

Change in plant functional traits across a warming tundra biome

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44

Anne D. Bjorkman^{1,2,3*}, Isla Myers-Smith², Sarah Elmendorf^{4,5}, Signe Normand¹, Nadja Rüger^{3,6}, Pieter S.A. Beck⁷, Anne Blach-Overgaard¹, Daan Blok⁸, J. Hans C. Cornelissen⁹, Bruce C. Forbes¹⁰, Damien Georges^{11,2}, Scott Goetz¹², Kevin Guay¹³, Gregory H.R. Henry¹⁴, Janneke HilleRisLambers¹⁵, Robert Hollister¹⁶, Dirk N. Karger¹⁷, Jens Kattge^{18,3}, Janet S. Prevéy¹⁹, Christian Rixen¹⁹, Gabriela Schaepman-Strub²⁰, Haydn Thomas², Mark Vellend²¹, Martin Wilmking²², Sonja Wipf¹⁹, Michele Carbognani²³, Luise Hermanutz²⁴, Esther Levesque²⁵, Ulf Molau²⁶, Alessandro Petraglia²³, Nadejda A. Soudzilovskaia²⁷, Marko Spasojevic²⁸, Marcello Tomaselli²³, Tage Vowles²⁹, Juha Alatalo³⁰, Heather Alexander³¹, Alba Anadon-Rosell^{32,33}, Sandra Angers-Blondin², Mariska Te Beest^{34,35}, Logan Berner¹², Robert G. Björk²⁹, Agata Buchwal^{36,37}, Allan Buras³⁸, Katie Christie³⁹, Laura S Collier²⁴, Elisabeth J. Cooper⁴⁰, Stefan Dullinger⁴¹, Bo Elberling⁴², Anu Eskelinen^{43,3,44}, Esther R. Frei¹⁴, Maitane Iturrate Garcia²⁰, Oriol Grau^{45,46}, Paul Grogan⁴⁷, Martin Hallinger⁴⁸, Karen Harper⁴⁹, Monique Heijmans⁵⁰, James Hudson⁵¹, Karl Hülber⁴¹, Colleen M. Iversen⁵², Francesca Jaroszynska^{53,19}, Jill Johnstone⁵⁴, Rasmus Halfdan Jorgensen⁵⁵, Elina Kaarlejärvi^{34,56}, Rebecca Klady⁵⁷, Sara Kuleza⁵⁴, Aino Kulonen¹⁹, Laurent J. Lamarque²⁵, Trevor Lantz⁵⁸, Amanda Lavalley⁴⁹, Chelsea J. Little^{20,59}, James David Mervyn Speed⁶⁰, Anders Michelsen^{61,62}, Ann Milbau⁶³, Jacob Nabe-Nielsen⁶⁴, Sigrid Schøler Nielsen¹, Josep Maria Ninot^{32,33}, Steve Oberbauer⁶⁵, Johan Olofsson³⁴, Vladimir G. Onipchenko⁶⁶, Sabine B. Rumpf⁴¹, Philipp Semenchuk⁴⁰, Rohan Shetti²², Lorna Street², Katharine Suding⁶⁷, Ken Tape⁶⁸, Andrew Trant⁶⁹, Urs Treier¹, Jean-Pierre Tremblay⁷⁰, Maxime Tremblay²⁵, Susanna Venn⁷¹, Stef Weijers⁷², Tara Zamin⁴⁷, Noemie Boulanger-Lapointe¹⁴, William A. Gould⁷³, Dave Hik⁷⁴, Annika Hofgaard⁷⁵, Inga Svala Jonsdottir^{76,77}, Janet Jorgenson⁷⁸, Julia Klein⁷⁹, Borgthor Magnusson⁸⁰, Craig Tweedie⁸¹, Philip A. Wookey⁸², Michael Bahn⁸³, Benjamin Blonder^{84,85}, Peter van Bodegom⁸⁶, Benjamin Bond-Lamberty⁸⁷, Giandiego Campetella⁸⁸, Bruno E.L. Cerabolini⁸⁹, F. Stuart Chapin III⁹⁰, Will Cornwell⁹¹, Joseph Craine⁹², Matteo Dainese⁹³, Franciska T. de Vries⁹⁴, Sandra Diaz⁹⁵, Brian J. Enquist^{96,97}, Walton Green⁹⁸, Peter Manning⁹⁹, Ruben Milla¹⁰⁰, Ülo Niinemets¹⁰¹, Yusuke Onoda¹⁰², Jenny Ordóñez¹⁰³, Wim A. Ozinga^{104,105}, Josep Penuelas^{106,46}, Hendrik Poorter¹⁰⁷, Peter Poschold¹⁰⁸, Peter Reich^{109,110}, Brody Sandel¹¹¹, Brandon Schamp¹¹², Serge Sheremetev¹¹³, Evan Weiher¹¹⁴

1. Ecoinformatics and Biodiversity & Arctic Research Center, Department of Bioscience, Aarhus University, Ny Munkegade 114-116, DK-8000 Aarhus C
2. School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, UK
3. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
4. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA
5. National Ecological Observatory Network, 1685 38th St, Boulder, CO 80301, USA
6. Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa Ancón, Panama
7. European Commission, Joint Research Centre, Directorate D - Sustainable Resources, Bio-Economy Unit, Via Enrico Fermi 2749, 21027, Ispra, Italy
8. Department of Physical Geography and Ecosystem Science, Lund University, Lund S-223 62, Sweden

- 45 9. Systems Ecology, Department of Ecological Science, Vrije Universiteit, Amsterdam, The
46 Netherlands
- 47 10. Arctic Centre, University of Lapland, FI-96101 Rovaniemi, Finland
- 48 11. International Agency for Research in Cancer, Lyon, France
- 49 12. Northern Arizona University, Flagstaff, Arizona, USA
- 50 13. Bigelow Laboratory for Ocean Sciences, East Boothbay, Maine, USA
- 51 14. Department of Geography, University of British Columbia, Vancouver, BC V6T 1Z4,
52 Canada
- 53 15. Biology Department, University of Washington, Seattle, USA, 98195-1800
- 54 16. Biology Department, Grand Valley State University, 1 Campus Drive, Allendale Michigan
55 USA
- 56 17. Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf,
57 Switzerland
- 58 18. Max Planck Institute for Biogeochemistry, Jena, Germany
- 59 19. WSL Institute for Snow and Avalanche Research SLF, 7260 Davos, Switzerland
- 60 20. Department of Evolutionary Biology and Environmental Studies, University of Zurich,
61 Zurich, Switzerland
- 62 21. Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada J1K
63 2R1
- 64 22. Institute of Botany and Landscape Ecology, Greifswald University, Greifswald, Germany
- 65 23. Department of Chemistry, Life Sciences and Environmental Sustainability, University of
66 Parma, Parco Area delle Scienze 11/A, I-43124 Parma, Italy
- 67 24. Department of Biology, Memorial University, St. John's, Newfoundland and Labrador,
68 Canada A1B3X9
- 69 25. Département des Sciences de l'environnement et Centre d'études nordiques, Université
70 du Québec à Trois-Rivières, Trois-Rivières, QC, G9A 5H7, Canada
- 71 26. Department of Biological and Environmental Sciences, University of Gothenburg,
72 Gothenburg, Sweden
- 73 27. Conservation Biology Department, Institute of Environmental Sciences, Leiden
74 University, The Netherlands
- 75 28. Department of Evolution, Ecology, and Organismal Biology, University of California
76 Riverside, Riverside, CA.
- 77 29. Department of Earth Sciences, University of Gothenburg, P.O. Box 460, SE-405 30
78 Gothenburg, Sweden
- 79 30. Department of Biological and Environmental Sciences, Qatar University, Qatar
- 80 31. Department of Forestry, Forest and Wildlife Research Center, Mississippi State University,
81 MS 39762
- 82 32. Department of Evolutionary Biology, Ecology and Environmental Sciences, University of
83 Barcelona, Av. Diagonal 643 E-08028 Barcelona
- 84 33. Biodiversity Research Institute, University of Barcelona, Av. Diagonal 643 E-08028
85 Barcelona
- 86 34. Department of Ecology and Environmental Science, Umeå University, Sweden
- 87 35. Department of Environmental Sciences, Copernicus Institute, Utrecht University, the
88 Netherlands

- 89 36. Adam Mickiewicz University, Institute of Geocology and Geoinformation, B.Krygowskiego
90 10, 61-680 Poznan, Poland
- 91 37. University of Alaska Anchorage, Department of Biological Sciences, 3151 Alumni Loop,
92 Anchorage, Alaska 99508, USA
- 93 38. Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2,
94 85354 Freising
- 95 39. The Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska
96 99518
- 97 40. Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and
98 Economics, UiT- The Arctic University of Norway, NO-9037 Tromsø, Norway
- 99 41. Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, A-
100 1030 Vienna, Austria
- 101 42. Center for Permafrost (CENPERM), Department of Geosciences and Natural Resource
102 Management, University of Copenhagen, DK-1350 Copenhagen, Denmark
- 103 43. Department of Physiological Diversity, Helmholtz Center for Environmental Research -
104 UFZ, Permoserstrasse 15, Leipzig 04103, Germany
- 105 44. Department of Ecology, University of Oulu, 90014 University of Oulu, Finland
- 106 45. Global Ecology Unit, CREAM-CSIC-UAB, Bellaterra, Catalonia 08193, Spain
- 107 46. CREAM, Cerdanyola del Vallès, Catalonia 08193, Spain
- 108 47. Department of Biology, Queen's University, Kingston, ON, Canada
- 109 48. Biology Department, Swedish Agricultural University (SLU), Uppsala, Sweden
- 110 49. Biology Department, Saint Mary's University, Halifax, NS, Canada
- 111 50. Plant Ecology and Nature Conservation Group, Wageningen University & Research,
112 Wageningen, The Netherlands
- 113 51. British Columbia Public Service, Canada
- 114 52. Climate Change Science Institute and Environmental Sciences Division, Oak Ridge
115 National Laboratory, Oak Ridge, TN, USA 37831
- 116 53. Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen,
117 AB24 3UU
- 118 54. Department of Biology, University of Saskatchewan, Saskatoon SK S7N 5E2 Canada
- 119 55. Department of Geosciences and Natural Resource Management, University of
120 Copenhagen, Denmark
- 121 56. Department of Biology, Vrije Universiteit Brussel (VUB), Belgium
- 122 57. Department of Forest Resources Management, Faculty of Forestry, University of British
123 Columbia, Vancouver, BC, Canada
- 124 58. School of Environmental Studies, University of Victoria, Victoria, BC, Canada
- 125 59. Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and
126 Technology, Dübendorf, Switzerland
- 127 60. NTNU University Museum, Norwegian University of Science and Technology, NO-7491
128 Trondheim, Norway
- 129 61. Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100
130 Copenhagen, Denmark
- 131 62. Center for Permafrost (CENPERM), University of Copenhagen, Oster Voldgade 10, DK-
132 1350 Copenhagen, Denmark

- 133 63. Research Institute for Nature and Forest (INBO), Kliniekstraat 25, 1070 Brussels, Belgium
134 64. Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde,
135 Denmark
136 65. Department of Biological Sciences, Florida International University, Miami FL 33199 USA
137 66. Department of Geobotany, Lomonosov Moscow State University, Moscow, Russia
138 67. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder CO
139 68. Institute of Northern Engineering, University of Alaska Fairbanks, USA
140 69. School of Environment, Resources and Sustainability, University of Waterloo, Waterloo,
141 Ontario, Canada N2L 3G1
142 70. Département de biologie, Centre d'études nordiques and Centre d'étude de la forêt,
143 Université Laval, QC, G1V 0A6, Canada
144 71. Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin
145 University, 221 Burwood Highway, Burwood, VIC, Australia 3125
146 72. Department of Geography, University of Bonn, Meckenheimer Allee 166, D-53115 Bonn,
147 Germany
148 73. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, Puerto Rico
149 74. Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9,
150 Canada
151 75. Norwegian Institute for Nature Research, PO Box 5685 Sluppen, NO-7485 Trondheim,
152 Norway
153 76. Faculty of Life and Environmental Sciences, University of Iceland, 101 Reykjavík, Iceland
154 77. University Centre in Svalbard, N-9171 Longyearbyen, Norway
155 78. Arctic National Wildlife Refuge, U. S. Fish and Wildlife Service
156 79. Department of Ecosystem Science & Sustainability, Colorado State University, Campus
157 Delivery 1476, Fort Collins, CO 80523-1476 USA
158 80. Icelandic Institute of Natural History, Gardabaer, Iceland
159 81. University of Texas at El Paso, El Paso, Texas, USA
160 82. Biology and Environmental Sciences, Faculty of Natural Sciences, University of Stirling,
161 Stirling, FK9 4LA, Scotland, UK
162 83. Institute of Ecology, University of Innsbruck, Innsbruck, Austria
163 84. Environmental Change Institute, School of Geography and the Environment, South Parks
164 Road, University of Oxford, Oxford OX1 3QY, UK
165 85. Rocky Mountain Biological Laboratory, PO Box 519, Crested Butte, Colorado, 81224 USA
166 86. Institute of Environmental Sciences, Leiden University, 2333 CC Leiden, the Netherlands
167 87. Joint Global Change Research Institute, Pacific Northwest National Laboratory, College
168 Park, MD, USA
169 88. School of Biosciences & Veterinary Medicine - Plant Diversity and Ecosystems
170 Management unit, University of Camerino, via Pontoni, 5 - 62032, Italy
171 89. DiSTA - University of Insubria, via Dunant 3, 21100 Varese, Italy
172 90. Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99709, USA
173 91. School of Biological, Earth & Environmental Sciences, Ecology and Evolution Research
174 Centre, UNSW Australia, Sydney, NSW 2052, Australia
175 92. Jonah Ventures, Manhattan KS 66502, USA

- 176 93. Department of Animal Ecology and Tropical Biology, University of Würzburg, Biozentrum -
177 Am Hubland, 97074 Würzburg, Germany
- 178 94. School of Earth and Environmental Sciences, The University of Manchester, UK
- 179 95. Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET and FCEfYN,
180 Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina
- 181 96. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona
182 85719, USA
- 183 97. The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA
- 184 98. Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street,
185 Cambridge, MA 02138 USA
- 186 99. Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Centre
187 (BiK-F), Senckenberganlage 25, Frankfurt, Germany
- 188 100. Área de Biodiversidad y Conservación. Departamento de Biología, Geología, Física y
189 Química Inorgánica. Universidad Rey Juan Carlos, 28933 Móstoles (Madrid), Spain
- 190 101. Estonian University of Life Sciences, Kreutzwaldi 1, 51014 Tartu, Estonia
- 191 102. Graduate School of Agriculture, Kyoto University, Oiwake, Kitashirakawa, Kyoto, 606-
192 8502 Japan
- 193 103. World Agroforestry Centre - Latin America, Av. La Molina 1895, La Molina, Lima, Perú
- 194 104. Team Vegetation, Forest and Landscape ecology, Wageningen Environmental Research
195 (Alterra), P.O. Box 47, NL-6700 AA Wageningen, The Netherlands
- 196 105. Institute for Water and Wetland Research, Radboud University Nijmegen, 6500 GL
197 Nijmegen, The Netherlands
- 198 106. Global Ecology Unit CREAM-CSIC-UAB, Bellaterra, Catalonia 08193, Spain
- 199 107. Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, Jülich 52425, Germany
- 200 108. Ecology and Conservation Biology, Institute of Plant Sciences, University of Regensburg,
201 D-93040 Regensburg
- 202 109. Department of Forest Resources, University of Minnesota, St. Paul, MN 55108 USA
- 203 110. Hawkesbury Institute for the Environment, Western Sydney University, Penrith NSW
204 2751, Australia
- 205 111. Department of Biology, Santa Clara University, 500 El Camino Real, Santa Clara, CA,
206 95053 USA
- 207 112. Department of Biology, Algoma University, Sault Ste. Marie, Ontario, Canada
- 208 113. Komarov Botanical Institute, Prof. Popov Street 2, St Petersburg 197376, Russia
- 209 114. Department of Biology, University of Wisconsin - Eau Claire, Eau Claire, WI 54702, USA

211 * Corresponding author (current address: Senckenberg Biodiversity and Climate Research
212 Centre, Frankfurt, Germany, anne.bjorkman@senckenberg.de)

213

214 Summary paragraph

215 Rapid climate warming in Arctic and alpine regions is driving changes in the structure and
216 composition of tundra plant communities^{1,2}, with unknown consequences for ecosystem
217 functioning. Because plant functional traits are directly related to vital ecosystem processes
218 such as primary productivity and decomposition, understanding trait-environment relationships

219 is critical to predicting high-latitude climate feedbacks^{3,4}, yet such relationships have never been
220 quantified at the biome scale. Here, we explore the biome-wide relationship between
221 temperature, soil moisture, and key plant functional traits (plant height, leaf area, leaf nitrogen
222 content (leaf N), specific leaf area (SLA), and leaf dry matter content (LDMC), as well as
223 community woodiness and evergreenness. We integrated more than 56,000 trait observations
224 with nearly three decades of plant community vegetation surveys at 117 Arctic and alpine
225 tundra sites spanning the northern hemisphere. We found strong spatial relationships between
226 summer temperature and community height, SLA, and LDMC. Soil moisture had a marked
227 influence on the strength (SLA and LDMC) and direction (leaf area and leaf N) of the
228 temperature-trait relationship, highlighting the potentially important influence of changes in
229 water availability on future plant trait change. Over the past three decades, community plant
230 height increased with warming across all sites, but other traits lagged far behind rates of change
231 predicted from spatial temperature-trait relationships. Our findings highlight the challenge of
232 using space-for-time substitution to predict the consequences of future warming on functional
233 composition and suggest that tundra ecosystem functions tied closely to plant height (e.g.,
234 carbon uptake) will show the most rapid changes with near-term climate warming. Our results
235 reveal the strength with which environmental factors shape biotic communities at the coldest
236 extremes of the planet and will enable improved projections of tundra functional change with
237 climate warming.

238

239 **Main text**

240 The tundra is warming more rapidly than any other biome on Earth, and the potential
241 ramifications are far-reaching due to global-scale vegetation-climate feedbacks⁵. Up to 50% of
242 the world's belowground carbon stocks are contained in permafrost soils⁵, and tundra regions
243 are expected to contribute the majority of warming-induced soil carbon loss over the next
244 century⁶. Plant traits directly impact carbon cycling and energy balance, which can in turn
245 influence regional and global climates^{4,7,8}. Traits related to the resource economics spectrum⁹,
246 such as specific leaf area, leaf nitrogen content, and leaf dry matter content, affect primary
247 productivity, litter decomposability, and nutrient cycling^{3,4,7,10}, while changes in size-related traits
248 such as leaf area and plant height influence carbon storage, albedo, and hydrology¹¹ (Table S1).
249 Quantifying the link between environment and plant functional traits is critical to understanding
250 the consequences of climate change, but such studies rarely extend into the tundra^{12,13}. As
251 such, the full extent of the relationship between climate and plant traits in the planet's coldest

252 ecosystems has never been assessed, and the consequences of climate warming for tundra
253 functional change are largely unknown.

254

255 Here, we quantify for the first time biome-wide relationships between temperature, soil moisture,
256 and key traits that represent the foundation of plant form and function¹⁴, using the largest
257 dataset of tundra plant traits ever assembled (56,048 measured trait observations; Fig. 1a and
258 S1, Table S2). We examine five continuous traits related to plant size - including adult plant
259 height and leaf area - and to resource economy - including specific leaf area (SLA), leaf nitrogen
260 content (leaf N), and leaf dry matter content (LDMC) - as well as two categorical traits related to
261 community-level structure (woodiness) and leaf phenology/lifespan (evergreenness). We
262 analyze two underlying components of biogeographic patterns in the five continuous traits:
263 intraspecific variability (phenotypic plasticity or genetic differences among populations) and
264 community-level variability (species turnover or shifts in species' abundances over space; Fig.
265 S2). Intraspecific trait variability is thought to be especially important where diversity is low or
266 where species have wide geographic ranges¹⁵, as in the tundra. We ask: 1) How do plant traits
267 vary with temperature and soil moisture across the tundra biome? 2) What is the relative
268 influence of intraspecific trait variability (ITV) versus community-level trait variation (estimated as
269 community-weighted trait means, CWM) for spatial temperature-trait relationships? 3) Are
270 spatial temperature-trait relationships explained by among-site differences in species
271 abundance or species turnover (presence-absence)?

272

273 A major impetus for quantifying spatial temperature-trait relationships is to better predict the
274 potential consequences of future warming^{16,17}. Thus, we also estimate realized rates of temporal
275 community-level trait change using nearly three decades of vegetation survey data at 117
276 tundra sites (Fig. 1a, Table S3). Focusing on interspecific trait variation, we ask: 4) How do
277 community trait changes over three decades of ambient warming compare to predictions from
278 spatial temperature-trait relationships? We expect greater temporal trait change when spatial
279 temperature-trait relationships are a) strong, b) independent of moisture, and c) due primarily to
280 abundance shifts instead of species turnover, given that species turnover over time depends on
281 immigration and is likely to be slow¹⁸. Finally, because total realized trait change over time in
282 continuous traits is comprised of both community-level variation and intraspecific trait variation
283 (ITV), we estimated the latter's *potential* contribution to overall trait change (CWM+ITV) using
284 the modeled intraspecific temperature-trait relationships described above (see supplementary
285 methods and Fig. S2). For all analyses we used a novel, generalizable hierarchical Bayesian

286 modeling approach, which allowed us to account for the hierarchical spatial, temporal and
287 taxonomic structure of the data as well as multiple sources of uncertainty.

288

289 We found strong spatial associations between temperature and community height, SLA, and
290 LDMC (Fig. 2a and S4) across the 117 survey sites. Both height and SLA increased significantly
291 with summer temperature overall, but the temperature-trait relationship for SLA was much
292 stronger at wet than at dry sites. LDMC was negatively related to temperature overall, and more
293 strongly so at wet than at dry sites. Woodiness decreased overall with warmer temperatures,
294 particularly in wet sites, but the relative proportion of evergreen woody species increased,
295 particularly in dry sites (Fig. S4, Table S5). These spatial temperature-trait relationships suggest
296 that long-term climate warming should cause pronounced shifts toward communities of non-
297 woody, taller plants with more resource-acquisitive leaves (high SLA and low LDMC).

298

299 Our results reveal a substantial moderating influence of soil moisture on community traits across
300 spatial temperature gradients^{2,19}. Both leaf area and leaf N decreased with warmer temperatures
301 in dry sites but increased with warmer temperatures in wet sites (Fig. 2a). Soil moisture was
302 important in explaining spatial variation in all seven traits investigated here, even when
303 temperature was not (Fig. 2a and S4). Thus, future warming-driven changes in traits and
304 associated ecosystem functions (e.g. decomposability) will likely depend on current soil
305 moisture conditions at a site¹⁹. Furthermore, future changes in water availability (e.g., via
306 changes in precipitation, snow melt timing, permafrost, and hydrology²⁰) could cause substantial
307 shifts in these traits and their associated functions irrespective of warming.

308

309 We found significant intraspecific temperature-trait relationships for all five continuous traits, but
310 these relationships were not always consistent with community-level patterns (Fig. 2b, Table
311 S6). Intraspecific plant height and leaf area showed strong positive relationships with summer
312 temperature (i.e., individuals were taller and had larger leaves in warmer locations). Intraspecific
313 LDMC, leaf N and SLA were significantly related to winter but not summer temperature (Fig.
314 S3). The differing responses of intraspecific trait variation to summer versus winter temperature
315 may indicate that size-related traits better reflect summer growth potential while leaf economics
316 traits reflect cold-stress tolerance. These results, although correlative, suggest that trait
317 variation expressed at the individual or population level is related to the growing environment
318 and that warming may therefore lead to substantial intraspecific trait change in many traits.

319 Thus, the potential for trait change over time is likely to be underestimated by using community-

320 weighted trait means alone. Future work is needed to disentangle the role of plasticity and
321 genetic differentiation in explaining the observed intraspecific temperature-trait relationships, as
322 this will also influence the rate of future trait change²¹. Trait measurements collected over time
323 and under novel (experimental) conditions, as yet unavailable, would enable more accurate
324 predictions of the magnitude of future intraspecific trait change.

325

326 Partitioning the underlying causes of community temperature-trait relationships revealed that
327 species turnover explained most of the variation in traits across space (Fig 2c), suggesting that
328 dispersal and immigration processes will play a key role in governing the rate of ecosystem
329 responses to warming. Shifts in species' abundances and intraspecific trait variation contributed
330 only a minor proportion of the overall temperature-trait relationship (Fig 2c). Furthermore, the
331 local trait pool in the coldest tundra sites (mean summer temperature < 3 °C) is constrained
332 relative to the tundra as a whole for many traits (Fig. S5). Together, these results indicate that
333 major community trait shifts with climate change will occur only with the arrival of novel species
334 from warmer climates.

335

336 Community plant height was the only trait that changed significantly over the 27 years of the
337 study; it increased rapidly at nearly every survey site (Fig 3 a&b, Fig S4, Table S7). Including
338 potential intraspecific trait variation (ITV) doubled the average estimate of plant height change
339 over time, from ~0.03 to ~0.06 cm/year. Because spatial patterns in ITV can be due to both
340 phenotypic plasticity and genetic differences among populations, this is likely a maximum
341 estimate of the ITV contribution, for example if it is due entirely to phenotypic plasticity. The
342 increase in community height is consistent with a finding of increasing vegetation height in
343 response to experimental warming at a subset of these sites²² and with studies of increased
344 shrub growth over time¹¹. Inter-annual variation in community height was significantly sensitive
345 to summer temperature (Fig. 3c, Fig. S3, Table S8), implying that increases in community height
346 are responding to warming. However, neither the rate of temperature change nor soil moisture
347 predicted the rate of CWM change in any trait (Fig. S6, Table S9).

348

349 Increasing community height over time was due largely to species turnover (rather than shifts in
350 abundances of resident species; Fig 3b) and was driven by the immigration of taller species
351 rather than the loss of shorter ones (Fig S7, Table S10). The magnitude of temporal change was
352 comparable to that predicted from the spatial temperature-trait relationship (Fig. 4a), indicating
353 that temporal change in plant height does not yet appear to be substantially limited by

354 immigration rates. The importance of turnover in explaining community height change is
355 surprising given the relatively short study duration and long lifespan of tundra plants, but is
356 nonetheless consistent with a previous finding of shifts towards warm-associated species in
357 tundra plant communities^{17,23}. Turnover could reflect the movement of tall species upward in
358 latitude and elevation or from local species pools in warmer microclimates. If the observed rate
359 of trait change continues (e.g., if immigration were unlimited), community height (excluding
360 potential change due to ITV) could increase by 20-60% by the end of the century, depending on
361 carbon emission, warming and water availability scenarios (Fig. S8).

362
363 Recent (observed) and future (predicted) changes in plant traits, particularly height, are likely to
364 have important implications for ecosystem functions and feedbacks involving soil
365 temperature^{24,25}, decomposition^{4,10}, and carbon cycling²⁶, as the potential for soil carbon loss is
366 particularly great in high-latitude regions⁶. For example, negative feedbacks of increasing plant
367 height to climate could occur with greater carbon storage, increased woody litter production⁴, or
368 if shading reduces soil temperatures and thus decomposition rates in summer^{5,24,26}. Positive
369 feedbacks are also possible if branches or leaves above the snowpack reduce winter and spring
370 albedo¹¹ or increase snow accumulation, leading to warmer winter soil temperatures and
371 increased decomposition rates^{5,11}. The balance of these feedbacks and thus the net impact of
372 trait change on carbon cycling may depend on the interaction between warming and changes in
373 water availability²⁷, which remains a major unknown in the tundra biome.

374
375 The lack of an observed temporal trend in SLA and LDMC despite strong temperature-trait
376 relationships over space highlights the limitations of using space-for-time substitution for
377 predicting short-term changes. This disconnect could reflect the influence of unmeasured
378 changes in water availability, e.g. due local-scale variation in the timing of snowmelt or
379 hydrology, that counter or swamp the effect of static soil moisture estimates. For example, we
380 would not expect significant changes in traits demonstrating a significant spatial temperature *
381 moisture interaction (LDMC, leaf area, leaf N or SLA), even in wet sites, if warming over time
382 also leads to drier soils. Perhaps tellingly, plant height was the only continuous trait for which a
383 temperature * moisture interaction was not significant, and was predicted to increase across all
384 areas of the tundra regardless of soil moisture change (Fig. 4c&d). Spatial-temporal
385 disconnects could also reflect dispersal limitation of potential immigrants (e.g., with low LDMC
386 and high SLA), or establishment failure due to novel biotic or abiotic conditions other than

387 temperature to which immigrants are maladapted^{18,28}. Furthermore, community responses to
388 climate warming could be constrained by soil properties (e.g., organic matter, mycorrhizae,
389 mineralization) that themselves respond slowly to warming¹⁷ or biotic conditions such as grazing
390 pressure²⁹.

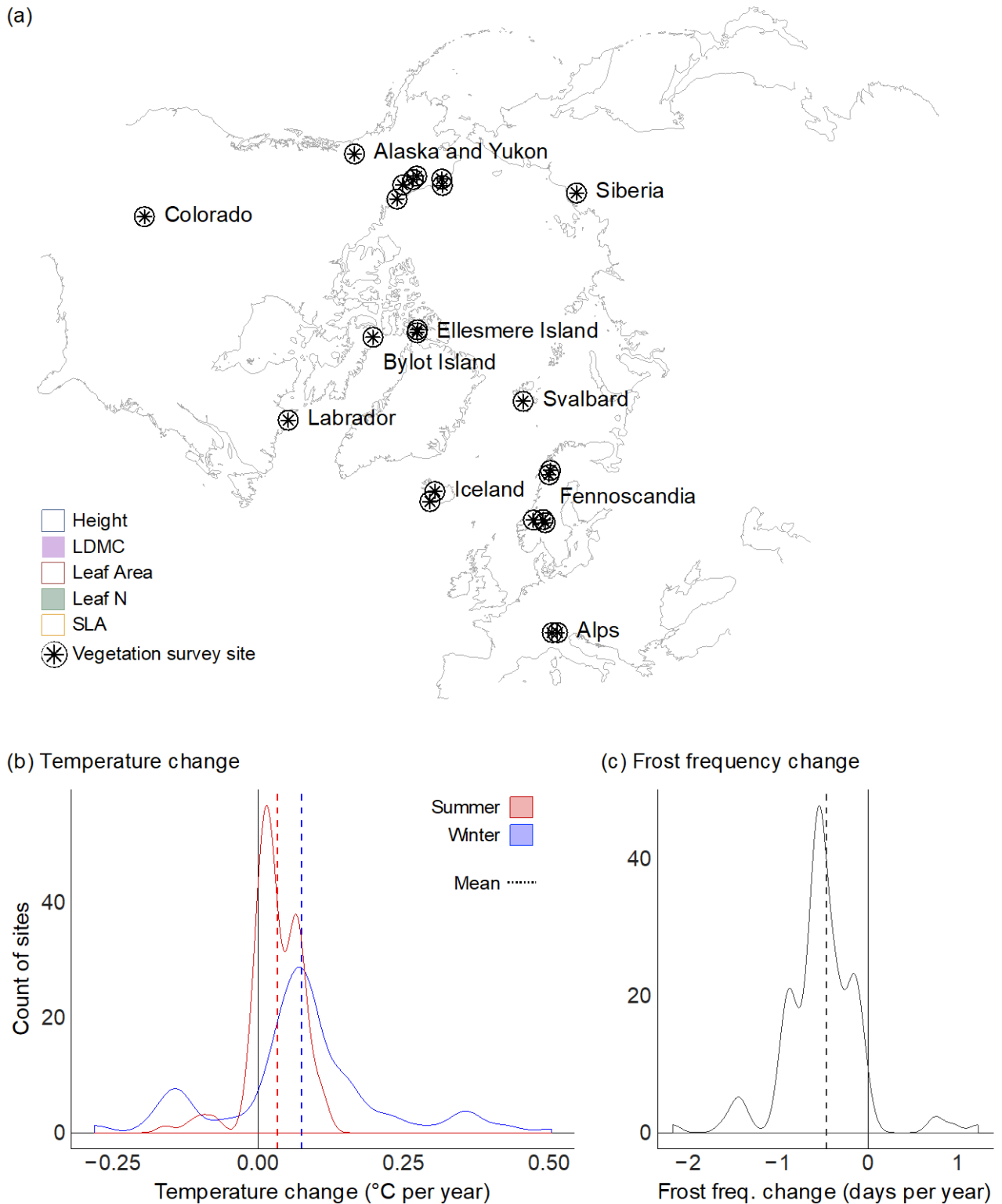
391

392 The patterns in functional traits described here reveal the extent to which environmental factors
393 shape biotic communities in the tundra. Strong temperature- and moisture-related spatial
394 gradients in traits related to competitive ability (e.g., height) and resource capture (e.g., leaf
395 nitrogen, SLA) reflect tradeoffs in plant ecological strategy^{9,14} from benign (warm, wet) to
396 extreme (cold, dry) conditions. Community-level ordination axes are also strongly related to
397 both temperature and moisture, suggesting that environmental drivers structure not only
398 individual traits but also trait combinations and thus lead to a reduced subset of successful
399 functional strategies in some environments (e.g. woody, low-SLA and low-leaf N communities in
400 warm, dry sites; Fig. S9). Thus, warming may lead to a community-level shift toward more
401 exploitative plant strategies³⁰ at wet tundra sites, but toward more conservative strategies in dry
402 sites as moisture becomes more limiting.

403

404 Earth system models are increasingly moving to incorporate trait-environment relationships into
405 modeling efforts, as this can substantially improve estimates of ecosystem change^{31,32}. Our
406 results inform these projections of future tundra functional change with warming³¹ by explicitly
407 quantifying the link between temperature, moisture, and key functional traits across the biome.
408 In particular, our study highlights the importance of accounting for future changes in water
409 availability, as this will likely influence both the magnitude and direction of change for many
410 traits. In addition, we demonstrate that spatial trait-environment relationships are driven largely
411 by species turnover, suggesting that modeling efforts will need to account for rates of species
412 immigration when predicting the speed of future functional shifts. While the failure of many traits
413 (e.g. specific leaf area) to match expected rates of change suggests that using space-for-time
414 substitution alone may inaccurately represent near-term ecosystem change, the ubiquitous
415 increase in community plant height reveals that rapid functional change is already underway in
416 tundra ecosystems.

417



418

419

420

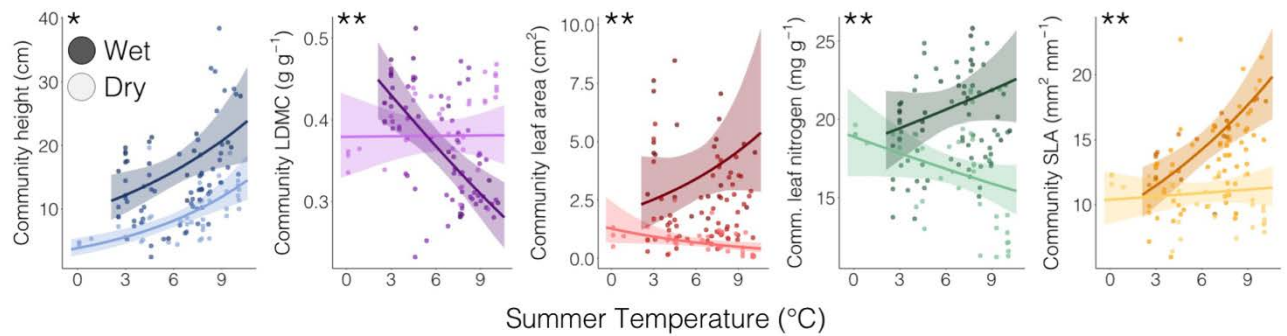
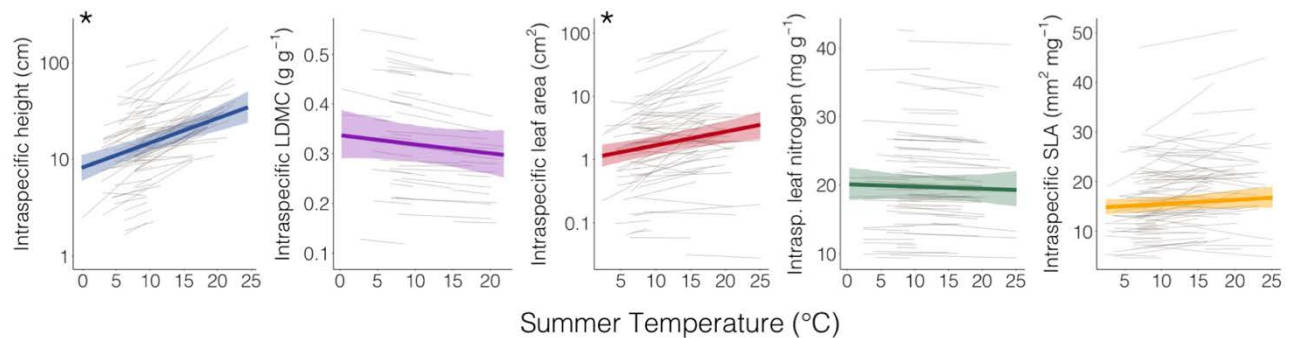
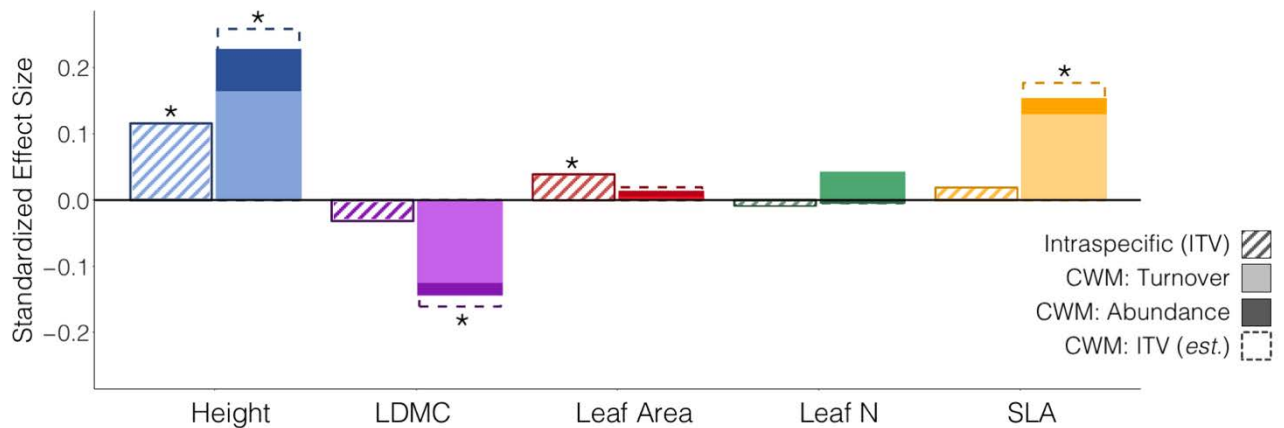
421

422

Figure 1. Map of all 56,048 tundra trait records and vegetation survey sites (a) and climatic change across the period of monitoring at the 117 vegetation survey sites, represented as mean winter (coldest quarter) and summer (warmest quarter) temperature (b) and frost day frequency (c). The size of the colored points on the map indicates the relative quantity of trait

423 measurements (larger circles = more measurements of that trait at a given location) and the
424 color indicates which trait was measured. The black stars indicate the vegetation survey sites
425 used in the community trait analyses. Trait data were included for all species that occur in at
426 least one tundra vegetation survey site; thus, while not all species are unique to the tundra, all
427 do occur in at least one tundra site. Temperature change and frost frequency change were
428 estimated for the interval over which sampling was conducted at each site plus the preceding
429 four years in order to best reflect the time window over which tundra plant communities respond
430 to temperature change^{17,23}.

431

(a) Temperature – trait relationship: across communities (CWM)**(b) Temperature – trait relationship: intraspecific trait variation (ITV)****(c) Temperature – trait relationship: standardized effect size**

433

434 Figure 2. Strong spatial relationships in traits across temperature and soil moisture gradients

435 are primarily explained by species turnover. Community-level (CWM) variation in functional traits

436 across space as related to mean summer (warmest quarter) temperature and soil moisture

437 (ordinal on a scale of 1 to 3; a), and within-species variation (ITV) across space as related to

438 summer temperature (b; note the log scale for height and leaf area). Standardized effect sizes

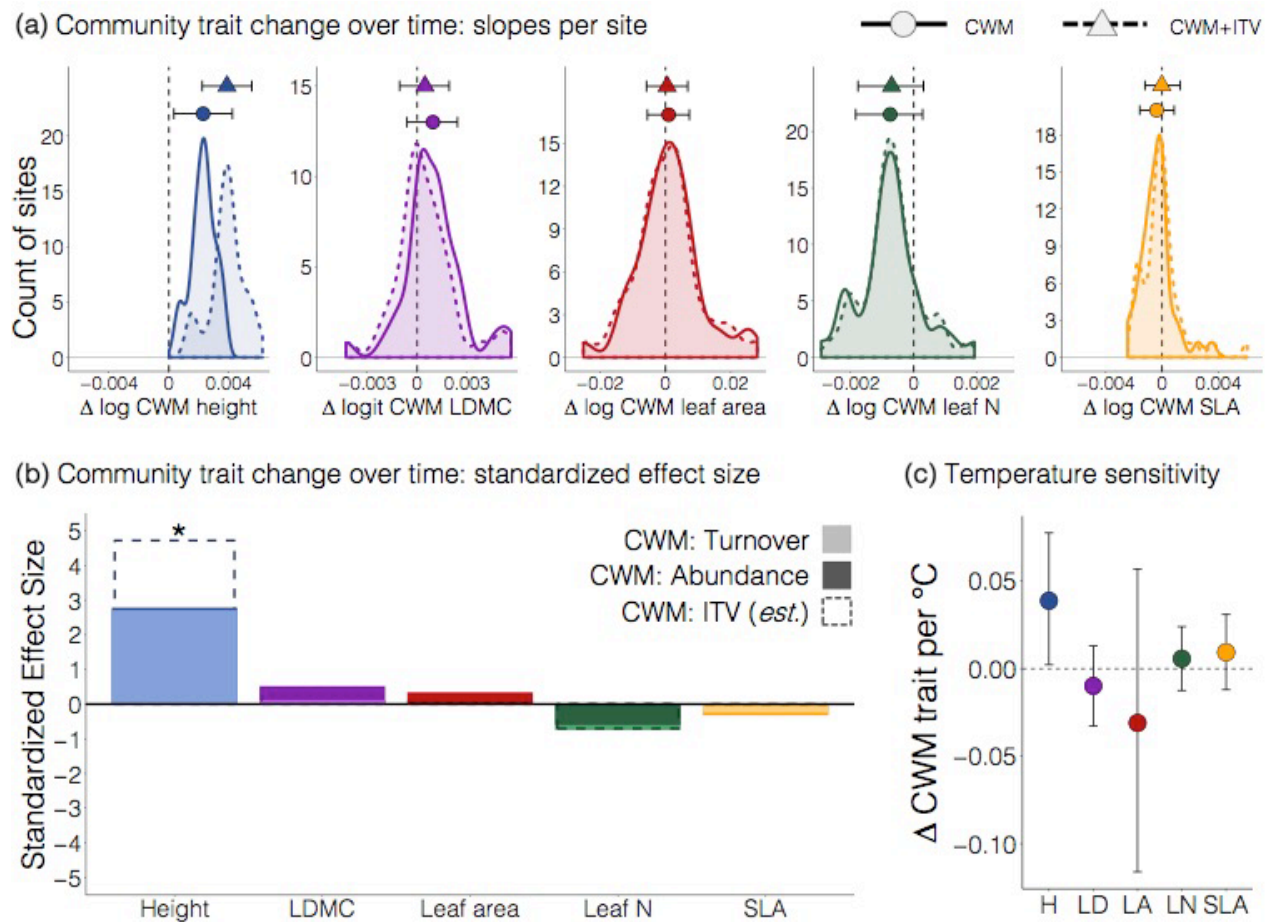
439 were estimated for all temperature-trait relationships (c) both across communities (CWM; solid

440 bars) and within species (ITV; striped bars). Effect sizes for CWM temperature-trait relationships

441 were further partitioned into the proportion of the effect driven solely by species turnover (light

Bjorkman, Anne D. et. al. Plant functional trait change across a warming tundra biome. *Nature* 2018 DOI [10.1038/s41586-018-0563-7](https://doi.org/10.1038/s41586-018-0563-7)

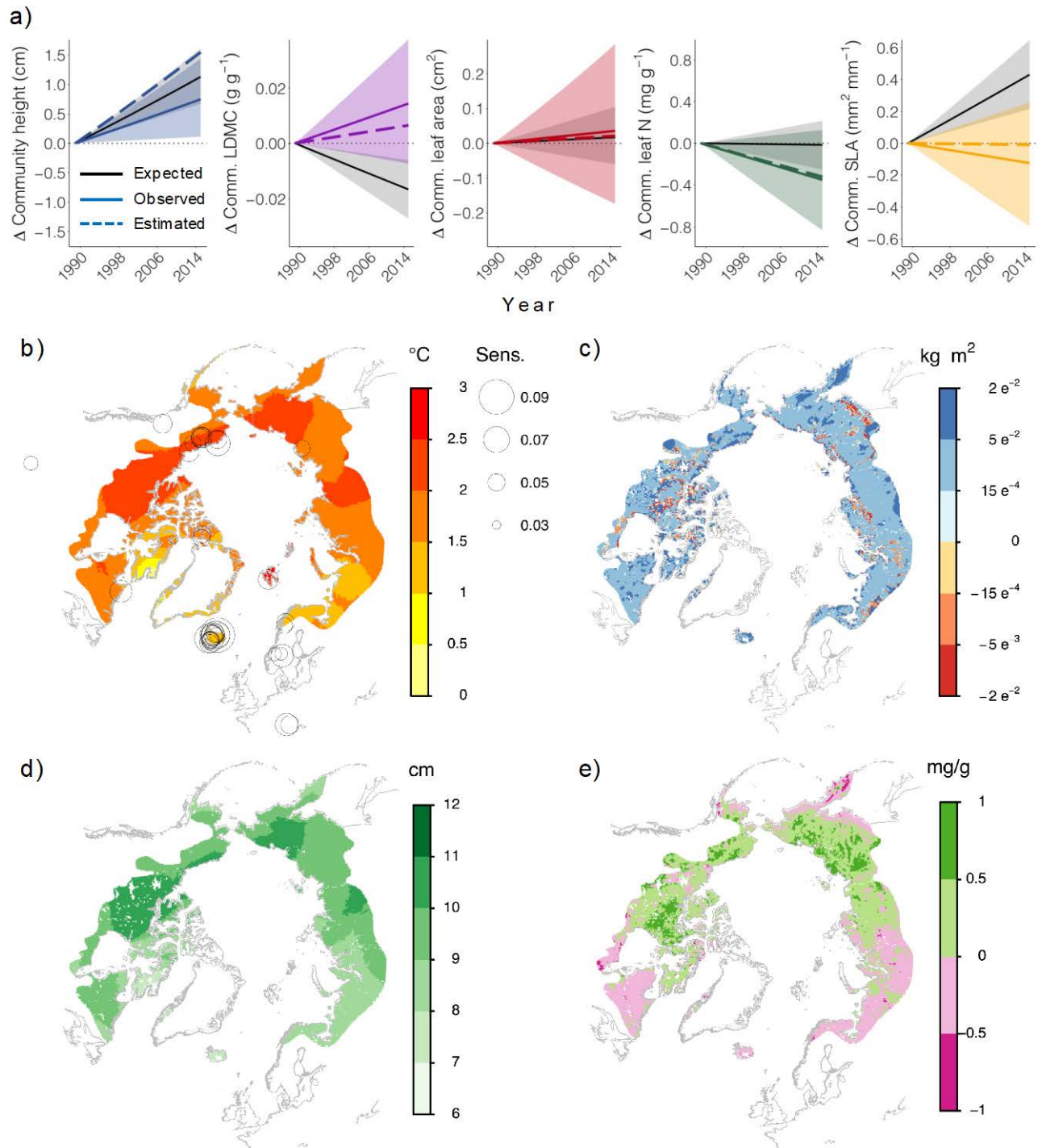
442 bars) and abundance shifts (dark bars) over space. Dashed lines indicate the estimated total
443 temperature-trait relationship over space if intraspecific trait variability is also accounted for
444 (CWM: ITV). Effect sizes for CWM estimates were obtained by dividing the slope of the
445 temperature-trait relationship by the standard deviation of the CWM model residuals. Effect
446 sizes for ITV, turnover only, and CWM: ITV were estimated relative to the CWM value for that
447 same trait based on the slope values of each temperature-trait relationship. Transparent ribbons
448 in (a) and (b) indicate 95% credible intervals for model mean predictions. Grey lines in (b)
449 represent intraspecific temperature-trait relationships for each species. In all panels, asterisks
450 indicate that the 95% credible interval on the slope of the temperature-trait relationship did not
451 overlap zero. In panel (a), two asterisks designate a significant interaction between temperature
452 and soil moisture. Winter temperature – trait relationships are shown in Fig. S3. Community
453 woodiness and evergreenness are shown in Fig. S4.
454



456

457 Figure 3. Observed community trait change (transformed units) per site per year (a), with and
 458 and without estimated intraspecific trait variation (ITV). Solid lines indicate the distribution of
 459 community-weighted mean (CWM) model slopes (trait change per site) while dashed lines
 460 indicate the community-weighted mean plus potential intraspecific trait variation (CWM+ITV)
 461 slopes. Circles (CWM), triangles (CWM+ITV) and error bars indicate the mean and 95%
 462 credible interval for the overall rate of trait change across all sites. The vertical black dashed line
 463 indicates 0 (no change over time). Standardized effect sizes (b) for CWM change over time
 464 were further partitioned into the proportion of the effect driven solely by species turnover (light
 465 bars) or shifts in abundance of resident species (dark bars) over time. Dashed lines indicate the
 466 estimated total trait change over time if predicted intraspecific trait variability is also included
 467 (CWM+ITV). Effect sizes for CWM estimates were obtained by dividing the slope of overall trait
 468 change over time by the standard deviation of the slopes per site. Effect sizes for turnover-only
 469 and CWM+ITV change are estimated relative to the CWM change value for that trait based on
 470 the slope values of each. Temperature sensitivity (c) of each trait as related to summer
 471 temperature (i.e., correspondence between interannual variation in CWM trait values with

472 interannual variation in temperature). Temperatures associated with each survey year were
473 estimated as five-year means (temperature of the survey year and four previous years) because
474 this interval has been shown to be most relevant to vegetation change in tundra¹⁷ and alpine²³
475 plant communities. Changes in community woodiness and evergreenness are shown in Fig. S4.
476



477

478 Figure 4. Observed community (CWM) trait change over time (colored lines) vs. expected CWM
 479 change over the duration of vegetation monitoring (1989-2015) based on the spatial
 480 temperature-trait (CWM) relationship and the average rate of recent summer warming across all
 481 sites (solid black lines; a). Colored dashed lines indicate the potential change over time if
 482 predicted intraspecific trait variability is also included (CWM+ITV). Values on the y-axis
 483 represent the magnitude of change relative to 0 (i.e., trait anomaly), with 0 representing the trait
 484 value at t_0 . Total recent temperature change (b) and soil moisture change (c) across the Arctic

Bjorkman, Anne D. et. al. Plant functional trait change across a warming tundra biome. *Nature* 2018 DOI [10.1038/s41586-018-0563-7](https://doi.org/10.1038/s41586-018-0563-7)

485 tundra (1979-2016). Temperature change estimates are derived from CRU gridded
486 temperature data, soil moisture change estimates are derived from downscaled ERA-Interim soil
487 moisture data. Circles in (b) represent the sensitivity (cm per °C) of CWM plant height to
488 summer temperature at each site (see Fig. 3c). Areas of high temperature sensitivity are
489 expected to experience the greatest increases in height with warming. Spatial trait-temperature-
490 moisture relationships (Fig. 2a) were used to predict total changes in height (d) and leaf N (e)
491 over the entire 1979-2016 period based on concurrent changes in temperature and soil
492 moisture. Note that (d) and (e) reflect *expected* and not observed trait change. See methods for
493 details of temperature change and soil moisture change estimates. The outline of Arctic areas is
494 based on the Circumpolar Arctic Vegetation Map (<http://www.geobotany.uaf.edu/cavm>).
495

496 **References**

- 497 1. Post, E. et al. Ecological dynamics across the Arctic associated with recent climate
498 change. *Science* 325, 1355–1358 (2009).
- 499 2. Elmendorf, S. C. et al. Plot-scale evidence of tundra vegetation change and links to
500 recent summer warming. *Nature Climate Change* 2, 453–457 (2012).
- 501 3. Díaz, S. et al. The plant traits that drive ecosystems: Evidence from three continents.
502 *Journal of Vegetation Science* 15, 295–304 (2009).
- 503 4. Cornelissen, J. H. C. et al. Global negative vegetation feedback to climate warming
504 responses of leaf litter decomposition rates in cold biomes. *Ecology Letters* 10, 619–627
505 (2007).
- 506 5. Sistla, S. A. et al. Long-term warming restructures Arctic tundra without changing net soil
507 carbon storage. *Nature* 497, 615–618 (2013).
- 508 6. Crowther, T. W. et al. Quantifying global soil carbon losses in response to warming.
509 *Nature* 540, 104–108 (2016).
- 510 7. Lavorel, S. & Garnier, E. Predicting changes in community composition and ecosystem
511 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16, 545–556
512 (2002).
- 513 8. Pearson, R. G. et al. Shifts in Arctic vegetation and associated feedbacks under climate
514 change. *Nature Climate Change* 3, 673–677 (2013).
- 515 9. Wright, I. J. et al. The worldwide leaf economics spectrum. *Nature* 428, 821–827 (2004).
- 516 10. Cornwell, W. K. et al. Plant species traits are the predominant control on litter
517 decomposition rates within biomes worldwide. *Ecology Letters* 11, 1065–1071 (2008).
- 518 11. Myers-Smith, I. H. et al. Shrub expansion in tundra ecosystems: dynamics, impacts and
519 research priorities. *Environ. Res. Lett.* 6, 045509 (2011).
- 520 12. Moles, A. T. et al. Global patterns in plant height. *Journal of Ecology* 97, 923–932
521 (2009).
- 522 13. Moles, A. T. et al. Global patterns in seed size. *Global Ecology and Biogeography* 16,
523 109–116 (2006).
- 524 14. Díaz, S. et al. The global spectrum of plant form and function. *Nature* 529, 167–171
525 (2016).
- 526 15. Siefert, A. et al. A global meta-analysis of the relative extent of intraspecific trait variation
527 in plant communities. *Ecology Letters* 18, 1406–1419 (2015).
- 528 16. McMahon, S. M. et al. Improving assessment and modelling of climate change impacts
529 on global terrestrial biodiversity. *Trends Ecol. Evol.* 26, 249–259 (2011).
- 530 17. Elmendorf, S. C. et al. Experiment, monitoring, and gradient methods used to infer
531 climate change effects on plant communities yield consistent patterns. *Proc. Natl. Acad.*
532 *Sci. U.S.A.* 112, 448–452 (2015).
- 533 18. Sandel, B. et al. Contrasting trait responses in plant communities to experimental and
534 geographic variation in precipitation. *New Phytologist* 188, 565–575 (2010).
- 535 19. Ackerman, D., Griffin, D., Hobbie, S. E. & Finlay, J. C. Arctic shrub growth trajectories
536 differ across soil moisture levels. *Global Change Biology* (2017). doi:10.1111/gcb.13677
- 537 20. Wrona, F. J. et al. Transitions in Arctic ecosystems: Ecological implications of a changing
538 hydrological regime. *Journal of Geophysical Research: Biogeosciences* 121, 650–674
539 (2016).

- 540 21. Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G. & Violle, C. When and how
541 should intraspecific variability be considered in trait-based plant ecology? Perspectives in
542 Plant Ecology, Evolution and Systematics 13, 217–225 (2011).
- 543 22. Elmendorf, S. C. et al. Global assessment of experimental climate warming on tundra
544 vegetation: heterogeneity over space and time. Ecology Letters 15, 164–175 (2012).
- 545 23. Gottfried, M. et al. Continent-wide response of mountain vegetation to climate change.
546 Nature Climate Change 2, 111–115 (2012).
- 547 24. Blok, D. et al. Shrub expansion may reduce summer permafrost thaw in Siberian tundra.
548 Global Change Biology 16, 1296–1305 (2010).
- 549 25. Blok, D., Elberling, B. & Michelsen, A. Initial stages of tundra shrub litter decomposition
550 may be accelerated by deeper winter snow but slowed down by spring warming.
551 Ecosystems 19, 155–169 (2016).
- 552 26. Cahoon, S. M. P., Sullivan, P. F., Shaver, G. R., Welker, J. M. & Post, E. Interactions
553 among shrub cover and the soil microclimate may determine future Arctic carbon
554 budgets. Ecology Letters 15, 1415–1422 (2012).
- 555 27. Christiansen, C. T. et al. Enhanced summer warming reduces fungal decomposer
556 diversity and litter mass loss more strongly in dry than in wet tundra. Global Change
557 Biology 23, 406–420 (2017).
- 558 28. Bjorkman, A. D., Vellend, M., Frei, E. R. & Henry, G. H. R. Climate adaptation is not
559 enough: warming does not facilitate success of southern tundra plant populations in the
560 high Arctic. Global Change Biology 1–12 (2016). doi:10.1111/gcb.13417
- 561 29. Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. Herbivores rescue diversity in warming tundra
562 by modulating trait-dependent species losses and gains. Nat Comms 8, 1–8 (2017).
- 563 30. Reich, P. B. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto.
564 Journal of Ecology 102, 275–301 (2014).
- 565 31. Wulschleger, S. D. et al. Plant functional types in Earth system models: past experiences
566 and future directions for application of dynamic vegetation models in high-latitude
567 ecosystems. Annals of Botany 114, 1–16 (2014).
- 568 32. Butler, E. E. et al. Mapping local and global variability in plant trait distributions. Proc.
569 Natl. Acad. Sci. U.S.A. 114, E10937–E10946 (2017).
- 570

571 **Acknowledgements**

572 This paper is an outcome of the sTundra working group meeting supported by sDiv, the
573 Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-
574 Leipzig (DFG FZT 118). ADB was supported by an iDiv postdoctoral fellowship and The Danish
575 Council for Independent Research - Natural Sciences (DFF 4181-00565 to SN). ADB, IMS, HT
576 and SAB were funded by the UK Natural Environment Research Council (ShrubTundra Project
577 NE/M016323/1 to IMS) and SN by the Villum Foundation's Young Investigator Programme
578 (VKR023456). NR was supported by the DFG-Forschungszentrum 'German Centre for
579 Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig' and Deutsche
580 Forschungsgemeinschaft DFG (RU 1536/3-1). AB was supported by EU-F7P INTERACT
581 (262693) and MOBILITY PLUS (1072/MOB/2013/0). ABO and SSN were supported by the
582 Danish Council for Independent Research - Natural Sciences (DFF 4181-00565 to SN) and the
583 Villum Foundation (VKR023456 to SN). SSN was additionally supported by the Carlsberg
584 Foundation (2013-01-0825). AH was supported by the Research Council of Norway
585 (244557/E50). BE was supported by the Danish National Research Foundation (CENPERM
586 DNRF100). BS was supported by the Soil Conservation Service of Iceland. B.J.E. was
587 supported by an NSF ATB, CAREER, and Macrosystems award. CMI was supported by the
588 Office of Biological and Environmental Research in the U.S. Department of Energy's Office of
589 Science as part of the Next-Generation Ecosystem Experiments in the Arctic (NGEE Arctic)
590 project. DB was supported by The Swedish Research Council (2015-00465) and Marie
591 Skłodowska Curie Actions co-funding (INCA 600398). ERF was supported by the Swiss
592 National Science Foundation. EW was supported by the National Science Foundation (DEB-
593 0415383), UWEC - ORSP, and UWEC - BCDT. GC was supported by the University of Zurich
594 Research Priority Program on Global Change and Biodiversity. HP was supported by the NSF
595 PLR (1623764, 1304040). ISJ was supported by the Icelandic Research Fund (70255021) and
596 the University of Iceland Research Fund. JDMS was supported by the Research Council of
597 Norway (262064). JHRL was supported by the U. S. Fish and Wildlife Service. JO was
598 supported by Klimaat voor ruimte, Dutch national research program Climate Change and
599 Spatial Planning. JJ, PG and TZ were supported by the Natural Sciences and Engineering
600 Research Council of Canada. JP was supported by the European Research Council Synergy
601 grant SyG-2013-610028 IMBALANCE-P. KG was supported by NSF ANS-1418123. LS and
602 PAW were supported by the UK Natural Environment Research Council Arctic Terrestrial
603 Ecology Special Topic Programme and Arctic Programme (NE/K000284/1 to PAW). PAW was
604 additionally supported by the European Union 4th Environment and Climate Framework

605 Programme (Project Number ENV4-CT970586). MIG was supported by the University of Zurich
606 Research Priority Program on Global Change and Biodiversity. MD was supported by DFG RTG
607 2010. OG was supported by the Natural Sciences and Engineering Research Council of
608 Canada, Fonds de recherche du Quebec: Nature et technologies, the Northern Scientific
609 Training Program, the Centre d'études nordiques, ArcticNet, and the Polar Continental Shelf
610 Program. RH was supported by the US National Science Foundation. SS was supported by
611 NASA NNX15AU03A. VGO was supported by the Russian Science Foundation (#14-50-
612 00029). The study has been supported by the TRY initiative on plant traits ([http://www.try-
613 db.org](http://www.try-
613 db.org)), which is hosted at the Max Planck Institute for Biogeochemistry, Jena, Germany. TRY is
614 currently supported by DIVERSITAS/Future Earth and the German Centre for Integrative
615 Biodiversity Research (iDiv) Halle-Jena-Leipzig. We acknowledge the contributions of Steven
616 Mamet, Mélanie Jean, Kirsten Allen, Nathan Young, Jenny Lowe, and many others to trait and
617 community composition data collection, and thank the governments, parks, field stations and
618 local and indigenous people for the opportunity to conduct research on their land. We thank
619 Helge Bruelheide and Julian Ramirez-Villegas for helpful input at earlier stages of this project.

620

621 **Author contributions**

622 ADB, IMS and SCE conceived the study, with input from the sTundra working group (SN, NR
623 PSAB, AB-O, DB, JHCC, WC, BCF, DG, SG, KG, GHRH, RH, JK, JSP, JHRL, CR, GS-S, HT,
624 MV, MW, and SW). ADB performed the analyses, with input from IMS, SCE, SN, NR. DNK made
625 the maps of temperature, moisture, and trait change. ADB wrote the manuscript, with input from
626 IMS, SCE, SN, NR, and contributions from all authors. ADB compiled the Tundra Trait Team
627 database, with assistance from IMS, HT and SAB. Authorship order was determined as follows:
628 1) core authors, 2) sTundra participants (alphabetical) and other major contributors, 3) authors
629 contributing both trait (Tundra Trait Team) and community composition (ITEX, etc.) data
630 (alphabetical), 4) Tundra Trait Team contributors (alphabetical), 5) community composition data
631 only contributors (alphabetical), and 6) TRY trait data contributors (alphabetical).

632

633 **Author Information**

634

635 Reprints and permissions information is available at www.nature.com/reprints.

636

637 The authors declare no competing financial interests.

638

639 Correspondence and requests for materials should be addressed to
640 anne.bjorkman@senckenberg.de.
641

642 METHODS

643

644 Below we describe the data, workflow (Fig. S2) and detailed methods used to conduct all
645 analyses.

646

647 **COMMUNITY COMPOSITION DATA**

648 Community composition data used for calculating community-weighted trait means were
649 compiled from a previous synthesis of tundra vegetation resurveys¹ (including many
650 International Tundra Experiment (ITEX) sites) and expanded with additional sites (e.g., Gavia
651 Pass in the Italian Alps and three sites in Sweden) and years (e.g., 2015 survey data added for
652 Iceland sites, QHI, and Alexandra Fiord; Table S3). We included only sites for which community
653 composition data were roughly equivalent to percent cover (i.e., excluding estimates
654 approximating biomass), for a total of 117 sites (defined as plots in a single contiguous
655 vegetation type) within 38 regions (defined as a CRU² grid cell). Plot-level surveys of species
656 composition and cover were conducted at each of these sites between 1989 and 2015 (see¹ for
657 more details of data collection and processing). On average, there were 15.2 plots per site.
658 Repeat surveys were conducted over a minimum duration of 5 and up to 21 years between
659 1989 and 2015 (mean duration = 13.6 years), for a total of 1,781 unique plots and 5,507 plot-
660 year combinations. Plots were either permanent (i.e., staked; 62% of sites) or semi-permanent
661 (38%), such that the approximate but not exact location was resurveyed. The vegetation
662 monitoring sites were located in tree-less Arctic or alpine tundra and ranged in latitude from 40°
663 (Colorado Rockies) to 80° (Ellesmere Island, Canada) and were circumpolar in distribution
664 (Figure 1). Our analyses only include vascular plants because there was insufficient trait data for
665 non-vascular species. Changes in bryophytes and other cryptogams are an important part of
666 the trait and function change in tundra ecosystems^{3,4}, thus the incorporation of non-vascular
667 plants and their traits is a future research priority.

668

669 *Temperature extraction for community composition observations*

670 We extracted summer (warmest quarter) and winter (coldest quarter) temperature estimates for
671 each of the vegetation survey sites from both the WorldClim⁵ (for long-term averages;
672 <http://www.worldclim.org/>) and CRU² (for temporal trends; <http://www.cru.uea.ac.uk/>) gridded
673 climate datasets. WorldClim temperatures were further corrected for elevation (based on the
674 difference between the recorded elevation of a site and the mean elevation of the WorldClim
675 grid cell) according to a correction factor of -0.005 °C per meter increase in elevation. This
Bjorkman, Anne D. et. al. Plant functional trait change across a warming tundra biome. *Nature*
2018 DOI [10.1038/s41586-018-0563-7](https://doi.org/10.1038/s41586-018-0563-7)

676 correction factor was calculated by extracting the mean temperature and elevation (WorldClim
677 30s resolution maps) of all cells falling in a 2.5 km radius buffer around our sites and fitting a
678 linear mixed model (with site as a random effect) to estimate the rate of temperature change
679 with elevation.

680

681 The average long-term (1960-present) temperature trend across all sites was 0.26 (range -0.06
682 to 0.49) and 0.43 (range -0.15 to 1.32) °C/decade for summer and winter temperature,
683 respectively.

684

685 *Soil moisture for community composition observations*

686 A categorical measure of soil moisture at each site was provided by every site PI according to
687 the methods described in Elmendorf et al. 2012 and Myers-Smith et al. 2015 (1,6). Soil moisture
688 was considered to be 1) dry when during the warmest month of the year the top 2 cm of the soil
689 was dry to the touch, 2) moist when soils were moist year round, but standing water was not
690 present, and 3) wet when standing water was found during the warmest month of the year.

691

692 *Soil moisture change for maps of environmental and trait change (Fig. 4b-e)*

693 We used high-resolution soil moisture observations from ESA CCI SM v04.2. To calculate the
694 mean distribution of soil moisture, we averaged the observations from 1979-2016. Because the
695 ESA CCI SM temporal coverage is poor for our sites, temporal data were instead taken from
696 ERA-Interim (Volumetric soil water layer 1) for the same time period. We downscaled the ERA-
697 Interim data to the 0.05° resolution of ESA CCI SM v04.2 using climatologically aided
698 interpolation (delta change method) 7. The change in soil water content was then calculated
699 separately for each grid cell using linear regression with month as a predictor variable. To
700 classify the soil moisture data into 3 categories (wet, mesic, dry) to match the community
701 composition dataset, we used a quantile approach on the mean soil moisture within the extent
702 of the Arctic. We assigned the lowest quantile to dry and the highest to wet conditions. For the
703 trends in soil moisture between 1979-2016 we calculated the percentage in change in relation
704 to the mean first, and then calculated the change based on the categorical data (e.g. 5%
705 change from category 1 (dry) to category 2 (mesic)).

706

707 *Changes in water availability for analysis*

708 Although the strong effect of soil moisture on spatial temperature-trait relationships suggests
709 that change in water availability over time will play an important role in mediating trait change,

710 we did not use the CRU estimates of precipitation change over time because of issues with
711 precipitation records at high latitudes and the inability of gridded datasets to capture localized
712 precipitation patterns (e.g., ^{8,9}). The CRU precipitation trends at our sites included many data
713 gaps filled by long-term mean values, especially at the high-latitude sites⁶. As a purely
714 exploratory analysis, we used the downscaled ERA-Interim data described above to investigate
715 whether trait change is related to summer soil moisture change (June, July, and August; Fig.
716 S6). However, we caution that soil moisture change in our tundra sites is primarily controlled by
717 snow melt timing, soil drainage, the permafrost table and local hydrology¹⁰, and as such
718 precipitation records and coarse-grain remotely sensed soil moisture change data are unlikely
719 to accurately represent local changes in soil water availability. For this same reason we did not
720 use the ERA-Interim data to explore spatial relationships between temperature, moisture and
721 community traits, as the categorical soil moisture data (described above) were collected
722 specifically within each community composition site and are therefore a more accurate
723 representation of long-term mean soil moisture conditions in that specific location.

724

725 TRAIT DATA

726 Continuous trait data (adult plant height, leaf area (average one-sided area of a single leaf),
727 specific leaf area (leaf area per unit of leaf dry mass; SLA), leaf nitrogen content (per unit of leaf
728 dry mass; leaf N), and leaf dry matter content (leaf dry mass per unit of leaf fresh mass; LDMC);
729 Fig. 1a & S11, Table S2) were extracted from the TRY¹¹ 3.0 database (available at [www.try-](http://www.try-db.org)
730 [db.org](http://www.try-db.org)). We also ran a field & data campaign in 2014-15 to collect additional in-situ tundra trait
731 data (the “Tundra Trait Team” (TTT) dataset) to supplement existing TRY records. All species
732 names from the vegetation monitoring sites, TRY and TTT were matched to accepted names in
733 The Plant List using the R package Taxonstand¹² (v. 1.8) before merging the datasets.

734 Community-level traits (woodiness and evergreenness) were derived from functional group
735 classifications for each species (REF). Woodiness is estimated as the proportion (abundance) of
736 woody species in the plot, while evergreenness is the proportion of evergreen woody species
737 abundance out of all woody species (evergreen plus deciduous) in a plot. Because some sites
738 did not contain any woody species (and thus the proportion of evergreen woody species could
739 not be calculated), this trait is estimated only for 98 of the 117 total sites.

740

741 *Data cleaning - TRY*

742 TRY trait data were subjected to a multi-step cleaning process. First, all values that did not
743 represent individual measurements or approximate species means were excluded. When a

Bjorkman, Anne D. et. al. Plant functional trait change across a warming tundra biome. *Nature* 2018 DOI [10.1038/s41586-018-0563-7](https://doi.org/10.1038/s41586-018-0563-7)

744 dataset within TRY contained only coarse plant height estimates (e.g., estimated to the nearest
745 foot), we removed these values unless no other estimate of height for that species was
746 available. We then identified overlapping datasets within TRY and removed duplicate
747 observations whenever possible. The following datasets were identified as having partially
748 overlapping observations: GLOPNET – Global Plant Trait Network Database, The LEDA
749 Traitbase, Abisko & Sheffield Database, Tundra Plant Traits Database, and KEW Seed
750 Information Database (SID).

751

752 We then removed duplicates within each TRY dataset (e.g., if a value is listed once as “mean”
753 and again as “best estimate”) by first calculating the ratio of duplicated values within each
754 dataset, and then removing duplicates from datasets with more than 30% duplicated values.
755 This cutoff was determined by manual evaluation of datasets at a range of thresholds. Datasets
756 with fewer than 30% duplicated values were not cleaned in this way as any internally duplicate
757 values were assumed to be true duplicates (i.e., two different individuals were measured and
758 happened to have the same measurement value).

759

760 We also removed all species mean observations from the “Niwot Alpine Plant Traits” database
761 and replaced it with the original individual observations as provided by M.J. Spasojevic.

762

763 *Data cleaning – TRY & TTT combined*

764 Both datasets were checked for improbable values, with the goal of excluding likely errors or
765 measurements with incorrect units but without excluding true extreme values. We followed a
766 series of data-cleaning steps, in each case identifying whether a given observation (x) was likely
767 to be erroneous (i.e. “error risk”) by calculating the difference between x and the mean
768 (excluding x) of the group and then dividing by the standard deviation of the group.

769

770 We employed a hierarchical data cleaning method, because the standard deviation of a trait
771 value is related to the mean and sample size. First, we checked individual records against the
772 entire distribution of observations of that trait and removed any records with an error risk
773 greater than 8 (i.e., a value more than 8 standard deviations away from the trait mean). For
774 species that occurred in four or more unique datasets with TRY or TTT (i.e., different data
775 contributors), we estimated a species mean per dataset and removed observations for which
776 the species mean error risk was greater than 3 (i.e., the species mean of that dataset was more
777 than 3 SD’s away from the species mean across all datasets). For species that occurred in

778 fewer than 4 unique datasets, we estimated a genus mean per dataset and removed
779 observations in datasets for which the error risk based on the genus mean was greater than
780 3.5. Finally, we compared individual records directly to the distribution of values for that species.
781 For species with more than 4 records, we excluded values above an error risk Y , where Y was
782 dependent on the number of records of that species and ranged from an error risk of 2.25 for
783 species with fewer than 10 records to an error risk of 4 for species with more than 30 records.
784 For species with four or fewer records, we manually checked trait values and excluded only
785 those that were obviously erroneous, based on our expert knowledge of these species.

786

787 This procedure was performed on the complete tundra trait database – including species and
788 traits not presented here. In total 2,056 observations (1.6%) were removed. In all cases, we
789 visually checked the excluded values against the distribution of all observations for each species
790 to ensure that our trait cleaning protocol was reasonable.

791

792 Trait data were distributed across latitudes within the tundra biome (Fig. S1). All trait
793 observations with latitude/longitude information were mapped and checked for implausible
794 values (e.g., falling in the ocean). These values were corrected from the original publications or
795 by contacting the data contributor whenever possible.

796

797 *Final trait database*

798 After cleaning out duplicates and outliers as described above, we retained 56,048 unique trait
799 observations (of which 18,613 are contained in TRY and 37,435 were newly contributed by the
800 Tundra Trait Team field campaign) across the five traits of interest. Of the 447 identified species
801 in the ITEX dataset, 386 (86%) had trait data available from TRY or TTT for at least one trait
802 (range 52-100% per site). Those species without trait data generally represent rare or
803 uncommon species unique to each site; on average, trait data were available for 97% of total
804 plant cover across all sites (range 39-100% per site; Table S2).

805

806 *Temperature extraction for trait observations*

807 WorldClim climate variables were extracted for all trait observations with latitude/longitude
808 values recorded (53,123 records in total, of which 12,380 were from TRY and 33,621 from
809 TTT). Because most observations did not include information about elevation, temperature
810 estimates for individual trait observations were not corrected for elevation and thus represent
811 the temperature at the mean elevation of the WorldClim grid cell.

812

813 *Data Availability*

814 Data compiled through the Tundra Trait Team will be made available through a public GitHub
815 repository (Bjorkman et al. in revision as a data paper at Global Ecology & Biogeography). The
816 public TTT database will include traits not considered in this study as well as tundra species that
817 do not occur in our vegetation survey plots, for a total of 80,827 trait observations on 834
818 species.

819

820 **ANALYSES**

821 All analyses were conducted in JAGS and/or Stan through R (v. 3.3.3) using packages *rjags*¹³
822 (v. 4.6) and *rstan*¹⁴ (v. 2.14.1).

823

824 A major limitation of the species mean trait approach often employed in analyses of
825 environment-trait relationships has been the failure to account for intraspecific trait variation
826 (ITV) that could be as or more important than interspecific variation^{15,16}. We addressed this issue
827 by employing a hierarchical analysis that incorporates both within-species and community-level
828 trait variation across climate gradients to estimate trait change over space and time at the
829 biome scale. We used a Bayesian approach that accounts for the hierarchical spatial (plots
830 within sites within regions) and taxonomic (intra- and inter-specific variation) structure of the
831 data as well as uncertainty in estimated parameters introduced through absences in trait
832 records for some species, and taxa that were identified to genus or functional group (rather than
833 species) in vegetation surveys.

834

835 *Intraspecific trait variation*

836 We subsetted the trait dataset to just those species for which traits had been measured in at
837 least four unique locations spanning a temperature range of at least 10% of the entire
838 temperature range (2.6°C and 5.0 °C for summer and winter temperature, respectively), and for
839 which the latitude and longitude of the measured individual or group of individuals was
840 recorded. The number of species meeting these criteria varied by trait and temperature
841 variable: 108-109 for SLA, 80-86 for plant height, 74-72 for leaf nitrogen, 85-76 for leaf area,
842 and 43-52 for LDMC, for summer and winter temperature, respectively). These species counts
843 correspond to 53-73% of community abundance. The relationship between each trait and
844 temperature was estimated from a Bayesian hierarchical model, with temperature as the
845 predictor variable and species (*s*) and dataset-by-location (*d*) modeled as random effects:

846
847
848
849
850
851

$$\begin{aligned} \text{traitobs}_i &\sim \text{logNormal}(a_{s,d}, \sigma_s) \\ a_{s,d} &\sim \text{Normal}(\alpha_s + \beta_s \cdot \text{temperature}_d, \sigma) \\ \beta_s &\sim \text{Normal}(B, \sigma_1) \\ \alpha_s &\sim \text{Normal}(A, \sigma_2) \end{aligned}$$

852 where A and B are the intercept and slope hyperparameters, respectively. Because LDMC
853 represents a ratio and is thus bound between 0 and 1, we used a beta error distribution for this
854 trait. Temperature values were mean-centered within each species. We used non-informative
855 priors for all coefficients.

856
857
858
859
860
861
862
863
864

We further explored whether the strength of intraspecific temperature-height relationships varied by functional group. We find that all functional groups (including dwarf shrubs, which are genetically limited in their ability to grow upright) show similar temperature-trait relationships (Fig. S12). These results suggest that the intraspecific temperature-trait relationships may not only be a response of individual growth changes, and are not restricted to particular functional groups with greater capacity for vertical growth (e.g., tall shrubs and graminoids versus dwarf shrubs and certain forb species).

865 *Calculation of community weighted mean (CWM) values*

866 We calculated the community-weighted trait mean (i.e., the mean trait value of all species in a
867 plot, weighted by the abundance of each species), for all plots within a site. We employed a
868 Bayesian approach to calculate trait means for every species (s) using an intercept-only model
869 (such that the intercept per species (α_s) is equivalent to the mean trait value of the species) and
870 variation per species (σ_s) with a lognormal error distribution.

871
872
873

$$\text{traitobs}_i \sim \text{logNormal}(\alpha_s, \sigma_s)$$

874 Because LDMC is a ratio and thus bound between 0 and 1, we used a beta error distribution for
875 this trait. When a species was measured multiple times in several different locations, we
876 additionally included a random effect of dataset-by-location (d) to reduce the influence of a
877 single dataset with many observations at one site when calculating the mean per species:

878
879

$$\text{traitobs}_i \sim \text{logNormal}(\alpha_{s,d}, \sigma_d)$$

880 $\alpha_{s,d} \sim \text{Normal}(\alpha_s, \sigma_s)$

881

882 We used non-informative priors for all species intercept parameters for which there were four or
883 more unique trait observations, so that the species-level intercept and variance around the
884 intercept per species were estimated from the data. In order to avoid removing species with
885 little or no trait data from the analyses, we additionally employed a “gap-filling” approach that
886 allowed us to estimate a species’ trait mean while accounting for uncertainty in the estimation of
887 this mean. For species with fewer than four but more than one trait observation, we used a
888 normal prior with the mean equal to the mean of the observation(s) and variance estimated
889 based on the mean mean-variance ratio across all species. In other words, we calculated the
890 ratio of mean trait values to the standard deviation of those trait values per species for all
891 species with greater than four observations, then took the mean of these ratios across all
892 species and multiplied this number by the mean of species X (where X is a species with 1-4
893 observations) to get the prior σ . For species with no observations, we used a prior mean equal
894 to the mean of all species in the same genus and a prior variance estimated based on the mean
895 mean-variance ratio of all species in that genus or 1.5 times the mean, whichever was lower. If
896 there were no other species in the same genus, then we used a prior mean equal to the mean of
897 all other species in the family and a prior variance estimated based on the mean mean-variance
898 ratio of all species in the family or 1.5 times the mean, whichever was lower.

899

900 In order to include uncertainty about species trait means (due to intraspecific trait variation,
901 missing trait information for some species, or when taxa were identified to genus or functional
902 group rather than species) in subsequent analyses, we estimated community-level trait values
903 per plot by sampling from the posterior distribution (mean +/- SD) of each species intercept
904 estimate and multiplying this distribution by the relative abundance of each species in the plot to
905 get a community-weighted mean (CWM) distribution per plot. This approach generates a
906 distribution of CWM values per plot that propagates the uncertainty in each species’ trait mean
907 estimate into the plot-level (CWM) estimate. By using a Bayesian approach, we are able to carry
908 through uncertainty in trait mean estimates to all subsequent analyses and reduce the potential
909 for biased or deceptively precise estimates due to missing trait observations.

910

911 *Calculation of CWM values: partitioning turnover and estimating contribution of ITV*

912 To assess the degree to which the spatial temperature-trait relationships are caused by species
913 turnover versus shifts in abundance among sites, we repeated each analysis using the non-

914 weighted community mean (all species weighted equally) of each plot. Temperature-trait
915 relationships estimated with non-weighted community means are due solely to species turnover
916 across sites. Finally, we assessed the potential contribution of intraspecific trait variation (ITV) to
917 the community-level temperature-trait relationship by using the modeled intraspecific
918 temperature-trait relationship (described above) to predict trait “anomaly” values for each
919 species at each site based on the temperature of that site in a given year relative to its long-
920 term average.

921

922 An intraspecific temperature-trait relationship could not be estimated for every species due to
923 an insufficient number of observations for some species. Therefore, we used the mean
924 intraspecific temperature-trait slope across all species to predict trait anomalies for species
925 without intraspecific temperature-trait relationships. These site- and year-specific species trait
926 estimates were then used to calculate “ITV-adjusted” community-weighted means (CWM+ITV)
927 for each plot in each year measured, and modeled as for CWM alone. As these “adjusted”
928 values are estimated *relative to each species’ mean value*, the spatial temperature-trait
929 relationship that includes this adjustment does not remove any bias in the underlying species
930 mean data. For example, if southern tundra species tend to be measured at the southern edge
931 of their range while northern tundra species tend to be measured at the northern edge of their
932 range, the overall spatial temperature-trait relationship could appear stronger than it really is for
933 species with temperature-related intraspecific variation. This is a limitation of any species-mean
934 approach.

935

936 Estimates of temporal CWM+ITV temperature-trait relationships are not prone to this same
937 limitation as they represent relative change, but should also be interpreted with caution as
938 intraspecific temperature-trait relationships may be due to genetic differences among
939 populations rather than plasticity, thus suggesting that trait change would not occur
940 instantaneously with warming. We therefore caution that the CWM+ITV analyses presented here
941 represent estimates of the potential contribution of ITV to overall CWM temperature-trait
942 relationships over space and time, but should not be interpreted as measured responses.

943

944 In sum, we incorporate intraspecific variation into our analyses in three ways. First, by using the
945 posterior distribution (rather than a single mean value) of species trait mean estimates in our
946 calculations of CWM values per plot, so that information about the amount of variation within
947 species is incorporated into all the analyses in our study. Second, by explicitly estimating

948 intraspecific temperature-trait relationships based on the spatial variation in individual trait
949 observations. And finally, by using these modeled temperature-trait relationships to inform
950 estimates of the potential contribution of ITV to overall (CWM+ITV) temperature-trait
951 relationships over space and time.

952

953 *Spatial community trait models*

954 To investigate spatial relationships in plant traits with summer and winter temperature and soil
955 moisture we used a Bayesian hierarchical modeling approach in which soil moisture and soil
956 moisture x temperature vary at the site level while temperature varies by WorldClim region
957 (unique WorldClim grid x elevation groups). In total, there were 117 sites (s) nested within 73
958 WorldClim regions (r). We used only the first year of survey data at each site to estimate spatial
959 relationships in community traits.

960

$$961 \quad cwmtrait_p \sim Normal(\alpha_s + \alpha_r, traitsd_p)$$

$$962 \quad \alpha_s \sim Normal(\gamma_1 \cdot moisture_s + \gamma_2 \cdot moisture_s \cdot temperature_s, \sigma_1)$$

$$963 \quad \alpha_r \sim Normal(\gamma_0 + \gamma_3 \cdot temperature_r, \sigma_2)$$

964

965 Where $cwmtrait_p$ is the estimated community-weighted mean (CWM) trait value per plot (p) and
966 $traitsd_p$ is the standard deviation of the posterior distribution of this mean per plot, as described
967 above.

968

969 As woodiness and evergreenness represent proportional data (bounded between 0 and 1,
970 inclusive), we used a beta-Bernoulli mixture model of the same structure as above to estimate
971 trait-temperature-moisture relationships for these traits. Because Arctic and alpine tundra sites
972 might differ in their trait-environment relationships due to differences in e.g. soil drainage, we
973 also present a version of the spatial community trait analyses in which the altitude of each site is
974 indicated (Fig. S13). We do not attempt to separately analyze trait-environment relationships for
975 Arctic and alpine sites due to the ambiguity in defining this cut-off (i.e., many sites can be
976 categorized as both Arctic and alpine, particularly in Scandinavia and Iceland) and the small
977 number of “true” alpine sites (European Alps and Colorado Rockies).

978

979 For estimation of the overall temperature-trait relationship, we used a model structure similar to
980 that above but with only temperature as a predictor (i.e., without soil moisture). This model was
981 used for both community-weighted mean (CWM) and non-weighted mean estimates in order to

982 determine the degree to which temperature-trait relationships over space are due to species
983 turnover alone (non-weighted mean) and for CWM+ITV plot-level estimates to determine the
984 likely additional contribution of intraspecific trait variation to the overall temperature-trait
985 relationship, as described above.

986

987 *Trait change over time*

988 Change over time was modeled at the CRU grid cell (region) level (r), with site (s) as a random
989 effect when there was more than one site per region (to account for non-independence of sites
990 within a region) and plot (p) as a random effect for those sites with permanent (repeating) plots
991 (to account for repeated measures on the same plot over time). We did not account for
992 temporal autocorrelation as most plots were not measured annually (average survey interval =
993 7.2 years) and did not have more than 3 observations over the study period (average number of
994 survey years per plot = 3.1). Year (y) was centered within each region.

995

$$996 \quad cwmtrait_{p,y} \sim Normal(\alpha_p + a_s + a_{r,y}, traitsd_{p,y})$$

997

998 For non-permanent plots and for sites that were the only site within a region, α_p or α_s ,
999 respectively, were set to 0. Region-level slopes were used to fit an average trend of community
1000 trait values over time:

1001

$$1002 \quad \alpha_{r,y} \sim Normal(a_r + \beta_r \cdot year_{y,r}, \sigma)$$

1003

$$\beta_r \sim Normal(B, \sigma_1)$$

1004

$$\alpha_r \sim Normal(A, \sigma_2)$$

1005

1006 where A and B are the intercept and slope hyperparameters, respectively. This model was used
1007 for both community-weighted mean (CWM) and non-weighted mean plot-level estimates in
1008 order to determine the degree to which temporal trait change is due to species turnover alone
1009 (non-weighted mean) and for CWM+ITV plot-level estimates to determine the potential
1010 additional contribution of intraspecific trait variation to overall trait change.

1011

1012 For the spatial community trait models, we used a beta-Bernoulli mixture model of the same
1013 form described above to estimate change in the proportion of woody and evergreen species.

1014 We additionally assessed whether the rate of observed trait change over time was related to the

1015 duration of vegetation monitoring at each site (Fig. S10). There was no significant influence of
1016 monitoring duration for any trait.

1017

1018 *Species gains and losses as a function of traits*

1019 We estimated species gains and losses at the site (rather than plot) level to reduce the effect of
1020 random fluctuations in species presences/absences due to observer error. Thus, sites with
1021 repeating and non-repeating plots were treated the same. A “gain” was defined as a species
1022 that did not occur in a site in the first survey year but did in the last survey year, while a “loss”
1023 was the reverse. We then modeled the probability of gain or loss separately as a function of the
1024 mean trait value of each species. For example, for “gains,” all newly observed species received
1025 a response type of 1 while all other species in the site received a response type of 0:

1026

$$1027 \quad \text{response}_i \sim \text{Bernoulli}(\alpha_s + \alpha_r + \beta_r \cdot \text{trait}_i)$$

1028

$$\alpha_r \sim \text{Normal}(A, \sigma_1)$$

1029

$$\beta_r \sim \text{Normal}(B, \sigma_2)$$

1030

$$\alpha_s \sim \text{Normal}(0, \sigma_r)$$

1031

1032 We included a random effect for site (s) only when there were multiple sites within the same
1033 region (r), otherwise α_s was set to 0. We considered species' responses to be significantly
1034 related to a given trait when the 95% credible interval on the slope hyperparameter (B) did not
1035 cross 0.

1036

1037 *Observed vs. expected trait change*

1038 We first calculated the mean rate of temperature change across the 38 regions in our study,
1039 and then estimated the *expected* degree of change in each trait over the same period based on
1040 this temperature change and the spatial relationship between temperature and CWM trait
1041 values. We then compared this *expected* trait change to actual trait change over time, as
1042 estimated from the model described above. To create Fig. 4a we used the overall predicted
1043 mean value of each trait in the first year of survey (1989) as an intercept, and then used the
1044 expected and observed rates of change (+/- uncertainty) to predict community trait values in
1045 each year thereafter. We subtracted the intercept from all predicted values in order to show trait
1046 change as anomaly (difference from 0). The difference between the expected (black) and
1047 observed (colored) lines in Fig. 4a represents a deviation from expected.

1048

1049 *Trait projections with warming*

1050 We projected trait change (Fig. S8) for the minimum (2.6) and maximum (8.5) IPCC carbon
1051 emission scenarios from the NIMR HadGEM2-AO Global Circulation Model. We used the
1052 midpoint years of the WorldClim (1975) and HadGem2 (2090) estimates to calculate the
1053 expected rate of temperature change over this time period. We then predicted trait values for
1054 each year into the future based on the projected rate of temperature change and the spatial
1055 relationship between temperature and community trait values.

1056

1057 These projections are not intended to predict actual expected trait change over the next
1058 century, as many other factors not accounted for here will also influence this change. In
1059 particular, future changes in functional traits will likely depend on concurrent changes in
1060 moisture availability, which are less well understood than temperature change. Recent modeling
1061 efforts predict increases in precipitation across much of the Arctic¹⁷, but it is unknown whether
1062 increasing precipitation will also lead to an increase in soil moisture/water availability for plants,
1063 as the drying effect of warmer temperatures (e.g. due to increased evaporation and/or
1064 decreased duration of snow cover¹⁸) may outweigh the impact of increased precipitation.

1065 Instead, these projections are an attempt to explore theoretical trait change over the long-term
1066 when using a space-for-time substitution approach.

1067

1068 *Temperature sensitivity*

1069 Temperature sensitivity (Fig. 3c) was modeled as the variation in CWM trait values with variation
1070 in the five-year mean temperature (i.e., the mean temperature of the survey year and the four
1071 preceding years). A four-year lag was chosen because this interval has been shown to best
1072 explain vegetation change in tundra¹⁹ and alpine²⁰ plant communities. The model specifics are
1073 exactly as shown above for trait change over time, but with temperature in the place of year.

1074 Temperatures were centered within each region.

1075

1076 *Trait change vs. temperature change and soil moisture*

1077 To determine whether the rate of trait change can be explained by the rate of temperature
1078 change at a site, the (static) level of soil moisture of a site, or their interaction, we modeled the
1079 rate of trait change as described above (“Trait change over time”) and compared it to the rate
1080 of temperature change over the same time interval (minus a lag of four years) and soil moisture:

1081

1082
$$\beta_r \sim \text{Normal}(\gamma_0 + \gamma_1 \cdot \text{temp}_r + \gamma_2 \cdot \text{moisture}_r + \gamma_3 \cdot \text{temp}_r \cdot \text{moisture}_r, \sigma)$$

1083

1084 where β_r is the rate of trait change per region (Fig. S6a). When sites within a region were
1085 measured over different intervals or contained different soil moisture estimates they were
1086 modeled separately in order to match with temperature change estimates over the same
1087 interval and soil moisture estimates, which vary at the site level.

1088

1089 We also conducted this analysis using estimates of soil moisture change (with a lag of four
1090 years) from downscaled ERA-Interim (volumetric soil water layer 1). This model took the same
1091 form as above, but with moisture change in place of static soil moisture estimates (Fig. S6b).
1092 Trait change was modeled at the site (rather than region) level because estimates of soil
1093 moisture change vary at the site level. Because ERA-Interim data were not available for every
1094 site, this analysis was conducted with a total of 101 rather than 117 sites. We note that the
1095 results of this analysis should be interpreted cautiously, as local changes in soil moisture may
1096 not be well represented by coarse-scale remotely sensed data, as described previously.

1097

1098 *Principal component analysis (PCA)*

1099 We performed an ordination of community-weighted trait mean values per plot on all seven
1100 traits. Because community evergreenness could only be estimated for plots with at least one
1101 woody species, the total number of plots included in this analysis is reduced compared to the
1102 entire dataset (1098 plots out of 1520 in total). We used the R package *vegan*²¹ (v. 2.4.6) to
1103 conduct a principal component analysis of these data. This analysis uses only trait means per
1104 plot, and therefore information about CWM uncertainty due to intraspecific trait variation and/or
1105 missing species is lost. We extracted the axis coordinates of each plot from the PCA analysis
1106 and used the spatial trait-temperature-moisture model described above (section “*Spatial*
1107 *community trait models*”) to determine whether plot distributions along both PCA axes varied
1108 significantly with temperature, moisture, and their interaction.

1109

1110 *Trends in species abundance [NOT YET COMPLETE]*

1111 In order to provide more insight into the species-specific changes occurring over time in tundra
1112 ecosystems, we calculated trends in abundance for the most common (widespread and
1113 abundant) species in the community composition dataset (Fig. SX). We estimated trends for all
1114 species that occurred in at least 10 sites at a minimum abundance of 10% cover (mean of all
1115 plots within a site) in at least one year and a minimum abundance of 5% across all years. We
1116 additionally included species that occurred at low abundance (1% or more) but were

1117 widespread (at least 20 sites). Because percent cover is bounded between 0 and 1 (inclusive)
1118 we used a beta-Bernoulli mixture model to estimate abundance change over time.

1119

1120 **Methods References**

- 1121 1. Elmendorf, S. C. et al. Plot-scale evidence of tundra vegetation change and links to
1122 recent summer warming. *Nature Climate Change* 2, 453–457 (2012).
- 1123 2. Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of
1124 monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of*
1125 *Climatology* 34, 623–642 (2014).
- 1126 3. Blok, D. et al. The Cooling Capacity of Mosses: Controls on Water and Energy Fluxes in a
1127 Siberian Tundra Site. *Ecosystems* 14, 1055–1065
- 1128 4. Soudzilovskaia, N. A., van Bodegom, P. M. & Cornelissen, J. H. C. Dominant bryophyte
1129 control over high-latitude soil temperature fluctuations predicted by heat transfer traits,
1130 field moisture regime and laws of thermal insulation. *Functional Ecology* 27, 1442–1454
1131 (2013).
- 1132 5. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, J. L. & Jarvis, A. Very high resolution
1133 interpolated climate surfaces for global land areas. *International Journal of Climatology*
1134 25, 1965–1978 (2005).
- 1135 6. Myers-Smith, I. H. et al. Climate sensitivity of shrub growth across the tundra biome.
1136 *Nature Climate Change* 5, 887–891 (2015).
- 1137 7. Willmott, C. J. & Robeson, S. M. Climatologically aided interpolation (CAI) of terrestrial air
1138 temperature. *International Journal of Climatology* 15, 221–229 (1995).
- 1139 8. Sperna Weiland, F. C., Vrugt, J. A., van Beek, R. L.). P. H., Weerts, A. H. & Bierkens, M.
1140 F. P. Significant uncertainty in global scale hydrological modeling from precipitation data
1141 errors. *Journal of Hydrology* 529, 1095–1115 (2015).
- 1142 9. Beguería, S., Vicente Serrano, S. M., Tomás Burguera, M. & Maneta, M. Bias in the
1143 variance of gridded data sets leads to misleading conclusions about changes in climate
1144 variability. *International Journal of Climatology* 36, 3413–3422 (2016).
- 1145 10. Wrona, F. J. et al. Transitions in Arctic ecosystems: Ecological implications of a changing
1146 hydrological regime. *Journal of Geophysical Research: Biogeosciences* 121, 650–674
1147 (2016).
- 1148 11. Kattge, J. et al. TRY—a global database of plant traits. *Global Change Biology* 17, 2905–
1149 2935 (2011).
- 1150 12. Cayuela, L., Granzow-de la Cerda, Í., Albuquerque, F. S. & Golicher, D. J.
1151 TAXONSTAND: An R package for species names standardisation in vegetation
1152 databases. *Methods in Ecology and Evolution* 3, 1078–1083 (2012).
- 1153 13. Plummer, M. rjags: Bayesian graphical models using MCMC. (2016).
- 1154 14. Stan Development Team. RStan: the R interface to Stan. (2016).
- 1155 15. Messier, J., McGill, B. J. & Lechowicz, M. J. How do traits vary across ecological scales?
1156 A case for trait-based ecology. *Ecology Letters* 13, 838–848 (2010).
- 1157 16. Violle, C. et al. The return of the variance: intraspecific variability in community ecology.
1158 *Trends Ecol. Evol.* 27, 245–253 (2012).

- 1159 17. Bintanja, R. & Selten, F. M. Future increases in Arctic precipitation linked to local
1160 evaporation and sea-ice retreat. *Nature* 509, 479–482 (2014).
- 1161 18. AMAP. Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017. (Arctic Monitoring
1162 and Assessment Programme (AMAP), 2017).
- 1163 19. Elmendorf, S. C. et al. Experiment, monitoring, and gradient methods used to infer
1164 climate change effects on plant communities yield consistent patterns. *Proc. Natl. Acad.*
1165 *Sci. U.S.A.* 112, 448–452 (2015).
- 1166 20. Gottfried, M. et al. Continent-wide response of mountain vegetation to climate change.
1167 *Nature Climate Change* 2, 111–115 (2012).
- 1168 21. Oksanen, J., Blanchet, F., Kindt, R. & Legendre, P. Package ‘vegan’. (2011).
- 1169