

# Dispersal and fire limit Arctic shrub expansion

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# 1                    **Dispersal and fire limit Arctic shrub expansion**

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## 11   **Abstract**

12   Arctic shrub expansion has been widely reported in recent decades, with large impacts on carbon  
13   budgets, albedo, and warming rates in high latitudes. However, predicting shrub expansion  
14   across regions remains challenging because the underlying controls remain unclear.

15   Observational studies and models typically use relationships between observed shrub presence  
16   and current environmental suitability (climate and topography) to predict shrub expansion, but  
17   such approaches omit potentially important biotic-abiotic interactions and non-stationary  
18   relationships. Here, we use long-term high-resolution satellite imagery across Alaska and  
19   western Canada to show that observed shrub expansion has not been controlled by environmental  
20   suitability during 1984-2014, but rather can only be explained by accounting for seed dispersal  
21   and fire. These findings provide the impetus for better observations of recruitment and for  
22   incorporating currently underrepresented processes of seed dispersal and fire in land models to  
23   project shrub expansion and future climate feedbacks. Integrating these dynamic processes with  
24   projected fire extent and climate, we estimate that shrubs will expand into 25% of the non-shrub

25 tundra by 2100, in contrast to 39% predicted using a relationship with increasing suitability  
26 alone. Thus, using environmental suitability alone likely overestimates and misrepresents the  
27 spatial pattern of shrub expansion and its associated carbon sink.

28

## 29 **Main**

30 The Arctic has warmed more than twice as fast as the global average and is projected to continue  
31 outpacing lower latitudes over the 21st century<sup>1</sup>. Rapid climate warming in recent decades and  
32 associated feedbacks have led to shifts in Arctic vegetation composition and abundance<sup>2-4</sup>. In  
33 particular, increased tundra shrub cover has been widely observed through field surveys<sup>5</sup>, aerial  
34 photographs<sup>6,7</sup>, and satellite remote sensing<sup>8,9</sup>. Pervasive shrub expansion can heat the  
35 atmosphere through decreased albedo and increased greenhouse warming induced by  
36 atmospheric water vapor, resulting from increased evapotranspiration and regional ocean  
37 feedbacks<sup>10-12</sup>. Locally, shrubs can warm the soil in the winter due to insulation of accumulated  
38 snow, which deepens the active layer and accelerates soil carbon loss compared to non-shrub  
39 tundra<sup>13,14</sup>. Moreover, the distribution of shrubs also affects nutrient cycling, animal  
40 populations<sup>15</sup>, and wildfire risk and associated carbon emissions<sup>16,17</sup>. Understanding controls of  
41 shrub expansion patterns is therefore crucial to predicting climate feedbacks and ecological  
42 consequences of the rapidly changing Arctic.

43         The area where temperature limits the growth of Arctic vegetation has been declining  
44 over the past decades<sup>18</sup>. Increasing temperature has been identified as a major control of shrub  
45 expansion<sup>5,19,20</sup>. However, the influence of temperature can be attenuated or reversed by soil  
46 moisture limitation, snow distribution, and topography<sup>4,21-25</sup>. The majority of observational-  
47 based studies focus on environmental factors and attribute the heterogeneity of shrub expansion

48 to spatial variation of environment-based suitability, i.e., the likelihood of shrub presence given  
49 environmental conditions<sup>26</sup>. Based on space-for-time substitutions, some of those studies used  
50 derived spatial environment-vegetation relationships to assess future shrub expansion<sup>5,20,21</sup>,  
51 assuming stationary relationships between species and the environment. Although this approach  
52 has been found effective in predicting species distributions when ecosystems are in dynamic  
53 equilibrium, e.g., under a relatively stable climate or over a sufficiently long time scale<sup>27</sup>, it  
54 ignores transient responses and non-stationary ecological processes, thus causing errors in  
55 projected ecosystem change<sup>28-30</sup>. As the Arctic tundra deviates from the historical quasi-  
56 equilibrium due to climate change, evaluating the dynamic roles of plant migration and  
57 disturbance becomes especially relevant.

58         With changes in growing conditions under a warmer climate, successful establishment of  
59 new shrub patches depends on seed dispersal. Seeds can be dispersed through many biotic and  
60 abiotic vectors, such as gravity, animals, wind, ocean currents, and drifting sea ice, which result  
61 in dispersal ranges from meters to hundreds of kilometers<sup>31,32</sup>. Seed dispersal has been found  
62 important in explaining shifts in vegetation composition at sites in alpine<sup>33</sup>, mediterranean<sup>34,35</sup>,  
63 and tropical biomes<sup>36,37</sup>. Nonetheless, the impact of seed dispersal on vegetation patterns is also  
64 compounded by suitable environmental niches and thus is not always the limiting factor<sup>38-40</sup>. In  
65 the Arctic, genetic analysis has revealed repeated long-distance seed dispersal to a remote  
66 archipelago from multiple source regions since the last glacial retreat, while the resulting species  
67 distribution is predominantly shaped by temperature that limits suitability for establishment<sup>39</sup>. In  
68 contrast to a relatively stable climate over the past several millennia, the fast changing climate  
69 over recent decades might lead to shifts in the relative dominance of environmental suitability  
70 and seed dispersal in shaping Arctic shrub expansion.

71           The dynamic trajectory of ecosystems may also be affected by disturbance. Although  
72 historically rare in Arctic ecosystems, wildfire is expected to become more intense and frequent  
73 as the climate warms<sup>16,41</sup>. In the short term, wildfires may cause seed and seedling mortality,  
74 which could limit post-fire recruitment. On the other hand, wildfires can alter post-fire  
75 vegetation trajectories by heating the soil during the fire, cause long-term soil warming by  
76 removing surface litter, and improve seedbed nutrient availability, thus facilitating germination  
77 and seedling establishment<sup>42–46</sup>. For example, modeling and site-based field studies have  
78 reported both enhanced expansion and diminished recovery of shrubs from four years to two  
79 decades after wildfires at several sites in Alaska<sup>43,45,47–49</sup>. How wildfires affect shrub expansion  
80 across large gradients of environmental suitability and seed dispersal has barely been evaluated  
81 using observations.

82           We focused on shrub expansion from 1984 to 2014 across the northwestern region of  
83 North America covering Alaska and western Canada, i.e., the NASA Arctic-Boreal Vulnerability  
84 Experiment (ABOVE) core domain. Shrub expansion was detected using an annual dominant  
85 land-cover product derived from Landsat surface reflectance and trained over field photography  
86 and very high resolution imagery<sup>3</sup>. Here, shrub expansion is defined as shrub dominance in  
87 tundra originally dominated by non-woody species at a 30 m scale. We collected topographic  
88 and regionally downscaled bioclimatic variables across the domain to identify the variables most  
89 informative for observed shrub expansion (Methods). Based on these selected topographic and  
90 bioclimatic conditions, averaged over three decades prior to 1984, we estimated environmental  
91 suitability for shrubs in 1984 using a random forest model. The same model was then used to  
92 calculate the suitability for shrubs in 2014 using 1985-2014 average bioclimatic conditions. We  
93 analyzed whether changes in suitability could explain shrub expansion from 1984 to 2014. Seed

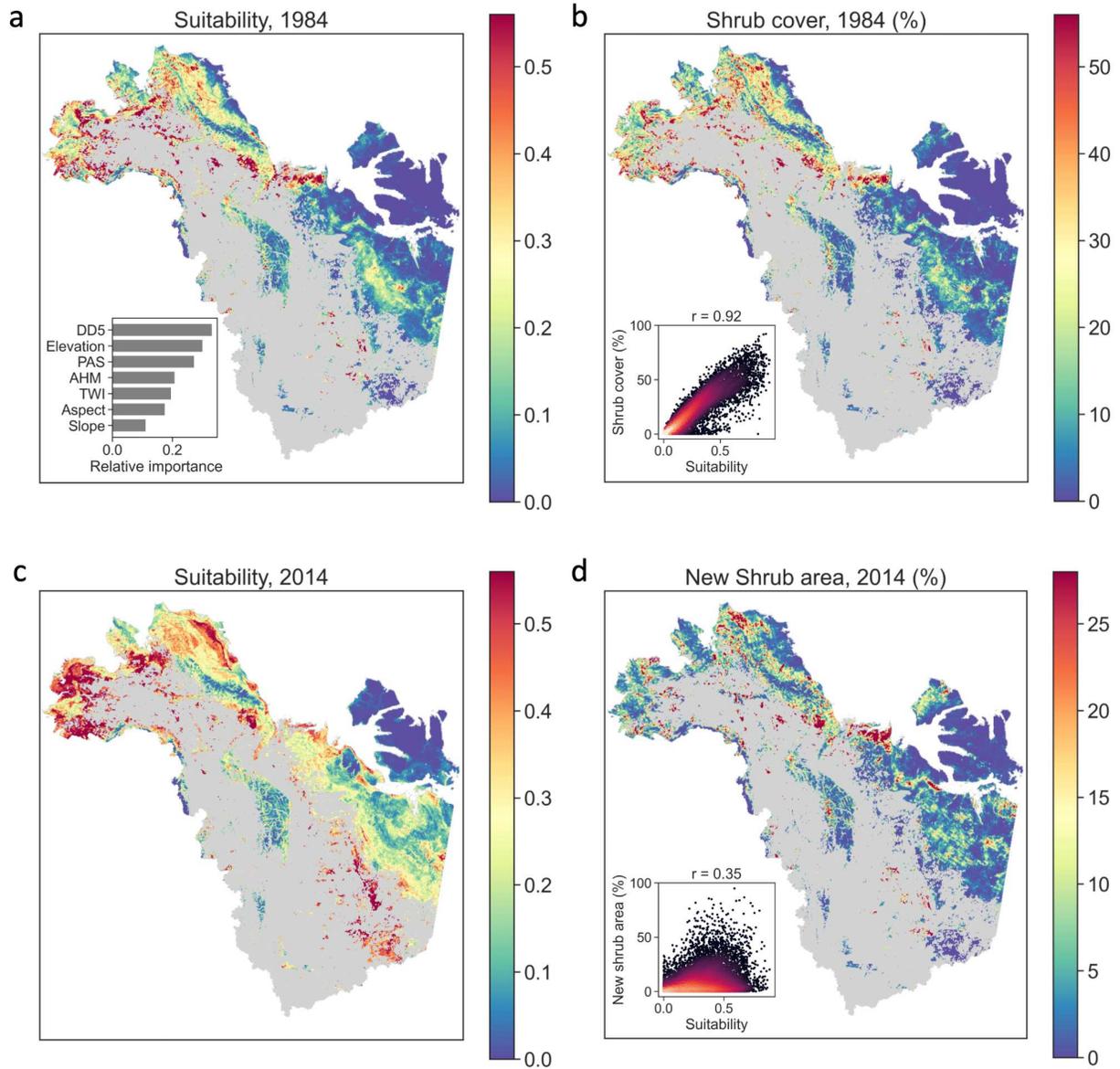
94 arrival probability, a measure of spatial proximity to existing shrub patches, was calculated  
95 through convolution of seed-dispersal kernels over 1984 shrub cover images. Given the variety  
96 of dispersal mechanisms, we considered both short- and long-distance dispersal kernels, and  
97 optimized the range and shape parameters to fit observed shrub expansion. The year and location  
98 of fires were obtained from a Landsat-derived annual burn scar product. We investigated  
99 individual and compound impacts of environmental suitability, seed dispersal, and fire  
100 occurrence on observed 1984-2014 shrub expansion. Based on the resulting sensitivities and the  
101 projection of bioclimatic conditions and fire from climate models, we estimated shrub expansion  
102 in 2040, 2070, and 2100, and explored the relative importance of suitability change, fire, and  
103 seed dispersal on projected shrub expansion.

104

### 105 **Environmental suitability of shrubs**

106 We first estimated bioclimatic and topographic suitability for shrubs as of 1984. Among the 27  
107 variables, the seven most informative variables, as identified based on variance inflation factors  
108 (Extended Data Table 1, Extended Data Fig. 1), were three bioclimatic variables (degree days  
109 above 5 °C, annual heat moisture index, and precipitation as snow) and four topographic  
110 variables (elevation, slope, aspect, and topographic wetness index). Based on the random forest  
111 model, degree days above 5 °C was the most important variable for suitability in 1984, followed  
112 by elevation and precipitation as snow (Fig. 1a). In terms of the direction and shape of response,  
113 higher suitability was associated with higher degree days above 5 °C, lower elevation, and higher  
114 precipitation as snow (Extended Data Fig. 2), although suitability responds to these variables  
115 nonlinearly across different combinations of climate and topographic conditions (Extended Data  
116 Fig. 3).

117 Suitability conditions in 1984 were higher in southwestern Alaska, eastern Seward  
118 Peninsula, and northern Northwest Territories of Canada, but lower on the northern edge of the  
119 North Slope of Alaska and northern Canada and mountainous regions such as the Brooks Range  
120 and the Mackenzie Mountains (Fig. 1a, reference locations noted in Extended Data Fig. 1c). This  
121 pattern of suitability was largely consistent with observed shrub distribution in 1984 ( $r = 0.92$ ,  
122 Fig. 1b), supporting the effectiveness of the suitability metric in describing the shrub-  
123 environment relationship under quasi-equilibrium conditions. Due to climate warming since  
124 1984, the domain became more suitable in 2014 on average, especially in southwestern Alaska,  
125 eastern Seward Peninsula, the North Slope, and the southeast of the domain (Fig. 1c). The area  
126 with high suitability ( $> 0.4$ ) increased from 13.4% to 28.3% of the region. However, these highly  
127 suitable regions experienced limited shrub expansion (Fig. 1d). Instead, hot spots of shrub  
128 expansion were found in the west of the North Slope and northwestern Canada. Across the entire  
129 domain, suitability was much less related to new (i.e., expanded) shrub area in 2014 ( $r = 0.35$ )  
130 than to existing shrub cover in 1984 ( $r = 0.92$ ). Accounting for different initial land cover types  
131 of the non-woody tundra and change of suitability also barely contributed to explaining the  
132 pattern of shrub expansion (Extended Data Fig. 4). These results suggest environmental  
133 suitability was not the major limiting factor of shrub expansion between 1984 and 2014.



134

135 **Fig. 1 | Suitability did not explain shrub expansion between 1984 and 2014.** Suitability of  
 136 shrubs in (a) 1984 and (c) 2014 estimated using topographic and bioclimatic conditions,  
 137 including annual degree-days above 5°C (DD5), annual degree precipitation as snow (PAS),  
 138 annual heat-moisture index (AHM), elevation, slope, aspect, and topographic wetness index  
 139 (TWI). The inset of (a) shows the relative importance of these factors on suitability. (b) Fraction  
 140 of shrub cover in 1984. (d) Fraction of new shrub area in 2014, i.e., non-shrub tundra in 1984

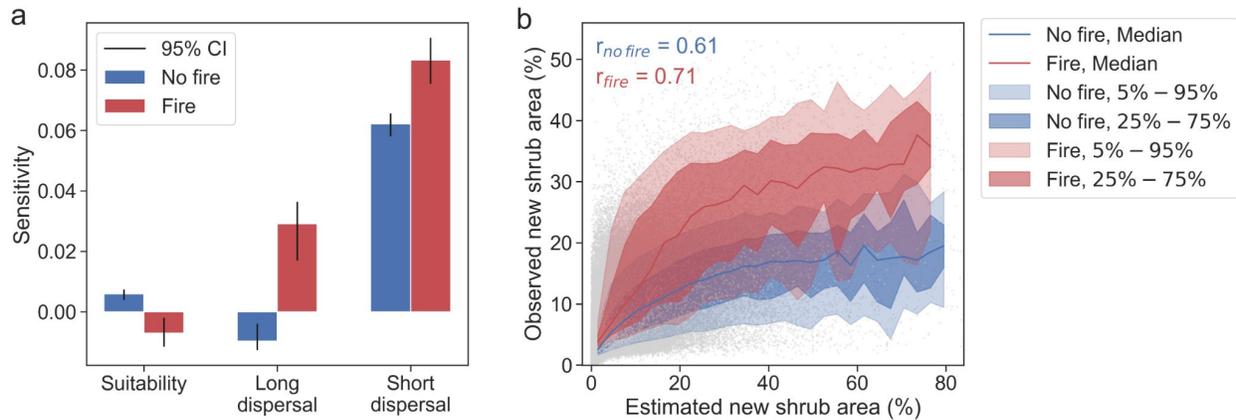
141 that became dominated by shrubs by 2014. The insets of (b) and (d) show the corresponding  
142 relationships with suitability, where brighter colors represent higher dot density.

143

#### 144 **Impacts of seed dispersal and fire**

145 The best-fitting long-distance dispersal was represented using a flat-tail kernel ( $c = 0.5$  in Eq. 1  
146 in Methods) with a range parameter of 39 km (Extended Data Fig. 5); and the short-distance  
147 dispersal was best represented using an exponential power kernel ( $c = 1.5$  in Eq. 1 in Methods),  
148 which is between an exponential kernel and a Gaussian kernel and has a range parameter of 600  
149 m. Notably, in regions not disturbed by fire, the area fraction of shrub expansion was the most  
150 sensitive to short-distance dispersal, 9.5 times more sensitive than to suitability based on the  
151 regression coefficients (Fig. 2a). The weak negative sensitivity to long-distance dispersal likely  
152 arose from the trade-off between the sensitivities to short- and long-distance dispersal, which  
153 might not be precisely separated based on the data due to their spatial correlation ( $r = 0.71$ ).  
154 However, both long- and short-distance dispersal became significantly more important in  
155 facilitating shrub expansion after fire, compared to areas without fire (Fig. 2a). The median of  
156 the sensitivities to long- and short-distance dispersal increased from -0.010 to 0.029 and from  
157 0.062 to 0.083, respectively, for areas that experienced fire; whereas the sensitivity to suitability  
158 reduced from 0.006 to -0.007. Across the entire domain, fire disturbance enhanced the likelihood  
159 of shrub expansion, especially in highly suitable areas with high seed arrival probability (Fig.  
160 2b). Accounting for seed arrival probability and suitability improved the estimation accuracy of  
161 shrub expansion from  $r = 0.35$  (Fig. 1d) to  $r = 0.61$  (areas with fire) and  $r = 0.71$  (areas without  
162 fire) (Fig. 2b). These findings show that, over recent decades, dispersal has been a stronger  
163 limiting factor than suitability on shrub expansion. Non-woody tundra locations becoming more

164 suitable is not sufficient for shrub expansion to occur. By contrast, fire disturbance and proximity  
 165 to existing shrub patches make shrub expansion more likely in the newly suitable areas.



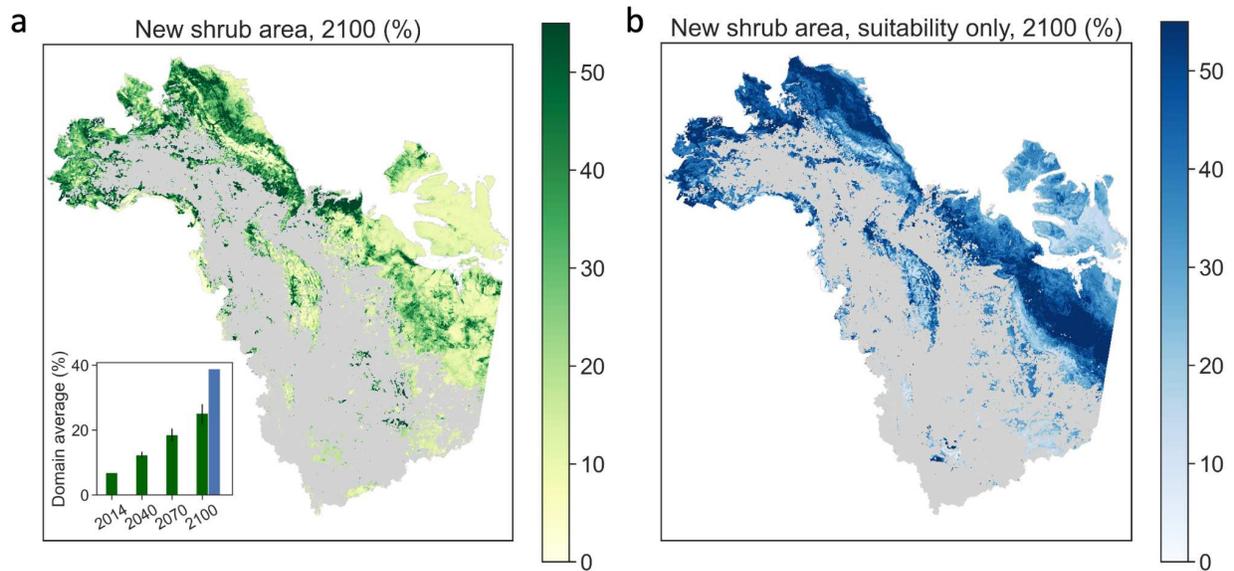
166  
 167 **Fig. 2 | Dispersal and fire explain shrub expansion during 1984-2014.** (a) Sensitivity of new  
 168 shrub area to suitability and probabilities of seed arrival via short- and long-distance dispersal at  
 169 locations with (red bars) and without (blue bars) fire. Vertical black lines denote the range of the  
 170 95% confidence interval of the regression coefficients across optimal dispersal kernel  
 171 parameters. (b) Observed and estimated new shrub area in 2014 at locations with (red) and  
 172 without (blue) fire. The lines and shaded bands represent the medians and ranges of observed  
 173 new shrub area (grey dots) for each bin of estimates with a width of 2%.

174

### 175 Predicted shrub expansion

176 Across the domain, 6.8% of non-shrub tundra in 1984 had become dominated by shrubs by 2014.  
 177 Using our established relationships (Fig. 2), we estimated that the shrubified area fraction would  
 178 increase progressively to  $25.1\% \pm 3.0\%$  by 2100 (Fig. 3a, Extended Data Fig. 6) corresponding  
 179 to  $253,651 \pm 30,317$  km<sup>2</sup> more shrub cover than in 2014, with the uncertainty originating from  
 180 uncertainty in the empirically derived sensitivities (Fig. 2a). The results suggest substantial shrub  
 181 expansion in southwestern Alaska, southern and eastern Seward Peninsula, south and north of

182 the Brooks Range, and northern Northwest Territories of Canada. The Victoria Island, western  
183 Nunavut, the Brooks Range, and the Mackenzie Mountains will likely experience limited shrub  
184 expansion. Note that projected shrub expansion estimated here originates from the combined  
185 impacts of suitability under projected climate change, seed dispersal, and projected burn area.  
186 The resulting pattern (Fig. 3a) does not account for shrub loss due to competition, pests, and  
187 herbivores, which requires future work to better characterize loss mechanisms. By contrast,  
188 without considering the impact of dispersal and fire, the relationship between shrub presence and  
189 increased suitability alone (Fig. 1a, b) predicts a higher fraction (38.9%) of non-shrub tundra in  
190 1984 will become shrublands by 2100. Notably, the shrub expansion pattern predicted using  
191 suitability alone shows substantial increase of shrub cover in the North Slope and northern  
192 Canada (Fig. 3b), which is significantly different from the expansion if dispersal and fire  
193 limitations are considered (Fig. 3a). Thus, relying on environmental suitability alone likely  
194 results in predictions that overestimate shrub expansion and misrepresent the spatial patterns. As  
195 a result, observational studies and models that project shrub expansion without considering the  
196 biological and physical constraints of dispersal and fire likely overestimate the 21<sup>st</sup> century  
197 carbon sink in Arctic tundra due to shrub responses to warming.



198

199 **Fig. 3 | A quarter of non-woody tundra in 1984 will be colonized by shrubs by 2100.** Spatial

200 pattern of new shrub area in 2100 predicted using (a) suitability, dispersal and fire, and (b)

201 suitability alone. The inset of (a) shows the domain average of new shrub area predicted with

202 (green bars) and without (blue bar) considering dispersal and fire. The vertical black lines

203 illustrate the uncertainty due to uncertainty of the estimated sensitivities, i.e., vertical black lines

204 in Fig. 2a. Using suitability alone overestimates shrub expansion and misrepresents the spatial

205 pattern.

206

### 207 **Relative impact of suitability, fire, and dispersal**

208 We investigated the spatial patterns of projected changes in suitability, burn area, and seed

209 arrival probability in 2100, and used synthetic scenarios, i.e., turning-off on factor at a time, to

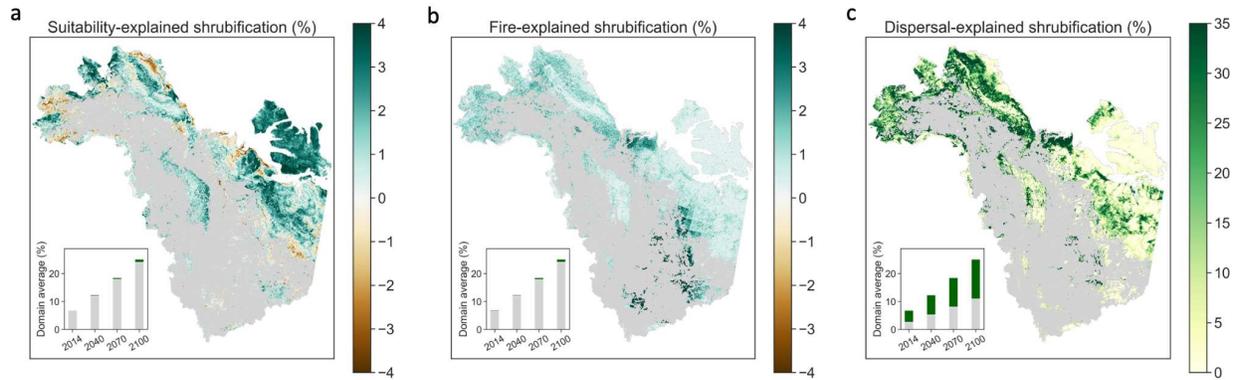
210 disentangle their individual impacts on projected shrub expansion shown in Fig. 3 (see Methods).

211 Compared to 1984, suitability in 2100 increased in most of the region due to climate warming,

212 although it decreased in some low elevation areas experiencing reduced snow inputs (Extended

213 Data Fig. 7a). Suitability change had a spatially heterogeneous impact on shrub expansion, i.e.,

214 increasing in most areas but decreasing in parts of southwestern Alaska, the North slope, and  
215 northern Canada. Given the low sensitivity of shrub expansion to suitability (Fig. 2a) and the  
216 spatial compensation, the net result of suitability changes was small averaged across the region  
217 (~1%) by 2100. Fires burned 3.2% of the area during 1984-2014, which was projected to  
218 increase to 7% during 2070-2100 based on the CMIP6 ensemble average. Burn area in CMIP6  
219 models was mostly concentrated in the southeast (Extended Data Fig. 7b), which had limited  
220 impact on shrub expansion due to low initial shrub cover and thus seed arrival probability in that  
221 region (Extended Data Fig. 7c). In the majority of Alaska and northern Canada the burn area was  
222 projected to be close to zero until the end of the 21<sup>st</sup> century. As a result, although areas  
223 disturbed by fire were found more likely to experience shrub expansion (Fig. 2), projected fire  
224 only contributed one percentage point out of the 25% shrub expansion by 2100, equivalent to the  
225 impact of projected suitability change (Fig. 4b). The spatial pattern of seed arrival probability  
226 mostly followed existing shrub cover, i.e., high in the majority of Alaska and middle of the  
227 Northwest Territories in Canada, and low in coastal regions of Alaska, and southeast and north  
228 of the Northwest Territories (Extended Data Fig. 7c). Dispersal largely explained shrub  
229 expansion in these regions (Fig. 4c). Notably, although the Brooks Range had moderate seed  
230 arrival probability (Extended Data Fig. 7c), shrubs were found unlikely to expand into this region  
231 (Fig. 3) due to the limitation of low suitability (Fig. 1c, Extended Data Fig. 7), highlighting the  
232 compound impact of suitability and seed dispersal. Across the domain, seed dispersal explained  
233 14% out of the 25% shrubified tundra from 1984 to 2100 (Fig. 4c). Given the dominant control  
234 of seed dispersal on the spatial pattern of shrub expansion, omitting dispersal likely leads to mis-  
235 represented shrub cover change.



236

237 **Fig 4 | Shrub expansion over the 21<sup>st</sup> century was primarily attributed to seed dispersal.**

238 Shrub expansion driven by (a) suitability change from 2014 to 2100, (b) projected fire and (c)  
 239 short- and long-distance seed dispersal. The insets show the domain average of shrub expansion  
 240 from 2014 to 2100; the grey sections show shrub expansion in a scenario where the  
 241 corresponding factor was turned off and the green sections represent its contribution.

242

243 **Discussion and implications**

244 Climate warming has made the Arctic tundra substantially more suitable for shrubs over recent  
 245 decades. However, we demonstrate that more suitable areas do not necessarily experience more  
 246 extensive shrub expansion, which, instead, is found in areas close to existing shrub patches  
 247 and/or disturbed by fire. In contrast to previous findings that suggest a stronger limitation of  
 248 environmental suitability than seed dispersal over the past millennia<sup>39</sup>, the results here indicate  
 249 dispersal processes limit shrub expansion over recent decades. Our findings provide  
 250 observational evidence for the importance of seed dispersal in Arctic shrub expansion under  
 251 rapid warming as the ecosystem deviates from its historical equilibrium. The fact that shrubs did  
 252 not expand into all suitable areas implies shrub establishment might not have kept up with the  
 253 pace of recent climate change. In the scenario where suitability is kept the same as in 2014  
 254 through 2100, shrub cover is still predicted to substantially increase across the domain (grey bars

255 in Fig. 4a). Therefore, shrubs will likely continue to expand across the Arctic tundra, even under  
256 a net-zero emission scenario, where global warming will be limited to 1.5 °C by 2050 and  
257 stabilized by 2100<sup>50</sup>.

258         Complex ecosystem processes introduce uncertainties in predicted suitability, identified  
259 shrub expansion, and the relationship to seed dispersal and fire disturbance. Uncertainties related  
260 to future suitability can be influenced by future bioclimatic conditions exceeding the historical  
261 ranges used to establish their relationships with suitability (Extended Data Fig. 8). For example,  
262 nutrient availability could increase much faster with temperature in a warmer climate due to an  
263 exponential increase of N mineralization rate and deepening active layer<sup>43</sup>. Thus, the data-driven  
264 suitability model trained using historical data could underestimate future suitability. However,  
265 mechanistic models could contribute to addressing such uncertainties. Shrub expansion was  
266 identified based on remotely-sensed shrub dominance at a 30 m scale and over 30 years<sup>3</sup>,  
267 therefore it may not precisely distinguish the underlying causes of seed dispersal and emergence  
268 of pre-existing shrubs<sup>3,9</sup>. However, because shrub emergence is expected to be controlled by  
269 environmental suitability, the low impact of suitability supports seed dispersal being the  
270 dominant cause of shrub expansion across the domain. Moreover, as dispersal is estimated based  
271 on spatial proximity, our results highlight the importance of spatially connected processes.  
272 Although seed dispersal is the originating mechanism and has been recognized as a dominant  
273 spatial process controlling vegetation range shifts<sup>33–37</sup>, the impact of spatial proximity identified  
274 here might also be partially attributed to other spatially connected factors, such as active layer  
275 depth, soil thermal-hydro conditions, surface litter, nutrient availability, and herbivore  
276 activities<sup>51–54</sup>. These factors may contribute to the spatial connectivity of shrub expansion via  
277 rates of seed germination and seedling establishment. However, these factors are unlikely to be

278 the dominant explanation for the identified impact of spatial proximity, as they are partially  
279 related to suitability via climate and topographic conditions, and they tend to exhibit smaller  
280 spatial ranges than those identified for long-distance dispersal (~40 km). Field surveys and  
281 measurements are required to investigate the confounding roles of these spatial processes.

282         Although fires can either enhance or inhibit plant regeneration depending on local soil  
283 and climate conditions<sup>25</sup>, our results suggest fire enhances shrub expansion where it does occur,  
284 consistent with palaeoecological studies<sup>42</sup> and model simulations<sup>43,55</sup> across a large scale. The  
285 strong compounding effect of fire and seed dispersal on shrub expansion (Fig. 2) highlights that  
286 fire promotes shrub expansion especially at locations close to preexisting shrub patches, where  
287 seeds are more likely to arrive and establish after fire. Because fire is projected to be rare in the  
288 Arctic tundra based on climate models, we find it only marginally contributes to shrub expansion  
289 by 2100. However, a recent study suggests lightning in Arctic tundra, the dominant source of  
290 burning<sup>56</sup>, will significantly increase to a rate similar to that in boreal forests<sup>16</sup>. Lightning-driven  
291 fire increases could trigger positive vegetation-fire feedbacks, leading to twofold more burn area  
292 by 2100 than the ensemble average of CMIP6 models (Extended Data Fig. 9)<sup>16,57</sup>. Therefore, fire  
293 likely exerts greater impacts on shrub expansion compared to the estimates here when  
294 considering these positive feedbacks, though further investigation is required to constrain the  
295 large uncertainty (Extended Data Fig. 9). As post-fire regeneration strongly controls how much  
296 fire-induced carbon loss is attenuated<sup>17</sup>, future work on the strength and spatial heterogeneity of  
297 the feedback between fire and shrub expansion will contribute to a better assessment of carbon  
298 budget in Arctic tundra.

299         Our results highlight that predicting shrub expansion cannot be based on climate alone.  
300 Models that do not account for fire disturbance and seed dispersal may misrepresent future shrub

301 cover. In Earth system models, seed production and dispersal have been recognized as the most  
302 under-developed vegetation demographic processes<sup>58</sup>. Representing seed dispersal, especially  
303 over long distances, requires seed transport across spatially discretized grids, which does not  
304 exist in most land models. Improved representation of seed dispersal therefore could contribute  
305 to better prediction of vegetation shifts. In addition to the factors investigated here, shrub  
306 expansion is also modulated by species competition for water, nutrients, and light<sup>59-61</sup>. Recent  
307 observational evidence suggests climate change can result in different competitive abilities  
308 across species due to divergent shifts of plant functional traits in Arctic tundra<sup>62-64</sup>, highlighting  
309 the potential of employing dynamic vegetation models that explicitly represent competition.  
310 These findings motivate improving process-based representations of seed dispersal, fire  
311 disturbance, and species competition in dynamic vegetation models as a fundamental component  
312 to better prediction of Arctic shrub change and corresponding climate feedbacks.

313 **Methods**

314 **Datasets**

315 Shrub expansion was identified based on the Landsat-derived product of annual dominant land  
316 cover across ABoVE core domain from 1984 to 2014<sup>65</sup>. The dataset provides annual dominant  
317 plant functional type at a 30 m resolution derived from Landsat surface reflectance, very high  
318 resolution imagery, and field photography across the ABoVE domain. We focused on pixels  
319 dominated by shrubs and non-woody species, i.e., excluding boreal forests. Pixels consistently  
320 classified as shrublands during 1984-1986 and 2012-2014 were considered as shrub cover in  
321 1984 and 2014, minimizing the uncertainty of noise in annual time series of land cover types.  
322 New shrub area was identified as pixels that had been dominated by non-woody species in 1984  
323 and became dominated by shrubs in 2014. We used climate and topographic conditions to  
324 estimate environmental suitability for shrublands. The climate conditions came from  
325 ClimateNA<sup>66</sup>, a product locally downscaled for North America at a 4 km resolution. The  
326 historical data (1955-2014) was downscaled from the gridded Climatic Research Unit Time-  
327 series data version 4.02 (CRU TS4.02), and the projected data (2014-2100) was downscaled  
328 from CMIP5 under the RCP8.5 scenario. The elevation data was obtained from the Advanced  
329 Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation  
330 Model Version 3 with a 30 m resolution<sup>67</sup>. Slope, aspect, and the topographic wetness index  
331 were derived from elevation using a terrain analysis software RichDEM<sup>68</sup>. Fire occurrence  
332 during 1985-2009 was identified using the annual product of differenced Normalized Burned  
333 Ratio (dNBR) at a 30 m resolution<sup>69</sup>, where the perimeters came from the Alaskan Interagency  
334 Coordination Center and the Natural Resources Canada fire occurrence datasets. Only fires that  
335 occurred at least 5 years prior to 2014 were considered to allow vegetation recovery. Burn area

336 during 2015-2100 was obtained from CMIP6 projections under a SSP585 scenario. Datasets at  
337 coarse resolutions (climate and projected burn area) were resampled to a 30 m resolution using  
338 the nearest neighbour method.

339

#### 340 **Estimation of environmental suitability**

341 We considered 23 bioclimatic variables (Extended Data Table 1) and 4 topographic conditions,  
342 i.e., elevation, slope, aspect, and topographic wetness index. To reduce the risk of overfitting, we  
343 identified the most informative variables based on the variance inflation factor, which measures  
344 the multicollinearity among the explanatory variables. Starting from all 27 variables, we  
345 excluded the variable with the highest variance inflation factor, i.e., the variable that can be best  
346 represented by a linear combination of other variables, one at a time, until the variance inflation  
347 factors of all variables are below the commonly used threshold of five<sup>70</sup>. This procedure ensured  
348 that the identified variables are most statistically informative in representing the bioclimatic and  
349 topographic conditions across the domain. Based on the identified variables, we applied 10  
350 species distribution models to estimate whether a pixel was shrubland. The models include  
351 generalized linear model, generalized additive model, boosted regression trees, classification tree  
352 analysis, artificial neural network, surface range envelope, flexible discriminant analysis,  
353 multiple adaptive regression splines, random forest, and maximum entropy, all applied using the  
354 *biomod2*<sup>71</sup> software in R<sup>72</sup>. Due to the large computation load, we trained each model using 5%  
355 of the pixels randomly selected within the target area, including both shrub and non-shrub pixels.  
356 The model accuracies were evaluated using all pixels across the entire domain. The random  
357 forest model had the highest accuracy based on the true skill statistic and the area under the  
358 receiver operating characteristic curve. Therefore, the environmental suitability, i.e., the

359 probability of a given 30 m pixel being shrubland given its bioclimatic and topographic  
360 conditions, was calculated using only the random forest model. We assumed a relatively stable  
361 climate prior to 1984. Thus, the average bioclimatic conditions during 1955-1984 were used to  
362 train the random forest model and assess suitability in 1984. Suitability in 2014, 2040, 2070, and  
363 2100 were estimated by replacing the bioclimatic conditions to the averages over the previous 30  
364 years, respectively. We evaluated the relative importance of each variable in explaining  
365 suitability. We also analyzed the response curve of suitability to the variation of each variable,  
366 and the response surfaces to the covariation of the most important three variables, while setting  
367 other variables as the domain average.

368

### 369 **Seed arrival probability**

370 The impact of seed dispersal was quantified using the probability of seed arrival at a given  
371 location, calculated using kernel convolution over the spatial pattern of shrublands. The  
372 following exponential power kernel was used to describe the relationship between seed arrival  
373 probability and distance to parent shrub patches.

$$374 \quad k(x_i) = \frac{b}{2\pi a^2 \Gamma(2/b)} \exp\left(-\left(\frac{x_i}{a}\right)^b\right) \quad (1)$$

375 where  $x_i$  is the distance to the  $i$ th shrubland pixel within a maximum range, which is considered  
376 as the distance where the kernel function first falls below  $10^{-9}$ ;  $a$  and  $b$  are the range and shape  
377 parameters, respectively. Large  $a$  represents high seed arrival probability from distant parent  
378 shrub patches and vice versa. Large  $b$  denotes a fast decay rate of seed arrival probability with  
379 distance and vice versa. The exponential power kernel is a generalized form of the Gaussian ( $b =$   
380 2), exponential ( $b = 1$ ), and flat-tailed ( $b = 0.5$ ) kernels, and has been widely used in literature<sup>73</sup>.

381 The seed arrival probability of a given location ( $s$ ) is calculated as follows:

382 
$$p(s) = \frac{I}{P_{\max}} \sum_{i=1}^N k(x_i) \Delta x \quad (2)$$

383 where  $N$  is the total number of shrub pixels within the maximum range;  $\Delta x = 30$  m is the width  
384 of a pixel; and  $P_{\max}$  is the normalization factor such that  $p(s) = I$  when the location is  
385 completely surrounded by shrublands within the maximum range. The seed arrival probability  
386  $p(s)$  measures the spatial proximity to existing shrublands. Assuming the same seed production  
387 of all shrublands, the seed arrival probability  $p(s)$  is also proportional to the expectation of the  
388 arriving seed amount. Based on the shrub cover in 1984, we calculated the seed arrival  
389 probability during 1984-2014 using the above described algorithm implemented in the  
390 multidimensional image processing software of *scipy.ndimage*<sup>74</sup>. To account for various  
391 dispersal vectors<sup>32</sup>, we considered both short-distance and long-distance dispersal kernels. For  
392 short-distance dispersal, we evaluated all combinations of  $100 \text{ m} \leq a \leq 1000 \text{ m}$  with an interval  
393 of 100 m and  $0.5 \leq b \leq 2.5$  with an interval of 0.5. For long-distance dispersal, we evaluated all  
394 combinations of  $1 \text{ km} < a \leq 60 \text{ km}$  with an interval of 2 km and  $0.5 \leq b \leq 2.5$  with an interval of  
395 0.5. We identified the parameters that resulted in the best 5% accuracy in estimating shrub  
396 expansion during 1984-2014.

397

### 398 **Sensitivity of observed shrub expansion to control factors**

399 Observed shrub expansion was quantified as the fraction of 30 m pixels that were not identified  
400 as shrublands in 1984, i.e., non-shrub tundra, but became shrublands in 2014 within each 4 km  
401 by 4 km gridcell. Suitability and seed arrival probabilities through short- and long-distance  
402 dispersal were aggregated by average to a 4 km scale and used to explain the spatial pattern of  
403 shrub expansion using multivariate linear regression. We calculated the regression accuracy and  
404 the sensitivities (regression coefficients) to the z-scores of the explanatory variables for gridcells

405 with and without fire occurrence, respectively. The 95% confidence intervals of the sensitivities  
406 were estimated.

407

#### 408 **Prediction of shrub expansion by 2100**

409 Based on the estimated empirical relationships, we predicted shrub expansion by 2040, 2070, and  
410 2100. For each 30-year period, suitability was estimated using topographic conditions and the  
411 averages of projected bioclimatic conditions. Seed arrival probability was estimated using shrub  
412 cover at the start of the period. Fire was assigned for each 30 m pixel with a probability  
413 represented by the cumulative burn area fraction, ensuring the aggregation from a 30 m scale  
414 consistent with the climate model projection at a coarser scale. Each non-shrub pixel at the start  
415 of the 30-year period was changed to shrubland at the end with a probability calculated using the  
416 estimated sensitivities to its suitability, seed arrival probability, and fire occurrence. We further  
417 quantified the uncertainty of projected shrub expansion due to the uncertainty in the estimated  
418 sensitivities. Instead of a computationally expensive bootstrapping approach, we used the lower  
419 and upper boundaries of the 95% confidence intervals for all the regression coefficients in each  
420 30-year period, which provided an overestimate of the uncertainty range of projected shrub  
421 expansion. To disentangle the impacts of suitability change, seed dispersal, and fire on the  
422 projected shrub expansion, we used synthetic scenarios where each of the three factors was  
423 turned off, i.e., suitability kept the same as in 2014, zero seed arrival probability, and no fire  
424 occurrence, respectively. The difference between the synthetic scenarios and the actual  
425 projection illustrated the contribution of the corresponding factor on the projected shrub  
426 expansion. To diagnose potential bias and spatial patterns of predicted shrub expansion using the  
427 suitability-based approach in previous studies, the shrub expansion by 2100 predicted here was

428 also compared to the prediction without considering dispersal and fire, i.e., by applying 2100  
429 suitability to the relationship established between shrub presence and suitability alone in 1984.

430

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600 **Extended Data**

601 **Extended Data Table 1 | The Full set of candidate climate variables.** Details of each variable

602 were described in Wang et al. (2016).

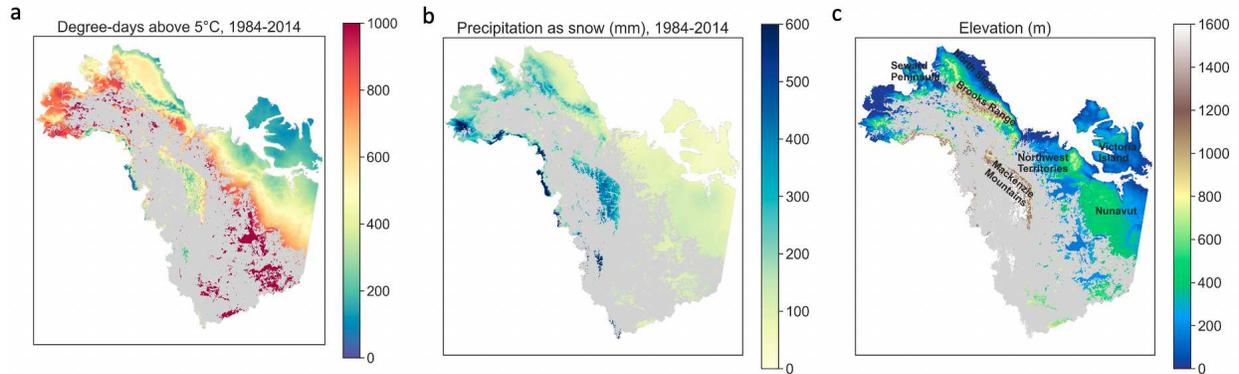
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**Variable name and unit**

---

- Mean annual temperature (°C)
  - Mean warmest month temperature (°C)
  - Mean coldest month temperature (°C)
  - Temperature difference between MWMT and MCMT, or continentality (°C)
  - Mean annual precipitation (mm),
  - May to September precipitation (mm),
  - Annual heat-moisture index  $(MAT+10)/(MAP/1000)$
  - Summer heat-moisture index  $((MWMT)/(MSP/1000))$
  - Degree-days below 0°C, chilling degree-days
  - Degree-days above 5°C, growing degree-days
  - Degree-days below 18°C, heating degree-days
  - Degree-days above 18°C, cooling degree-days
  - Number of frost-free days
  - Frost-free period
  - The day of the year on which FFP begins
  - The day of the year on which FFP ends
  - Precipitation as snow (mm). For individual years, it covers the period between August in the previous year and July in the current year.
  - Extreme minimum temperature over 30 years
  - Extreme maximum temperature over 30 years
  - Hargreaves reference evaporation (mm)
  - Hargreaves climatic moisture deficit (mm)
  - Mean annual solar radiation ( $MJ\ m^{-2}\ d^{-1}$ )
  - Mean annual relative humidity (%)
- 

603



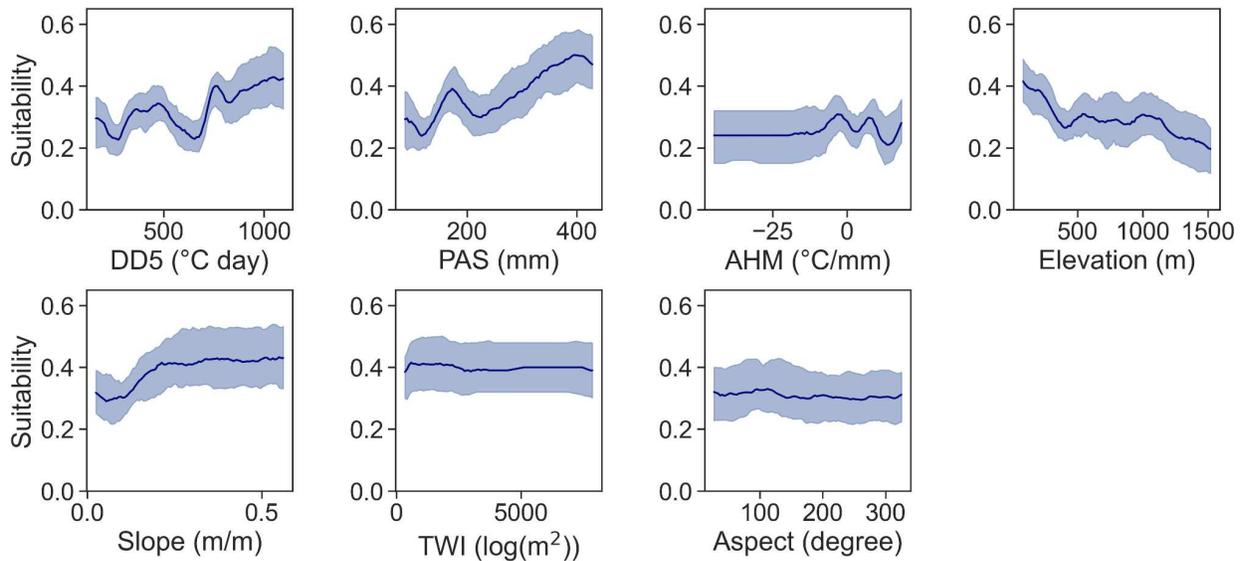
604

605 **Extended Data Fig. 1 | Spatial patterns of the dominant climate and topographic conditions**

606 **on environmental suitability.** Average (a) degree-days above 5 °C and (b) precipitation as

607 snow during 1984-2014. (c) Elevation across the domain, illustrated using a 4 km resolution.

608



609

610 **Extended Data Fig. 2 | Response curve of suitability to climate and topographic conditions.**

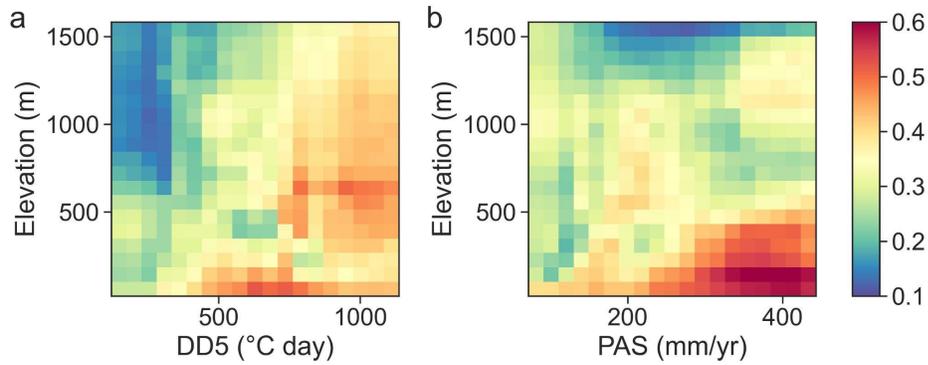
611 The conditions include annual degree-days above 5 °C (DD5), annual precipitation as snow

612 (PAS), annual heat-moisture index (AHM), elevation, slope, topographic wetness index (TWI),

613 and aspect. The line and shaded band in each panel show the median and 5%-95% uncertainty

614 range uncertainty across 100 random forest runs.

615

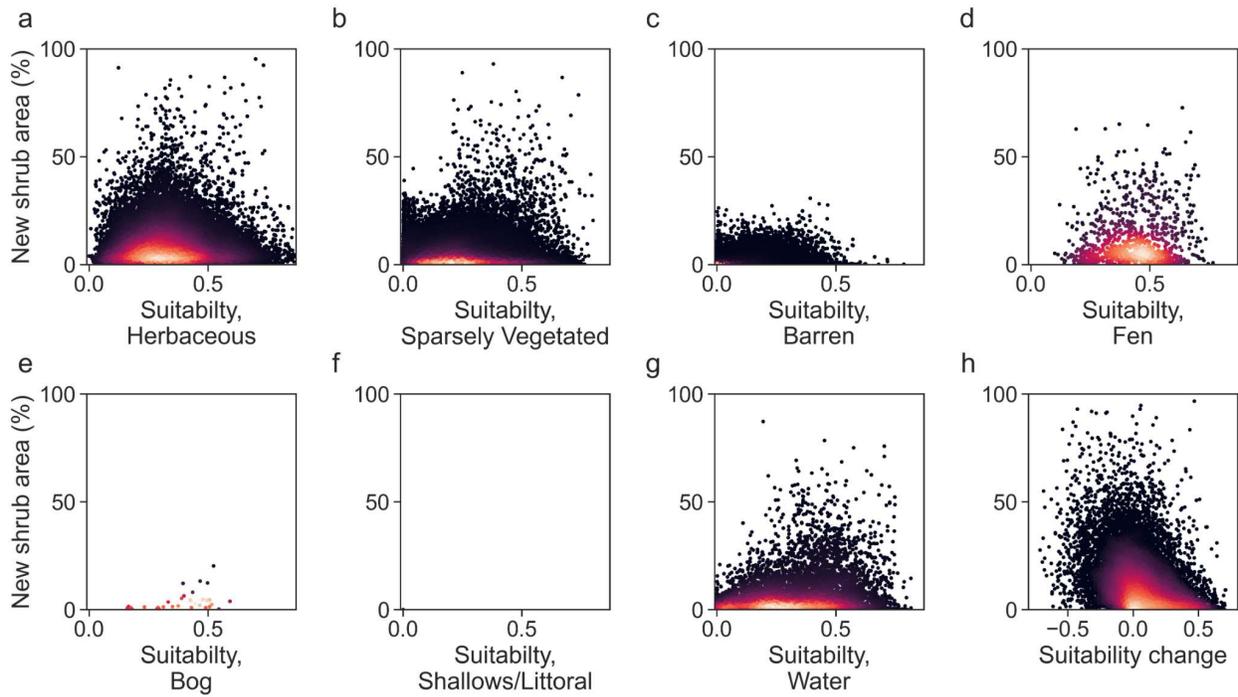


616

617 **Extended Data Fig. 3 | Response surface of suitability to annual degree-days above 5 °C**

618 **(DD5), annual precipitation as snow (PAS), and elevation.**

619

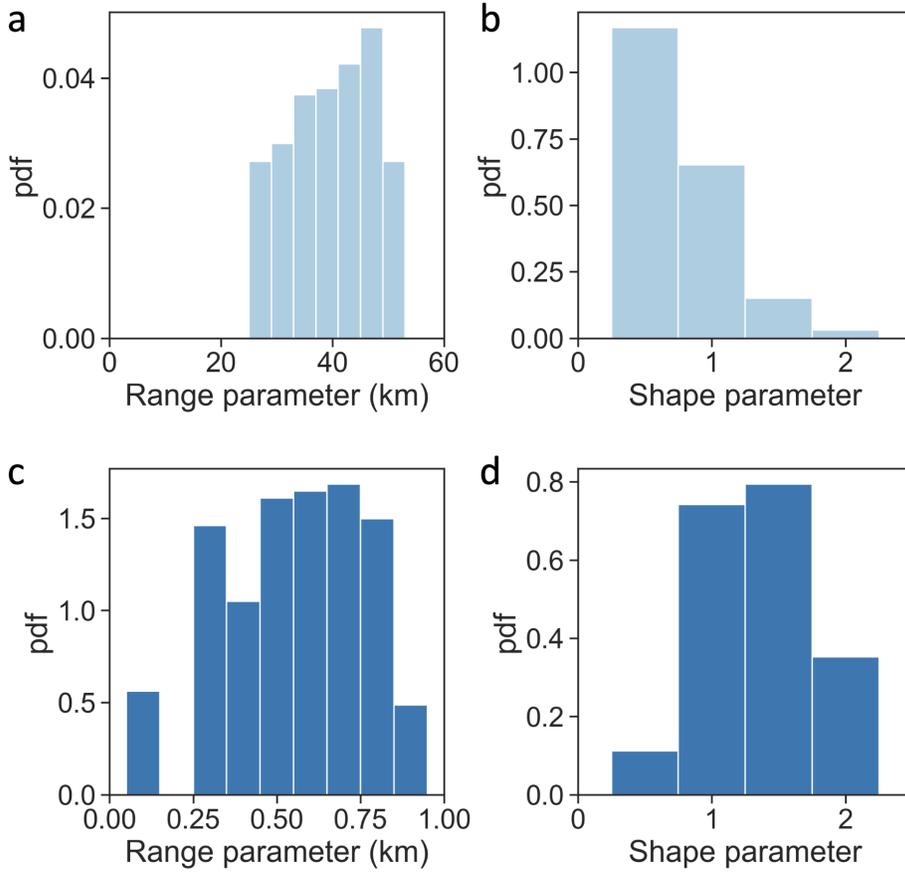


620

621 **Extended Data Fig. 4 | Relationships of new shrub area in 2014 with suitability in different**

622 **initial land cover types in 1984, and with suitability change between 1984-2014.**

623



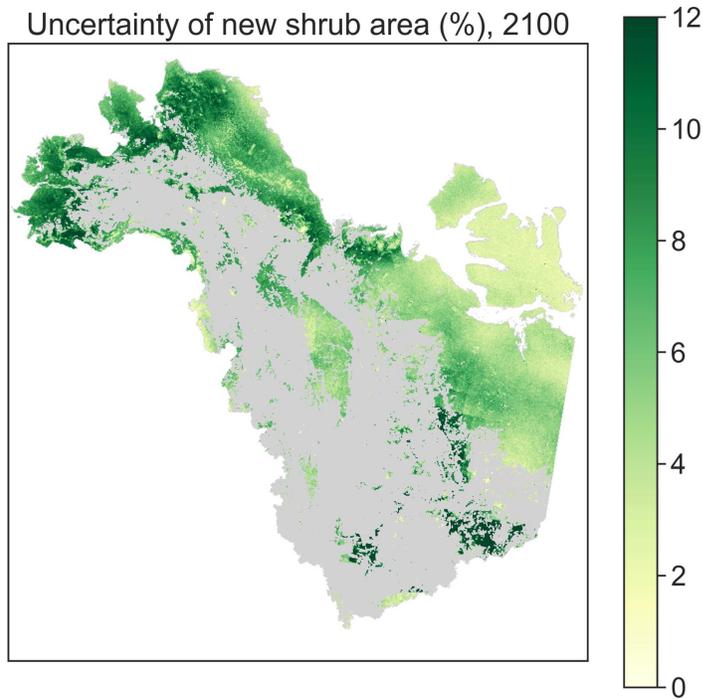
624

625 **Extended Data Fig. 5 | Probabilistic distributions of the seed dispersal kernel parameters**

626 **across the top 5% ensembles that match with observation.** Parameters of the (a, b) long-

627 distance and (c, d) short-distance dispersal kernels.

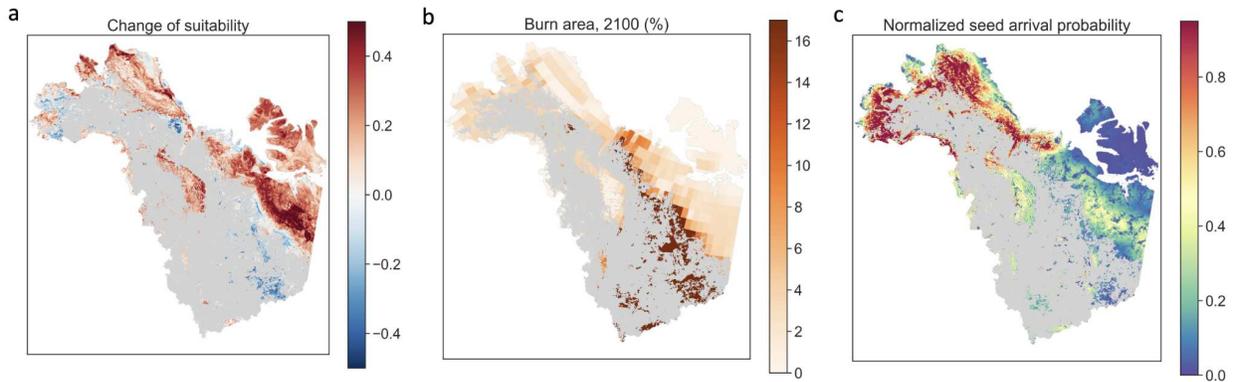
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630 **Extended Data Fig. 6 | Uncertainty range of estimated new shrub area in 2100.**

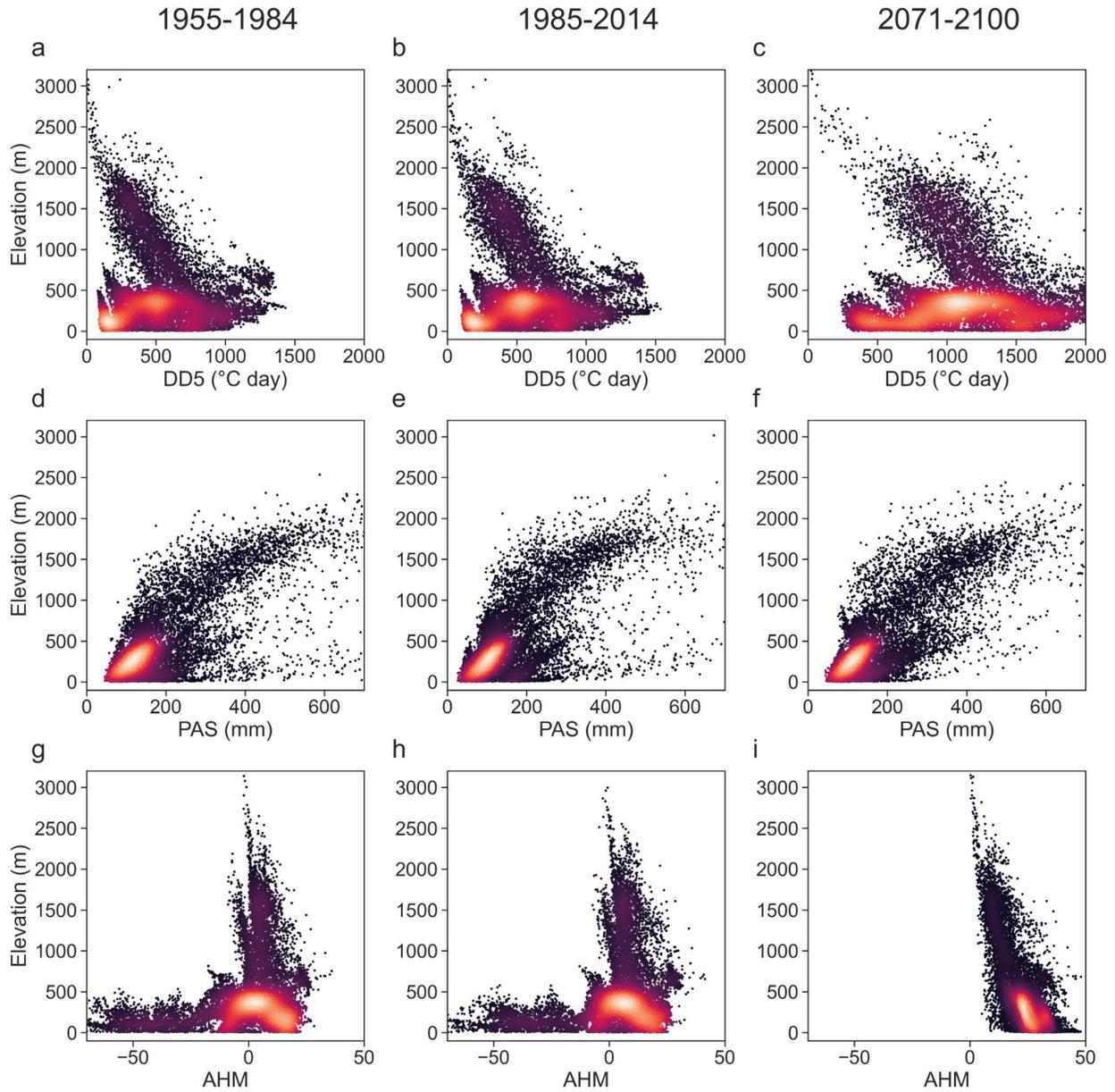
631



632

633 **Extended Data Fig. 7 | Spatial patterns of suitability change from 2014 to 2100, 30-year**  
 634 **cumulative burn area by 2100 projected in CMIP6, and seed arrival probability. Seed**  
 635 **arrival probability includes both short and long distance dispersal and is normalized to the scale**  
 636 **of 0-1.**

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639 **Extended Data Fig. 8 | Historical and projected bioclimatic conditions and elevation across**

640 **the domain.** Joint distribution of (a-c) degree-days above 5°C and elevation, (d-f) annual

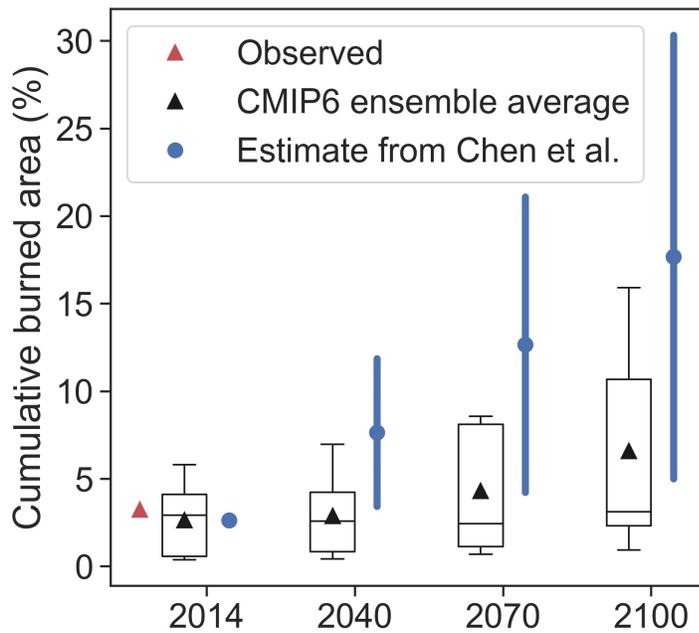
641 precipitation as snow and elevation, (g-i) annual heat moisture index and elevation during (a, d,

642 g) 1955-1984, (b, e, h) 1985-2014, and (c, f, i) 2071-2100. Brighter colors represent higher point

643 density.

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647 **Extended Data Fig. 9 | Domain average of observed and projected 30-year cumulative burn**

648 **area from 2014 to 2100 based on CMIP6 and Chen et al. (2021).** Red triangle shows the

649 domain average of the observed burn area during 1984-2014. Black triangles denote the

650 ensemble average , the upper and lower boundaries of the boxes correspond to the 25th and 75th

651 quantiles, and the whiskers show the range of projections across CMIP6 models. Blue dots and

652 vertical lines represent the predicted mean and uncertainty of burn area in 2100, linearly

653 interpolated from 2014 to 2100, based on Chen et al. (2021) where vegetation-fire feedback was

654 considered.

655

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [codeanddemoinputdata.docx](#)