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REVIEW AND SYNTHESES

Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time

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Abstract

Understanding the sensitivity of tundra vegetation to climate warming is critical to forecasting future biodiversity and vegetation feedbacks to climate. *In situ* warming experiments accelerate climate change on a small scale to forecast responses of local plant communities. Limitations of this approach include the apparent site-specificity of results and uncertainty about the power of short-term studies to anticipate longer term change. We address these issues with a synthesis of 61 experimental warming studies, of up to 20 years duration, in tundra sites worldwide. The response of plant groups to warming often differed with ambient summer temperature, soil moisture and experimental duration. Shrubs increased with warming only where ambient temperature was high, whereas graminoids increased primarily in the coldest study sites. Linear increases in effect size over time were frequently observed. There was little indication of saturating or accelerating effects, as would be predicted if negative or positive vegetation feedbacks were common. These results indicate that tundra vegetation exhibits strong regional variation in response to warming, and that in vulnerable regions, cumulative effects of long-term warming on tundra vegetation – and associated ecosystem consequences – have the potential to be much greater than we have observed to date.

Keywords

Alpine, Arctic, climate warming, long-term experiment, meta-analysis, plants.

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INTRODUCTION

The past few decades have witnessed dramatic shifts in vegetation composition, biomass and diversity in numerous Arctic and alpine tundra sites (Grabherr *et al.* 1994; van Wijk *et al.* 2004; Tape *et al.* 2006; Hudson & Henry 2009; Post *et al.* 2009b; Callaghan *et al.* 2011; Hill & Henry 2011). Remote sensing studies also indicate widespread changes in tundra vegetation over the same period (Pouliot *et al.* 2009; Bhatt *et al.* 2010). Such transformations are widely hypothesised to be the result of recent climate warming. In the past 40 years, surface air temperatures over the Arctic have increased at an average of 0.4 °C per decade, a rate nearly double that of climate warming observed at lower latitudes (Kattsov *et al.* 2005; McBean *et al.* 2005; Anisimov *et al.* 2007). General circulation models consistently indicate that air temperatures will continue to rise most rapidly in polar latitudes, lending increased urgency to understanding vegetation–climate interactions across the tundra biome (IPCC 2007).

Tundra vegetation affects ecosystem processes, services and climatic regulation on scales ranging from the local to the global. Therefore, climate-induced changes in tundra vegetation could have wide-ranging consequences. For example, plant composition directly influences nitrogen cycling, productivity and decomposition, active layer depth, forage quantity and quality, snow distribution and surface albedo (Chapin *et al.* 1996, 2005; Sturm *et al.* 2005; Cornelissen *et al.* 2007; Blok *et al.* 2010). Net effects of future warming on the vast carbon stores contained in tundra soils (Tarnocai *et al.* 2009) depend on whether increases in primary productivity can offset warming-induced increases in heterotrophic soil respiration (CO_2 release; Euskirchen *et al.* 2009) and methanogenesis in thawing permafrost (CH_4 release; McGuire *et al.* 2009). On a local scale, shifts in vegetation are expected to substantially alter key resources, such as medicinal plants and faunal biodiversity, with strong ramifications for subsistence harvest, ecotourism and local livelihoods (Klein *et al.* 2008; Post *et al.* 2009b; Wookey *et al.* 2009).

Motivated by both the severe climate projections and unique services provided by the tundra biome, there has been a proliferation of warming studies in tundra sites throughout the globe. To date, these experimental warming studies have offered numerous examples of vegetation changing, not changing, or changing in unexpected directions. A robust framework for forecasting when and where particular vegetation changes will occur is, however, lacking. For example, recent studies in high Arctic tundra (Hollister *et al.* 2005; Hudson & Henry 2010), low-Arctic peat (Keuper *et al.* 2011), subarctic moss heath (Jonsdottir *et al.* 2005) and alpine tundra (Klanderud 2008) have found considerable vegetation stability and ecological resistance to experimental warming. These site-specific results contrast with an alpine study that found that warming caused > 25% loss in species richness (Klein *et al.* 2004); a high elevation study from the sub-arctic, which found that evergreen shrubs in warmed plots increased at twice the rate of that in control plots over a 12-year period (Molau 2010); and a sub-arctic heath, where substantial changes in shrubs, moss and lichens were detected after 20 years of warming (P.L. Sorensen, S. Lett & A. Michelsen, unpublished data). They also differ from the conclusions of a previously published meta-analysis, which detected experimental warming effects on vegetation composition in as little as 2 years (Walker *et al.* 2006). Extrapolating decadal-scale predictions based on short-term warming experiments is further complicated by observations that short (1–3 years) and longer term (5–9 years) responses to climate warming may vary even within the same experiment (Chapin *et al.* 1995; Hollister *et al.* 2005).

There is ample reason to expect that tundra vegetation response to climate warming should vary spatially and temporally. The tundra biome spans a gradient of over 10 °C in average summer temperature, a moisture gradient from polar desert to wetlands, and also contains considerable variation in soil pH, organic matter content, nutrient availability and herbivore populations (Epstein *et al.* 2004). The structure and species composition of tundra plant communities also vary regionally, with warmer sites typically supporting a greater number of vascular species, a taller and denser shrub canopy and fewer cryptogams than cooler sites (Walker 2000; Walker *et al.* 2005). In addition, tundra vegetation is relatively slow-growing, and sexual reproduction is highly variable and dependent on climatic conditions. As a result, long-term effects of warming could differ markedly from short-term responses, particularly when growth and reproductive processes respond differently to warming (Arft *et al.* 1999; Doak & Morris 2010). Differences between short-term and long-term warming effects can also result from vegetation-feedbacks. For example, if air-temperature warming stimulates an increase in the height and density of canopy vegetation and litter production, shading of the soil surface may increase after long-term warming (Blok *et al.* 2010; Sorensen *et al. in review*). This shading, in turn, can result in reduced soil temperatures, and an associated slowing of nutrient cycling and decreased thaw depth.

Previous efforts to rigorously address heterogeneity in tundra responses to warming over space and time through multi-site synthesis have been hindered by a lack of sufficient data and statistical tools; most experiments were short-term and conducted at a relatively small group of research stations. Dormann & Woodin (2002) found no statistically significant moderating effects of duration of warming experiment, latitude, elevation, or ambient summer temperature in their analysis of experimental warming effects on plant biomass. In contrast, meta-analyses of growth, biomass, reproduction, cover and height (Arft *et al.* 1999; van Wijk *et al.* 2004; Walker *et al.* 2006) strongly suggest that plant responses to warming vary with time, location, and/or moisture regime. However, meta-analysis is unable to account for repeated measures of the same experiment, which occurred in these syntheses, and could cause effects to be exaggerated. Moreover, authors of the syntheses stressed that their results should be interpreted with caution as geographical location, soil moisture, length of experiment and growth form partially co-vary, and because the total number of studies included was relatively small and of short duration (the majority of data points represented < 6 years of experimental warming). These short-comings are of concern because the ultimate goal of climate change experimentation is to forecast the long-term effects of climate warming over a wide region.

To quantify warming effects on tundra plant communities worldwide and hone forecasts for particular abiotic regimes and time horizons, we synthesised vegetation responses from 1–20 years of experimental warming in 61 separate experiments conducted at 27 distinct geographical locations (Fig. 1; Table S1). Our specific objectives were to quantify (1) mean responsiveness of tundra plant growth forms to experimental warming over all studies and years; (2) temporal trends in responsiveness of these growth forms and (3) differences in responses based on the soil moisture and summer temperature of the study locale.

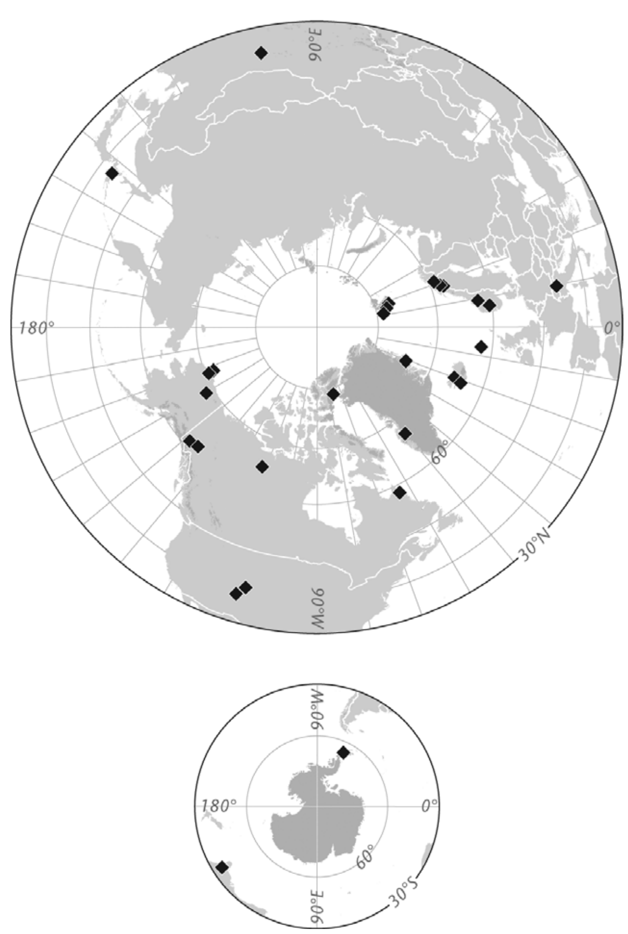

Figure 1 Study areas. Locations included Stepping Stone Islands (Antarctic Peninsula); Australian Alps (Australia); Alexandra Fiord, Daring Lake, Kluane, Torngat Mtns Natl. Park and Wolf Creek (Canada); Haibei (China); Kilpisjärvi (Finland); Kangerlussuaq Fjord and Zackenberg (Greenland); Dovre, Finse, Longyearbyen and Ny-Ålesund (Norway); Sornfelli (Faroe Islands); Audkuluheidi and Thingvellir (Iceland), Taisetsu Mountains (Japan); Abisko and Latnjajaure (Sweden); Val Bercla (Switzerland); Atqasuk, Barrow, Niwot Ridge, Rocky Mtn Biol. Lab. and Toolik Lake (U.S.).

METHODS

Warming experiments

We amassed plot level data on plant abundance and height from 61 *in-situ* warming experiments conducted throughout the tundra biome between 1981 and 2010 (Table S1). The majority of the studies are part of the International Tundra Experiment (ITEX: http://www.geog.ubc.ca/itex; Henry & Molau 1997). ITEX experiments use a passive warming design with open-top chambers consisting of angled, transparent fibreglass or polycarbonate sides that typically raises the mean daily summer air temperature by 1–3 °C (Molau & Mølgaard 1996; Marion *et al.* 1997). We also included studies with other experimental warming designs, including greenhouses and infrared heaters. On the basis of the 35 experiments included that had recorded temperature inside and outside of plots during at least one summer, we estimate that the warming treatment resulted in a mean daily summer air temperature increase of 1.5 °C and a mean daily summer soil temperature increase of 1.0 °C. This increase is similar to the mean increase in Arctic summer air temperature (1.8 °C) expected by the year 2050 (ACIA 2005).

The techniques used to quantify the amount and type of vegetation per plot included biomass harvests, visual cover estimates, frequency of subplots in which a particular taxon occurred, or total number of point frame hits per taxon using point-intercept sampling. The point-intercept sampling technique in these studies employed a fixed, square frame, with 20–100 sampling points spaced equidistantly within the frame (Molau & Mølgaard 1996). At each point, the identity and status (alive or dead) of plant tissue intercepted by a vertically-dropped pin were recorded. Some researchers, using the point-intercept technique, recorded only the top vegetation layer at each intercept point or only the top and bottom vegetation layer at each point, whereas others recorded all vegetation layers. Within a study, the same measurement technique was used in all years (Table S1). An effort was made to identify all taxa to species, but in some cases, plants were classified only to morphospecies, or growth forms. This was done for species that are difficult to identify in the field, such as cryptogams, so that within a study, the same taxonomic groups were used consistently across years. A subset of studies also included measurements of mean canopy height (average of 25–100 canopy height measurements over a sampling grid) and a subset of these studies also recorded the identity of the tallest plant at each grid point.

From these raw data, we derived the following vegetation response metrics in each study plot: the % cover of bare ground (either visual estimates, or proportion of gridded sampling points encountering only bare soil, rock or cryptogamic crusts); the mean canopy height; the maximum height by growth form (derived from the height of the tallest plant per growth form that was measured over the sampling grid); total abundance (biomass, cover, frequency or point-frame hits) of above-ground live material by growth form; total abundance of dead material (litter and standing dead); total abundance of the dominant species (single most common species in each study site) and diversity (Simpson's index). We used a hierarchical grouping scheme to define growth forms, first assigning plants to five broad groups (shrubs, graminoids forbs, mosses and lichens), and then further subdividing into 11 narrow groups (deciduous shrubs, evergreen shrubs, grasses, rushes, sedges, forbs, acrocarpous mosses, pleurocarpous mosses, crustose lichens, foliose lichens and fruticose lichens). We selected these groups because individual species within them are known to cluster well by functional effects, with the caveat that some species within the groups may respond individualistically to climate warming (Chapin *et al.* 1996; Dorrepaal 2007; Klein *et al.* 2007). We also investigated the responses of shrubs grouped by height rather than leaf-longevity, classifying species according to their maximum potential heights as recorded in online flora [Argus (2001), Australian Plants Society – NSW Region (2011), E-Flora BC (2011), Flora of the Canadian Arctic Archipelago (2011), Flora of North America (2011), Flora of NW Europe (2011), FloreAlpes (2011), The Gymnosperm Database (2011), PlantNET – NSW FloraOnline (2011), USDA PLANTS Database (2011)], with dwarf shrubs < 15 cm tall, low-shrubs 15–50 cm, and tall shrubs > 50 cm, as two of the most important ecosystem effects of shrubs (snow trapping and spring albedo) are directly linked to canopy height (Sturm *et al.* 2001).

The aggregated growth form totals we used are heavily influenced by the responses of numerical dominants within a given growth form, and do not necessarily reflect the mean response of all species within a growth form. This response metric met our goal of describing changes in the structure and composition of vegetation with climate warming, but does not explicitly test whether growth forms are useful in predicting the response of individual species. We used the maximum height per growth form as a conservative estimate of growth-form-specific height changes, rather than the mean observed height (average of all top canopy hits) used in previous studies, as overtopping of shorter individuals could cause the apparent mean height to increase without any actual change in height.

Mean summer (July – Northern Hemisphere, January – Southern Hemisphere) temperature per study was derived directly from local climate sensors at or near the study sites whenever possible. For five studies that lacked local climate data, we estimated mean summer temperature over the study period based on the 0.5° resolution climate grid provided by the University of East Anglia Climate Research Unit (CRU) TS3.0 dataset, which showed a high degree of correlation (Pearson $r = 0.75$) with the local climate sensor data. For studies where the climate data source differed in elevation from the study site, and for the CRU-based estimates, we adjusted temperature estimates based on a standard lapse rate of 6°C/1000 m. The individual(s) responsible for data collection at each study also classified their study into one of three soil moisture classes: dry, containing roughly < 20% gravimetric soil moisture content (GMC); moist 20–60% GMC; or wet > 60% GMC, and one of three grazing intensity classes (low, medium, high), and qualified whether the dominant grazers were small or large mammals, birds or insects. Time (duration of warming) was calculated as the number of summers the treatment had been imposed, not calendar year, as studies were initiated at different time points. All data have been archived at the Polar Data Catalogue (http://polardata.ca/).

Analyses

Effect size calculation

We used the standardised mean difference (unbiased estimator Hedge's g^*) as an effect size (Hedges & Olkin 1985). This unit-free metric, which estimates effect size as the difference between treatment and control plot means, scaled by the pooled standard deviation, allowed a quantitative assessment of large-scale patterns when methodology varied among studies (see Cardinale *et al.* 2006; Stewart 2010; Vilà *et al.* 2011 and references therein for other examples and discussion of the benefits and limitations of this approach). Along with the weighted mean effect size, we also report the median percent change over all measurement years in all studies.

Statistical analysis

We used linear mixed models both to quantify the mean responsiveness of tundra vegetation to experimental warming over all studies and measurement years, and to analyse variation in effect size with duration of warming, study site moisture and ambient temperature. We chose to use mixed models as our dataset included repeated measurements of the same sites at multiple time-points. This structure presents problems for meta-analysis because repeat measurements of the same study are not independent, and we expected responses to change with the duration of warming. Within a traditional meta-analysis framework, options for analysing such datasets are limited to reducing each study to a single measurement, either by (1) analysing responses at each time point separately, (2) discarding results from all but a single time point or (3) averaging effect sizes over moments in time and calculating a composite variance. While these options are statistically sound, (1) results in a much reduced data set for any given time point as well as difficulties in disentangling true effects of experimental duration unless all studies are measured in all years, and (2) and (3) preclude comparisons of temporal variation in effect size. Our use of linear mixed models allowed us to overcome these limitations. A similar approach has been used in several previous studies to account for complex data structures (e.g. Dormann & Woodin 2002; Cardinale *et al.* 2006; Yang *et al.* 2010).

To estimate mean effects over all studies and time-periods, we fit weighted intercept-only linear mixed models, weighting each data point (effect size per study per time-point) by the inverse of its estimated sampling variance and using study-identity as a random effect to account for non-independence of repeat measurements from the same study. Using inverse variance weighting is a recommended approach that increases both the precision of the estimated effect sizes and statistical power in meta-analyses (Gurevitch & Hedges 1999). Weighting by sample size achieves essentially the same purpose, but simulation studies contrasting weighting by sample size versus weighting by inverse variance suggest that the latter is preferable (Marín-Martínez & Sánchez-Meca 2010). Credible intervals (95%) were calculated using Markov Chain Monte Carlo methods to sample from the posterior distribution of the intercept for each model. These intervals were extremely similar to bootstrapped confidence intervals from a traditional meta-analysis, in which we eliminated pseudo-replication by averaging effect sizes by time and calculated a composite variance prior to analysis following the methodology outlined in Borenstein *et al.* (2009) (Elmendorf *et al.* unpublished data).

To examine differences in effect size over space and time, we used a top-down strategy to arrive at the best descriptive model for each response variable (Zuur *et al.* 2009). Our basic approach was to first fit a saturated linear mixed model with all possible fixed and random effects included, then sequentially remove unimportant random effects terms, and last sequentially remove unimportant fixed effects terms, resulting in a single reduced model for each response variable that retained only terms that were at least marginally ($P < 0.1$) significant. Fixed effects included time (duration of experiment), summer ambient temperature, site moisture and pairwise interactions between time and moisture and time and summer temperature. To examine the possibility that warming effects saturate or accelerate over time, as would be expected under negative or positive vegetation feedback scenarios respectively, we fit quadratic as well as linear terms for time. Given that studies could vary randomly in both their mean effect size and trajectory over time, we began with random intercept terms for study identity, as well as random study-specific slopes over time. Time and temperature were centred for each response variable by subtracting the mean to improve model convergence and estimation of variance components.

To prevent differences in sampling method (abundance metric used) from unduly influencing results, initial models were also tested for significant effects of the abundance metric or abundance metric and time interaction terms. When either term had a significant or marginally significant effect ($P < 0.1$), we removed this source of variation by removing datasets sampled using metrics that yielded consistently different effect sizes. Chi-squared likelihood ratio tests were used to determine the significance of all fixed effect terms based on single-term deletions, and simulated restricted likelihood ratio tests were used to determine the significance of random effects terms. On the basis of the final (simplified) fitted model for each variable, we used Markov Chain Monte Carlo methods to sample from the posterior distribution of the parameters to derive 95% credible intervals to graphically depict how the predicted effect of warming on each variable varies over space and time. Temperature was modelled as a continuous variable, but to display variation in effect size over both time and summer temperature in a single figure, we show predicted responses at three representative mean summer temperatures (5.5, 8.0 and 10.5 °C) that represent the approximate quarter, midpoint and three-quarter temperature points between the minimum (2.7 °C) and maximum (13.4 °C) summer temperatures of studies included in this synthesis. All linear mixed models were analysed in R (version 2.11) using the packages lme4, languageR and RLRsim (Baayen 2010; Bates & Maechler 2010; Scheipl 2010).

Sample sizes varied due to both absences of individual taxa across study sites and the level of detail used when sampling (for example most sites identified cryptogams only to broad group). We omitted studies from individual analyses if unknown species comprised > 5% of the potential vegetation for any group. Similarly, diversity analyses included only studies where > 95% of the vascular vegetation was identified to species (only six studies had > 95% of nonvascular vegetation recorded to species), and studies were removed from the dominance analysis if the most abundant taxon at the study was not identified to species. Only response variables measured at > 15 studies were included in the analyses of average effect sizes and only response variables measured at > 25 studies were included in the analyses of spatial and temporal variation in warming effects to ensure that we had adequate power and spatial representation to detect broad patterns.

A commonly raised concern about using warming chambers is that grazers may be unintentionally excluded or deterred (Wookey 2008), an effect we minimised by using fenced data as controls in all studies in which fenced and unfenced plot data were available (10 studies). This effect could still be substantial in unfenced areas where mammals were the dominant grazers and the intensity of grazing was medium or high. Thus, we also re-ran the mean-effects analysis excluding such sites. If overall effects were largely caused by chambers excluding these grazers, removing the data from these sites should substantially reduce the estimated mean effect-size. As no such reduction was observed, we ran the remainder of the analyses using the full dataset.

RESULTS

Average effect size

When responses were averaged over all sites, weighted mean effect size estimates indicated that experimental warming significantly increased dead plant material and shrubs (especially deciduous, low and tall shrubs), while mosses (especially acrocarpous mosses) and lichens (especially foliose and fruticose lichens) decreased (Fig. 2a). Warming also significantly increased the mean canopy height and the height of all broad vascular groups (Fig. 2b).

Spatial and temporal variation in warming effects

A common result from the analysis of warming effects over space and time was heterogeneity in the direction and magnitude of vegetation response with duration of warming experiment, ambient summer temperature and moisture (Table 1). Effects of time, time x moisture or time x temperature were retained in the final models for a majority of response variables (Table 1). This effect typically reflected a linear increase in the absolute magnitude of effect sizes over time over all site conditions, or a subset of site conditions. Less commonly, we also observed decreases in effect size over time, or saturating effects. The *direction* of the moderating effect of site temperature and moisture conditions on long-term response varied by the vegetation group examined (see details below).

Abundance

For total shrub abundance, warming had the greatest long-term positive effect in sites that were already relatively warm, and had moist to wet soil (Fig. 3a–c). In cold, dry sites, there was an initial positive response of shrubs, which was not sustained. The total shrub response appeared to be dominated by low-growing and deciduous shrubs, which showed similar trends to the total shrubs (Fig. S1). In contrast, evergreen shrub changes were influenced only by study site moisture, not by summer temperature (Fig. 3d); tall shrubs increased with climate warming over their entire range, especially after 10 years of warming, whereas dwarf shrubs actually decreased significantly over time with warming (Fig. 3e,f).

Forbs and total graminoids showed no consistent temporal trends, but warming had the greatest positive effects on graminoid abundance at colder sites, and neutral to negative effects at warm sites (Fig. 4a). Among graminoids, grasses, rushes and sedges differed from one another in their responses to warming over a moisture gradient. Sedges had the greatest long-term positive response in wet sites, whereas grasses had the greatest long-term positive response in dry sites, and rushes were generally unresponsive, with a slight tendency for negative responses to warming in dry sites (Fig. S2).

Lichens consistently declined in abundance irrespective of site moisture or temperature (Fig. 4b). Negative long-term effects of experimental warming on moss abundance were primarily found in moist sites (Fig. 4c). Sample sizes for narrow subgroups of mosses and lichens were insufficient to address how their responses may have varied over space and time.

Community attributes and height

Dead plant material rapidly accumulated in response to warming, but the magnitude of this response remained constant after *c.* 10 years of warming (Fig. 5a). Vascular plant diversity showed declines with long-term warming only in moist sites (Fig. 5b). The abundance of the dominant species showed no overall trends, nor spatial or temporal variation in response to warming. The cover of bare ground increased with warming in warm moist sites, but decreased in cold dry sites (Fig. 5c). Cold sites showed an initial increase in canopy height, which was not sustained over the long-term (Fig. 5d). In contrast, moderate-to-warm sites showed continued increases in canopy height.

DISCUSSION

Our global synthesis of 61 tundra warming experiments found significant mean positive effects of warming on canopy height, the maximum observed height of vascular growth forms, and the abundance of shrubs and dead material, and negative effects on the abundance of non-vascular cryptogams, both lichens and mosses. However, the effects of warming were rarely consistent over space or time. As a result, the magnitudes of these mean-responses are adequate for forecasting the aggregate response of the tundra biome only insofar as the study sites and measurement years included are an accurate representation of the tundra biome as a whole over the time-scale of anticipated warming.

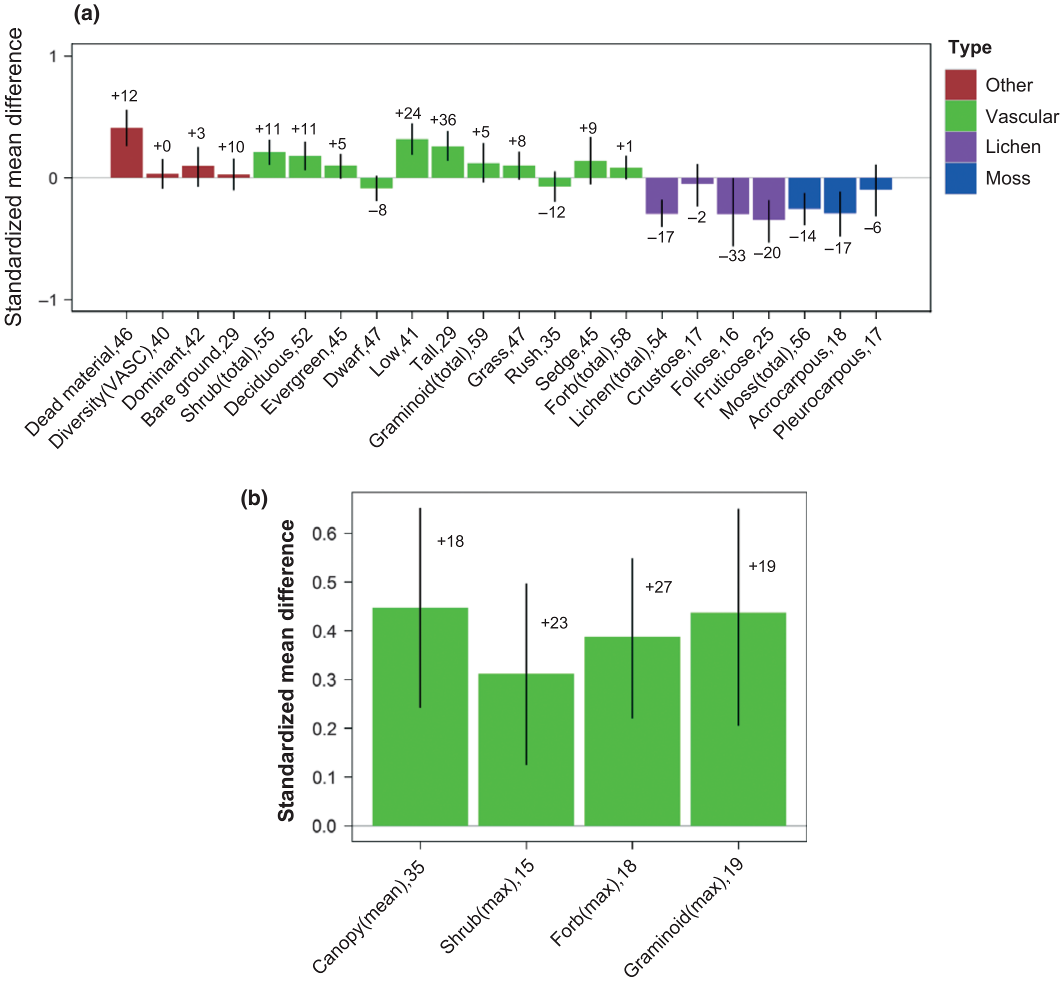

Figure 2 Average effects of warming on community attributes and growth form abundance (a) and vegetation height (b). Bars show the weighted mean effect size (standardised mean difference) based on intercept-only weighted linear mixed models of all studies and sampling years. Error bars show 95% credible intervals. Median per cent change recorded over all studies and years is inset above or below the corresponding bar. The *x*-axis labels show response variable and number of studies included in the analysis.

Temporal variation

Differences between short-term and long-term responses to climate warming are expected because changes in temperature affect a wide variety of ecosystem processes – ranging from direct influence on photosynthetic rates and plant tissue allocation patterns to biogeochemical cycling and soil organic matter – but at different rates (Shaver *et al.* 2000). As a result, the severity and even direction of warming effects are anticipated to change over time, particularly when indirect effects are taken into consideration. Previous syntheses of experimental warming on plant growth and abundance have variously found no effect of duration (Dormann & Woodin 2002), transient effects (Arft *et al.* 1999), or effects that were sustained at roughly the same magnitude after 2–6 years of warming (Walker *et al.* 2006). In contrast, we commonly found linear increases in the absolute magnitude of effect sizes with experimental duration, over either all site conditions (e.g. dwarf and tall shrubs, lichens), or a subset of site conditions (e.g. total shrubs in moderate-to-warm and moist to wet sites; grasses in cold, dry sites).

This synthesis provides an understanding of decadal-scale effects of climate warming, given that the average duration of experiments was 10 years. Yet, because both long-term and short-term studies are included, and as most long-term studies measured vegetation response at multiple time-points throughout the experiment, even these results are dominated by short-term findings. This distribution is not uncommon in the global change literature, given the expense, time and difficulty in maintaining long-term experiments and incentives to publish short-term results. However, our analyses of temporal variation in effect size underscore how qualitative reviews and quantitative syntheses that combine studies of different experimental duration may underestimate potential long-term effects. This may partially explain, for example, why the two earlier meta-analyses of warming effects on tundra plant biomass (Dormann & Woodin 2002; van Wijk *et al.* 2004) failed to detect significant declines in cryptogams. Such a pattern also suggests that the median rates of change presented in this paper (Fig. 2) underestimate the potential long-term effects in responsive regions.

We also identified several instances of resistance (lack of change), resilience (transient effects only), and saturating responses to climate warming. In nearly all cases where effects varied with site moisture or temperature, there was at least one set of conditions where there was essentially no mean response over all time periods (e.g. total graminoids and forbs in moderate and warm areas). The positive responses of shrubs appeared to be transitory in dry, cold zones and

Table 1 Summary of moderators of the responses to experimental warming, based on linear mixed models. Time = summers of warming; Moisture = soil moisture classes of study site; Temp. = mean summer (July or January) temperature of study sites (see Methods). Fixed effect terms retained in the reduced models for each response variable are indicated by shading. Time was included as a linear term except in cases denoted by (Q) where time was retained as a quadratic term in the final models. Significance of fixed effects terms (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, †$P < 0.10$) was assessed by chi-squared likelihood ratio tests (LRT) using single-term deletions. LRTs for main effects terms in the presence of significant interactions were not performed. The two right-most columns list random effects terms retained in the final models and figures illustrating the best-fit models.

	Fixed effects terms						
Response variable	Time	Time × Moisture	Time × Temp.	Moisture	Temp.	Random effects terms	Figure(s)
Shrub (Total)	▨	▨ *	▨ ***	▨	▨	Study, study × time	*3a–c*
Deciduous	▨	▨ **	▨ ***	▨	▨	Study	*S1a–c*
Evergreen	▨ *(Q)	▨ *		▨		Study, study × time, study × time^2	*3d*
Dwarf	▨ *					Study, study × time	*3e*
Low	▨	▨ **	▨ **	▨	▨	Study, study × time	*S1d–f*
Tall	▨ *					Study	*3f*
Forb (Total)						Study, study × time	
Graminoid (Total)					▨ *	Study, study × time	*4a*
Grass	▨	▨ *		▨	▨ *	Study, study × time	*S2a–c*
Rush	▨	▨ †		▨	▨ †	Study, study × time, study × time^2	*S2d–f*
Sedge	▨	▨ *		▨		Study	*S2g*
Lichen (Total)	▨ ***					Study, study × time	*4b*
Moss (Total)	▨ †			▨ †		Study, study × time, study × time^2	*4c*
Dead material	▨ *(Q)					Study, study × time	*5a*
Diversity (vascular)	▨	▨ †		▨		Study	*5b*
Dominant species						Study, study × time	
Bare				▨ ***	▨ **	Study	*5c*
Canopy height (mean)	▨		▨ *		▨	Study, study × time, study × time^2	*5d*

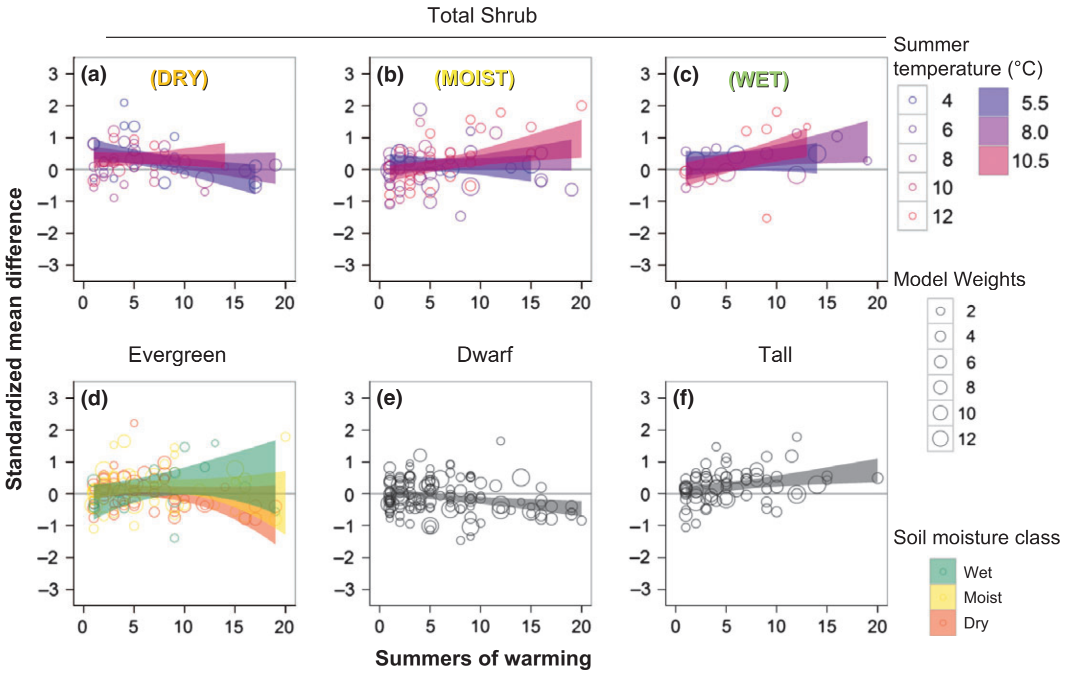

Figure 3 Total, evergreen, tall and dwarf shrub response to experimental warming. Points show effect sizes (standardised mean differences) for individual studies and measurement years; the area of circles is proportional to weights assigned to individual data points (inverse variance). For each response, shaded areas show 95% credible intervals for predictors included in the best-fit explanatory models. For total shrubs, contrasting effects of warming over time between dry, moist and wet soils are illustrated in panels (a), (b) and (c), respectively; contrasting effects of warming with ambient summer temperature are illustrated by colours of points and bands within panels (a), (b) and (c). Temperature was measured and modelled as a continuous variable, but to simplify the presentation, we generated predicted responses at three representative summer temperatures (5.5, 8.0 and 10.5 °C; the actual data range was from 2.7 to 13.4 °C). Response of low-growing and deciduous shrubs was extremely similar to the total shrub response and is presented in Fig. S1. For evergreen shrubs, contrasting effects of warming between dry, moist and wet soils aggregated over all temperatures are illustrated in d, colour of points and predicted response trajectories illustrate different responses by soil moisture. Responses of dwarf (e) and tall (f) shrubs aggregated over all moisture and temperatures varied only with time. A single point with weight < 1 and an effect size of 4.2 is omitted from panels (b), (e) and (f).

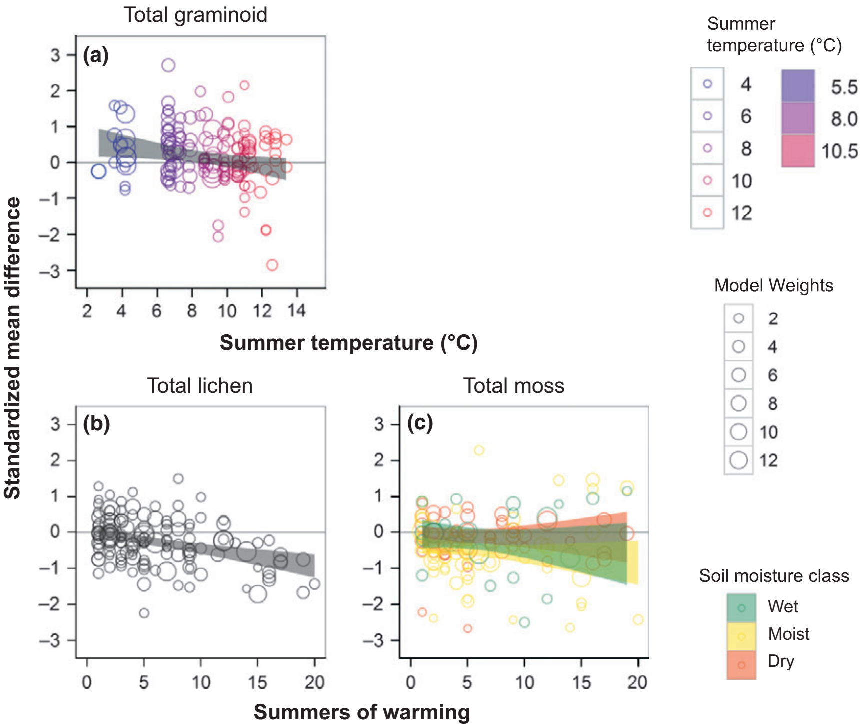

Figure 4 Total graminoid, lichen and moss response to experimental warming. The response of graminoids (a) varied only by summer temperature as shown in the *x*-axis. Lichen response varied only with time (b). Moss response varied with time and soil moisture (c). Three points with weight < 1 and effect sizes between −3.8 and −5.1 are omitted from panel (a). See Fig. 3 for further explanation of the graph.

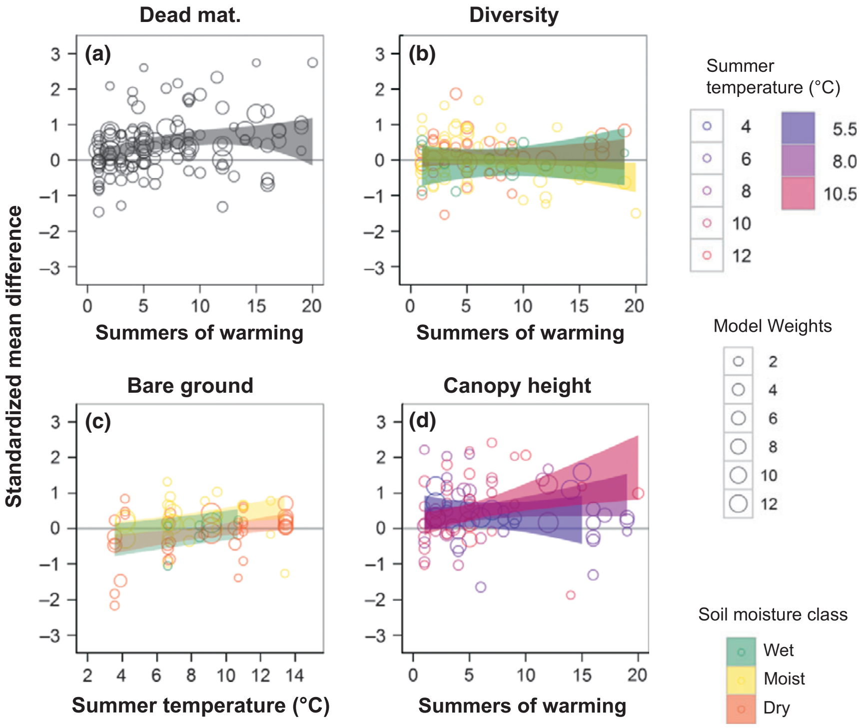

Figure 5 Response of community attributes (dead plant material, vascular diversity, bare ground cover, and mean canopy height) to experimental warming. The response of dead plant material varied only with time (a). The response of diversity varied with time and soil moisture (b). The response of cover of bare ground varied with soil moisture and summer temperature (c). The response of canopy height varied with time and summer temperature (d). Note that the *x*-axis differs for panel (c). Two points with weights ≤ 1 and effect sizes < 4.4 are omitted from panel (c) and a single point with weight < 1 and effect size of −3.9 is omitted from panel (d). See Fig. 3 for further explanation of the graph.

dead plant material accumulated rapidly during the first decade of warming with little further change in the second decade. The latter effect could be due to increases in rates of decomposition over time, perhaps also in response to warming. Changes in effect size were frequently statistically significant, but confidence intervals were wider for the later years – and there were fewer studies with 10+ years of warming – suggesting that additional data would improve the precision of forecasts for the second decade of warming.

Some groups, such as forbs and total graminoids, showed no predictable temporal variation in effect size. This pattern may result either from high year-to-year variability in above-ground growth, which would make long-term trends more difficult to detect, or from compensatory responses of different species. Inter-annual fluctuations in the above-ground biomass or cover of herbaceous growth forms are expected to be common due to their more flexible morphology and high proportion of stored plant reserves (Arft *et al.* 1999). Both the degree of warming (Marion *et al.* 1997) and other co-limiting factors of plant growth (e.g. sunlight, precipitation, nutrient availability) probably varied among years within studies and among studies. Only a handful of studies included consistent, multi-year records of treatment plot temperature, solar radiation, or windspeed, which precluded an explicit test of these covariates on the observed responses here. However, a previous meta-analysis found no significant effect of either the warming design used nor among-study variation in soil warming on plant productivity, soil respiration and nitrogen mineralisation responses to experimental warming (Rustad *et al.* 2001). Within graminoids, there was also some indication of opposing responses to long-term warming by grasses, sedges and rushes, so it is possible that gains in one group were sometimes offset by losses in another.

Spatial variation

Plant groups varied in whether or not effects of warming depended on moisture or temperature, and the direction of the moderating effects, when such effects were detected. Despite these idiosyncrasies, some general trends can be inferred. In particular, our data suggest that the response of vascular plants to warming depends on the ambient temperature at a site, with shrubs expanding most in the warm tundra regions and graminoids and forbs expanding predominantly in the colder regions. These shifts in response reflect existing gradients in vegetation structure. In Arctic tundra regions, there is a sharp decline in canopy closure and height from south to north, largely due to reductions in the height and density of the shrub canopy (Walker *et al.* 2005). The tallest growth forms in cold areas tend to be herbaceous (frequently graminoids), which can easily overtop dwarf shrubs, whereas the tallest growth forms in warm areas are woody (low and tall shrubs). Accordingly, in this synthesis, the groups that increased most in abundance under simulated warming were graminoids in cold regions and primarily shrubs in warm regions. We also found that tall shrubs, which are typical of more moderate tundra climates, generally increased under warming, whereas dwarf shrubs, which are more common in colder tundra regions, actually declined under experimental warming. These patterns probably result from an increase in light competition with warming as the canopy closes, which would favour species capable of vertical growth.

Where the same traits affect both ecosystem function and which species respond to climate change, we can expect nonlinear feedbacks between the two (Suding *et al.* 2008). Canopy height seems to be one such key trait here because tall shrubs have the potential to extensively modify ecosystem function, and seem to proliferate with warming. Consequences of shrub expansion include an increase in summer sensible heat flux and a decrease in winter surface albedo, which can result in a positive feedback loop between climate warming and shrub expansion (Sturm *et al.* 2001; Thompson *et al.* 2004), as well as soil shading and increased production of recalcitrant litter, which have the potential to buffer climate warming effects (Cornelissen *et al.* 2007; Blok *et al.* 2010). The impact of shrub expansion is currently quite low because the area of land affected remains relatively small (Chapin *et al.* 2005). However, further expansions in shrub cover have the potential to instigate more severe changes. Projecting the land-surface area vulnerable to expansion of shrubs is therefore critical to understanding future regional and global climate scenarios.

Our results suggest that future climate-induced shrub expansion will be most extensive in the *c.* 66% of the Arctic tundra that has 'warm' summer temperatures and is dominated by tall shrubs (Subzones D & E on the Circumpolar Arctic Vegetation map; Walker *et al.* 2005), and particularly in moist to wet areas within these zones. Our projections contrast with the results of two previous studies that explicitly compared the sensitivity to global change of different tundra regions (van Wijk *et al.* 2004; Lloyd *et al.* 2011), and found the largest effects in more northern and/or lower biomass communities. The narrower focus of this synthesis (on solely warming effects rather than warming, shading, and fertilisation effects) and a broader geographical scope probably explain the different results. Observational data seemingly support our conclusions. Analyses of NDVI trends over time within Canada indicate that greening areas are concentrated in the Low Arctic and Subarctic zones (Pouliot *et al.* 2009); shrub expansion in the Alps occurs predominantly at lower elevations (Cannone *et al.* 2007); repeat vegetation surveys in the High Arctic sometimes fail to find dramatic changes (Prach *et al.* 2010; but see Hudson & Henry 2009), whereas prominent shrub expansion has been noted in the low arctic in Russia and Alaska, particularly in drainages (Silapaswan *et al.* 2001; Tape *et al.* 2006; Forbes *et al.* 2010).

Approximately 34% of the vegetated Arctic tundra region is in the high Arctic, with a mean July temperature < 7 °C and where dwarf shrubs are the most common form of woody vegetation. Our data indicate that, in next few decades, cold regions are likely to remain resistant to shrub expansion. It is possible that shrub species or genotypes with the potential to respond favourably to warming are currently absent from these colder regions, but long-distance migration or gene-flow could overcome some of these genetic constraints (Alsos *et al.* 2007; Aitken *et al.* 2008). Furthermore, low amounts of plant-available nitrogen and slow species turnover at high latitudes are likely to constrain shrub expansion in the high Arctic for the next 50 years, but perhaps less so thereafter (Epstein *et al.* 2000). Increases in soil organic layer thickness have been documented in some warming studies (Björk *et al.* 2007). Thus, although our data-set contains numerous 10–20 year warming experiments, lack of response over this time does not necessarily indicate stasis in the years beyond.

Nutrient-based simulation models suggest that mosses should expand substantially under climate warming in the high Arctic and to a lesser degree in the low Arctic (Epstein *et al.* 2000). However, we found that ambient summer temperature was rarely a significant factor explaining moss responses to experimental warming. Instead, trends from the current synthesis suggest that moisture, rather than temperature, moderates moss susceptibility to climate warming (Lang *et al.* 2009). Lacking true roots, the capacity of mosses to take advantage of warmer conditions may be particularly constrained by seasonal water availability (Potter *et al.* 1995). This may partly explain why *Sphagnum*, the dominant genus in wet ecosystems in the tundra biome, does not generally decline with temperature increase in peatlands (Lang *et al.* 2009, in press; Keuper *et al.* 2011). Humidity tends to be at least slightly reduced within warming chambers (Marion *et al.* 1997). This drying effect could have contributed to the long-term declines in mosses with warming. In general, our findings are consistent with a parallel in-depth study on arctic bryophyte diversity and abundance responses to temperature (Lang *et al.* 2011). Both along natural temperate gradients and in three warming experiments in Sweden and Alaska, most bryophytes, except *Sphagnum* and a few subarctic pleurocarpous mosses, declined with warmer climatic regimes.

In contrast to the varied regional responses among vascular growth forms, after more than 10 years of warming, lichens declined in almost all places they occurred. Furthermore, rates of decline were substantial (median decline recorded in lichens over all sampling times and sites was 17%). This value is likely to be a significant underestimate of long-term declines; the median time point at which lichen abundance was measured was after five summers of warming, but our temporal analysis indicates that lichens continued to decline substantially beyond this point. This result is somewhat surprising, given that lichen declines with warming are often attributed to increased shade and litter produced by vascular plants, especially expanding shrubs in lower Arctic and lower-altitude tundra (Cornelissen *et al.* 2001), and a previous meta-analysis found that lichens were resistant to short-term warming in the high Arctic (Walker *et al.* 2006). It is possible that in harsher, more herbaceous tundra, lichen decline becomes evident mostly at the decadal scale following only multiple years of litter accumulation. These results are of concern from a conservation perspective because, while lichens are found throughout the tundra, they are relatively more abundant and diverse in the colder tundra areas, where they are particularly important sources of both animal forage and nitrogen inputs (through biological fixation by bacterial symbionts).

Concluding remarks

Our results demonstrate that the responsiveness of growth forms and resulting ecosystem feedbacks from climate warming can have pronounced regional heterogeneity within a single biome and that small sustained changes in plant abundance can have large long-term consequences. Congruent with many intraspecific comparisons of regional sensitivity to climate warming (Grøtan *et al.* 2008; Post *et al.* 2009a; Lloyd *et al.* 2011), we found that growth forms often responded differently to experimental warming across their distribution, suggesting that 'hotspots' of physiognomic change with future warming are also likely. However, despite our success in identifying several important moderators of climate warming effects, there was a substantial amount of unexplained variation (scatter) in effect size and the confidence intervals of mean effect size were wide (particularly for the long-term effects). Summer air temperature is just one factor that influences plant growth in the tundra biome and indeed in all landscapes. Striking differences in plant responses to warming have been observed in years with herbivore outbreaks and inside versus outside of exclosures (Post & Pedersen 2008; Olofsson *et al.* 2009; Li *et al.* 2011), which suggests that herbivores can strongly alter the development of warmed tundra plant communities. Differences in soil nutrient pools and pH, precipitation, winter temperatures and snow cover, species composition and density add further complexity to the links between vegetation and summer climate change. As the full spectrum of environmental variability across the Arctic tundra was not systematically factored into the design and execution of the studies synthesised here, these unknowns may have influenced both the mean and regional estimates of response in the current study, despite our large sample size. Such heterogeneity in biological response to warming should be accounted for in the design of monitoring networks. Understanding and accounting for the complexity of tundra vegetation response to warming are necessary to properly parameterise global models that forecast the impacts of climate change on carbon cycling and the surface energy balance of the tundra biome.

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AUTHORSHIP

All authors participated in maintaining experiments and data collection. SCE analysed the data; SCE, GHRH and RDH wrote the paper, with input from the other authors.

REFERENCES

ACIA (2005). *Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.*, 1, 95–111.

Alsos, I.G., Eidesen, P.B., Ehrich, D., Skrede, I., Westergaard, K., Gro Hilde Jacobsen, G.H. *et al.* (2007). Frequent long-distance plant colonization in the changing Arctic. *Science*, 316, 1606–1609.

Anisimov, O.A., Vaughan, D.G., Callaghan, T., Furgal, C., Marchant, H., Prowse, T.D. *et al.* (2007). Polar regions (Arctic and Antarctic). In: *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden & C.E. Hanson). Cambridge University Press, Cambridge, UK, pp. 653–685.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M. *et al.* (1999). Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol. Monogr.*, 69, 491–511.

Argus, G.W. (2001). A guide to the identification of willows in Alaska, the Yukon Territory and adjacent regions. In: *Workshop on Willow Identification*. George W. Argus, Ontario, Canada.

Australian Plants Society – NSW Region (2011). Available at: http://137.229.141.57/wp-content/uploads/2011/02/GuideSalixAK-YT11May05.pdf. Last accessed 30 March 2011.

Baayen, R.H. (2010). languageR: data sets and functions with "analyzing linguistic data: a practical introduction to statistics".

Bates, D.M. & Maechler, M. (2010). Lme4: Linear mixed-effects models using S4 classes. [Computer software manual]. R Package Version 0.999375-34. Available: http://cran.r-project.org/web/packages/l?me4/index.html.

Bhatt, U.S., Walker, D.A., Raynolds, M.K., Comiso, J.C., Epstein, H.E., Jia, G.S. *et al.* (2010). Circumpolar Arctic tundra vegetation change is linked to sea ice decline. *Earth Interact.*, 14, 1–20.

Björk, R.G., Majdi, H., Klemedtsson, L., Lewis-Jonsson, L. & Molau, U. (2007). Long-term warming effects on root morphology, root mass distribution, and microbial activity in two dry tundra plant communities in northern Sweden. *New Phytol.*, 176, 862–873.

Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C. & Berendes, F. (2010). Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Glob. Change Biol.*, 16, 1296–1305.

Borenstein, M., Hedges, L.V., Higgins, J.P.T. & Rothstein, H.R. (2009). *Introduction to Meta-analysis*. John Wiley & Sons, West Sussex.

Callaghan, T.V., Tweedie, C.E., Åkerman, J., Andrews, C., Bergstedt, J., Butler, M.G. *et al.* (2011). Multi-decadal changes in tundra environments and ecosystems: synthesis of the International Polar Year – Back to the Future project (IPY-BTF). *Ambio*, 40, 705–716.

Cannone, N., Sgorbati, S. & Guglielmin, M. (2007). Unexpected impacts of climate change on alpine vegetation. *Front. Ecol. Environ.*, 5, 360–364.

Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M. *et al.* (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443, 989–992.

Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995). Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, 76, 694–711.

Chapin, F.S., Bret-Harte, M.S., Hobbie, S.E. & Zhong, H.L. (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. *J. Veg. Sci.*, 7, 347–358.

Chapin, F.S., Sturm, M. III, Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H. *et al.* (2005). Role of land-surface changes in arctic summer warming. *Science*, 310, 657–660.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E. *et al.* (2001). Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *J. Ecol.*, 89, 984–994.

Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J. *et al.* (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecol. Lett.*, 10, 619–627.

Doak, D.F. & Morris, W.F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature*, 467, 959–962.

Dormann, C.F. & Woodin, S.J. (2002). Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Funct. Ecol.*, 16, 4–17.

Dorrepaal, E. (2007). Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? *J. Ecol.*, 95, 1167–1180.

E-Flora, BC. (2011). Available at: http://www.geog.ubc.ca/biodiversity/eflora/. Last accessed 30 March 2011.

Epstein, H.E., Walker, M.D., Chapin, F.S. & Starfield, A.M. (2000). A transient, nutrient-based model of Arctic plant community response to climatic warming. *Ecol. Appl.*, 10, 824–841.

Epstein, H.E., Beringer, J., Gould, W.A., Lloyd, A.H., Thompson, C.D., Chapin, F.S. *et al.* (2004). The nature of spatial transitions in the Arctic. *J. Biogeogr.*, 31, 1917–1933.

Euskirchen, E.S., McGuire, A.D., Chapin, F.S., Yi, S. & Thompson, C.C. (2009). Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks. *Ecol. Appl.*, 19, 1022–1043.

Flora of North America (2011). Available at: http://fna.huh.harvard.edu/. Last accessed 30 March 2011.

Flora of NW Europe (2011). Available at: http://nlbif.eti.uva.nl/. Last accessed 30 March 2011.

Flora of the Canadian Arctic Archieplago (2011). Available at: http://www.mun.ca/biology/delta/arcticf/. Last accessed 30 March 2011.

FloreAlpes (2011). Available at: http://www.florealpes.com/. Last accessed 30 March 2011.

Forbes, B.C., Fauria, M.M. & Zetterberg, P. (2010). Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Glob. Change Biol.*, 16, 1542–1554.

Grabherr, G., Gottfried, M. & Pauli, H. (1994). Climate effects on mountain plants. *Nature*, 369, 448–448.

Grøtan, V., Sæther, B.-E., Filli, F. & Engen, S. (2008). Effects of climate on population fluctuations of ibex. *Glob. Change Biol.*, 14, 218–228.

Gurevitch, J. & Hedges, L.V. (1999). Statistical issues in ecological meta-analyses. *Ecology*, 80, 1142–1149.

Hedges, L.V. & Olkin, I. (1985). *Statistical Methods for Meta-analysis*. Academic Press, San Diego, CA.

Henry, G.H.R. & Molau, U. (1997). Tundra plants and climate change: the International Tundra Experiment (ITEX). *Glob. Change Biol.*, 3(Suppl. 1), 1–9.

Hill, G.B. & Henry, G.H.R. (2011). Responses of high arctic wet sedge Tundra to climate warming since 1980. *Glob. Change Biol.*, 17, 276–287.

Hollister, R.D., Webber, P.J. & Tweedie, C.E. (2005). The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Glob. Change Biol.*, 11, 525–536.

Hudson, J.M.G. & Henry, G.H.R. (2009). Increased plant biomass in a high Arctic heath community from 1981 to 2008. *Ecology*, 90, 2657–2663.

Hudson, J.M.G. & Henry, G.H.R. (2010). High Arctic plant community resists 15 years of experimental warming. *J. Ecol.*, 98, 1035–1041.

IPCC (ed.) (2007). *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, New York.

Jonsdottir, I.S., Magnusson, B., Gudmundsson, J., Elmarsdottir, A. & Hjartarson, H. (2005). Variable sensitivity of plant communities in Iceland to experimental warming. *Glob. Change Biol.*, 11, 553–563.

Kattsov, V.M., Källén, E., Cattle, H., Christensen, J., Drange, H., Hanssen-Bauer, I. *et al.* (2005). Future climate change: modeling and scenarios for the Arctic. In: *Arctic Climate Impact Assessment* (ACIA). Cambridge University Press., Cambridge, UK, pp. 1042.

Keuper, F., Dorrepaal, E., Van Bodegom, P.M., Aerts, R., Van Logtestijn, R.S.P., Callaghan, T.V. *et al.* (2011). A race for space? How *Sphagnum fuscum* stabilizes vegetation composition during long-term climate manipulations. *Glob. Change Biol.*, 17, 2162–2171.

Klanderud, K. (2008). Species-specific responses of an alpine plant community under simulated environmental change. *J. Veg. Sci.*, 19, 363–372.

Klein, J.A., Harte, J. & Zhao, X.Q. (2004). Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecol. Lett.*, 7, 1170–1179.

Klein, J.A., Harte, J. & Zhao, X.Q. (2007). Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. *Ecol. Appl.*, 17, 541–557.

Klein, J.A., Harte, J. & Zhao, X.Q. (2008). Decline in medicinal and forage species with warming is mediated by plant traits on the Tibetan Plateau. *Ecosystems*, 11, 775–789.

Lang, S.I., Cornelissen, J.H.C., Holzer, A., ter Braak, C.J.F., Ahrens, M., Callaghan, T.V. *et al.* (2009). Determinants of cryptogam composition and diversity in Sphagnum-dominated peatlands: the importance of temporal, spatial and functional scales. *J. Ecol.*, 97, 299–310.

Lang, S.I., Cornelissen, J.H.C., Shaver, G.R., Ahrens, M., Callaghan, T.V., Molau, U. *et al.* (2011). Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Glob. Change Biol.*, DOI: 10.1111/j.1365-2486.2011.02570.x

Li, G., Liu, Y., Frelich, L.E. & Sun, S. (2011). Experimental warming induces degradation of a Tibetan alpine meadow through trophic interactions. *J. Appl. Ecol.*, 48, 659–667.

Lloyd, A.H., Bunn, A.G. & Berner, L. (2011). A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Glob. Change Biol.*, 17, 1935–1945.

Marín-Martínez, F. & Sánchez-Meca, J. (2010). Weighting by inverse variance or by sample size in random-effects meta-analysis. *Educ. Psychol. Meas.*, 70, 56–73.

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H. *et al.* (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Change Biol.*, 3, 20–32.

McBean, G., Alekseev, G., Chen, D., Førland, E., Fyfe, J., Groisman, P.Y. *et al.* (2005). Arctic climate: past and present. In: *Arctic Climate Impact Assessment* (ACIA). Cambridge University Press, Cambridge, UK, pp. 21–60.

McGuire, A.D., Anderson, L.G., Christensen, T.R., Dallimore, S., Guo, L.D., Hayes, D.J. *et al.* (2009). Sensitivity of the carbon cycle in the Arctic to climate change. *Ecol. Monogr.*, 79, 523–555.

Molau, U. (2010). Long-term impacts of observed and induced climate change on tussock tundra near its southern limit in northern Sweden. *Plant Ecol. Divers.*, 3, 29–34.

Molau, U. & Mølgaard, P. (eds.) (1996). *ITEX Manual*. Danish Polar Centre, Copenhagen, Denmark. Available at: http://www.geog.ubc.ca/itex/. Last accessed on 30 March 2011.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T. & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob. Change Biol.*, 15, 2681–2693.

PlantNET – NSW FloraOnline (2011). Available at: http://plantnet.rbg-syd.nsw.gov.au/floraonline.htm. Last accessed 30 March 2011.

Post, E. & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proc. Natl. Acad. Sci.*, 105, 12353–12358.

Post, E., Brodie, J., Hebblewhite, M., Anders, A.D., Maier, J.A.K. & Wilmers, C.C. (2009a). Global population dynamics and hot spots of response to climate change. *Bioscience*, 59, 489–497.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B. *et al.* (2009b). Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325, 1355–1358.

Potter, J.A., Press, M.C., Callaghan, T.V. & Lee, J.A. (1995). Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-arctic. *New Phytol.*, 131, 533–541.

Pouliot, D., Latifovic, R. & Olthof, I. (2009). Trends in vegetation NDVI from 1 km AVHRR data over Canada for the period 1985–2006. *Int. J. Remote Sens.*, 30, 149–168.

Prach, K., Košnar, J., Klimešová, J. & Hais, M. (2010). High Arctic vegetation after 70 years: a repeated analysis from Svalbard. *Polar Biol.*, 33, 635–639.

Rammig, A., Jonas, T., Zimmermann, N.E. & Rixen, C. (2010). Changes in alpine plant growth under future climate conditions. *Biogeosciences*, 7, 2013–2024.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E. *et al.* (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126, 543–562.

Scheipl, F. (2010). RLRsim: exact (Restricted) Likelihood Ratio tests for mixed and additive models. R package version 2.0-5. Available at: http://CRAN.R-project.org/package=RLRsim.

Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G. *et al.* (2000). Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience*, 50, 871–882.

Silapaswan, C.S., Verbyla, D.L. & McGuire, A.D. (2001). Land cover change on the Seward Peninsula: the use of remote sensing to evaluate the potential influences of climate warming on historical vegetation dynamics. *Can. J. Remote Sens.*, 27, 542–554.

Stewart, G. (2010). Meta-analysis in applied ecology. *Biol. Lett.*, 6, 78–81.

Sturm, M., McFadden, J.P., Liston, G.E., Chapin, F.S.I., Racine, C.H. & Holmgren, J. (2001). Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. *J. Clim.*, 14, 336–344.

Sturm, M., Schimel, J., Michaelson, G., Welker, J.M., Oberbauer, S.F., Liston, G. *et al.* (2005). Winter biological processes could help convert arctic tundra to shrubland. *Bioscience*, 55, 17–26.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E. *et al.* (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.*, 14, 1125–1140.

Tape, K., Sturm, M. & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Glob. Change Biol.*, 12, 686–702.

Tarnocai, C., Canadell, J.G., Schuur, E.A.G., Kuhry, P., Mazhitova, G. & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem. Cycles*, 23, GB2023.

The Gymnosperm Database (2011). Available at: http://www.conifers.org/. Last accessed 30 March 2011.

Thompson, C., Beringer, J., Iii, F.S.C. & McGuire, A.D. (2004). Structural complexity and land-surface energy exchange along a gradient from Arctic tundra to boreal forest. *J. Veg. Sci.*, 15, 397–406.

University of East Anglia Climatic Research Unit (CRU). [Phil Jones, Ian Harris]. CRU Time Series (TS) high resolution gridded datasets, [Internet]. NCAS British Atmospheric Data Centre, 2008. Available at: http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_1256223773328276. Last accessed 3 September 2010.

USDA PLANTS Database (2011). Available at: http://plants.usda.gov/java/. Last accessed 30 March 2011.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L. *et al.* (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.*, 14, 702–708.

Walker, D.A. (2000). Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography. *Glob. Change Biol.*, 6, 19–34.

Walker, D.A., Raynolds, M.K., Daniels, F.J.A., Einarsson, E., Elvebakk, A., Gould, W.A. *et al.* (2005). The circumpolar Arctic vegetation map. *J. Veg. Sci.*, 16, 267–282.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M. *et al.* (2006). Plant community responses to experimental warming across the tundra biome. *Proc. Natl Acad. Sci. USA*, 103, 1342–1346.

van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin, F.S. *et al.* (2004). Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Glob. Change Biol.*, 10, 105–123.

Wookey, P.A. (2008). Experimental approaches to predicting the future of tundra plant communities. *Plant Ecol. Divers.*, 1, 299–307.

Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., Brathen, K.A., Cornelissen, J.H.C. *et al.* (2009). Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Glob. Change Biol.*, 15, 1153–1172.

Yang, L.H., Edwards, K.F., Byrnes, J.E., Bastow, J.L., Wright, A.N. & Spence, K.O. (2010). A meta-analysis of resource pulse – consumer interactions. *Ecol. Monogr.*, 80, 125–151.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Deciduous and low-growing shrub responses to experimental warming.
Figure S2 Graminoid sub-groups (grass, rush and sedge) responses to experimental warming.
Table S1 Study details.

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