

**Climate sensitivity of shrub growth across the tundra biome**

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59 **Abstract**

60 Rapid temperature increases in the tundra biome have been linked to increasing shrub dominance<sup>1-4</sup>.  
61 Shrub expansion can modify climate by altering surface albedo, energy and water balance, and  
62 permafrost<sup>2,5-8</sup>, yet the drivers of shrub growth remain poorly understood. Dendroecological data  
63 consisting of multi-decadal time series of annual shrub growth provide an underused resource to  
64 explore climate-growth relationships. Here we analyse circumpolar data from 37 arctic and alpine sites  
65 in 9 countries, including 25 species, and ~42 000 annual growth records from 1821 individuals. Our  
66 analyses demonstrate that the sensitivity of shrub growth to climate was: 1) heterogeneous, with  
67 European sites showing greater summer temperature sensitivity than North American sites, and 2)  
68 higher at sites with greater soil moisture and for taller shrubs (e.g., alders, willows) growing at their  
69 northern or upper elevational range edges. Across latitude, climate sensitivity of growth was greatest at  
70 the boundary between the low and high Arctic, where permafrost is thawing<sup>4</sup> and the majority of the  
71 global permafrost soil carbon pool is stored<sup>9</sup>. The observed variation in shrub climate-growth  
72 relationships need to be incorporated into earth system models to improve future projections of climate  
73 change impacts across the tundra biome.

74

75 The Arctic is warming more rapidly than other biomes due to climate amplification involving  
76 temperature, water vapour, albedo and sea ice feedbacks<sup>5,7</sup>. For this reason tundra ecosystems are  
77 predicted to respond more rapidly to climate change than other terrestrial ecosystems<sup>4</sup>. The tundra  
78 biome spans arctic and alpine regions that have very similar plant species pools and mean climates, yet  
79 vary in topography, seasonality and land-use history. Concurrent with the recent high-latitude warming  
80 trend<sup>7</sup>, repeat photography and vegetation surveys have shown widespread expansion of shrubs in both  
81 arctic and alpine regions<sup>1-3</sup>, characterised by increased canopy cover, height and abundance. However,  
82 climate warming<sup>7</sup> and shrub increases<sup>2,10</sup> have not been observed at all sites. Modelling studies predict  
83 that annual warming of 2-10 °C<sup>11</sup> could increase the dominance of shrub species and convert as much  
84 as half of current tundra to ‘shrubland’ by the end of the 21<sup>st</sup> century<sup>8</sup>. However, the uniformity of the  
85 frequently cited relationship between tundra shrub expansion and climate change<sup>5,12-15</sup> has yet to be  
86 quantified across the tundra biome as a whole.

87

88 Shrubs are woody perennial species that live from decades to centuries, and when growing in highly  
89 seasonal climates, form annual growth rings allowing for the analysis of radial growth over time. Many  
90 shrub species are widely distributed across the tundra biome and are often the dominant vegetation  
91 type, due to their canopy height, longevity and ability to outcompete other low-growing tundra plant  
92 species. Due to their wide geographic distributions and annual growth records, shrubs species are  
93 ideally suited for quantifying tundra vegetation responses to a warming climate. Assembled annual  
94 growth records for shrub species from sites across the tundra biome provide a unique opportunity to  
95 test competing hypotheses of shrub responses to climate warming over the past half century.

96

97 Previous ecological monitoring and dendroecological studies have identified temperature, growing  
98 season length, summer precipitation and snow cover as important variables explaining variation in

99 growth at different sites and for different shrub species<sup>1,10,13,14,16–18</sup>. However, there is a lack of  
100 consensus in the literature regarding which climate variables best explain growth in tundra ecosystems.  
101 We therefore do not know if growth-climate relationships are consistent in direction and magnitude  
102 among species and at sites where plant composition, climate trends and environmental parameters  
103 differ. Currently, most large-scale vegetation models assume the latter: high climate sensitivity and a  
104 uniform growth response to warming among shrub species and populations<sup>8,23</sup>. These models also  
105 predict pronounced positive climate feedbacks as a result of future tundra vegetation change<sup>5,8</sup>. Yet, if  
106 shrub growth responses to climate are constrained, then ecosystem-level changes in shrub dominance  
107 should vary regionally, and feedbacks across the tundra biome as a whole could be weaker than  
108 currently predicted.

109

110 We quantified the climate sensitivity of shrub growth – i.e., the strength of relationship between annual  
111 growth and climate variables (including temperature and precipitation variables, specific calculations  
112 described below) – to test the following four hypotheses: 1) The greatest climate sensitivity of growth  
113 should occur at northern or high elevation range edges if plant performance is more climate limited for  
114 these peripheral populations than in the centre of the species distribution<sup>19–21</sup>. 2) Climate sensitivity of  
115 growth should be greatest in the centre of the species distribution if populations growing under more  
116 stressful conditions at range edges have evolved conservative life history strategies limiting their ability  
117 to respond when conditions improve<sup>22</sup>. 3) Climate sensitivity of growth should vary along gradients  
118 across the species distribution if the response of species to a warming climate is limited by other  
119 factors, such as soil nutrients, soil moisture or biotic interactions<sup>20</sup>. Alternatively, 4) the climate  
120 sensitivity of growth could be uniform.

121

122 We conducted a biome-scale data synthesis of both existing and new time series of shrub growth from  
123 across the tundra biome. This dataset extends beyond previous analyses by including sites across the

124 circumpolar Arctic, comprising dwarf, low and tall canopy species, and encompassing 60 years of  
125 annual-resolution shrub growth. We used crossdated, radial and axial growth measurements spanning  
126 1950 to 2010, collected at 37 sites, and including a total of 25 shrub species from eight genera. We  
127 analysed climate-growth relationships for 46 different genus-by-site combinations encompassing  
128 variation between sites and across taxa. We used linear mixed models to investigate the climate  
129 sensitivity for each genus-by-site combination using 33 climate models as predictors of shrub growth  
130 increments. All data were normalized at the genus-by-site-level before analysis and model terms  
131 included seasonal temperatures and precipitation as fixed effects and year as a random effect (see Supp.  
132 Info.).

133

134 We calculated four complementary indices of climate sensitivity from the mixed model analysis for  
135 each genus-by-site combination: 1) the difference in AIC value between the best climate model and a  
136 null model (delta AIC), 2) the  $R^2$  value for the best climate model, 3) the absolute value of the slope of  
137 the relationship between growth and summer temperature and 4) the proportion of individuals that had  
138 significant linear relationships between growth and the summer temperature (i.e., the best predictor  
139 variables from the overall analysis). We then assessed these indices of climate sensitivity across abiotic  
140 (wet day frequency, soil moisture, growing season length) and biotic gradients (distance to range edge  
141 and the species-level, maximum canopy height, see Supp. Info.). In Fig. 1, we report both the delta AIC  
142 index and model slopes to demonstrate the spatial variation in climate sensitivity (including the  
143 direction of the temperature effect) around the tundra biome (all indices reported in Fig. S12). In Fig. 2  
144 we report the percentage of models that indicated climate (temperature or precipitation) sensitivity in  
145 the model comparison analysis and in Fig. 3 we report the relationships between all four climate  
146 sensitivity indices across environmental and biological gradients.

147

148 Our results indicate that growth-climate relationships were not uniform across the tundra biome (Fig.  
149 1), which contrasts with the common assumption used in tundra-biome scale vegetation models<sup>23</sup>.  
150 Overall climate sensitivity was high with 83% or 38 of 46 genus-by-site combinations exhibiting  
151 climate-sensitive growth (Table S5). Summer temperature variables best explained variation in shrub  
152 growth across the 46 genus-by-site combinations and 33 climate models (Fig. 2), with 46% or 21 of 46  
153 genus-by-site combinations showing positive growth-summer temperature relationships, and 8 showing  
154 negative relationships (Fig. 1, Table S5). Individual-level climate sensitivity of growth varied  
155 considerably with 5 – 97% of individuals at each site and only ~36% of the total individuals sampled  
156 showing significant summer temperature sensitivity (Table S5). A moving window analysis  
157 demonstrated the relatively consistent climate sensitivity of shrub growth over time, despite the  
158 increase in sample size in recent years across the dataset (Fig. S13).

159  
160 Our analysis demonstrates substantial heterogeneity in the climate sensitivity of shrub growth across  
161 the tundra biome (Fig. 1). The greatest climate sensitivity of growth was found in the Northwest  
162 Russian Arctic and Northern Europe, whereas more heterogeneous climate sensitivity occurred among  
163 sites in the North American Arctic (Fig. 1), where many sites exhibited weak relationships between  
164 growth and summer temperatures (Table S5). When comparing across gradients, we found greater  
165 climate sensitivity for shrubs growing in wetter sites relative to drier sites as indicated by the number of  
166 days with precipitation and satellite-derived soil moisture (Fig. 3a and b). We found support for our  
167 first hypothesis concerning biogeographic patterns of climate sensitivity of growth. Shrubs growing  
168 near their northern latitudinal or elevational range limits showed greater climate sensitivity, as did taller  
169 (>50cm maximum canopy height) versus shorter species (<50cm) (Fig. 3c and d). Overall, shrub  
170 growth-climate relationships were not uniform across the tundra biome, but instead varied along soil  
171 moisture gradients, between species with different canopy heights and among locations within the  
172 distribution of each species.

173

174 Our results highlight the importance of soil moisture and drought as drivers of climate sensitivity of  
175 shrub growth. In tundra environments, soil moisture is influenced by a variety of factors including  
176 rainfall during the summer, snow distribution, duration and melt, permafrost status, soil properties and  
177 landscape-to-micro-scale topography, making it more challenging to quantify than climate variables<sup>24</sup>.  
178 We observed high climate sensitivity and positive growth-climate relationships at many sites with high  
179 soil moisture (Figs. 1 and 3); however, seven sites exhibited negative growth-climate relationships (Fig.  
180 1) and some of these sites were located in areas with high soil moisture at the landscape scale (Fig.  
181 S14). These negative relationships with summer temperatures could indicate drought limitation of  
182 growth in woody species, which can occur in wet as well as dry landscapes<sup>25</sup>.

183

184 Previous experimental and observational studies have pointed to the importance of summer  
185 temperatures as a driver of vegetation change<sup>1,13,14,26</sup>, but the role of soil moisture is less often  
186 examined. A recent synthesis of two decades of ecological monitoring data from the International  
187 Tundra Experiment Network showed that increases in shrub abundance were most pronounced at sites  
188 that experienced warmer summer and wetter versus drier conditions<sup>1</sup>. In addition, landscape-level  
189 studies of shrub change in Northern Alaska showed greater increases in wet floodplains relative to  
190 well-drained hill slopes<sup>3,10</sup>. Our study, using a new circum-Arctic dendroecological dataset consisting  
191 of almost exclusively different sites from those in the International Tundra Experiment dataset, shows  
192 broad geographic patterns in the climate sensitivity of shrub growth, with higher climate sensitivity at  
193 wetter versus drier sites. Taken together these results suggest that, with continued warming<sup>11</sup>,  
194 potentially more variable precipitation<sup>11</sup> and uncertainty in the future soil moisture regime<sup>11,24</sup>, water  
195 availability could play an increasingly important role in limiting future shrub expansion. However,  
196 analyses of changes in plant water availability in tundra ecosystems are currently limited by the lack of  
197 high-resolution soil moisture observations over time<sup>24</sup>.

198

199 In our study, climate sensitivity of shrub growth was greatest at the northern or elevational range  
200 margins of individual species (Fig. 3). This creates a pattern of greater climate sensitivity of shrub  
201 growth at the transition zone between tall and low shrub tundra (Fig. 1). The greatest ecosystem  
202 transitions in shrub dominance could occur at these mid-arctic latitudes, rather than at the northern  
203 limits of the tundra biome as a whole. The patterns of climate sensitivity of growth in tundra shrub  
204 species can be compared to patterns observed in treeline ecotones. Half of the global latitudinal and  
205 elevational treelines studied to date have been advancing poleward or upslope, and warming has often  
206 been associated with this treeline advance<sup>27</sup>. The greatest temperature sensitivity of tree growth has  
207 been observed at the upper or northern-most margin of the forest-tundra transition zone<sup>19,27</sup> and the  
208 greatest moisture sensitivity at southern or lower range edges<sup>28</sup>. Our results suggest that for tundra  
209 shrub species, both temperatures and soil moisture are dominant factors controlling shrub growth at  
210 range edges, while further from the range edge other factors such as competition, facilitation,  
211 herbivory, and disease<sup>20</sup> may be more important. Herbivore densities vary spatially and temporally  
212 across our study locations<sup>12,29</sup>, and this could be one of the factors explaining the variation in climate  
213 sensitivity. The relationships between the climatic and biotic factors influencing growth are likely  
214 complex and deserve greater study.

215

216 We find that the growth of tall shrub species, i.e., those with a potential canopy height exceeding 50  
217 cm, is more climate-sensitive than the growth of low-statured species (Fig. 3b). This greater climate  
218 sensitivity for tall shrub species has important implications for earth system models, as changes in tall  
219 shrub cover will contribute more dramatically to ecosystem-climate feedbacks<sup>8</sup>. Increases in canopy  
220 height and abundance of taller species relative to lower-stature dwarf shrub species at warmer  
221 temperatures was a major finding of two recent syntheses of plot-based ecological monitoring and  
222 passive warming experiments, however these studies did not include taller alder and willow species<sup>1,26</sup>.

223 Tall shrub species may be able to take advantage of more favourable climate conditions, particularly at  
224 the transition zone from tall to low shrub tundra, by competing for limited light and nutrient resources  
225 through shading and belowground investment<sup>30</sup>. In particular, in contrast to this previous work that has  
226 not explicitly tested biogeographic patterns of climate sensitivity<sup>1</sup>, our analysis demonstrates that the  
227 sensitivity to climate of low shrub species was often greater towards their range margins (Fig. 3a). This  
228 results in a pattern of high climate sensitivity for some species growing in the High Arctic (Fig. 1).

229

230 In conclusion, our study demonstrates a high climate sensitivity of shrub growth at sites across the  
231 tundra biome, which provides strong evidence for the attribution of tundra shrub increases to climate  
232 warming<sup>4</sup>. However, our results indicate that dramatic increases in shrub growth with warming are  
233 unlikely to occur in all regions of the tundra biome, and that greatest shrub growth responses will  
234 instead occur in the transition-zone between tall- and low-statured shrub tundra and at sites where soil  
235 moisture is not limiting. The pressing question for future research is whether temperature-induced  
236 increases in shrub growth will continue to occur at current or accelerated rates or if factors such as  
237 water availability, herbivory, pathogen outbreaks, nutrient limitation, or fire will begin to limit the  
238 growth of shrubs in arctic and alpine tundra. Experimental tests involving manipulations of  
239 temperature<sup>26</sup>, moisture regime, and atmospheric CO<sub>2</sub> concentration are necessary to predict the growth  
240 responses of shrubs under future environmental scenarios. Increased monitoring of soil moisture<sup>24</sup> (see  
241 NASA and ESA initiatives including <http://smap.jpl.nasa.gov/>) and other locally-influenced climate and  
242 biological variables and expanded networks of *in-situ* tundra vegetation observations<sup>1</sup> will further  
243 improve predictions. Only with a combination of enhanced ecological monitoring, multifactorial  
244 experimentation and additional data synthesis, can we make the spatially-explicit and species-level  
245 projections of vegetation dynamics needed to improve estimates of feedbacks to future climate change.

246

247 **Methods Summary**

248 To examine the climate sensitivity of tundra shrub growth, we assembled a database of 37 arctic and  
249 alpine sites encompassing 25 species from eight genera (Tables S1 and S2) for a total of 46 genus-by-  
250 site combinations, 1,821 individual shrubs, and 41,576 yearly growth measurements. Growth  
251 measurements included annual ring widths (35 genus-by-site combinations) and stem increments (11  
252 genus-by-site combinations). Although, the data collection was not coordinated in advance and  
253 includes both published and unpublished data, the resulting dataset represents many of the dominant  
254 and widely distributed tundra shrub species found at sites across the tundra biome.

255

256 To test the correspondence between variation in annual growth and climate, we used monthly Climate  
257 Research Unit (CRU) TS3.21 gridded temperature and precipitation data (0.5° resolution, Table S3).  
258 We found high correlations between the CRU TS3.21 and station data for the 19 sites with a  
259 meteorological station in relatively close proximity (Table S4).

260

261 We used linear mixed models (package nlme, R version 2.15.3) and model selection including 33  
262 candidate models of temperature and precipitation variables to relate annual growth to climate (Tables  
263 S5 and S6). We analysed data from 1950 to 2010, as this is the period with the highest quality of  
264 climate data and greatest overlap between different individual shrub growth time series among sites.

265

266 We present four different indices of climate sensitivity for each genus-by-site combination (see above  
267 and Supp. Info.). We considered the overall climate sensitivity to be the comparison of the best model  
268 to a null model; summer temperature sensitivity was a comparison of only the models containing a  
269 summer temperature variable to a null model. We then compared the climate sensitivity of growth to  
270 environmental and biotic gradients including wet day frequency, soil moisture, distance to nearest  
271 range edge and the maximum potential canopy height for the sampled species. Detailed methods  
272 describing the data and analyses that were used are included in the supplementary information.

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360

361 **Author contributions**

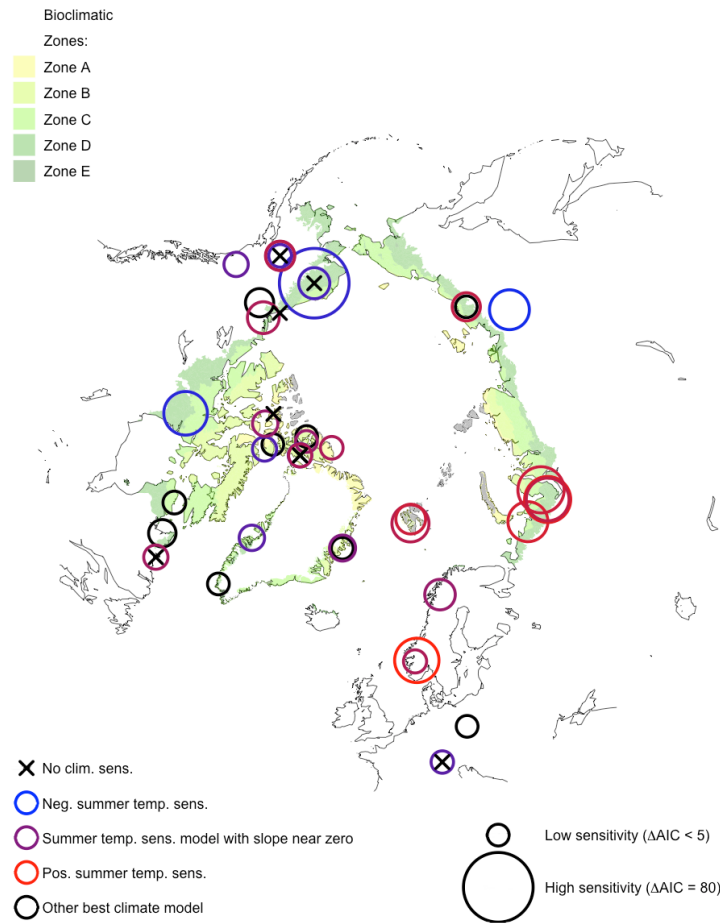
362 All authors designed the study, collected or processed data and assisted in writing the paper; IMS and  
363 MV took the lead in writing the paper; IMS analysed the data.

364

365 **Author information**

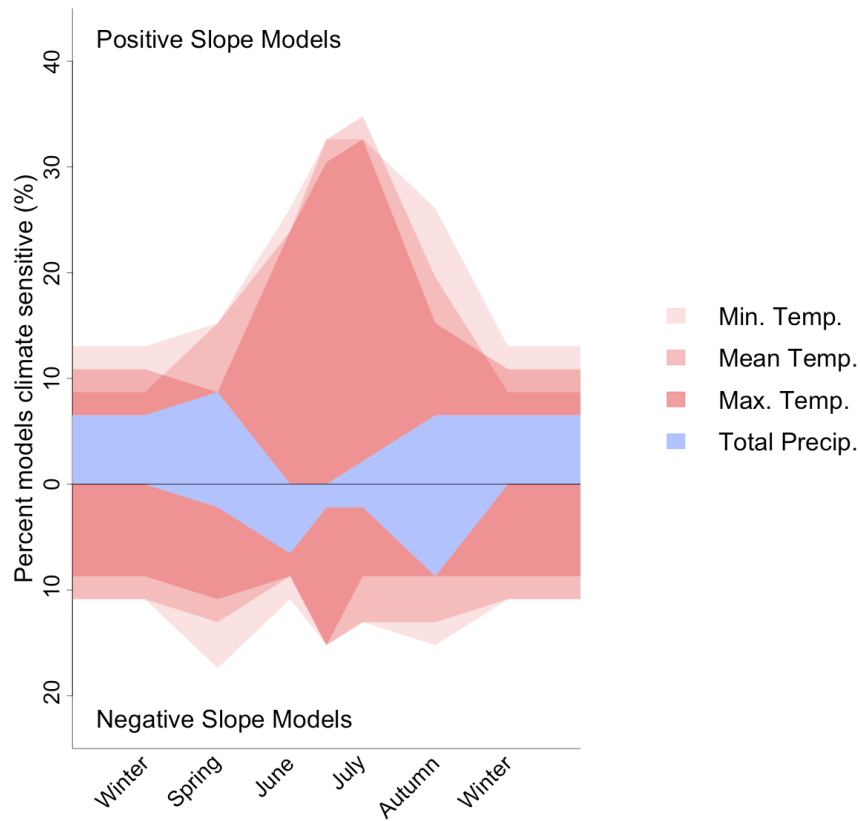
366 The authors declare no competing financial interests. Data have been archived at the Polar Data  
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369 **Figures**



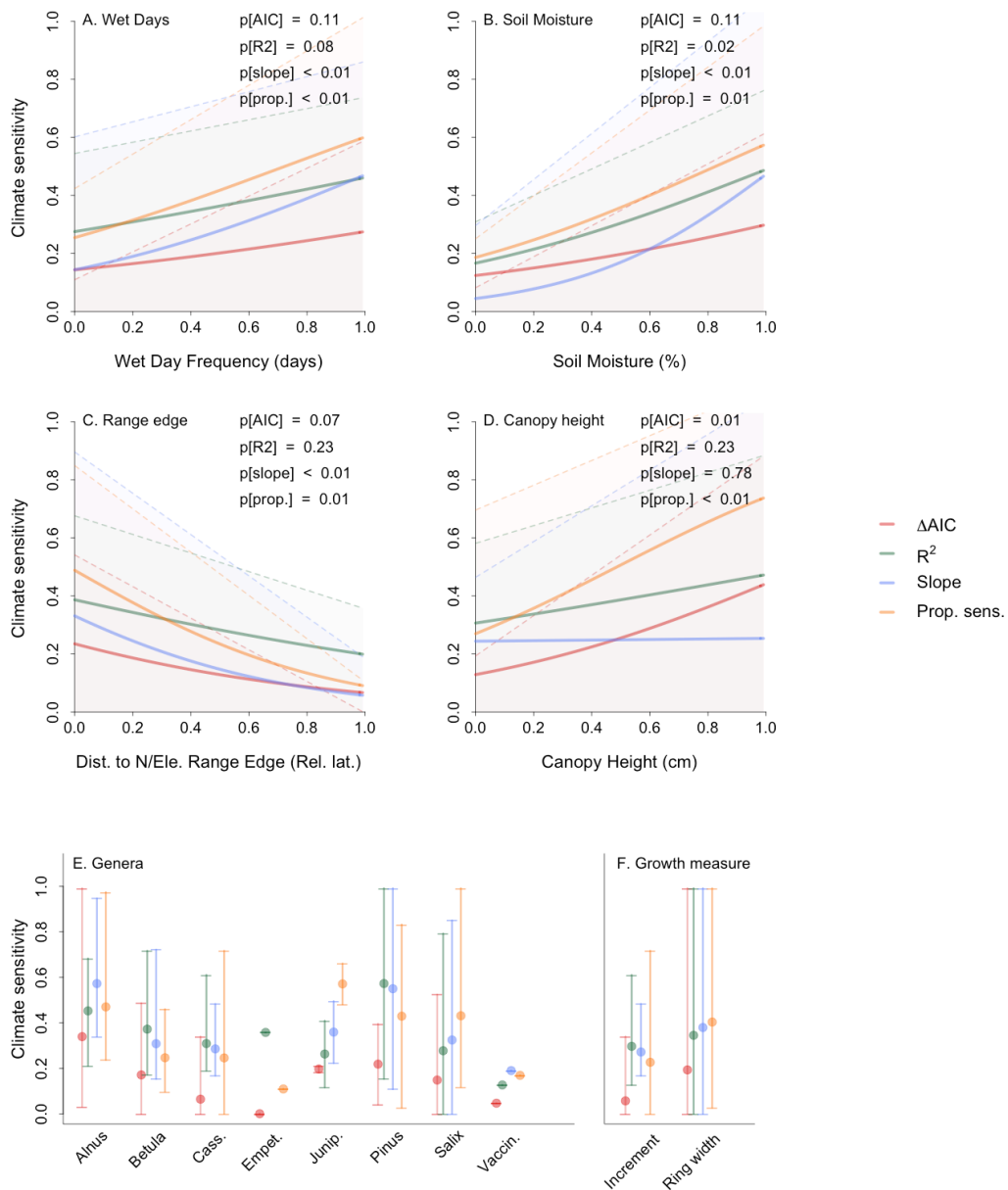
370

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



380

381 Figure 2. Comparison of climate models. Summer temperature models were more frequently climate  
 382 sensitive than other temperature or precipitation models in the model comparison analysis of 46 genus-  
 383 by-site combinations and 33 climate models (Table S4). The shaded colouring indicates the percent of  
 384 models that were considered climate sensitive for each of the four categories of climate variables for  
 385 each of the genus-by-site combinations with a difference in AIC value of greater than 2 between the  
 386 given climate model and the null model for all one parameter models in the model comparison analysis.



387

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

395 individuals that had significant linear relationships between growth and summer temperature variables.  
396 The lines and associated p-values indicate beta regression of the different climate sensitivity metrics,  
397 the dashed lines indicate the 90<sup>th</sup> quantile. The distance to the range edge (C) is the distance between  
398 the sampling location and the northern or elevation range edge for each species converted to relative  
399 latitudes (see Supp. Info.). This gives an index of how far a sample population is located from the  
400 maximum extent of the distribution of that species either northward in the Arctic or up slope in alpine  
401 tundra.