nature climate change

LETTERS

PUBLISHED ONLINE: XX MONTH XXXX | DOI: 10.1038/NCLIMATE2697

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 C. 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 A. Wheeler[15,26], Sonja Wipf[15], Kevin C. Guay[5], David S. Hik[27] and Mark Vellend[28]

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. Q.1 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: Q.2 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[4] and most 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 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 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], characterized 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 (ref. 11) could convert as much as half of current Q.3 tundra to 'shrubland' by the end of the twenty-first century[8], but the uniformity of the frequently cited relationship between climate

[1]School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JW, UK. [2]National Ecological Observatory Network, 1685 38th Street, Suite 100, Boulder, Colorado 80301, USA. [3]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309, USA. [4]European Commission, Joint Research Centre (JRC), Institute for Environment and Sustainability (IES), Forest Resources and Climate Unit, Via Enrico Fermi 2749, 21027 Ispra VA, Italy. [5]Woods Hole Research Center, 149 Woods Hole Road, Falmouth, Massachusetts 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, British Columbia 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, 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. *e-mail: isla.myers-smith@ed.ac.uk

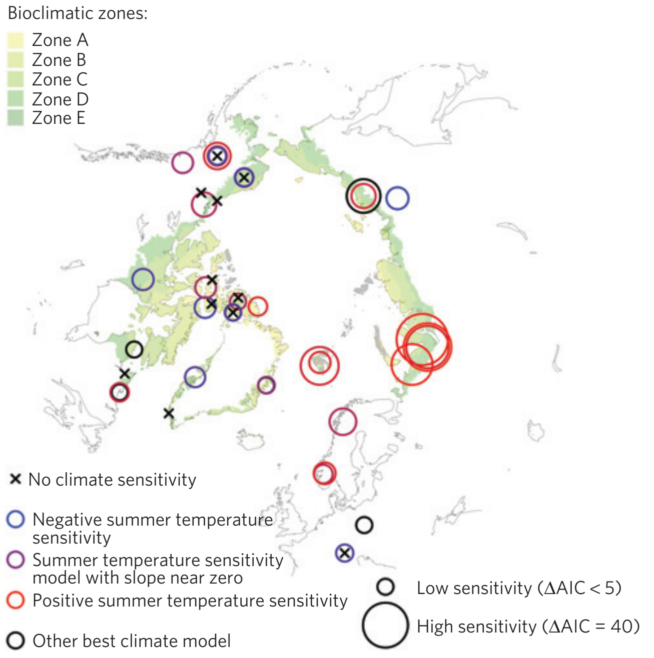

Figure 1 | Climate sensitivity across the tundra biome. The size of the circle shows the strength of the summer temperature sensitivity as indicated by the delta AIC. The colour of the circles indicates the direction of the relationship with summer temperature variables, with red circles indicating sites 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 representing genus-by-site combinations where climate sensitivity was not indicated by the model comparison analysis. 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 (CAVM. 2003. http://www.geobotany.uaf.edu/cavm). Q.4

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 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 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 Q.5 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 peripheral than central populations[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 improve[23]. 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[21]. Alternatively, 4) climate sensitivity of growth could be uniform.

We synthesized existing and new 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 AIC between the best climate model and a null model (delta AIC), 2) the R^2 for the best climate model, 3) Q.6 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 delta AIC 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 models[19]. 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, Supplementary Table 5). 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 (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

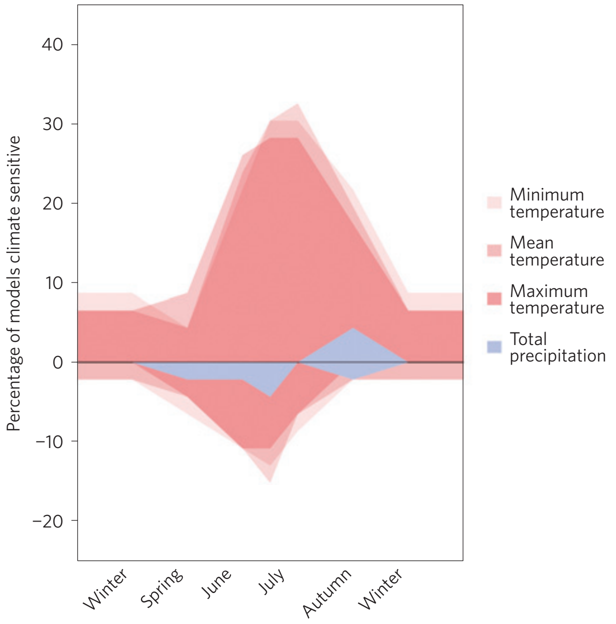

Figure 2 | Comparison of climate models. Summer temperature models were more frequently climate sensitive than other temperature or precipitation models in the model comparison analysis of 46 genus-by-site combinations and 33 climate models (Supplementary Table 4). The shaded Q.7 colouring indicates the percentage 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.

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 variables[24]. 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 landscapes[25], although in sites with increasing soil moisture, standing water can also lead to 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 sites that had experienced summer warming and in wetter versus drier 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 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 warming[11], potentially more variable precipitation[11] 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 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 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 warming[27]. 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 edges[28]. Our results suggest that for tundra shrubs, both temperature and soil moisture control growth at range edges, while further from the range Q.8 edge other factors such as competition, facilitation, herbivory and disease[21] 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 likely complex and deserve greater study. Q.9

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 cover[8]. 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 resources[30]. In particular, in contrast to previous work that has not explicitly tested biogeographic patterns of climate sensitivity[1], our analysis demonstrates that the climate sensitivity of both tall and dwarf shrub species was often greater towards range margins (Fig. 3a). This results in an overall pattern of high climate sensitivity at mid-latitudes by also for some species growing in the high Arctic (Fig. 1). Q.10

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, pronounced 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 research question is whether temperature-induced increases in shrub growth will continue to occur at current or accelerated rates or whether factors such as

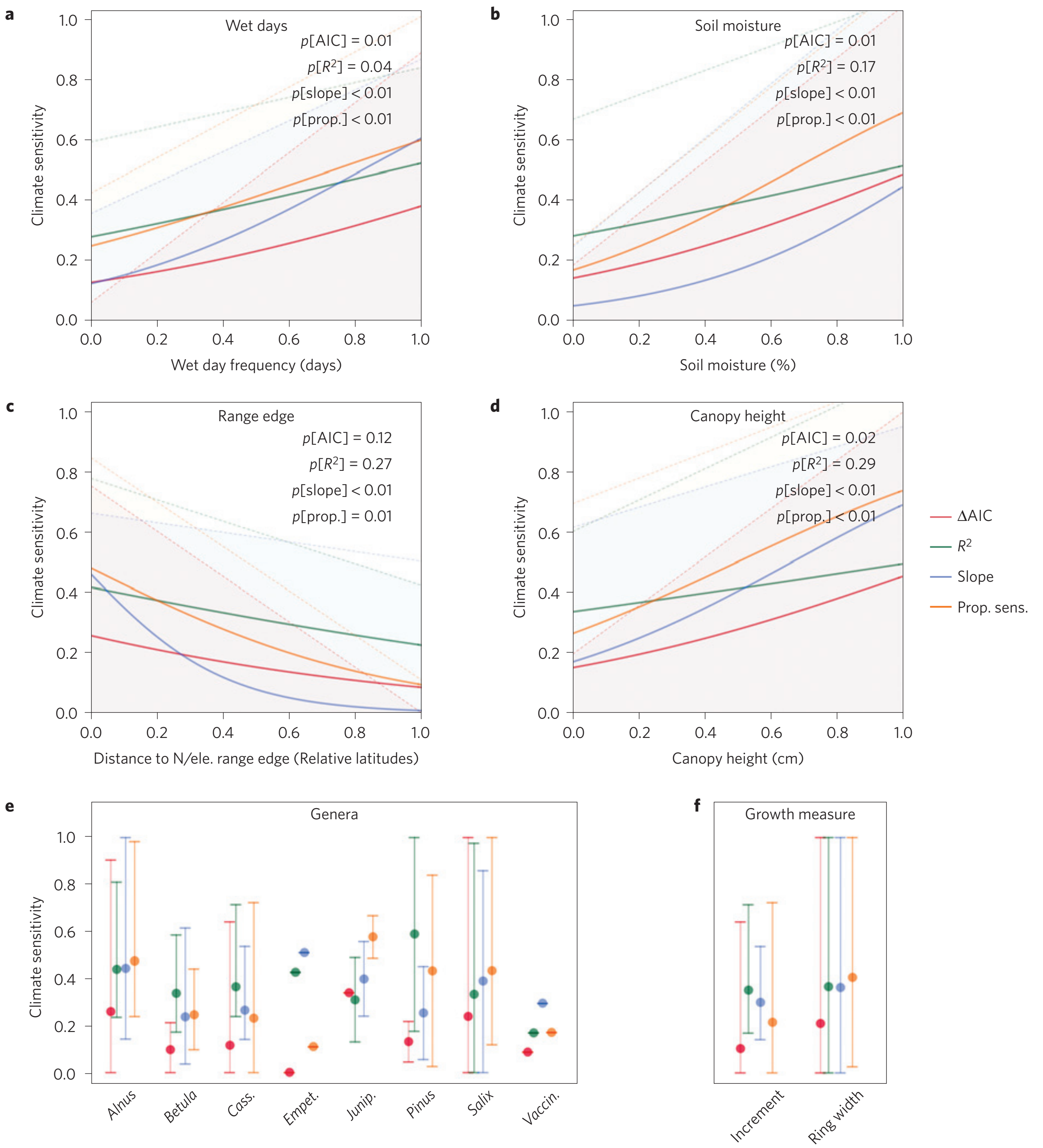

Figure 3 | Climate sensitivity across gradients. a–d, Greater climate sensitivity was found for shrub species growing at sites with a greater number of wet days (**a**), higher soil moisture (**b**), closer to northern/elevational range limits (**c**) and for species with higher maximum canopy heights (**d**). **e**,**f**, Climate sensitivity varied among genera (**e**) 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 shaded areas indicate the 90th quantile of these regressions. 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.

water availability, herbivory, pathogen outbreaks, nutrient limitation or fire will play a greater role in limiting future tundra shrub expansion. Further experimental manipulations of temperature[26], moisture regime, biotic interactions and atmospheric CO_2 concentration are necessary to predict shrub growth responses under future environmental scenarios. Improved soil moisture records[24] (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 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

Methods and any associated references are available in the online version of the paper.

Received 4 July 2014; accepted 13 May 2015; published online XX Month XXXX

References

1. Elmendorf, S. C. *et al.* Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature 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. Q.12 IPCC *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. *Nature 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* (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. *Nature 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. 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.* Q.13 http://dx.doi.org/10.1093/aob/mcu077 (2014).
20. 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).
21. 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. NY Acad. Sci.* **1297,** 112–125 (2013).
22. MacArthur, R. H. *Geographical Ecology: Patterns in the Distribution of Species* (Princeton Univ. Press, 1972).
23. 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).
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 local and indigenous people for the opportunity to conduct research on their land. Financial support was provided by the International Arctic Science Committee (All), German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (sTUNDRA working group), the EnviroNorth CREATE grant (I.H.M-S.), International Polar Year Programs of the Government of Canada, Natural Sciences and Engineering Research Council of Canada and Northern Scientific Training Program (I.H.M-S., D.S.H., M.V., S.A.R., N.B-L., E.L., A.J.T., L.H., L.S.C., T.C.L.), INTERACT (262693), 7th Framework Programme, Virtual Institute ICLEA of the Helmholtz Foundation (M.W. and A.Buras), Wageningen University, Research Center, Darwin Center for Biogeosciences, Danish National Research Foundation (CENPERM DNRF100) (D.B.), Swedish Polar Secretariat (S.A.R.), Academy of Finland, Nordic Centre of Excellence TUNDRA, NASA Land Cover/Land-Use Change Program (B.C.F. and M.M-F.), Natural Environment Research Council Independent Research Fellowship (NE/L011859/1) (M.M-F.), Research Council of Norway (Project 212897) (J.D.M.S.), Fonds de recherche du Québec: Nature et technologies (N.B-L., E.L., M.V.) and Centre d'études Nordiques, ArcticNet—a network of centres of excellence (S.A.R., N.B-L., E.L., A.J.T., L.H., L.S.C.), Polar Continental Shelf Program (S.A.R., N.B-L., E.L.), Canada Foundation for Innovation (T.C.L.), WSL Institute for Snow and Avalanche Research SLF (to C.R., M.A.D., J.A.W., S.Wipf), Knud Højgaard Charity Foundation (N.M.S.), The Northern Worlds initiative of the National Museum of Denmark (C.B.), IPY-NWO (project 851.40.051) (S.Weijers), Polish National Science Centre (project N306 009139) (A.Buchwal), Virtual Institute ICLEA of the Helmholtz Foundation (A.Buras), National Science Foundation (ARC-0806506) (A.T.N.), University of Zurich Research Priority Program 'Global Change and Biodiversity' (G.S-S.), Woods Hole Research Center (K.C.G.) and The Research Council of Norway (V.R.). Q.14

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. Data have been archived at the Polar Data Catalogue (https://www.polardata.ca Ref No. 12131). Correspondence and requests for materials should be addressed to I.H.M-S.

Competing financial interests

The authors declare no competing financial interests.

 DOI: 10.1038/NCLIMATE2697

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 including 33 candidate models of 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. Detailed methods describing the data and analyses that were used are included in the Supplementary Information.

Queries for NPG paper nclimate2697

Page 1

Query 1:
Please check the use of 'Arctic' (meaning: relating to the regions around the North Pole) versus 'arctic' (informal, meaning 'cold', which should be avoided). Can we use the former throughout?

Query 2:
Please amend the text here and throughout, including in figure captions, to avoid numbered lists (that is, amend the text to remove the numbers).

Query 3:
Please note that reference numbers are formatted according to style in the text, so that any reference numbers following a symbol or acronym are given as 'ref. XX' on the line, whereas all other reference numbers are given as superscripts.

Page 2

Query 4:
Differences were found between the two versions of figure 1 supplied (right portion of map). Please check that the correct version has been followed.

Query 5:
References should be cited in numerical order; they have been renumbered starting from here. Please check and confirm.

Query 6:
Please amend the text here to define 'AIC', and can the use of 'delta' versus the symbol be made consistent throughout the text and figures?

Page 3

Query 7:
Y axis label of figure 2 amended. Please check.

Query 8:
Please amend the text here to avoid non-time-related use of 'while' ('whereas'?).

Query 9:
To avoid non-style use (Americanism) of 'likely' here; is it best changed to, for example, 'are likely to be complex', or can 'likely' simply be replaced by, for example, 'probably' or 'possibly'?

Query 10:
Please check/amend the sentence 'This results in ... Arctic' for clarity.

Page 4

Query 11:
Please provide species name in full in the x axis of figure 3e.

Page 5

Query 12:
Please provide publisher for refs 4, 11.

Query 13:
Please provide volume and page range for ref. 19.

Query 14:
Would the text here be better as 'collection, and governments'?