# Climate sensitivity of shrub growth across the tundra biome

**Citation for published version:**
Myers-Smith, IH, Elmendorf, SC, Beck, PSA, Wilmking, M, Hallinger, M, Blok, D, Tape, KD, Rayback, SA, Macias-Fauria, M, Forbes, BC, Speed, JDM, Boulanger-Lapointe, N, Rixen, C, Lévesque, E, Schmidt, NM, Baittinger, C, Trant, AJ, Hermanutz, L, Collier, LS, Dawes, MA, Lantz, TC, Weijers, S, JØrgensen, RH, Buchwal, A, Buras, A, Naito, AT, Ravolainen, V, Schaepman-Strub, G, Wheeler, JA, Wipf, S, Guay, KC, Hik, DS & Vellend, M 2015, 'Climate sensitivity of shrub growth across the tundra biome', *Nature Climate Change*, vol. 5, no. 9, pp. 887-891. https://doi.org/10.1038/nclimate2697

**Digital Object Identifier (DOI):**
10.1038/nclimate2697



**Published In:**
Nature Climate Change

# Climate sensitivity of shrub growth across the tundra biome

Isla H. Myers-Smith[1], Sarah C. Elmendorf[2,3], Pieter S. A. Beck[4,5], Martin Wilmking[6], Martin Hallinger[6], Daan Blok[7], Ken D. Tape[8], Shelly A. Rayback[9], Marc Macias-Fauria[10], Bruce C. Forbes[11], James D. M. Speed[12], Noémie Boulanger-Lapointe[13,14], Christian Rixen[15], Esther Lévesque[13], Niels Martin Schmidt[16], Claudia Baittinger[17], Andrew J. Trant[18,19], Luise Hermanutz[19], Laura Siegwart Collier[19], Melissa A. Dawes[15], Trevor Lantz[18], Stef Weijers[20], Rasmus Halfdan Jørgensen[21], Agata Buchwal[22], Allan Buras[6], Adam T. Naito[23], Virve Ravolainen[24], Gabriela Schaepman-Strub[25], Julia Wheeler[15,26], Sonja Wipf[15], Kevin Guay[5], David S. Hik[27], and Mark Vellend[28]

1. School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JW, United Kingdom
2. National Ecological Observatory Network, 1685 38th St., Suite 100, Boulder, CO, 80301, USA
3. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, 80309, USA
4. European Commission, Joint Research Centre (JRC), Institute for Environment and Sustainability (IES), Climate Change Unit, Via Enrico Fermi 2749, 21027, Ispra VA, Italy
5. Woods Hole Research Center, 149 Woods Hole Road, Falmouth, MA, 02540, USA
6. Institute of Botany and Landscape Ecology, Ernst-Moritz-Arndt University Greifswald, D-17487, Greifswald, Germany
7. Center for Permafrost (CENPERM), Department of Geosciences and Natural Resource Management, University of Copenhagen, DK-1350 Copenhagen, Denmark
8. Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, 99775-7000, USA
9. Department of Geography, 213 Old Mill Building, 94 University Place, University of Vermont, Burlington, Vermont, 05405, USA

10. School of Geography and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY, UK
11. Arctic Centre, University of Lapland, Box 122, FI-96101, Rovaniemi, Finland
12. University Museum, Norwegian University of Science and Technology, NO-7491, Trondheim, Norway
13. Département des Sciences de l'environnement et Centre d'études nordiques, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, Québec, G9A 5H7, Canada
14. Department of Geography, University of British Columbia, 1984 West Mall, Vancouver, BC, V6T 1Z2, Canada
15. WSL Institute for Snow and Avalanche Research SLF, Fluelastrasse 11, CH-7260, Davos Dorf, Switzerland
16. Arctic Research Centre, Aarhus University, Frederiksborgvej 399, 4000, Roskilde, Denmark
17. National Museum of Denmark, Frederiksholms Kanal 12, 1220, Copenhagen, Denmark
18. School of Environmental Studies, PO Box 3060 STN CSC, University of Victoria, Victoria, British Columbia, V8W 3R4, Canada
19. Department of Biology, Memorial University, St John's, Newfoundland, A1B 3X9, Canada
20. Climatology and Landscape Ecology, Department of Geography, University of Bonn, Meckenheimer Allee 166, D-53115, Bonn, Germany
21. Department of Plant & Environmental Sciences, University of Copenhagen, Rolighedsvej 21, 1958, Frederiksberg C, Denmark
22. Institute of Geoecology and Geoinformation, Adam Mickiewicz University, Dziegielowa 27, 61-680, Poznan, Poland
23. Department of Geography, Texas A&M University, 810 Eller O&M Building, Mailstop 3147 TAMU, College Station, Texas, 77843-3147, USA
24. Norwegian Polar Institute, Fram Centre, NO-9296, Tromsø, Norway

25. Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057, Zürich, Switzerland

26. University of Basel, Institute of Botany, CH-4056 Basel, Switzerland

27. Department of Biological Sciences, Biological Sciences Bldg., University of Alberta, Edmonton, Alberta, T6G 2E9, Canada

28. Département de biologie, Faculté des Sciences, 2500, boulevard de l'Université, Université de Sherbrooke, Sherbrooke, Québec, J1K 2R1, Canada

**Abstract**

Rapid temperature increases in the tundra biome have 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 1821 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 (e.g., alders, 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[4] and the majority of the global permafrost soil carbon pool is stored[9]. 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 due 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 ecosystems[4]. 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 trend[7], repeat photography and vegetation surveys have shown widespread expansion of shrubs[1–3], characterised by increased canopy cover, height and abundance. However, climate warming[7] and shrub increase[2,10] have not occurred at all sites. Models predict that warming of 2-10 °C[11] could convert as much as half of current tundra to 'shrubland' by the end of the 21st century[8], 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 entire tundra biome.

Shrubs are woody perennial species that live from decades to centuries. In highly 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, due 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 if climate-growth relationships are consistent in direction and magnitude among species and among sites where plant composition, climate trends and environmental parameters differ. Currently, most large-scale vegetation models assume high climate sensitivity and a uniform growth response to warming among shrub species and populations[8,23]. 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 currently predicted.

We quantified the climate sensitivity of shrub growth – i.e., 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 peripheral than central populations[19–21]. 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 improve[22]. 3) Climate sensitivity of growth should vary along gradients if the response of species to warming is limited by other factors, such as soil nutrients, soil moisture or biotic interactions[20]. Alternatively, 4) climate sensitivity of growth could be uniform.

We synthesized existing and new time series of shrub growth across the tundra biome. Our dataset 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 to 2010, collected at 37 sites, and for 25 shrub species in eight 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 at the genus-by-site level before analysis and model terms included seasonal temperatures and precipitation as fixed effects and year as a random effect (see Supp. Info.).

We calculated four complementary indices of climate sensitivity from the mixed model analysis for each genus-by-site combination: 1) the difference in AIC between the best climate model and a null model (delta AIC), 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 Supp. Info.). In Fig. 1, we report both delta AIC and model slopes to illustrate spatial variation in climate sensitivity (all indices reported in Fig. S12). 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 models[23]. Overall climate sensitivity was high: 83% (38/46) genus-by-site combinations exhibited climate-sensitive growth (Table S5). 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; 8 showed negative relationships (Fig. 1, Table S5). Individual-level climate sensitivity of growth varied considerably: 5 – 97% of individuals at each site and ~36% of all individuals showed significant summer temperature sensitivity (Table S5). A moving window analysis demonstrated the relatively consistent climate sensitivity of shrub growth over time, despite the increase in sample size in recent years (Fig. S13).

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 (Table S5). 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 and 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 (>50cm maximum canopy height) versus shorter species (<50cm) (Fig. 3c and d). Overall, shrub growth-climate 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 and drought as drivers 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 variables[24]. We observed high climate sensitivity and positive growth-climate relationships at many sites with high soil moisture (Figs. 1 and 3); however, seven sites exhibited negative growth-climate relationships (Fig. 1) and some of these sites were located in areas with high soil moisture at the landscape scale (Fig. S14). These negative relationships with summer temperatures could indicate drought limitation of growth in woody species, which can occur in both wet and dry landscapes[25], although in sites with increasing soil moisture and standing water can also experience reduced growth and shrub dieback[6].

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 warmer (in summer) and wetter sites [1]. 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 dataset 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 wetter versus drier sites. Taken together these results suggest that, with continued warming[11], potentially more variable precipitation[11] and uncertainty in the future soil moisture regime[11,24], water availability 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 data[24].

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 greatest 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 to date have been advancing poleward or upslope, often associated with warming[27]. Temperature sensitivity of tree growth is greatest at the upper or northern-most margin of the forest-tundra transition zone[19,27] and moisture sensitivity is greatest at southern or lower range edges[28]. Our results suggest that for tundra shrubs, both temperature and soil moisture control growth at range edges, while further from the range edge other factors such as competition, facilitation, herbivory, and disease[20] 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 variation in climate sensitivity. Relationships between the climatic and biotic factors influencing growth are likely complex and deserve greater study.

We find that climate sensitivity of growth is greater for tall shrubs, than for low-statured species (Fig. 3b). This has important implications for earth system models, as changes in tall shrub cover will contribute more dramatically to ecosystem-climate feedbacks[8]. Increases in canopy height and abundance of taller species relative to lower-stature dwarf 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 resources[30]. In particular, in contrast to this previous work that has not explicitly tested biogeographic patterns of climate sensitivity[1], our analysis demonstrates that the sensitivity to climate of low shrub species was often greater towards their range margins (Fig. 3a). This results in a pattern of 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 warming[4]. However, dramatic increases in shrub growth with warming are unlikely to occur in all regions, and the greatest 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 open question is whether temperature-induced increases in shrub growth will continue to occur at current or accelerated rates or if factors such as water availability, herbivory, pathogen outbreaks, nutrient limitation, or fire will limit growth in arctic and alpine tundra. Experiments manipulating temperature[26], moisture regime, herbivory and atmospheric $CO_2$ concentration are necessary to predict shrub growth responses under future environmental scenarios. Improved soil moisture records[24] (resulting from e.g., 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 observations[1] 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 Summary**

To examine climate sensitivity of tundra shrub growth, we assembled a database of 37 arctic and alpine sites encompassing 25 species from eight genera (Tables S1 and S2) 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, the data collection was not coordinated in advance and includes both published and unpublished data, the resulting dataset represents many of the dominant and widely distributed tundra 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, Table S3). We found high correlations between the CRU TS3.21 and station data for the 19 sites with a meteorological station in relatively close proximity (Table S4).

We used linear mixed models (package nlme, R version 2.15.3) and model selection including 33 candidate models of temperature and precipitation variables to relate annual growth to climate (Tables S5 and S6). We analysed data from 1950 to 2010, the period with the highest climate data quality 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 Supp. Info.). 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 to a null model. 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. Detailed methods describing the data and analyses that were used are included in the supplementary information.

## References


1. Elmendorf, S. C. *et al.* Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat. Clim. Change* **2,** 453–457 (2012).
2. Myers-Smith, I. H. *et al.* Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ. Res. Lett.* **6,** 045509 (2011).
3. Tape, K. D., Sturm, M. & Racine, C. H. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Glob. Change Biol.* **12,** 686–702 (2006).
4. IPCC Working Group II. *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. (2014).
5. Chapin, F. S. *et al.* Role of land-surface changes in arctic summer warming. *Science* **310,** 657–660 (2005).
6. Blok, D. *et al.* Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Glob. Change Biol.* **16,** 1296–1305 (2010).
7. Hinzman, L. D. *et al.* Trajectory of the Arctic as an integrated system. *Ecol. Appl.* **23,** 1837–1868 (2013).
8. Pearson, R. G. *et al.* Shifts in Arctic vegetation and associated feedbacks under climate change. *Nat. Clim. Change* **3,** 673–677 (2013).
9. Hugelius, G. *et al.* The Northern Circumpolar Soil Carbon Database: spatially distributed datasets of soil coverage and soil carbon storage in the northern permafrost regions. *Earth Syst. Sci. Data* **5,** 3–13 (2013).
10. Tape, K., Hallinger, M., Welker, J. & Ruess, R. Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* **15,** 711–724 (2012).
11. IPCC. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (2013).
12. Post, E. *et al.* Ecological dynamics across the Arctic associated with recent climate change. *Science* **325,** 1355–1358 (2009).
13. Forbes, B. C., Macias-Fauria, M. & Zetterberg, P. Russian arctic warming and 'greening' are closely tracked by tundra shrub willows. *Glob. Change Biol.* **16,** 1542–1554 (2010).
14. Macias-Fauria, M., Forbes, B. C., Zetterberg, P. & Kumpula, T. Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nat. Clim. Change* **2,** 613–618 (2012).
15. Sturm, M., Racine, C. H. & Tape, K. D. Increasing shrub abundance in the Arctic. *Nature* **411,** 546–547 (2001).
16. Hallinger, M., Manthey, M. & Wilmking, M. Establishing a missing link: Warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol.* **186,** 890–899 (2010).
17. Blok, D. *et al.* What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* **8,** 1169–1179 (2011).
18. Weijers, S. *et al.* No divergence in Cassiope tetragona: Persistence of growth response along a latitudinal temperature gradient and under multi-year experimental warming. *Ann. Bot.* **110,** 653–665 (2012).
19. Ettinger, A. K., Ford, K. R. & HilleRisLambers, J. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* **92,** 1323–1331 (2011).
20. HilleRisLambers, J., Harsch, M. A., Ettinger, A. K., Ford, K. R. & Theobald, E. J. How will biotic interactions influence climate change–induced range shifts? *Ann. N. Y. Acad. Sci.* **1297,** 112–125 (2013).
21. MacArthur, R. H. *Geographical Ecology: Patterns in the Distribution of Species*. (Princeton University Press, 1972).

22. Grime, J. P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111,** 1169–1194 (1977).
23. Wullschleger, S. D. *et al.* Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Ann. Bot.* mcu077 (2014). doi:10.1093/aob/mcu077
24. Seneviratne, S. I. *et al.* Investigating soil moisture–climate interactions in a changing climate: A review. *Earth-Sci. Rev.* **99,** 125–161 (2010).
25. Wilmking, M. & Myers-Smith, I. Changing climate sensitivity of black spruce (Picea mariana Mill.) in a peatland-forest landscape in Interior Alaska. *Dendrochronologia* **25,** 167–175 (2008).
26. Elmendorf, S. C. *et al.* Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecol. Lett.* **15,** 164–175 (2012).
27. Harsch, M. A., Hulme, P. E., McGlone, M. S. & Duncan, R. P. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.* **12,** 1040–1049 (2009).
28. Beck, P. S. A. *et al.* Changes in forest productivity across Alaska consistent with biome shift. *Ecol. Lett.* **14,** 373–379 (2011).
29. Olofsson, J. *et al.* Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob. Change Biol.* **15,** 2681–2693 (2009).
30. Bret-Harte, M. S., Shaver, G. R. & Chapin, F. S. Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. *J. Ecol.* **90,** 251–267 (2002).

**Acknowledgements**

We thank the many field and laboratory assistants for help with data collection, governments, parks, field stations and the local and indigenous people for the opportunity to conduct research on their land. Financial support was provided by the International Arctic Science Committee [All], the EnviroNorth CREATE grant [IMS], International Polar Year Programs of the Government of Canada, Natural Sciences and Engineering Research Council of Canada and Northern Scientific Training Program [IMS, DSH, MV, NBL, EL, AT, LH, LSC], INTERACT (262693) European Community's Seventh Framework Programme [MW and ABur], Wageningen University and Research Center, Darwin Center for Biogeosciences, Danish National Research Foundation (CENPERM DNRF100) [DB], NSERC, Swedish Polar Secretariat [SR], Academy of Finland and NASA Land Cover/Land-Use Change Program [BCF and MMF], Oxford Martin School Programme on Resource Stewardship [MMF], Research Council of Norway (Project 212897) [JDMS], Fonds de recherche du Québec: Nature et technologies [NBL, EL, MV] and Centre d'études Nordiques, ArcticNet – a network of centres of excellence [NBL, EL, AT, LH, LSC], Polar Continental Shelf Program [NBL, EL], WSL Institute for Snow and Avalanche Research SLF [to CR, MD, JW, SWi], Knud Højgaard Charity Foundation [NMS], The Northern Worlds initiative of the National Museum of Denmark [CB], IPY-NWO (project 851.40.051) [SWe], Polish National Science Centre (project N306 009139) [ABuc], Virtual Institute ICLEA of the Helmholtz Foundation [ABur], National Science Foundation (ARC-0806506) [AN], University of Zurich Research Priority Program 'Global Change and Biodiversity' [GSS] and The Research Council of Norway [VR].

**Author contributions**

All authors designed the study, collected or processed data and assisted in writing the paper; IMS and MV took the lead in writing the paper; IMS analysed the data.

**Author information**

The authors declare no competing financial interests. Data have been archived at the Polar Data Catalogue (https://www.polardata.ca/ Ref No 12131). Supplementary information accompanies this paper. Correspondence and requests for materials should be addressed to IMS (isla.myers-smith@ed.ac.uk).

## Figures

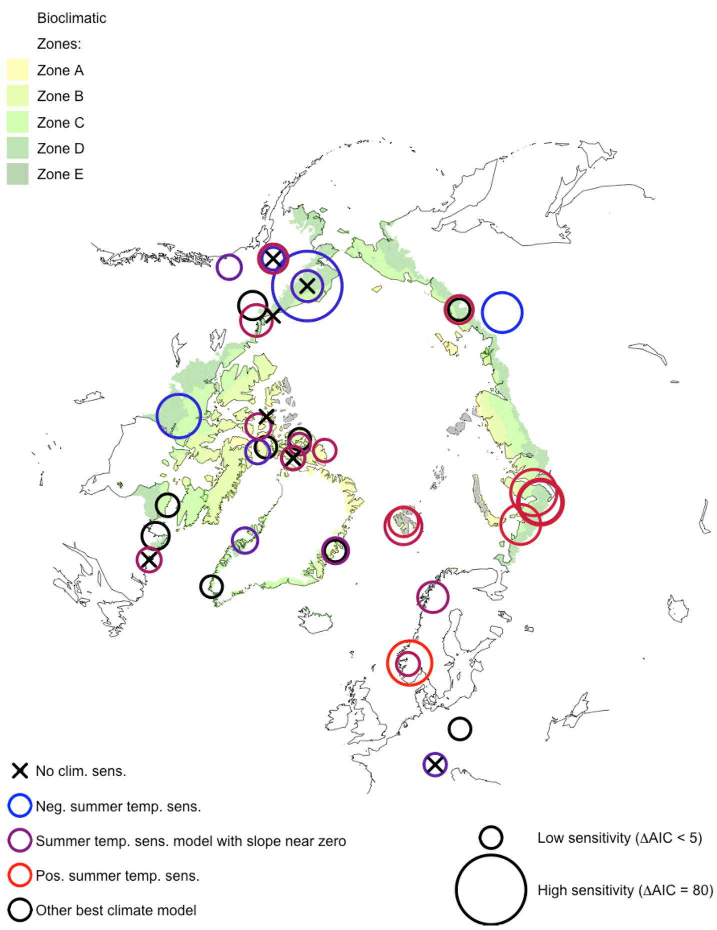


Figure 1. Climate sensitivity across the tundra biome. The size of the circle shows the strength of the summer temperature sensitivity as indicated by the delta AIC. The colour of the circles indicates the direction of the relationship with summer temperature variables, with red circles indicating sites that have a positive relationship, blue circles indicating sites with a negative relationship, purple circles indicating sites with slopes near zero, black circles indicating sites where the best model was not a summer temperature model and crosses indicating genus-by-site combinations where summer temperature sensitivity was not indicated by the model comparison analysis. Sites with multiple circles indicate study sites where multiple species were sampled. The coloured regions indicate the bioclimatic zones of the Circumpolar Arctic Vegetation Map (CAVM. 2003. http://www.geobotany.uaf.edu/cavm/).

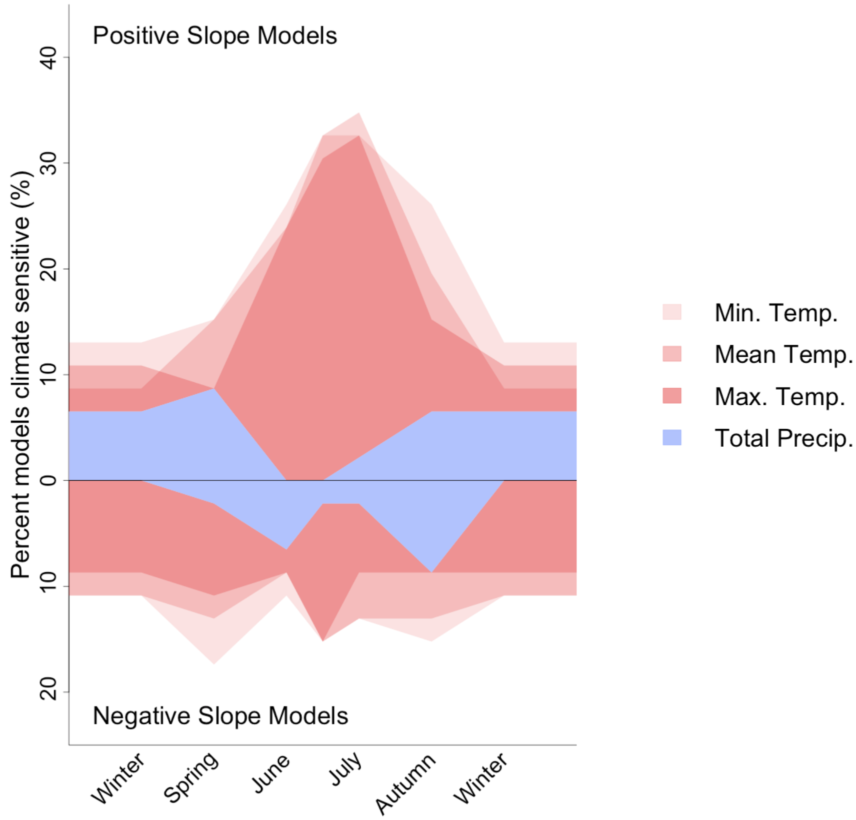


Figure 2. Comparison of climate models. Summer temperature models were more frequently climate sensitive than other temperature or precipitation models in the model comparison analysis of 46 genus-by-site combinations and 33 climate models (Table S4). The shaded colouring indicates the percent of models that were considered climate sensitive for each of the four categories of climate variables for each of the genus-by-site combinations with a difference in 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.

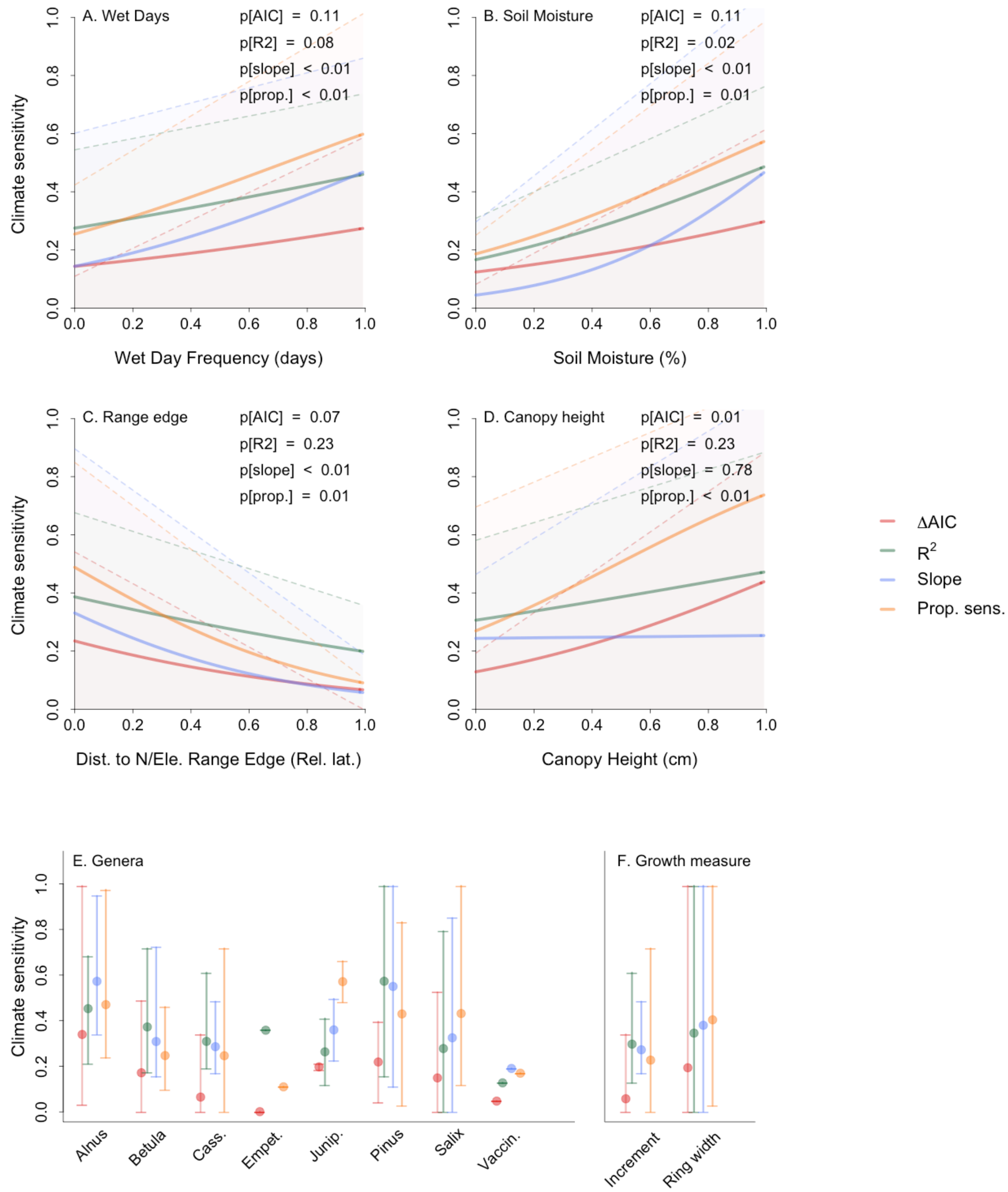


Figure 3. Climate sensitivity across gradients. Greater climate sensitivity was found for shrub species growing at sites with a greater number of wet days (A), higher soil moisture (B), closer to northern/elevational range limits (C) and for species with higher maximum canopy heights (D). Climate sensitivity varied among genera (E) and between the two growth measures of stem increments and annual ring widths (F). Climate sensitivity is indicated by four metrics: 1) the difference in AIC value between the best climate model and a null model, 2) the $R^2$ value for the best climate model, 3) the absolute value of the slope of the best summer temperature model and 4) the proportion of

individuals that had significant linear relationships between growth and summer temperature variables. The lines and associated p-values indicate beta regression of the different climate sensitivity metrics, the dashed lines indicate the 90$^{th}$ quantile. 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 Supp. Info.). 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 up slope in alpine tundra.