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1 **Running Title:** Climate and shrubline advance

2

3 **Climate warming as a driver of tundra shrubline advance**

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6

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12

13 *Key-words.* shrub, alpine, tundra, high-latitude, range expansion, recruitment, age distributions,
14 climate, willow (*Salix*), Yukon

15

16 *Tweetable Abstract.* Shrubs advance into northern alpine tundra as climate warms: summer
17 temperature influences growth; winter temperature influences recruitment

18

19 **Summary**

20 1. Climate warming is predicted to alter ecological boundaries in high-latitude ecosystems
21 including the elevational or latitudinal extent of tall shrubs in Arctic and alpine tundra. Over
22 60 studies from 128 locations around the tundra biome have investigated shrub expansion in
23 tundra ecosystems; however, only six studies test whether shrublines are actually advancing
24 up hill-slopes or northward into tundra where tall shrubs are currently absent.

25

- 26 2. We test the hypothesis that willow shrublines have expanded to higher elevations in relation
27 to climate across a 50 x 50 km area in the Kluane Region of the southwest Yukon Territory,
28 Canada by surveying of 379 shrubs at 14 sites and sampling of 297 of the surveyed shrubs at
29 10 sites. We compared growth and recruitment to climate variables to test the climate
30 sensitivity of shrub increase using annual radial growth analysis, age distributions and repeat
31 field surveys to estimate the current rate of shrubline advance.
- 32
- 33 3. We found consistent and increasing rates of recruitment of alpine willows, with estimates of
34 faster advancing shrublines on shallower hill-slopes. Mortality was extremely low across the
35 elevation gradient. Aspect, elevation and species identity did not explain variation in
36 recruitment patterns, suggesting a regional factor, such as climate, as the driver of the
37 observed shrubline advance.
- 38
- 39 4. Annual radial growth of willows was best explained by variation in summer temperatures,
40 and recruitment pulses by winter temperatures. Measured recruitment rates are $\sim 20 \pm 5$
41 individuals per hectare per decade (mean \pm SE) and measured rates of increased shrub cover
42 of $\sim 5 \pm 1$ % per decade (mean \pm SE) measured at the Pika Camp site between field surveys
43 in 2009 and 2013. Our results suggest that shrubline will continue to advance over the next
44 50 years, if growing conditions remain suitable. However, if future conditions differ
45 between summer and winter seasons, this could lead to contrasting trajectories for
46 recruitment versus growth, and influence the vegetation change observed on the landscape.

47

48 *Synthesis.* Our findings in the context of a review of the existing literature indicate that elevational
49 and latitudinal shrublines, like treelines, are advancing in response to climate warming; however,
50 the trajectories of change will depend on the climate drivers controlling recruitment versus growth.

51 **Introduction**

52 Species distributions are expected to track climate at the global scale (Gaston 2009), and tundra
53 ecosystems are an excellent place to test for climate-induced range expansion, as the tundra biome
54 is climate constrained and experiencing the most rapid change of any terrestrial biome on the planet
55 (Post *et al.* 2009). Climate warming has already altered ecological boundaries in high-latitude
56 ecosystems, and is thought to have contributed to the expansion of at least half of treelines into
57 Arctic and alpine tundra globally (Harsch *et al.* 2009). Beyond the treeline, tall-statured shrub
58 species are projected to expand their ranges with climate warming into previously low-statured
59 tundra communities (Post *et al.* 2009; Myers-Smith *et al.* 2011a), hereafter referred to as shrubline
60 advance. Though we have ample evidence of treeline advance from sites around the world (Harsch
61 *et al.* 2009), an advancing shrubline in northern alpine tundra has been reported in only a few
62 studies (Dial *et al.* 2007, 2016; Hallinger, Manthey & Wilmking 2010; Upshall 2011; Rundqvist *et*
63 *al.* 2011) Wipf, Rixen and Stoeckli *op. cit.*, Fig. 1). In tundra ecosystems, advance of the shrubline
64 ecotone will alter albedo, soil temperatures, nutrient turnover times, carbon cycling and
65 biodiversity, which could create feedbacks to future shrub expansion and Arctic warming (Myers-
66 Smith *et al.* 2011a; Pearson *et al.* 2013; Williamson *et al.* 2016). Thus, it is necessary to understand
67 the rates and drivers of shrubline advance, in addition to increased shrub growth and recruitment, to
68 project future vegetation change in tundra ecosystems and resulting feedbacks to ecosystem
69 functions with warming.

70

71 Tundra ecosystems have been dominated by woody vegetation in the past (Higuera *et al.* 2008) and
72 there is ample evidence that shrub expansion is currently underway at sites across the tundra biome
73 (Fig. 1, Myers-Smith *et al.* 2011a). Paleoecological records indicate that shrub species were much
74 more abundant in high-latitude ecosystems during the warmer and wetter period of the early
75 Holocene (Higuera *et al.* 2008). Recent observations from sites around the Arctic indicate a
76 transition towards more dense shrubland (Sturm, Racine & Tape 2001; Tape, Sturm & Racine 2006;

77 Forbes, Macias-Fauria & Zetterberg 2010; Myers-Smith *et al.* 2011a; Macias-Fauria *et al.* 2012;
78 Ropars & Boudreau 2012; Tremblay, Lévesque & Boudreau 2012; Lantz, Marsh & Kokelj 2013;
79 Frost & Epstein 2014; Naito & Cairns 2015). And, future climate warming in tundra ecosystems is
80 projected to again lead to deciduous tree or shrub dominated tundra (Swann *et al.* 2010; Pearson *et*
81 *al.* 2013). However, evidence is lacking for advances of shrubline ecotones up hill-slopes in
82 mountain regions or northward into the Arctic, as most studies instead test for changes in the cover
83 or abundance of tundra shrubs (Fig. 1).

84
85 Climate is linked to the position of the shrubline ecotone (Lantz, Gergel & Kokelj 2010b) and is
86 often invoked as the cause of tree or shrubline advance (Truong, Palmé & Felber 2007; Harsch *et*
87 *al.* 2009; Hallinger *et al.* 2010). Experimental studies also indicate that warming will increase the
88 dominance of shrub species in tundra ecosystems (Arft *et al.* 1999; Walker *et al.* 2006; Elmendorf
89 *et al.* 2012a), and this is corroborated by observations of greater shrub increases at sites that have
90 experienced greater warming (Elmendorf *et al.* 2012b). Shrub growth has been demonstrated to be
91 climate sensitive (Forbes *et al.* 2010; Hallinger *et al.* 2010; Blok *et al.* 2011; Macias-Fauria *et al.*
92 2012; Myers-Smith *et al.* 2015a); however, new recruitment (Lantz, Gergel & Henry 2010a;
93 Boulanger-Lapointe *et al.* 2014; Büntgen *et al.* 2015), rather than growth alone, will drive shrubline
94 advance. Thus, it is still uncertain if the same climate or biological drivers will control shrubline
95 advance relative to shrub expansion in tundra ecosystems.

96
97 Treeline advance has been studied in more detail than changes in the elevation limit of tall shrub
98 species, and the reported drivers of treeline advance, though often linked to climate, are varied
99 (Harsch & Bader 2011). A global meta-analysis of 166 treelines found that over half had advanced
100 in elevation since 1900, while just under half remained unchanged over the same period (Harsch *et*
101 *al.* 2009). Climate sensitivity of tree growth has been identified at treeline (Ettinger, Ford &
102 HilleRisLambers 2011); however, the controls on tree recruitment at treeline are often related more

103 closely to winter (rather than summer) weather and microenvironmental conditions (Wilmking *et al.*
104 2012; Hagedorn *et al.* 2014) or biotic interactions (HilleRisLambers *et al.* 2013). Shrubby treelines
105 such as the often low-statured mountain birch (*Betula pubescens* subsp. *tortuosa*) treeline have been
106 documented to be advancing in alpine ecosystems in Norway (Tømmervik *et al.* 2009; Hofgaard,
107 Dalen & Hytteborn 2009) and Sweden (Kullman 2002; Sundqvist, Björk & Molau 2008). However,
108 shrubline dynamics have been little studied relative to treeline advance, with only a few studies
109 investigating shrubline advance (Dial *et al.* 2007, 2016; Hallinger *et al.* 2010; Upshall 2011;
110 Rundqvist *et al.* 2011; Stöckli *et al.* 2011) and recruitment (Lantz *et al.* 2010a; Boulanger-Lapointe
111 *et al.* 2014; Büntgen *et al.* 2015) in tundra ecosystems (Fig. 1). Because shrubline advance is so
112 infrequently studied, we lack a complete understanding of the drivers of ecological boundaries
113 beyond treelines.

114

115 In this study, we tested the hypothesis that the willow shrubline has advanced over the past 50 years
116 in our focal research site in the Kluane region of the southwest Yukon Territory, Canada. We
117 compared largest stem initiation and growth rates to climate variables to test the climate sensitivity
118 of shrub recruitment and growth. If shrubline advance is related to a large-scale regional driver such
119 as climate, we predict consistent evidence of new recruitment across the study region. If shrubline
120 advance is mediated by local-scale processes, such as microclimate, herbivory or disturbances, we
121 predict variation in recruitment patterns across the region. We used dendroecology to investigate
122 shrub largest stem initiation over the second half of the 20th century and repeat ecological
123 monitoring over a four-year period (2009 - 2013) to calculate current, and estimate future, rates of
124 cover change, recruitment, age distributions and shrub densities at the elevational shrubline in this
125 high-latitude alpine tundra ecosystem.

126

127 **Materials and Methods**

128 *Literature Review*

129 We surveyed the literature for all studies presenting evidence of shrub dynamics including:
130 patch/cover change, infilling or recruitment change in existing shrub tundra, and advance of the
131 latitudinal or elevational shrubline (Fig. 1). We began with existing reviews of shrub expansion
132 (Myers-Smith *et al.* 2011a; Büntgen *et al.* 2015) and then supplemented these literature reviews
133 using the search terms: “tundra” and “shrubs” and conducting a comprehensive search for the years
134 2011 to 2016 using both Web of Science and Google Scholar. We recorded the shrub change
135 observed, coordinates of the study sites, species under investigation, methods used, sample size and
136 other relevant information for all studies identified (Table S1).

137

138 *Field surveys*

139 We investigated shrubline advance along 26 hill-slopes in 14 sites in the Kluane region of the
140 southwest Yukon Territory (Table S2, Fig. 3a, Fig. S1 and S2) from 2007 to 2009. The Kluane
141 Region is located along the continental divide where the Pacific flora transitions into the Arctic
142 flora (Cody 2000). Glacial refugia are thought to have been located in this region (Brubaker *et al.*
143 2005), which could be a factor influencing the present-day variation in species composition (Fig.
144 S2).

145

146 At each site, we established a survey transect parallel to the contours of the valley hill-slope at
147 shrubline, the maximum elevation at which tall willow species grow (Fig. 2, Table S2). We
148 searched for the highest elevation at which a plant from any of the tall willow species grew along
149 the hill-slope. This individual became the first transect point and shrub to be surveyed along the
150 shrubline transect. We identified each willow individual for each different species found within 3 m
151 of a transect point located every 10 m along the hill-slope from the first shrub sampled, until we had
152 sampled 8 individuals for age determination and growth ring width measurements. If no willows

153 were present at a given transect point, we walked further along or slightly down towards the
154 shrubline transition until the next willow was reached. This survey method allowed for the distance
155 among individuals and the density of shrubs at the shrubline ecotone to be calculated.

156

157 After surveying at shrubline, we walked down the hill-slope until reaching a subjectively estimated
158 zone of approximately 50% tall willow shrub cover. At two sites, Burwash and Bison, cover was
159 closer to 20% as the topography of the valley did not permit surveying on the same aspect at a
160 lower elevation (Table S2). At all sites except Printers Pass and Copper Joe Creek, we repeated this
161 survey on the opposite aspect of the valley or in the case Five Lakes on the opposite side of the
162 ridge, and for Aishihik Ridge and Cranberry Ridge, at a location further along the ridge (Table S2).

163

164 The six most abundant tall willow species in the Kluane Region were *Salix pulchra* Cham.
165 (diamond-leaf willow), *Salix niphoclada* Rydb. (barren-ground willow), *Salix glauca* L. Hook.
166 (grey-leaf willow), *Salix richardsonii* Hook. (Richardson's willow), *Salix barrattiana* Hook.
167 (Barratt's willow), and *Salix alaxensis* Andersson (felt-leaf willow, Table S3, Fig. S2). During the
168 survey, we identified the species of each willow, and since these species are dioecious, we also
169 identified the sex, if the individual had visible catkins (Myers-Smith & Hik 2012). When catkins
170 were absent, we were not able to distinguish between the species *S. niphoclada* and *S. glauca*
171 during field surveys. We have therefore combined these individuals into one taxonomic category;
172 however, we believe that most individuals sampled in this group are *S. niphoclada*. Species
173 identifications were confirmed by George Argus (Emeritus, National Herbarium of Canada). The
174 location, elevation, hill-slope, and aspect were recorded, as well as the largest diameter of the shrub
175 patch and the maximum height.

176

177 *Climate data*

178 The Kluane Region has a continental climate that is also influenced by coastal weather patterns with
179 cold winters with October – February mean temperatures from -7°C to -15°C and relatively warm
180 summers with June – July mean temperatures from 7°C to 11°C at lower elevations around 800m
181 (Fig. S3). We used lapse rate corrected monthly Climate Western North America (ClimateWNA)
182 v5.30 gridded temperature and precipitation data (4 x 4 km resolution, Wang *et al.* 2011) and
183 Climate Research Unit (CRU) TS3.21 gridded temperature and precipitation data (0.5° resolution,
184 Harris, Ian 2013). These climate data correlate well with local meteorological station data (Myers-
185 Smith *et al.* 2015a).

186

187 *Sample collection*

188 We collected stem samples from 297 individuals across 20 of the 26 hill-slopes at 10 of the 14 sites.
189 We collected a 3-5 cm sample of the largest stem of each individual for growth ring analysis just
190 above the stem-root interface along two elevational transects on two hill-slopes for a total of eight
191 individuals per transect and 32 individuals per valley (see above). Occasionally, samples could not
192 be collected due to low shrub prevalence (e.g. Copper Joe Creek) or could not be processed due to
193 wood rot or growth deformities, thus reducing the final sample sizes slightly at some sites (Table
194 S2). Sampling was not conducted at the sites Aishihik and Cranberry Ridge, was only conducted at
195 one aspect in Bison Valley, and at one elevation for Printer's Pass and Copper Joe Creek (Table
196 S2). At two sites with longer continuous elevation gradients, Gladstones and Observation Plateau,
197 we sampled again at a lower elevation where shrub cover was approximately 75% (Table S2).

198

199 In these alpine ecosystems near the elevational shrubline where shrub plants have few stems (from
200 one to tens) and a stunted growth form, information from the base of the largest stem likely
201 represents similar information to that found in the root collar, which may not be the case in more
202 continuous shrub cover at lower elevations (Ropars *et al.* 2017). We restricted our sampling to
203 higher elevations where willow patches were smaller and were non-contiguous in their extent (the

204 average willow patch diameter was 100 cm and the average density of individuals was 17 per 100m,
205 Table S2), so that we were likely sampling only distinct genetic individuals. Although willow
206 species can spread laterally through clonal growth, individuals growing in these extreme
207 environments with shallow active-layer soil depths have been shown to be genetically distinct even
208 when growing in relatively close proximity (Douhovnikoff *et al.* 2010).

209

210 *Age estimates*

211 Age estimates were determined for all samples using dendrochronology following methods adapted
212 for tundra shrub species (Myers-Smith *et al.* 2015b). Rings were counted from thin cross sections of
213 the largest stems harvested just above the root collar. The age of shrub stems was estimated as the
214 maximum number of rings measured between four radii for each sample. We sampled two serial
215 sections ~5 cm apart along the largest stem of 25 individuals and age estimates differed by 2 ± 0.5
216 years (mean \pm SE). We compared age estimates between the first and second largest stems on 18
217 different shrub individuals, and found that the stem age varied by an average of 6 ± 2 years (mean \pm
218 SE) between these stems. Therefore, we assume that stem age estimates and the estimated initiation
219 dates of the largest stem could have an error of around ± 6 years. Stem ages are only minimum
220 estimates because sometimes rings are missing, the pith of the stem is rotten, or the largest stem or
221 basal stem section might not represent the oldest part of the willow shrub. However, the estimated
222 years of initiation of stems gives a good indication of the overall history of growth of these high-
223 elevation shrubs.

224

225 *Growth measurements*

226 To process samples for annual radial growth measurements, we made thin sections of the shrub
227 stems, mounted the sections on glass slides, and took digital images with a microscope mounted
228 digital camera. Each shrub section was measured along four radii for annual increment with a
229 resolution of $1\mu\text{m}$ (WinDendro, Québec, Canada or ImageJ, Research Services Branch, National

230 Institute of Mental Health, Maryland, USA). Each at 90° from the other unless the placement of
231 radii had to be moved to avoid growth deformities or rotten wood, which occurred in approximately
232 10% of samples. To account for measurement error, we repeated the count for the first radii after
233 completing the other three radii. Missing rings were accounted for during the visual crossdating
234 conducted on the raw ring width measurements using marker rings such as the 2004 high growth
235 year and the 2001 low growth year. We identified missing rings in 19% of samples of these
236 repeated measurements. Willow stem sections varied in the ease at which rings could be counted
237 and the information that these rings contained. A statistic of the repeatability of the measurement
238 was calculated by correlating the ring width measurements between the two repeated radii. The
239 repeatability correlations (Pearson's r) was greater than 0.8 for 96% of samples. The radii for each
240 stem sample were averaged. A statistic of uniformity between the four radii was calculated for each
241 sample by averaging the correlation for each radius with the mean of all four radii. Correlations
242 (Pearson's r) among all of the sample radii were greater than 0.8 for 88% of the samples.

243

244 *Growth data*

245 We removed the first five years of growth to account for irregular growth patterns during early life
246 stages. Data were not detrended to account for age-related growth, as these trends were not present
247 in most shrub individuals and we wanted to treat all individuals in the same manner (Myers-Smith
248 *et al.* 2015b). Growth data at the level of the individual and climate data at the site level were mean
249 centred and variance scaled using the standard score to convert all growth and climate data into the
250 same units and to meet the assumption of normality.

251

252 *Shrubline Advance Estimates*

253 Shrub densities were calculated from the sampling protocol as the number of shrub individuals
254 encountered along the length of the sampling transect with a final unit of shrubs per 100 m of
255 transect (Table S2). To calculate shrubline advance, we estimated the rate of change of shrub

256 density over time based on largest stem recruitment rates estimated from the dendroecological age
257 estimates among the two transect elevations. This was calculated as the slope of the linear
258 relationship between the number of shrubs per 100 m as recruitment progresses and time in years
259 (see Fig S5). Thus, our estimates of shrubline advance assumed that hill-slopes with higher rates of
260 shrubline advance had 1) greater rates of increasing shrub densities over time, and 2) greater
261 differences in age distributions among transects at shrubline versus at lower elevations (Fig. S5).

262

263 *Shrub cover change*

264 We surveyed shrub cover, density, growth and recruitment in six 50 x 50 m plots at the Pika Valley
265 site in July 2009 and 2013 following the Tall Shrub Monitoring Protocol (Myers-Smith *et al.* 2009).
266 Clonal species can have extremely long lifespans and might not experience any age-related
267 senescence over time (de Witte and Stöcklin, 2010); therefore, tundra willow patches, once
268 established and growing in conditions with limited herbivory and stem dieback, can continue to
269 expand for decades. We used willow densities calculated from distances among individuals, percent
270 cover and patch sizes collected in the field surveys to quantify current and future tall willow cover.

271

272 *Statistical analysis of age distributions*

273 Statistics were conducted with the software R (version 3.2.2, R Development Core Team, Vienna).
274 We used linear models to test for differences of shrubline advance and elevations between sites. We
275 compared the minimum age of shrub individuals among sites using Kruskal-Wallis tests or between
276 elevations among sites using Friedman rank sum tests using the package agricolae, because age
277 distributions at high elevations were right skewed and non-parametric tests were required. We used
278 mixed models with site as a random effect to test for a difference in patch width and height to
279 compare the patch size of shrubs between sites. We used MANOVA and ANOVA to test for
280 variation in patch size among species. We used a Shapiro-Wilk normality test to evaluate the age
281 distributions. The variables stem width, patch width, patch height, and age were log transformed to

282 meet criteria for normality and homogeneity of variance. We used time series analysis to test the
283 correspondence between pulses of largest stem initiation and weather data using the stats, mFilter
284 and TTR packages (Büntgen *et al.* 2015). We used linear models to test the correspondence
285 between detrended largest stem initiation (Hodrick-Prescott filter) and summer (June-July) and
286 winter (October-February) temperature and precipitation data including one-year lags.

287

288 *Statistical analysis of growth data*

289 We used a linear mixed model analysis to quantify the climate sensitivity of growth (Myers-Smith
290 *et al.* 2015b, a p.). Linear mixed models analysis can take into account hierarchical sampling
291 structure, temporal autocorrelation and unbalanced sampling (Crawley 2007). Linear mixed models
292 are growing in popularity in annual radial growth analysis because these models can account for
293 variance in growth among years within individuals and variance among individuals within sites as
294 well as heterogeneity in growth patterns over time of different individuals growing at the same site
295 (Lapointe-Garant *et al.* 2010; Schmidt *et al.* 2010; Ettinger *et al.* 2011; Speed *et al.* 2011a; Subedi
296 & Sharma 2013). We used the nlme package to conduct the mixed model analysis, using maximum
297 likelihood estimation for model selection and restricted maximum likelihood estimation for slope
298 estimates (Crawley 2007). We mean-centred and variance scaled all growth ring data at the
299 individual level and climate data at the site-level prior to analysis, so that we can calculate the
300 climate sensitivity among individuals at different sites. Our model structure included annual radial
301 growth as the response variable, fixed effects included climate variables, and random intercepts for
302 year and an autocorrelation structure (AR1, autoregressive process of order one). We calculated the
303 conditional R^2 value for each mixed model using the r.squaredGLMM function of the MuMIn
304 package (Nakagawa & Schielzeth 2013). We did not include random slopes in addition to random
305 intercepts as this level of complexity led to singular convergences.

306

307 Model selection can be used to identify a single best model from a set of competing models
308 (Johnson & Omland 2004). We tested 33 climate models chosen to represent the climate variables
309 that we hypothesized would best explain the variation in annual radial growth and a null model. The
310 33 models included seasonal temperatures or precipitation variables and a selection of models with
311 both temperature and precipitation variables. We used the same climate models as used by Myers-
312 Smith et al. (2015a; sup. info) in a tundra biome-wide synthesis of annual radial growth data.

313

314 *Estimates of shrub cover change*

315 We used our collected age distribution, shrub cover and field survey data to make a simple
316 projection of future patch expansion of tundra shrubs overtime across the Kluane Region. We used
317 exponential relationships to project patch size increase with age, based on the change in patch size
318 of currently existing shrub patches over a 50-year period, and compared these results to measured
319 increases over a four-year period (2009 – 2013). The 95% quantile relationship was calculated
320 using the quantreg package.

321

322 **Results**

323 Our literature review indicated few studies demonstrating shrubline advance and increased shrub
324 recruitment at sites around the tundra biome (Fig. 1, Table S1). Only six other studies at five study
325 sites investigated shrubline advance beyond current elevational limits of shrub species in addition to
326 this study (Dial *et al.* 2007, 2016; Hallinger *et al.* 2010; Upshall 2011; Rundqvist *et al.* 2011;
327 Stöckli *et al.* 2011), and none investigated shrubline advance beyond latitudinal limits of the
328 species. Ten studies investigated recruitment of tundra shrubs. All of the above studies find some
329 evidence for shrubline advance and increased recruitment at sites around the tundra biome (Table
330 S1), with two of the studies indicating both increases and decreases or stable shrublines (Rundqvist
331 *et al.* 2011) or recruitment rates (Boulanger-Lapointe *et al.* 2014).

332

333 Our field surveys of 379 individuals at 14 sites indicated that shrub density and the stature of tall
334 willows decreased from treeline with greater elevation (Table S2). Our sampling of 297 of the
335 surveyed individuals at 10 sites indicated skewed age distributions and younger willows at
336 shrubline transects than in the zone of 50% shrub cover (Fig. 5 and Fig. S4; Friedman rank sum test
337 = 14.22, $F_{2,144} = 64$, $P_{\chi^2} < 0.01$, $P < 0.01$). Ages at shrubline did not vary significantly between sites
338 (Kruskal-Wallis $\chi^2 = 34.40$, $df = 36$, $P = 0.54$). Shrub density differed between sites (Table S2);
339 however, all sites showed similar patterns of largest stem initiation and increasing density over time
340 (Fig. S5). Only one case of mortality was observed in the survey of 379 individuals, and
341 observations of stem mortality were very infrequent. When travelling between sites, only three dead
342 individuals were observed, with evidence of stem girdling present in each case, likely as a result of
343 small mammal herbivory. The rates of shrubline advance (Fig. 3a) and elevation of shrubline (Fig.
344 S1) varied across the Kluane Region. Shrubline advance was negatively correlated with the hill-
345 slope of the alpine valleys (Fig. 3a) and was not explained by aspect and elevation (linear model, P
346 = ns). Willows were smaller at shrubline relative to those found at lower elevations (Table S2,
347 linear mixed models, shrubline estimate \pm SE = -0.44 ± 0.06 m, t-value = -7.39 , $P < 0.01$).

348

349 Tall willow diversity was variable across the Kluane Region with different willow species growing
350 at the shrubline ecotone (Fig. S2). However, three species, *S. niphoclada*, *S. pulchra*, and *S.*
351 *richardsonii*, were most abundant and made up $\sim 80\%$ of all the individuals sampled. Age among
352 all willow species surveyed did not differ significantly (Kruskal-Wallis, $\chi^2 = 60.74$, $df = 51$, $P =$
353 0.17). Patch sizes, measured as both width and height, varied between species (MANOVA, Pillai's
354 trace = 0.25 , $F_{10,564} = 7.91$, $P < 0.01$) and this was due to variation in the growth form of the more
355 rarely sampled species. *Salix alaxensis* individuals grew taller, and *S. barratiana* individuals were
356 generally shorter in stature than the other species. No differences were observed in height of the
357 three most commonly surveyed species (ANOVA, $F_{2,224} = 1.39$, $P = 0.25$); however, patch sizes
358 were larger for *S. pulchra* (ANOVA, $F_{2,224} = 8.61$, $P < 0.01$, Tukey's Test pair-wise comparisons).

359

360 Largest stem initiation pulses were correlated with winter temperatures (Fig. 5) and the variation in
361 annual radial growth of willows was best explained by summer temperatures (Fig. 6, Fig. S6, Table
362 S4). Climate sensitivity of willow annual radial growth was variable across the Kluane Region (Fig.
363 6, Fig. S6, Table S4) and this variability was not explained by hill-slope, elevation or species
364 composition (linear mixed models, $P = ns$). We observed shrub recruitment rates of $\sim 20 \pm 5$
365 individuals per hectare per decade (mean \pm SE) and measured rates of increased shrub cover of $\sim 5 \pm$
366 1% per decade (mean \pm SE) from seedling and patch expansion surveys at the Pika Camp site over
367 the period 2009 to 2013. Using a simplified relationship between age and patch size constrained by
368 the monitoring data, and based on the assumption that conditions will remain similarly favourable,
369 we estimated that willow cover will increase by at least 20 percent at lower elevations and could
370 increase as much as five-fold at the shrubline ecotone over the next 50 years (Fig. 7).

371

372 **Discussion**

373 This study provides compelling evidence for wide-spread recent advance of the shrubline across
374 high-latitude alpine tundra of the Kluane Region. While it is commonly assumed that there is ample
375 evidence for shrubline advance in tundra ecosystems eg. IPCC Working Group II (2014), studies
376 documenting shrubline advance or increasing shrub recruitment are rare (Fig. 1, Table S1). In the
377 Kluane Region, we found uniform patterns of increases in the initiation of the largest stems among
378 species and sites with differing aspects and hill-slopes. This indicates that a regional driver such as
379 climate warming is likely to be responsible for the observed changes. Annual radial growth of these
380 willow species was best explained by interannual variation in summer temperatures, and pulses of
381 initiation of the largest stems by winter temperatures. A previous literature review of recruitment
382 rates of tundra shrubs did not identify a consistent timing of increased recruitment at sites around
383 the tundra biome (Büntgen *et al.* 2015).

384

385 In the Kluane Region, the earliest pulse in the initiation of the largest stems of shrubs at shrubline
386 occurred between 1989 and 1996, and began earlier, between 1980 – 1985, in the 50% shrub cover
387 zone (Fig. 4). Summer temperatures have been warming gradually in the region since 1960 and
388 general increase in winter temperatures have occurred since the early 1980s (Fig. S3). We observed
389 almost no dead individuals, and saw little evidence of dieback or dead stems in the field surveys,
390 indicating that adult willow mortality has been very low in recent years. In cold tundra
391 environments, woody material decomposes slowly (Hobbie 1996) and should be preserved on the
392 landscape for decades. The observed high recruitment rates and low mortality, climate sensitivity of
393 initiation of largest stems and growth indicate that a rapid change in shrub cover is currently
394 occurring in alpine tundra of the Kluane region. If conditions remain favourable for growth and
395 recruitment over the next 50 years, tall willow cover could increase by 20% or more and shrubline
396 could continue to advance in this region (Fig. 7).

397

398 *Shrubline advance*

399 We suggest that climate warming has improved growth and recruitment conditions, leading to the
400 observed increased shrub abundance and cover in the Kluane Region. We found a uniform pattern
401 of shrubline advance between the four dominant tall willow species and an increasing rate of largest
402 stem initiation across the Kluane Region. The age of willow stems was surprisingly uniform among
403 sites and between species, with a median shrubline age of 17 years at the shrubline ecotone, despite
404 variation in shrubline elevation. Rapid advance of white spruce treeline (*Picea glauca*) on south-
405 facing hill-slopes and stable treelines on north-facing hill-slopes have been observed in this region
406 (Danby & Hik 2007). However, we observed no variation in age, height or advance of shrubline
407 with valley aspect. Our results indicate a contrasting importance of microclimate for treeline versus
408 shrubline advance in this region, and that regional factors are more important than local factors as
409 drivers of shrubline advance.

410

411 *Climate warming*

412 Our results suggest that growth and initiation of largest stems are controlled by different climate
413 variables in the Kluane Region. Annual radial growth of willows correlated best with summer
414 temperatures, whereas pulses in the initiation of largest stems correlated best with winter
415 temperatures. Climate has been identified as a significant factor influencing the growth (Forbes *et al.*
416 *et al.* 2010; Hallinger *et al.* 2010; Blok *et al.* 2011; Macias-Fauria *et al.* 2012; Tape *et al.* 2012;
417 Elmendorf *et al.* 2012b; Weijers *et al.* 2012; Myers-Smith *et al.* 2015a p.) and establishment
418 (Harsch *et al.* 2009; Van Bogaert *et al.* 2010; Harsch & Bader 2011; Mamet & Kershaw 2012) of
419 woody species in northern alpine or tundra ecosystems. Summer temperatures could either
420 negatively influence (Shevtsova *et al.* 2009) or promote (Graae, Alsos & Ejrnaes 2008; Milbau *et al.*
421 *et al.* 2009; Büntgen *et al.* 2015) seedling establishment, and winter temperatures and cold
422 stratification can influence seed germination rates, seedling mortality and fungal infection (Graae *et al.*
423 *et al.* 2008; Wilmking *et al.* 2012; Hagedorn *et al.* 2014). In alpine ecosystems, where snow is
424 redistributed by wind, seedlings may be exposed to atmospheric temperatures rather than being
425 protected by an insulating snow pack and thus increasing winter mortality on exposed ridges (Wipf,
426 Stoeckli & Bebi 2009; Myers-Smith & Hik 2013).

427

428 Factors other than climate, such as cold-induced photoinhibition, permafrost disturbance, herbivory
429 or plant–plant interactions, could also influence growth and recruitment at elevational treelines and
430 shrublines (Harsch *et al.* 2009; Myers-Smith *et al.* 2011a; HilleRisLambers *et al.* 2013). In the
431 Kluane Region, shallow alpine tundra soils are underlain by bedrock, and thus permafrost thaw will
432 likely have less influence on surface conditions and shrub recruitment or productivity relative to
433 other tundra environments (Natali, Schuur & Rubin 2012; Wilmking *et al.* 2012). Signs of
434 herbivory on shrubs are low in the Kluane Region relative to other tundra ecosystems (Christie *et al.*
435 *et al.* 2015; Barrio *et al.* 2016). The major herbivores on tundra shrubs include ptarmigan browsing
436 new buds in spring, non-cyclic insect herbivores, stem herbivory by small mammals including

437 marmots and rare browsing by moose or other large herbivores. Although not the focus of this
438 study, we believe that herbivory is unlikely to be a major limiting factor for shrub expansion
439 currently in the Kluane Region. In summary, our results point to climate as a driver of shrub
440 expansion and shrubline advance in the Kluane Region.

441

442 Similar to our observations for shrublines, treeline advance has been documented in the Kluane
443 Region and has been attributed to summer warming (Danby & Hik 2007). Summer temperatures
444 have increased by approximately 1°C between 1980 and 2010 in the Kluane area (Fig. S3), and this
445 warming is likely linked to the climate regime shifts observed in the North Western Pacific in 1977
446 and 1989 (Hare & Mantua 2000). Sporadic pulses of recruitment are a common phenomenon at
447 treeline (Körner 2012), however age distributions of tall willow species in this study indicate
448 conditions for recruitment have gradually improved over the past half century. We found that pulses
449 in largest stem initiation were best explained by variation in winter temperatures indicating that
450 frost damage might be a driver of seedling mortality. We predict that if recruitment conditions
451 continue to remain favourable, increased recruitment will continue to occur in this region.

452

453 *Disturbance*

454 Disturbance can influence recruitment rates in tundra ecosystems. Fire (Lantz *et al.* 2010a, 2013)
455 and permafrost degradation (Lantz *et al.* 2009) have been positively associated with recruitment in
456 alder in the Western Canadian Arctic (*Alnus viridis* subsp. *fruticosa*) and caribou trampling has
457 been associated with increased recruitment of *Betula glandulosa* in Northern Quebec (Ropars &
458 Boudreau 2012). In contrast, herbivory can limit the advance of woody species up hill-slopes in
459 northern mountainous regions (Cairns & Moen 2004; Olofsson *et al.* 2009; Hofgaard *et al.* 2009;
460 Van Bogaert *et al.* 2010; Speed *et al.* 2010, 2011b, 2012) and shrub encroachment in tundra
461 ecosystems has been shown to be reduced or inhibited by herbivores (Post & Pedersen 2008;
462 Olofsson *et al.* 2009; Tape *et al.* 2010; Christie *et al.* 2015). Various animal species feed on willow

463 shrubs ranging from large herbivores such as caribou and reindeer (Olofsson *et al.* 2009; Forbes *et*
464 *al.* 2010; Zamin & Grogan 2013; Bernes *et al.* 2015), birds such as ptarmigan (Tape *et al.* 2010),
465 small mammals such as voles and lemmings (Predavec & Danell 2001; Olofsson *et al.* 2009), and
466 herbivorous insects (Olofsson & Strengbom 2000; Den Herder, Virtanen & Roininen 2004).
467 Herbivory can influence both the establishment of new recruits and reduce the survival of adults.
468 However, the impacts of herbivory on recruitment will likely have a larger influence on the
469 population age structure (Speed *et al.* 2010).

470

471 In the Kluane Region, herbivore damage causing shrub death was only observed once in surveys of
472 hundreds of willow individuals. Because seedlings are small and difficult to observe, we likely
473 under-sampled willows younger than ~10 years, and therefore we might not have entirely accounted
474 for seedling and sapling mortality. Willow seeds have variable and often low germination rates
475 (Shevtsova *et al.* 2009; Graae *et al.* 2010), and therefore studying the factors promoting recruitment
476 in these species is logistically difficult. It is likely that in addition to winter temperatures, growing
477 season conditions, disturbance regimes, nutrient availability, seed quality, seed production, other
478 reproductive factors, and variable herbivory could all interact to determine the new recruitment of
479 willow species. However, increasing recruitment in recent decades suggests that herbivory on
480 seedlings or other sources of mortality are not currently a major limiting factor of shrubline advance
481 in the Kluane Region.

482

483 *Limits to shrubline advance*

484 Our results indicate that the initiation of the largest stems of tall willows and shrub cover have
485 increased and will likely continue to increase, if growing conditions remain the same or continue to
486 improve as long as other factors do not become limiting. However, quantitatively projecting future
487 shrubline advance in this region is more difficult. Shrub growth and patch expansion is limited by
488 available resources (Tape *et al.* 2012), and shrubline advance is limited by factors such as substrate,

489 seed source and disturbance. Large-scale disturbances such as hill-slope erosion were observed at
490 many of the sites that had low elevation shrublines. Hill-slopes with talus, scree or exposed rock are
491 not sufficiently stable at higher elevations to support further willow range expansion. On many of
492 the hill-slopes with high shrublines, tall willows are already growing close to the tops of ridges.
493 Though these shrubline individuals were small in stature and did not make up a significant
494 proportion of the overall shrub cover, they had successfully established and were persisting at these
495 higher elevation sites.

496

497 We observed low reproductive effort and potential pollen or resource limitation in these individuals
498 (Myers-Smith, Saunders and Hik, unpublished data). Inadequate successful reproduction is one of
499 the common demographic explanations for range limits (Gaston 2009). Willows growing at the
500 highest elevations in Kluane might not be reproductive and many established seedlings at the
501 shrubline ecotone could come from seed sources located further down the hill-slope. Reproduction
502 could improve with age allowing greater recruitment of individuals from seeds produced at high
503 elevations in the future. Although we predict further increase in cover of willow shrubs in this
504 region, shrubline advance could be limited by active disturbance, available soil substrates, seed
505 source and poor high-elevation reproduction.

506

507 *Conclusions*

508 Our findings add to the growing evidence of increases in shrub abundance in tundra ecosystems,
509 and provide one of the few examples of both upslope advancement and increasing rate of initiation
510 of largest stems of shrubs in relation to climate warming in tundra ecosystems (Fig. 1). We find that
511 contrasting seasons influence growth (summer) and largest stem initiation (winter) in this system. A
512 significant change in tall shrub canopy cover and elevational range extent will begin to alter a
513 variety of factors from soil temperatures and nutrients (Blok *et al.* 2010; Buckeridge *et al.* 2010;
514 Myers-Smith & Hik 2013) to habitat availability for tundra-dwelling animal species (Wheeler &

515 Hik 2013; Boelman *et al.* 2015), which could feedback to influence tundra ecosystem functions as a
516 whole. If growing conditions remain the same or improve over the next 50 years, we predict that tall
517 willow cover will increase by at least 20% and enhanced recruitment will continue to lead to further
518 shrubline advance. However, our results highlight that with different climate drivers for growth and
519 recruitment, variation in the rates of future climate change between summer and winter seasons
520 could lead to different trajectories for vegetation dynamics in this high-latitude alpine tundra.

521

522 **Authors' contributions**

523 IMS and DH conceived the study; IMS collected and analysed the data; IMS wrote the paper with
524 contributions from DH.

525

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540

541 **Data Accessibility**

542 Data are available at the polar data catalogue (<https://www.polardata.ca> Reference Number = 1647).

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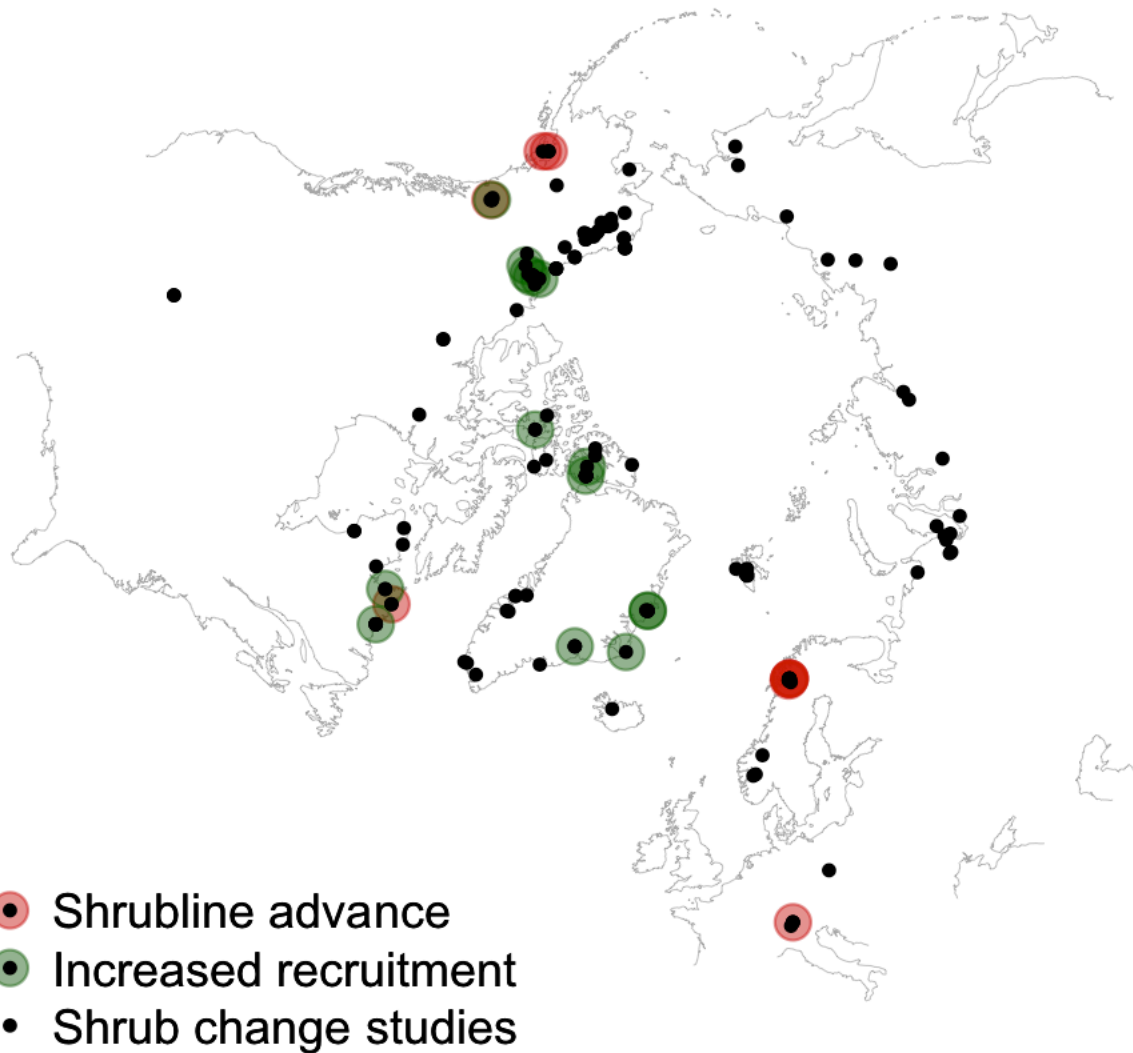
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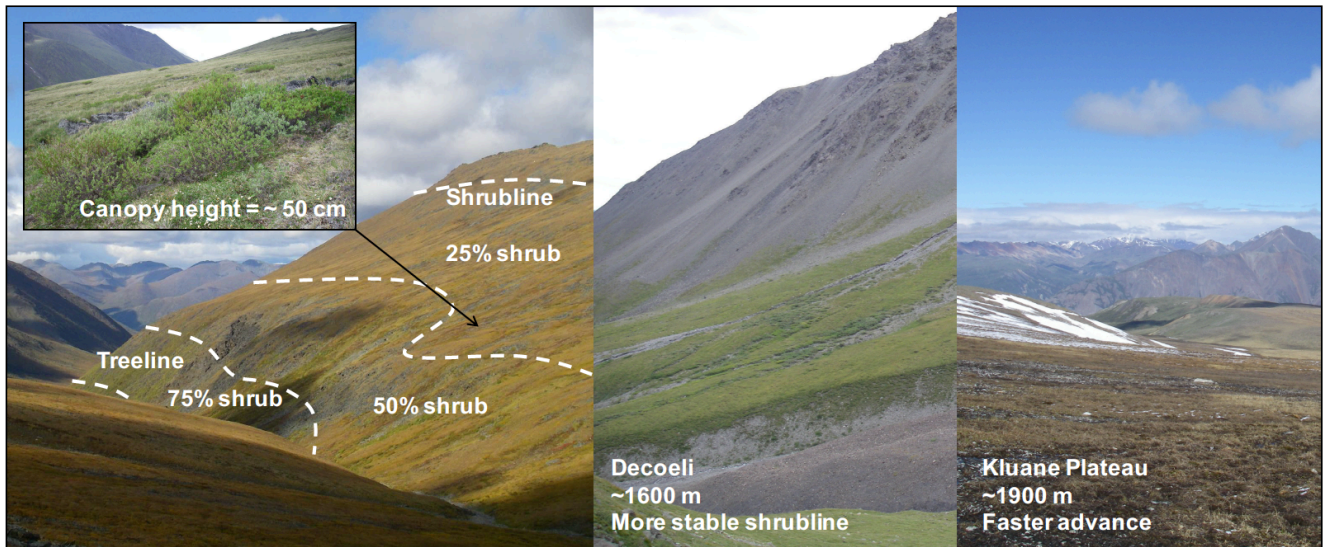
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24 **Figures**

25

26 Figure 1. Evidence of shrubline advance (red), increased recruitment (green) from the 60 studies of
 27 shrub change and 128 study locations at sites around the tundra biome identified in the literature. Six
 28 studies at five study sites investigated shrubline advance beyond current elevational limits of shrub
 29 species in addition to this study, and none investigated shrubline advance beyond latitudinal limits of
 30 the species. Ten studies investigated increased recruitment.



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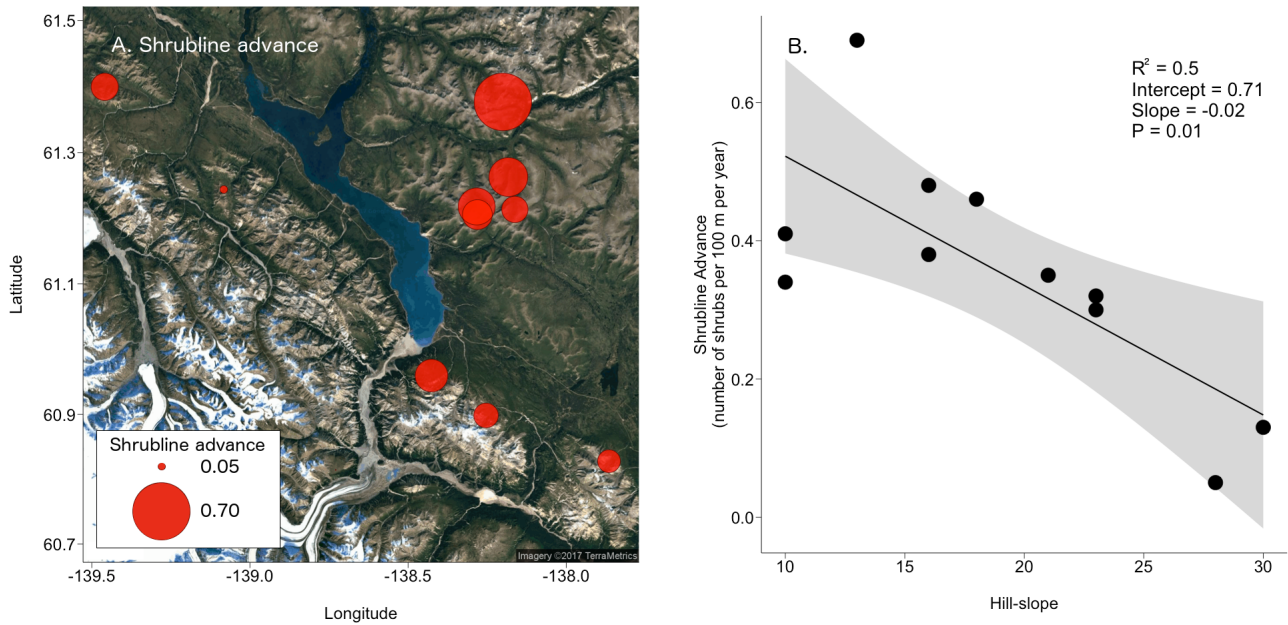
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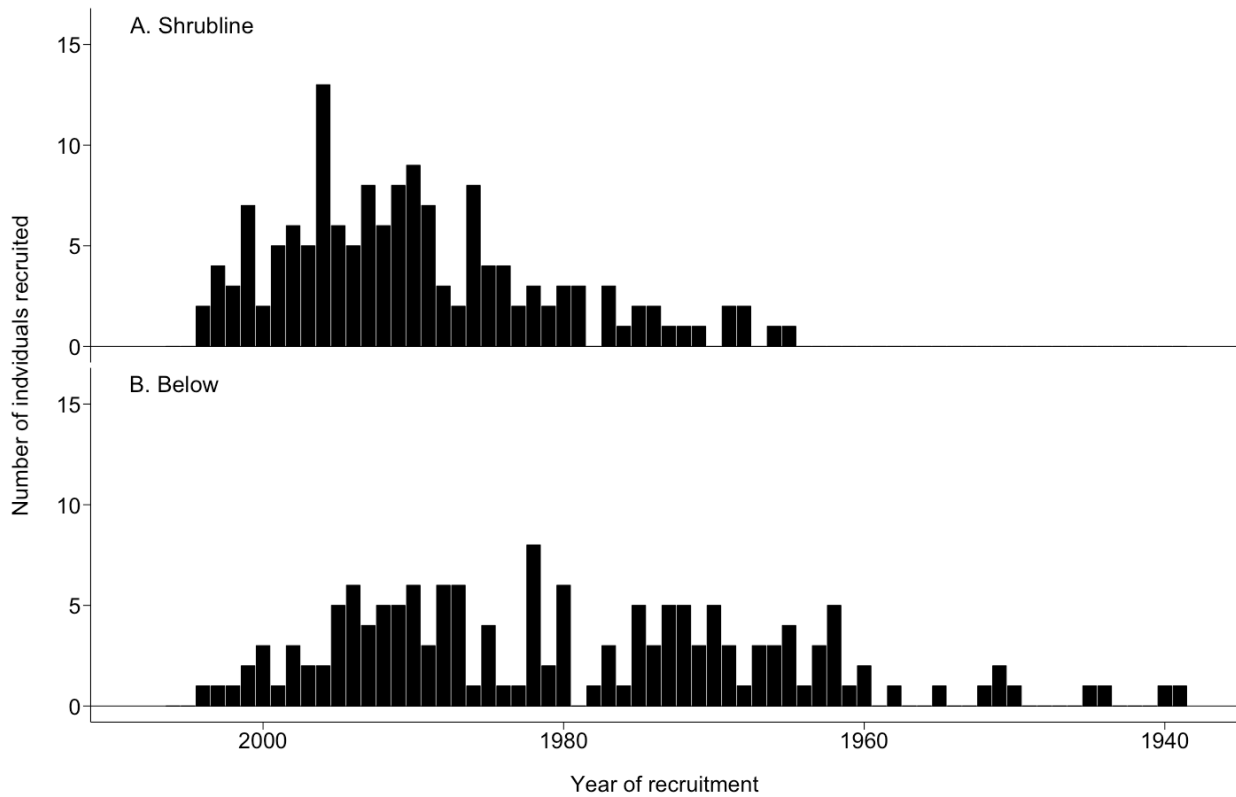
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Figure 2. Elevational shrub densities from treeline to shrubline (the maximum elevational extent at which tall shrubs grow) in the Kluane Region of the Southwest Yukon. At treeline willow shrubs can reach over 2m tall, at the 50% shrub zone canopy heights are around 50 cm, at shrubline canopy heights are often 30 cm or lower (Table S2). The hill-slopes and soil substrate vary across the region with more stable shrublines being found on steeper hill-slopes (such as the west-facing Decoeli hill-slope pictured here with a shrubline of approx. 1600 m) and faster-advancing and higher shrublines being found on shallower hill-slopes (such as the north-facing Kluane Plateau pictured here with a shrubline of approx. 1900 m).



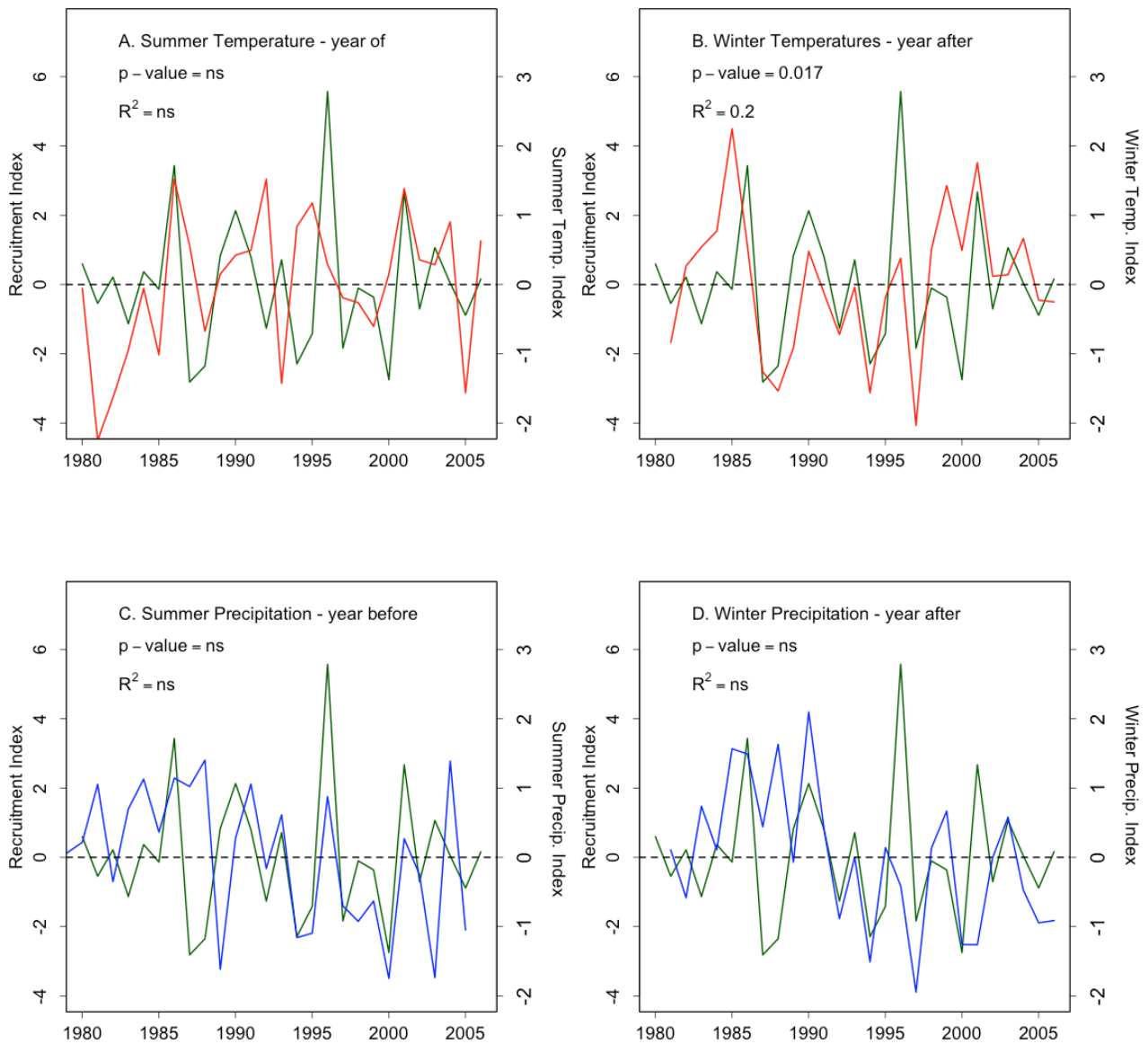
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041 Figure 3. Evidence of shrubline advance (slope of the relationship between the number of shrubs per
 042 100 m as recruitment progresses and time in years, see Fig S5) at sites across the Kluane Region of the
 043 Southwest Yukon. Shrublines that are advancing faster (a greater increase in shrub density over time)
 044 are indicated by larger red circles (A). Shrubline advance was higher for sites with more shallow hill-
 045 slopes across the 11 alpine valleys studied (B). Hill-slope was the only measured topographic or
 046 ecological variable that explained variation in shrubline advance among the 11 study sites.



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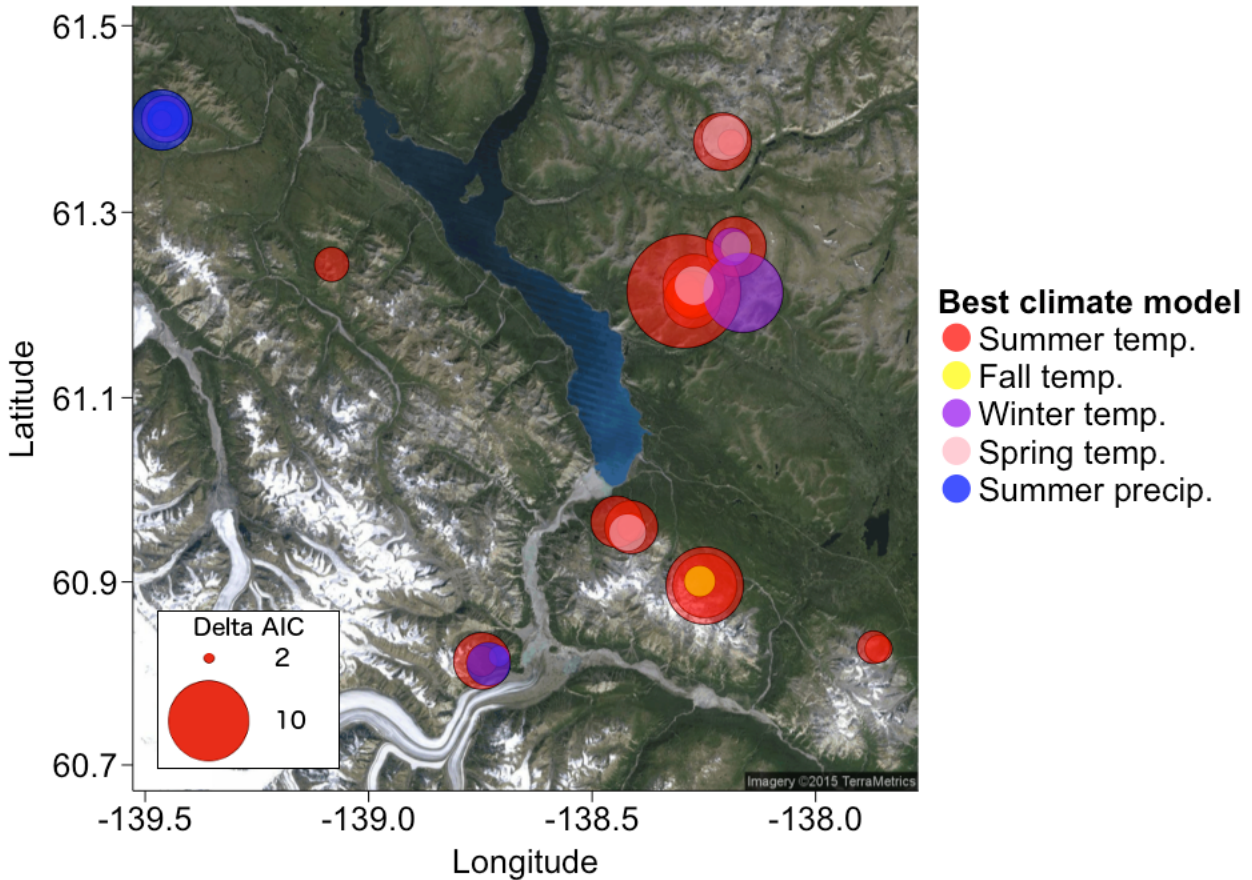
048 Figure 4. Age distributions indicate that shrublines are advancing in the Kluane Region of the
 049 Southwest Yukon. Age distributions of willows at (A) and below (B) shrubline are pooled for all sites
 050 at the shrubline and 50% shrub ecotones. The distribution of willows at shrubline is right skewed
 051 indicating a higher proportion of younger individuals at the shrubline ecotone (Shapiro-Wilk normality
 052 test, $W = 0.94$, $P < 0.01$).



353

354 Figure 5. Variation in willow recruitment at the elevational shrubline plotted as a detrended index from
 355 the time series analysis (green) in the Kluane Region of the Southwest Yukon is best explained by
 356 winter temperatures the year after germination (B). The red lines in plots A and B indicate the June –
 357 July mean and October – February mean temperatures and the blue lines indicate precipitation over the
 358 same periods. Climate data are CRU TS3.21 gridded temperature and precipitation data (0.5°
 359 resolution).

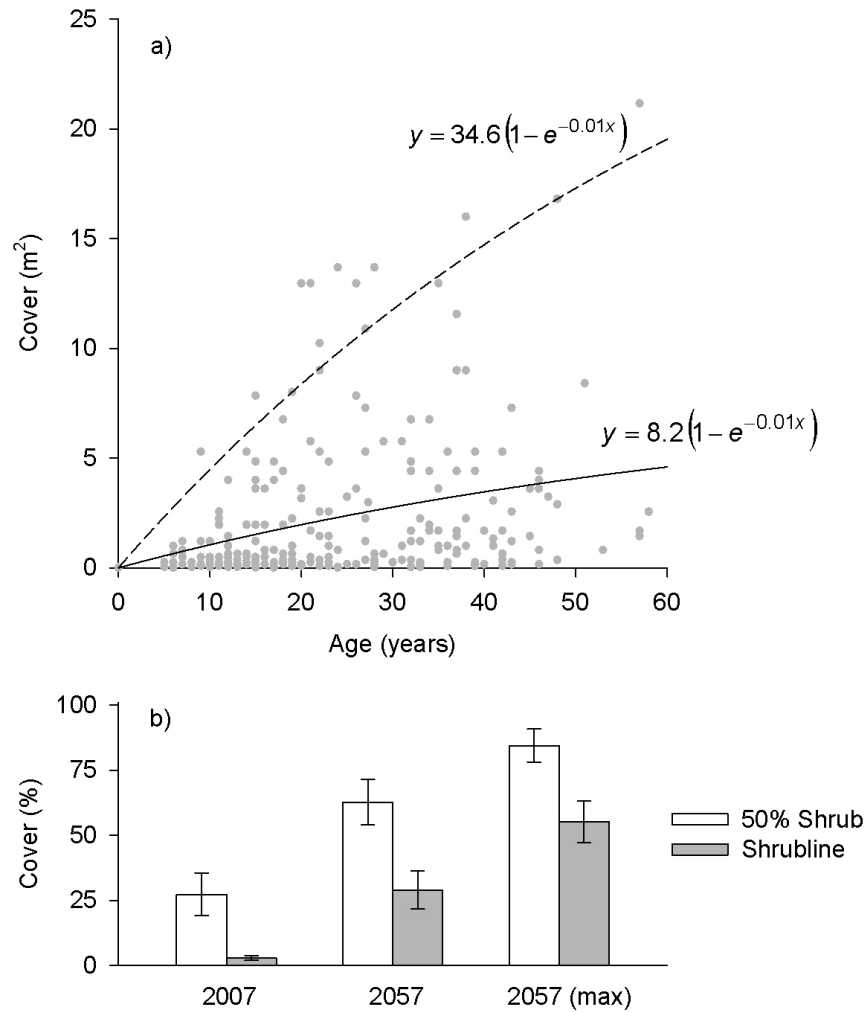
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061

062 Figure 6. Map of climate sensitivity of growth of willows across the Kluane Region of the Southwest
 063 Yukon. Summer temperatures best explained the variation in shrub growth at most sites. The size of the
 064 circle indicates the strength of the climate sensitivity (ΔAIC value, see Figure S5 for other indices of
 065 climate sensitivity); colour indicates the type of climate model that best explained the variation in
 066 growth. Climate data are ClimateWNA v5.30 gridded temperature and precipitation data (4 x 4 km
 067 resolution).

068 Figure 6.



069

070 Figure 7. Estimated current and future projected tall willow cover in alpine tundra of the Kluane
 071 Region of the Southwest Yukon. The solid line is the exponential regression between patch age and
 072 shrub cover indicating the average growth rate and the dashed line is the 95% exponential quantile
 073 regression indicating the estimated maximum growth rate (a). The error bars (b) indicate the standard
 074 error of the projections for the shrub patch cover increases from the survey data, but not the overall
 075 uncertainty of these simplified model estimates which would be much greater. These estimates suggest
 076 that shrub cover will double at lower elevations and increase 10-fold at the shrubline ecotone, if
 077 conditions remain unchanged and all the individuals surveyed continue to grow at the same rate over
 078 the next 50 years (b). New recruitment and continued improved growing conditions, which are not

079 incorporated into this simple projection, are likely to result in an even greater rate of increase if rates of
080 mortality, stem dieback and herbivory remain low. However, lack of suitable substrates further upslope
081 may limit shrub expansion.

