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Abstract: Rapid climate warming in the tundra biome has been linked to increasing shrub dominance. Shrub expansion can modify climate by altering surface albedo, energy and water balance, and permafrost yet the drivers of shrub growth remain poorly understood. Dendroecological data consisting of multi-decadal time series of annual shrub growth provide an underused resource to explore climate–growth relationships. Here, we analyse circumpolar data from 37 Arctic and alpine sites in 9 countries, including 25 species, and 42,000 annual growth records from 1,821 individuals. Our analyses demonstrate that the sensitivity of shrub growth to climate was: (1) heterogeneous, with European sites showing greater summer temperature sensitivity than North American sites, and (2) higher at sites with greater soil moisture and for taller shrubs (for example, alders and willows) growing at their northern or upper elevational range edges. Across latitude, climate sensitivity of growth was greatest at the boundary between the Low and High Arctic, where permafrost is thawing and most of the global permafrost soil carbon pool is stored. The observed variation in climate–shrubs growth relationships should be incorporated into Earth system models to improve future projections of climate change impacts across the tundra biome.

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Climate sensitivity of shrub growth across the tundra biome

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Rapid climate warming in the tundra biome has been linked to increasing shrub dominance^{1–4}. Shrub expansion can modify climate by altering surface albedo, energy and water balance, and permafrost^{2,5–8}, yet the drivers of shrub growth remain poorly understood. Dendroecological data consisting of multi-decadal time series of annual shrub growth provide an underused resource to explore climate-growth relationships. Here, we analyse circumpolar data from 37 Arctic and alpine sites in 9 countries, including 25 species, and ~42,000 annual growth records from 1,821 individuals. Our analyses demonstrate that the sensitivity of shrub growth to climate was: (1) heterogeneous, with European sites showing greater summer temperature sensitivity than North American sites, and (2) higher at sites with greater soil moisture and for taller shrubs (for example, alders and willows) growing at their northern or upper elevational range edges. Across latitude, climate sensitivity of growth was greatest at the boundary between the Low and High Arctic, where permafrost

is thawing⁴ and most of the global permafrost soil carbon pool is stored⁹. The observed variation in climate-shrub growth relationships should be incorporated into Earth system models to improve future projections of climate change impacts across the tundra biome.

The Arctic is warming more rapidly than lower latitudes owing to climate amplification involving temperature, water vapour, albedo and sea ice feedbacks^{5,7}. Tundra ecosystems are thus predicted to respond more rapidly to climate change than other terrestrial ecosystems⁴. The tundra biome spans Arctic and alpine regions that have similar plant species pools and mean climates, yet vary in topography, seasonality, land cover and glaciation history. Concurrent with the recent high-latitude warming trend⁷, repeat photography and vegetation surveys have shown widespread expansion of shrubs^{1–3}, characterized by increased canopy cover, height and abundance. However, climate warming⁷ and shrub increase^{2,10} have not occurred at all sites. Models predict that warming of 2–10 °C (ref. 11) could convert as much as half of current

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Bioclimatic zones:

- Zone A
- Zone B
- Zone C
- Zone D
- Zone E

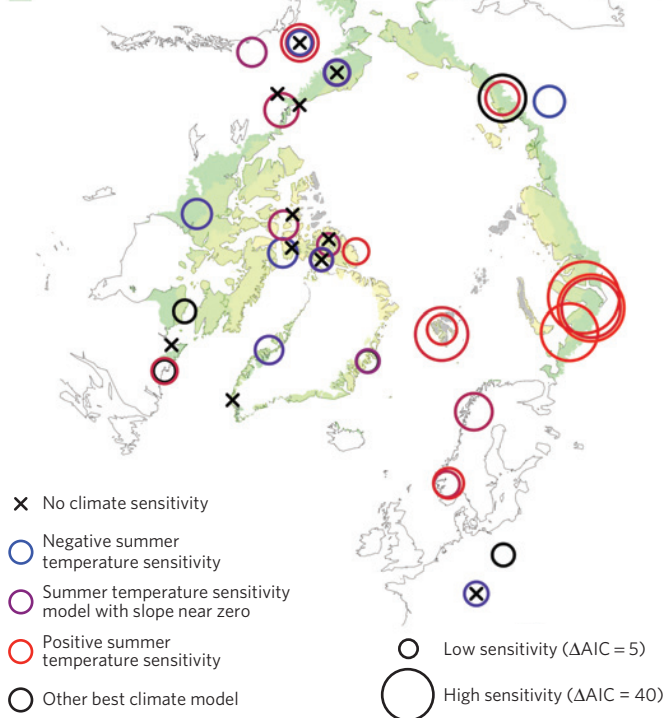


Figure 1 | Climate sensitivity across the tundra biome. The size of the circle shows the strength of the summer temperature sensitivity as indicated by the ΔAIC . The colour of the circles indicates the direction of the relationship with summer temperature variables. Locations with multiple circles indicate study sites where multiple species were sampled. The coloured regions indicate the bioclimatic zones of the Circumpolar Arctic Vegetation Map (<http://www.geobotany.uaf.edu/cavm>).

tundra to 'shrubland' by the end of the twenty-first century⁸, but the uniformity of the frequently cited relationship between climate change and tundra shrub expansion^{5,12–15} has yet to be quantified across the tundra biome as a whole.

Shrubs are woody perennial species that can live from decades to centuries. In seasonal climates, they form annual growth rings, allowing analysis of radial growth over time. Many shrub species are widely distributed across the tundra biome and are often dominant, owing to their canopy height, longevity and ability to outcompete low-growing plants. With wide geographic distributions and annual growth records, shrubs are ideally suited for quantifying tundra vegetation responses to climate warming. Assembled annual growth records from sites across the tundra biome provide a unique opportunity to test competing hypotheses of shrub responses to climate change over the past half-century.

Previous ecological monitoring and dendroecological studies have identified temperature, growing season length, summer precipitation and snow cover as important variables explaining spatial and interspecific variation in shrub growth^{1,10,13,14,16–18}. However, there is a lack of consensus regarding which climate variables best explain growth across all tundra ecosystems. We therefore do not know whether climate–growth relationships are consistent in direction, strength and magnitude among species and among sites where plant composition, climate trends and environmental parameters differ. At present, most large-scale vegetation

models assume high climate sensitivity and a uniform growth response to warming among shrub species and populations^{8,19}. These models predict pronounced positive climate feedbacks as a result of tundra vegetation change^{5,8}. Yet, if shrub growth responses to climate are constrained, then changes in shrub dominance should vary regionally, and feedbacks across the tundra biome as a whole could be weaker than predicted at present.

We quantified the climate sensitivity of shrub growth—that is, the strength of relationship between annual growth and climate variables (including temperature and precipitation, specific calculations described below)—to test four hypotheses: (1) The greatest climate sensitivity of growth should occur at northern or high-elevation range edges if plant performance is more climate limited in the harsher growing conditions at range edges than in the centre of species distributions^{20–22}. (2) Climate sensitivity of growth should be greatest in the centre of species distributions if populations growing under more stressful conditions at range edges have evolved conservative life history strategies limiting their ability to respond when conditions improve²³. (3) Climate sensitivity of growth should vary along spatial gradients if the response of species to warming is limited by other factors, such as soil nutrients, soil moisture or biotic interactions²¹. Alternatively, (4) climate sensitivity of growth could be uniform across the tundra biome.

We synthesized published and unpublished time series of shrub growth across the tundra biome. Our data set extends beyond previous analyses by including sites across the circumpolar Arctic, comprising dwarf, low and tall canopy species, and encompassing 60 years of annual-resolution shrub growth. We used crossdated, radial and axial growth measurements spanning 1950–2010, collected at 37 sites, and for 25 shrub species in 8 genera. We analysed climate–growth relationships for 46 genus-by-site combinations using linear mixed models to estimate climate sensitivity, with 33 candidate climate models as predictors of shrub growth increments. All data were normalized before analysis and model terms included seasonal temperatures and precipitation as fixed effects and year as a random effect (see Supplementary Information).

We calculated four complementary indices of climate sensitivity from the mixed model analysis for each genus-by-site combination: (1) the difference in Akaike information criterion (AIC) between the best climate model and a null model (ΔAIC), (2) the R^2 for the best climate model, (3) the absolute value of the slope of the relationship between growth and summer temperature and (4) the proportion of individuals that had significant linear relationships between growth and summer temperature (the best predictor from the overall analysis). We assessed these indices of climate sensitivity across abiotic (wet day frequency, soil moisture, growing season length) and biotic gradients (distance to range edge and species-level maximum canopy height, see Supplementary Information). In Fig. 1, we report both ΔAIC and model slopes to illustrate spatial variation in climate sensitivity (all indices reported in Supplementary Fig. 12). In Fig. 2 we report the percentage of models indicating climate (temperature or precipitation) sensitivity in the model comparison analysis; Fig. 3 shows relationships between all four climate-sensitivity indices across different gradients.

Climate–growth relationships were not uniform across the tundra biome (Fig. 1), contrasting with the common assumption used in Arctic vegetation models¹⁹. Overall climate sensitivity was high: 76% (35/46) genus-by-site combinations exhibited climate-sensitive growth (Supplementary Table 5). Summer temperature variables best explained variation in shrub growth across the 46 genus-by-site combinations and 33 climate models (Fig. 2), with 46% (21/46) genus-by-site combinations showing positive growth–summer temperature relationships and 17% (8/46) showing negative relationships (Fig. 1 and Supplementary Table 5). Individual-level climate sensitivity of growth varied considerably: 5–97% of individuals at each site and ~36% of all individuals

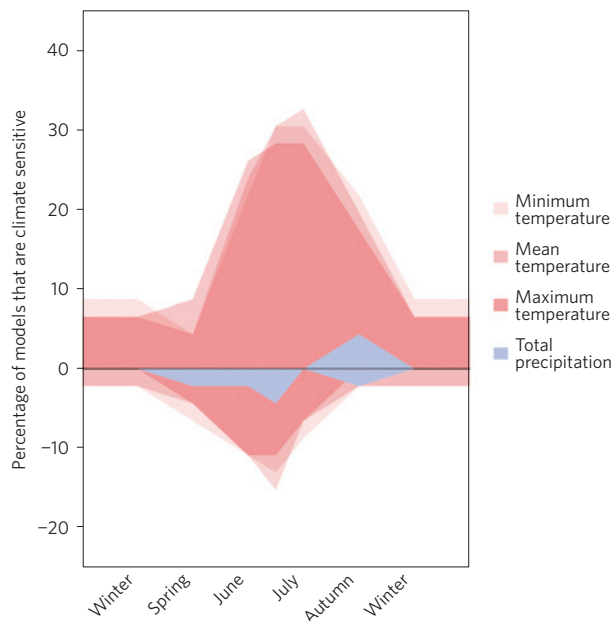


Figure 2 | Comparison of climate models. Summer temperature models were more frequently climate sensitive than other temperature or precipitation models in the model comparison analysis of 46 genus-by-site combinations and 33 climate models (Supplementary Table 4). The shaded colouring indicates the percentage of models that were considered climate sensitive (either positive or negative) for each of the four categories of climate variables for each of the genus-by-site combinations with a Δ AIC value of greater than 2 between the given climate model and the null model for all one-parameter models in the model comparison analysis.

showed significant summer temperature sensitivity (Supplementary Table 5). A moving window analysis demonstrated the relatively consistent climate sensitivity of shrub growth over time, despite the increase in sample size in recent years (Supplementary Fig. 13).

Climate sensitivity of shrub growth was highly heterogeneous across the tundra biome (Fig. 1). Climate sensitivity was greatest in the northwest Russian Arctic and northern Europe, and more heterogeneous among sites in North America (Fig. 1), where many sites exhibited weak relationships between growth and summer temperatures (Supplementary Table 5). Across gradients, climate sensitivity was greater in wetter sites relative to drier sites as indicated by the number of days with precipitation and satellite-derived soil moisture (Fig. 3a,b). We found support for our first hypothesis: shrubs growing near their northern latitudinal or elevational range limits showed greater climate sensitivity, as did taller (>50 cm maximum canopy height) versus shorter species (<50 cm; Fig. 3c,d). Overall, shrub climate–growth relationships were not uniform across the tundra biome, but instead varied according to soil moisture, species canopy height and geographic position within the species ranges.

Our results highlight the importance of soil moisture as a driver of climate sensitivity of shrub growth. In tundra environments, soil moisture is influenced by several factors including rainfall during the summer, snow distribution, duration and melt, permafrost status, soil properties and topography, making it more challenging to quantify than climate variables²⁴. We observed high climate sensitivity and positive climate–growth relationships at many sites with high soil moisture (Figs 1 and 3); however, eight sites exhibited negative summer temperature–growth relationships (Fig. 1) and some of these sites were located in areas with high soil moisture at the landscape scale (Supplementary Fig. 14). These negative relationships with summer temperatures could indicate drought limitation of growth in woody species, which can occur in both wet and dry landscapes²⁵, although in sites with increasing soil

moisture, standing water can also lead to reduced growth and shrub dieback⁶.

Previous studies have identified summer temperatures as an important driver of vegetation change^{1,13,14,26}, but the role of soil moisture is less often examined. A recent synthesis of two decades of ecological monitoring (the International Tundra Experiment Network) showed that increased shrub abundance was most pronounced at sites that had experienced summer warming and in wetter versus drier sites¹. In addition, landscape-level studies of shrub change in northern Alaska showed greater increases in wet floodplains relative to well-drained hill slopes^{3,10}. Our study, using a new circumarctic dendroecological data set consisting of almost exclusively different sites from those in previous studies, also demonstrates broad geographic patterns in the climate sensitivity of shrub growth, with higher climate sensitivity at sites with higher soil moisture. Taken together these results suggest that, with continued warming¹¹, potentially more variable precipitation¹¹ and uncertainty in the future soil moisture regime^{11,24}, water availability or flooding could play an increasingly important role in limiting future shrub expansion. However, analyses of plant water availability in tundra ecosystems are limited by the lack of high-resolution soil moisture data²⁴.

In our study, climate sensitivity of shrub growth was greatest at the northern or elevational range margins of individual species (Fig. 3). Climate sensitivity of shrub growth was thus greatest at the transition zone between tall and low shrub tundra (Fig. 1). The largest ecosystem transitions in shrub dominance could occur at these mid-Arctic latitudes, rather than at the northern limits of the tundra biome as a whole. The patterns of climate sensitivity of growth in tundra shrub species can be compared to patterns observed in treeline ecotones. Half of the latitudinal and elevational treelines studied so far have advanced poleward or upslope, often associated with warming²⁷. Temperature sensitivity of tree growth has been found to be highest at the upper or northern-most margin of the forest–tundra transition zone^{20,27} and moisture sensitivity to be highest at southern or lower range edges²⁸. Our results suggest that for tundra shrubs, both temperature and soil moisture control growth at range edges, whereas further from the range edge other factors such as competition, facilitation, herbivory and disease²¹ may be more important. Herbivore densities vary spatially and temporally across our study locations^{12,29}, and this could be one of the factors explaining the variation in climate sensitivity. Relationships between the climatic and biotic factors influencing growth are probably complex and deserve greater study.

We find that climate sensitivity of growth is greater for tall shrubs, than for low-statured shrub species (Fig. 3b). This has important implications for Earth system models, as changes in tall shrub cover will contribute more markedly to ecosystem–climate feedbacks than changes in dwarf shrub cover⁸. Increases in canopy height and abundance of taller species relative to lower-stature shrub species was a major finding of two recent syntheses of plot-based ecological monitoring and passive warming experiments; however, these studies did not include taller alder and willow species^{1,26}. Tall shrub species may more readily exploit favourable climate conditions, particularly at the transition zone from tall to low shrub tundra, by competing for limited light and nutrient resources³⁰. In particular, in contrast to previous work that has not explicitly tested biogeographic patterns of climate sensitivity¹, our analysis demonstrates that the climate sensitivity of both tall and dwarf shrub species was often greater towards colder range margins (Fig. 3a). This results in an overall pattern of high climate sensitivity at mid-latitudes, but also high climate sensitivity for some species growing in the High Arctic (Fig. 1).

In conclusion, climate sensitivity of shrub growth is generally high at sites across the tundra biome, which provides strong evidence for the attribution of tundra shrub increases to climate warming⁴. However, pronounced increases in shrub growth with warming are unlikely to occur in all regions, and the greatest

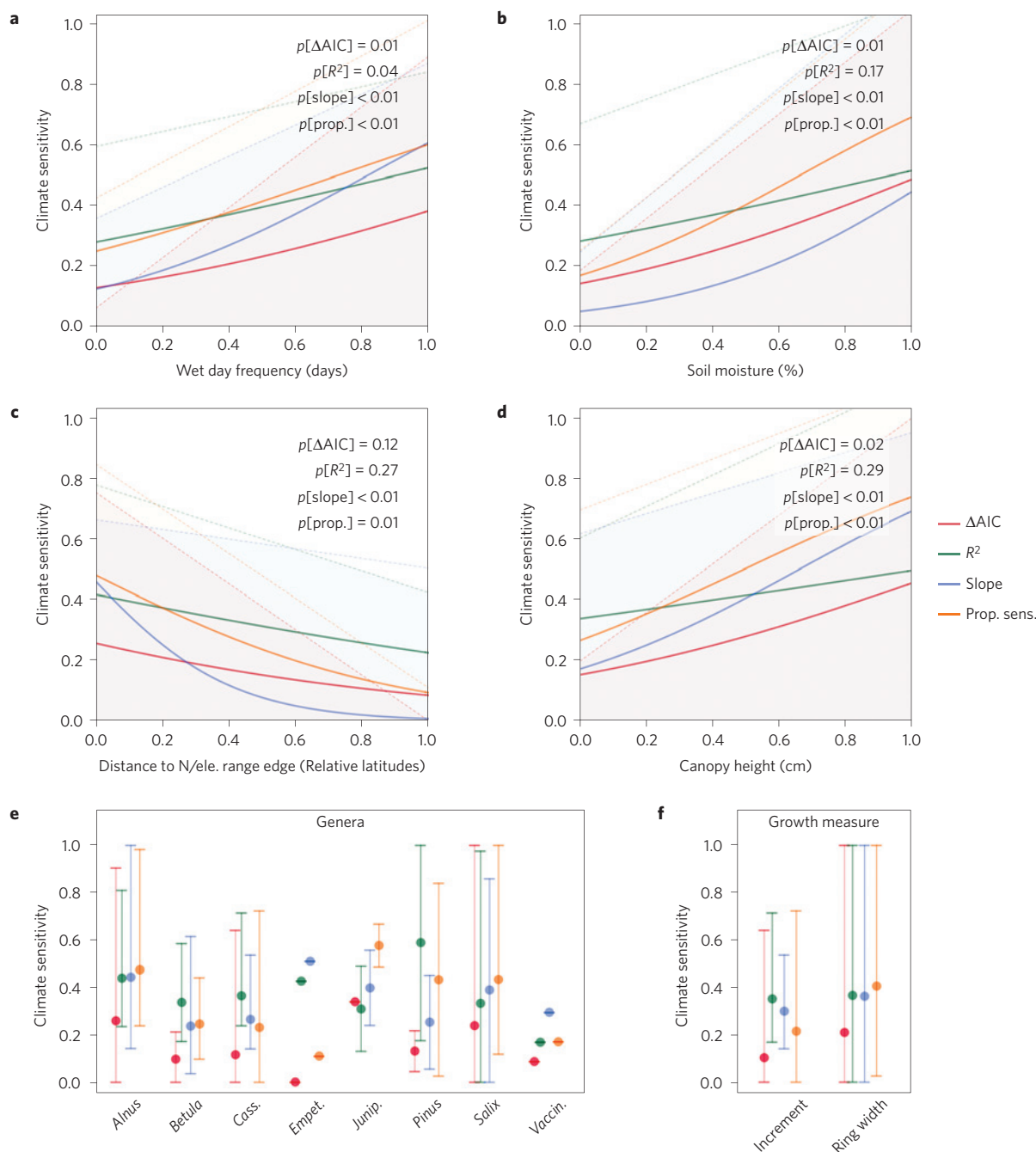


Figure 3 | Climate sensitivity across gradients. **a–d**, Greater climate sensitivity was found for shrub species growing at sites with a greater number of wet days (**a**), higher soil moisture (**b**), closer to northern/elevational range limits (**c**) and for species with higher maximum canopy heights (**d**). **e, f**, Climate sensitivity varied among genera (**e**; Supplementary Table 2) and between the two growth measures of stem increments and annual ring widths (**f**). The lines and associated p values indicate beta regression of the different climate-sensitivity metrics; the shaded areas indicate the 90th quantile of these regressions and the error bars (**e, f**) indicate the range of values. The distance to the range edge (**c**) is the distance between the sampling location and the northern or elevation range edge for each species converted to relative latitudes (see Supplementary Information). This gives an index of how far a sample population is located from the maximum extent of the distribution of that species either northward in the Arctic or upslope in alpine tundra.

shrub growth responses are instead likely to occur in the transition zone between tall- and low-statured shrub tundra and where soil moisture is not limiting. A pressing research question is whether temperature-induced increases in shrub growth will continue to occur at current or accelerated rates or whether factors such as water availability, herbivory, pathogen outbreaks, nutrient limitation or fire will play a greater role in limiting future tundra shrub expansion. Further experimental manipulations of temperature²⁶, moisture regime, biotic interactions and atmospheric CO₂ concentration are

necessary to predict shrub growth responses under future environmental scenarios. Improved soil moisture records²⁴ (resulting from, for example, ESA <http://www.esa-soilmoisture-cci.org> and NASA <http://smap.jpl.nasa.gov>) and other locally influenced climate and biological variables and expanded networks of *in situ* tundra vegetation observations¹ will further improve predictions. Only with a combination of enhanced ecological monitoring, multifactorial experimentation and additional data synthesis can we make improved projections of vegetation feedbacks to future climate change.

Methods

Methods and any associated references are available in the [online version of the paper](#).

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Author contributions

All authors designed the study, collected or processed data and assisted in writing the paper; I.H.M.-S. and M.V. took the lead in writing the paper; I.H.M.-S. analysed the data with assistance from S.C.E.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to I.H.M.-S.

Competing financial interests

The authors declare no competing financial interests.

Methods

To examine climate sensitivity of tundra shrub growth, we assembled a database of 37 Arctic and alpine sites encompassing 25 species from 8 genera (Supplementary Tables 1 and 2) for a total of 46 genus-by-site combinations, 1,821 individual shrubs, and 41,576 yearly growth measurements. Growth measurements included annual ring widths (35 genus-by-site combinations) and stem increments (11 genus-by-site combinations). Although data collection was not coordinated in advance and includes both published and unpublished data, the resulting data set represents many of the dominant and widely distributed shrub species found across the tundra biome.

To test the correspondence between variation in climate and annual growth, we used monthly Climate Research Unit (CRU) TS3.21 gridded temperature and precipitation data (0.5° resolution, Supplementary Table 3). We found high correlations between the CRU TS3.21 and station data for the 19 sites with a meteorological station in relatively close proximity (Supplementary Table 4).

We used linear mixed models (package nlme, R version 2.15.3) and model selection among 33 candidate models that included temperature and precipitation variables to relate annual growth to climate (Supplementary Tables 5 and 6). We analysed data from 1950 to 2010, the period with the highest quality climate data and overlap between different individual shrub growth time series.

We present four different indices of climate sensitivity for each genus-by-site combination (see above and Supplementary Information). We considered the overall climate sensitivity to be the comparison of the best model to a null model; summer temperature sensitivity was a comparison of only the models containing a summer temperature variable. We then compared the climate sensitivity of growth to environmental and biotic gradients including wet day frequency, soil moisture, distance to nearest range edge and the maximum potential canopy height for the sampled species. Data have been archived at the Polar Data Catalogue (<https://www.polardata.ca> Ref No. 12131). Detailed methods describing the data and analyses that were used are included in the Supplementary Information.

Corrigendum: Climate sensitivity of shrub growth across the tundra biome

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In the version of this Letter originally published online, the second affiliation for Martin Hallinger was missing: ⁷Department of Ecology, Swedish University of Agricultural Sciences, PO Box 7044, 75007 Uppsala, Sweden. The remaining affiliations have been renumbered.

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