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Running Title: Climate and shrubline advance

Climate warming as a driver of tundra shrubline advance

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

Summary

1. Climate warming is predicted to alter ecological boundaries in high-latitude ecosystems including the elevational or latitudinal extent of tall shrubs in Arctic and alpine tundra. Over 60 studies from 128 locations around the tundra biome have investigated shrub expansion in tundra ecosystems; however, only six studies test whether shrublines are actually advancing up hill-slopes or northward into tundra where tall shrubs are currently absent.
2. We test the hypothesis that willow shrublines have expanded to higher elevations in relation to climate across a 50 x 50 km area in the Kluane Region of the southwest Yukon Territory, Canada by surveying of 379 shrubs at 14 sites and sampling of 297 of the surveyed shrubs at 10 sites. We compared growth and recruitment to climate variables to test the climate sensitivity of shrub increase using annual radial growth analysis, age distributions and repeat field surveys to estimate the current rate of shrubline advance.

3. We found consistent and increasing rates of recruitment of alpine willows, with estimates of faster advancing shrublines on shallower hill-slopes. Mortality was extremely low across the elevation gradient. Aspect, elevation and species identity did not explain variation in recruitment patterns, suggesting a regional factor, such as climate, as the driver of the observed shrubline advance.

4. Annual radial growth of willows was best explained by variation in summer temperatures, and recruitment pulses by winter temperatures. Measured recruitment rates are \(~20 \pm 5\) individuals per hectare per decade (mean ± SE) and measured rates of increased shrub cover of \(~5 \pm 1\%\) per decade (mean ± SE) measured at the Pika Camp site between field surveys in 2009 and 2013. Our results suggest that shrubline will continue to advance over the next 50 years, if growing conditions remain suitable. However, if future conditions differ between summer and winter seasons, this could lead to contrasting trajectories for recruitment versus growth, and influence the vegetation change observed on the landscape.

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

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

Tundra ecosystems have been dominated by woody vegetation in the past (Higuera et al. 2008) and there is ample evidence that shrub expansion is currently underway at sites across the tundra biome (Fig. 1, Myers-Smith et al. 2011a). Paleoecological records indicate that shrub species were much more abundant in high-latitude ecosystems during the warmer and wetter period of the early Holocene (Higuera et al. 2008). Recent observations from sites around the Arctic indicate a transition towards more dense shrubland (Sturm, Racine & Tape 2001; Tape, Sturm & Racine 2006;
Climate is linked to the position of the shrubline ecotone (Lantz, Gergel & Kokelj 2010b) and is often invoked as the cause of tree or shrubline advance (Truong, Palmé & Felber 2007; Harsch et al. 2009; Hallinger et al. 2010). Experimental studies also indicate that warming will increase the dominance of shrub species in tundra ecosystems (Arft et al. 1999; Walker et al. 2006; Elmendorf et al. 2012a), and this is corroborated by observations of greater shrub increases at sites that have experienced greater warming (Elmendorf et al. 2012b). Shrub growth has been demonstrated to be climate sensitive (Forbes et al. 2010; Hallinger et al. 2010; Blok et al. 2011; Macias-Fauria et al. 2012; Myers-Smith et al. 2015a); however, new recruitment (Lantz, Gergel & Henry 2010a; Boulanger-Lapointe et al. 2014; Büntgen et al. 2015), rather than growth alone, will drive shrubline advance. Thus, it is still uncertain if the same climate or biological drivers will control shrubline advance relative to shrub expansion in tundra ecosystems.

Trees have been studied in more detail than changes in the elevation limit of tall shrub species, and the reported drivers of treeline advance, though often linked to climate, are varied (Harsch & Bader 2011). A global meta-analysis of 166 treelines found that over half had advanced in elevation since 1900, while just under half remained unchanged over the same period (Harsch et al. 2009). Climate sensitivity of tree growth has been identified at treeline (Ettinger, Ford & HilleRisLambers 2011); however, the controls on tree recruitment at treeline are often related more
closely to winter (rather than summer) weather and microenvironmental conditions (Wilmking et al. 2012; Hagedorn et al. 2014) or biotic interactions (HilleRisLambers et al. 2013). Shrubby treelines such as the often low-statured mountain birch (Betula pubescens subsp. tortuosa) treeline have been documented to be advancing in alpine ecosystems in Norway (Tømmervik et al. 2009; Hofgaard, Dalen & Hytteborn 2009) and Sweden (Kullman 2002; Sundqvist, Björk & Molau 2008). However, shrubline dynamics have been little studied relative to treeline advance, with only a few studies investigating shrubline advance (Dial et al. 2007, 2016; Hallinger et al. 2010; Upshall 2011; Rundqvist et al. 2011; Stöckli et al. 2011) and recruitment (Lantz et al. 2010a; Boulanger-Lapointe et al. 2014; Büntgen et al. 2015) in tundra ecosystems (Fig. 1). Because shrubline advance is so infrequently studied, we lack a complete understanding of the drivers of ecological boundaries beyond treelines.

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

Literature Review

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

Field surveys

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

At each site, we established a survey transect parallel to the contours of the valley hill-slope at shrubline, the maximum elevation at which tall willow species grow (Fig. 2, Table S2). We searched for the highest elevation at which a plant from any of the tall willow species grew along the hill-slope. This individual became the first transect point and shrub to be surveyed along the shrubline transect. We identified each willow individual for each different species found within 3 m of a transect point located every 10 m along the hill-slope from the first shrub sampled, until we had sampled 8 individuals for age determination and growth ring width measurements. If no willows
were present at a given transect point, we walked further along or slightly down towards the
shrubline transition until the next willow was reached. This survey method allowed for the distance
among individuals and the density of shrubs at the shrubline ecotone to be calculated.

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

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

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

**Sample collection**

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

In these alpine ecosystems near the elevational shrubline where shrub plants have few stems (from one to tens) and a stunted growth form, information from the base of the largest stem likely represents similar information to that found in the root collar, which may not be the case in more continuous shrub cover at lower elevations (Ropars et al. 2017). We restricted our sampling to higher elevations where willow patches were smaller and were non-contiguous in their extent (the
average willow patch diameter was 100 cm and the average density of individuals was 17 per 100m, Table S2), so that we were likely sampling only distinct genetic individuals. Although willow species can spread laterally through clonal growth, individuals growing in these extreme environments with shallow active-layer soil depths have been shown to be genetically distinct even when growing in relatively close proximity (Douhovnikoff et al. 2010).

Age estimates

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

Growth measurements

To process samples for annual radial growth measurements, we made thin sections of the shrub stems, mounted the sections on glass slides, and took digital images with a microscope mounted digital camera. Each shrub section was measured along four radii for annual increment with a resolution of 1µm (WinDendro, Québec, Canada or ImageJ, Research Services Branch, National
Institute of Mental Health, Maryland, USA). Each at 90° from the other unless the placement of radii had to be moved to avoid growth deformities or rotten wood, which occurred in approximately 10% of samples. To account for measurement error, we repeated the count for the first radii after completing the other three radii. Missing rings were accounted for during the visual crossdating conducted on the raw ring width measurements using marker rings such as the 2004 high growth year and the 2001 low growth year. We identified missing rings in 19% of samples of these repeated measurements. Willow stem sections varied in the ease at which rings could be counted and the information that these rings contained. A statistic of the repeatability of the measurement was calculated by correlating the ring width measurements between the two repeated radii. The repeatability correlations (Pearson’s $r$) was greater than 0.8 for 96% of samples. The radii for each stem sample were averaged. A statistic of uniformity between the four radii was calculated for each sample by averaging the correlation for each radius with the mean of all four radii. Correlations (Pearson’s $r$) among all of the sample radii were greater than 0.8 for 88% of the samples.

**Growth data**

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

**Shrubline Advance Estimates**

Shrub densities were calculated from the sampling protocol as the number of shrub individuals encountered along the length of the sampling transect with a final unit of shrubs per 100 m of transect (Table S2). To calculate shrubline advance, we estimated the rate of change of shrub
density over time based on largest stem recruitment rates estimated from the dendroecological age
estimates among the two transect elevations. This was calculated as the slope of the linear
relationship between the number of shrubs per 100 m as recruitment progresses and time in years
(see Fig S5). Thus, our estimates of shrubline advance assumed that hill-slopes with higher rates of
shrubline advance had 1) greater rates of increasing shrub densities over time, and 2) greater
differences in age distributions among transects at shrubline versus at lower elevations (Fig. S5).

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

Statistical analysis of age distributions
Statistics were conducted with the software R (version 3.2.2, R Development Core Team, Vienna).
We used linear models to test for differences of shrubline advance and elevations between sites. We
compared the minimum age of shrub individuals among sites using Kruskal-Wallis tests or between
elevations among sites using Friedman rank sum tests using the package agricolae, because age
distributions at high elevations were right skewed and non-parametric tests were required. We used
mixed models with site as a random effect to test for a difference in patch width and height to
compare the patch size of shrubs between sites. We used MANOVA and ANOVA to test for
variation in patch size among species. We used a Shapiro-Wilk normality test to evaluate the age
distributions. The variables stem width, patch width, patch height, and age were log transformed to
meet criteria for normality and homogeneity of variance. We used time series analysis to test the correspondence between pulses of largest stem initiation and weather data using the stats, mFilter and TTR packages (Büntgen et al. 2015). We used linear models to test the correspondence between detrended largest stem initiation (Hodrick-Prescott filter) and summer (June-July) and winter (October-February) temperature and precipitation data including one-year lags.

**Statistical analysis of growth data**

We used a linear mixed model analysis to quantify the climate sensitivity of growth (Myers-Smith et al. 2015b, a p.). Linear mixed models analysis can take into account hierarchical sampling structure, temporal autocorrelation and unbalanced sampling (Crawley 2007). Linear mixed models are growing in popularity in annual radial growth analysis because these models can account for variance in growth among years within individuals and variance among individuals within sites as well as heterogeneity in growth patterns over time of different individuals growing at the same site (Lapointe-Garant et al. 2010; Schmidt et al. 2010; Ettinger et al. 2011; Speed et al. 2011a; Subedi & Sharma 2013). We used the nlme package to conduct the mixed model analysis, using maximum likelihood estimation for model selection and restricted maximum likelihood estimation for slope estimates (Crawley 2007). We mean-centred and variance scaled all growth ring data at the individual level and climate data at the site-level prior to analysis, so that we can calculate the climate sensitivity among individuals at different sites. Our model structure included annual radial growth as the response variable, fixed effects included climate variables, and random intercepts for year and an autocorrelation structure (AR1, autoregressive process of order one). We calculated the conditional $R^2$ value for each mixed model using the r.squaredGLMM function of the MuMIn package (Nakagawa & Schielzeth 2013). We did not include random slopes in addition to random intercepts as this level of complexity led to singular convergences.
Model selection can be used to identify a single best model from a set of competing models (Johnson & Omland 2004). We tested 33 climate models chosen to represent the climate variables that we hypothesized would best explain the variation in annual radial growth and a null model. The 33 models included seasonal temperatures or precipitation variables and a selection of models with both temperature and precipitation variables. We used the same climate models as used by Myers-Smith et al. (2015a; sup. info) in a tundra biome-wide synthesis of annual radial growth data.

Estimates of shrub cover change

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

Results

Our literature review indicated few studies demonstrating shrubline advance and increased shrub recruitment at sites around the tundra biome (Fig. 1, Table S1). Only six other studies at five study sites investigated shrubline advance beyond current elevational limits of shrub species in addition to this study (Dial et al. 2007, 2016; Hallinger et al. 2010; Upshall 2011; Rundqvist et al. 2011; Stöckli et al. 2011), and none investigated shrubline advance beyond latitudinal limits of the species. Ten studies investigated recruitment of tundra shrubs. All of the above studies find some evidence for shrubline advance and increased recruitment at sites around the tundra biome (Table S1), with two of the studies indicating both increases and decreases or stable shrublines (Rundqvist et al. 2011) or recruitment rates (Boulanger-Lapointe et al. 2014).
Our field surveys of 379 individuals at 14 sites indicated that shrub density and the stature of tall willows decreased from treeline with greater elevation (Table S2). Our sampling of 297 of the surveyed individuals at 10 sites indicated skewed age distributions and younger willows at shrubline transects than in the zone of 50% shrub cover (Fig. 5 and Fig. S4; Friedman rank sum test $= 14.22, F_{2,144} = 64, P_{x^2} < 0.01, P < 0.01$). Ages at shrubline did not vary significantly between sites (Kruskal-Wallis $\chi^2 = 34.40, df = 36, P = 0.54$). Shrub density differed between sites (Table S2); however, all sites showed similar patterns of largest stem initiation and increasing density over time (Fig. S5). Only one case of mortality was observed in the survey of 379 individuals, and observations of stem mortality were very infrequent. When travelling between sites, only three dead individuals were observed, with evidence of stem girdling present in each case, likely as a result of small mammal herbivory. The rates of shrubline advance (Fig. 3a) and elevation of shrubline (Fig. S1) varied across the Kluane Region. Shrubline advance was negatively correlated with the hill-slope of the alpine valleys (Fig. 3a) and was not explained by aspect and elevation (linear model, $P = \text{ns}$). Willows were smaller at shrubline relative to those found at lower elevations (Table S2, linear mixed models, shrubline estimate $\pm$ SE = -0.44 $\pm$ 0.06 m, t-value = -7.39, $P < 0.01$).

Tall willow diversity was variable across the Kluane Region with different willow species growing at the shrubline ecotone (Fig. S2). However, three species, *S. niphoclada*, *S. pulchra*, and *S. richardsonii*, were most abundant and made up ~80% of all the individuals sampled. Age among all willow species surveyed did not differ significantly (Kruskal-Wallis, $\chi^2 = 60.74, df = 51, P = 0.17$). Patch sizes, measured as both width and height, varied between species (MANOVA, Pillai's trace = 0.25, $F_{10,564} = 7.91, P < 0.01$) and this was due to variation in the growth form of the more rarely sampled species. *Salix alaxensis* individuals grew taller, and *S. barratiana* individuals were generally shorter in stature than the other species. No differences were observed in height of the three most commonly surveyed species (ANOVA, $F_{2,224} = 1.39, P = 0.25$); however, patch sizes were larger for *S. pulchra* (ANOVA, $F_{2,224} = 8.61, P < 0.01$, Tukey's Test pair-wise comparisons).
Largest stem initiation pulses were correlated with winter temperatures (Fig. 5) and the variation in annual radial growth of willows was best explained by summer temperatures (Fig. 6, Fig. S6, Table S4). Climate sensitivity of willow annual radial growth was variable across the Kluane Region (Fig. 6, Fig. S6, Table S4) and this variability was not explained by hill-slope, elevation or species composition (linear mixed models, $P = \text{ns}$). We observed shrub recruitment rates of $\sim 20 \pm 5$ individuals per hectare per decade (mean $\pm$ SE) and measured rates of increased shrub cover of $\sim 5 \pm 1\%$ per decade (mean $\pm$ SE) from seedling and patch expansion surveys at the Pika Camp site over the period 2009 to 2013. Using a simplified relationship between age and patch size constrained by the monitoring data, and based on the assumption that conditions will remain similarly favourable, we estimated that willow cover will increase by at least 20 percent at lower elevations and could increase as much as five-fold at the shrubline ecotone over the next 50 years (Fig. 7).

**Discussion**

This study provides compelling evidence for wide-spread recent advance of the shrubline across high-latitude alpine tundra of the Kluane Region. While it is commonly assumed that there is ample evidence for shrubline advance in tundra ecosystems eg. IPCC Working Group II (2014), studies documenting shrubline advance or increasing shrub recruitment are rare (Fig. 1, Table S1). In the Kluane Region, we found uniform patterns of increases in the initiation of the largest stems among species and sites with differing aspects and hill-slopes. This indicates that a regional driver such as climate warming is likely to be responsible for the observed changes. Annual radial growth of these willow species was best explained by interannual variation in summer temperatures, and pulses of initiation of the largest stems by winter temperatures. A previous literature review of recruitment rates of tundra shrubs did not identify a consistent timing of increased recruitment at sites around the tundra biome (Büntgen et al. 2015).
In the Kluane Region, the earliest pulse in the initiation of the largest stems of shrubs at shrubline occurred between 1989 and 1996, and began earlier, between 1980 – 1985, in the 50% shrub cover zone (Fig. 4). Summer temperatures have been warming gradually in the region since 1960 and general increase in winter temperatures have occurred since the early 1980s (Fig. S3). We observed almost no dead individuals, and saw little evidence of dieback or dead stems in the field surveys, indicating that adult willow mortality has been very low in recent years. In cold tundra environments, woody material decomposes slowly (Hobbie 1996) and should be preserved on the landscape for decades. The observed high recruitment rates and low mortality, climate sensitivity of initiation of largest stems and growth indicate that a rapid change in shrub cover is currently occurring in alpine tundra of the Kluane region. If conditions remain favourable for growth and recruitment over the next 50 years, tall willow cover could increase by 20% or more and shrubline could continue to advance in this region (Fig. 7).

**Shrubline advance**

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

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

Factors other than climate, such as cold-induced photoinhibition, permafrost disturbance, herbivory or plant–plant interactions, could also influence growth and recruitment at elevational treelines and shrublines (Harsch et al. 2009; Myers-Smith et al. 2011a; HilleRisLambers et al. 2013). In the Kluane Region, shallow alpine tundra soils are underlain by bedrock, and thus permafrost thaw will likely have less influence on surface conditions and shrub recruitment or productivity relative to other tundra environments (Natali, Schuur & Rubin 2012; Wilmking et al. 2012). Signs of herbivory on shrubs are low in the Kluane Region relative to other tundra ecosystems (Christie et al. 2015; Barrio et al. 2016). The major herbivores on tundra shrubs include ptarmigan browsing new buds in spring, non-cyclic insect herbivores, stem herbivory by small mammals including
marmots and rare browsing by moose or other large herbivores. Although not the focus of this study, we believe that herbivory is unlikely to be a major limiting factor for shrub expansion currently in the Kluane Region. In summary, our results point to climate as a driver of shrub expansion and shrubline advance in the Kluane Region.

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

**Disturbance**

Disturbance can influence recruitment rates in tundra ecosystems. Fire (Lantz *et al*. 2010a, 2013) and permafrost degradation (Lantz *et al*. 2009) have been positively associated with recruitment in alder in the Western Canadian Arctic (*Alnus viridis* subsp. *fruticosa*) and caribou trampling has been associated with increased recruitment of *Betula glandulosa* in Northern Quebec (Ropars & Boudreau 2012). In contrast, herbivory can limit the advance of woody species up hill-slopes in northern mountainous regions (Cairns & Moen 2004; Olofsson *et al*. 2009; Hofgaard *et al*. 2009; Van Bogaert *et al*. 2010; Speed *et al*. 2010, 2011b, 2012) and shrub encroachment in tundra ecosystems has been shown to be reduced or inhibited by herbivores (Post & Pedersen 2008; Olofsson *et al*. 2009; Tape *et al*. 2010; Christie *et al*. 2015). Various animal species feed on willow
shrubs ranging from large herbivores such as caribou and reindeer (Olofsson et al. 2009; Forbes et al. 2010; Zamin & Grogan 2013; Bernes et al. 2015), birds such as ptarmigan (Tape et al. 2010), small mammals such as voles and lemmings (Predavec & Danell 2001; Olofsson et al. 2009), and herbivorous insects (Olofsson & Strengbom 2000; Den Herder, Virtanen & Roininen 2004).

Herbivory can influence both the establishment of new recruits and reduce the survival of adults. However, the impacts of herbivory on recruitment will likely have a larger influence on the population age structure (Speed et al. 2010).

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

**Limits to shrubline advance**

Our results indicate that the initiation of the largest stems of tall willows and shrub cover have increased and will likely continue to increase, if growing conditions remain the same or continue to improve as long as other factors do not become limiting. However, quantitatively projecting future shrubline advance in this region is more difficult. Shrub growth and patch expansion is limited by available resources (Tape et al. 2012), and shrubline advance is limited by factors such as substrate,
seed source and disturbance. Large-scale disturbances such as hill-slope erosion were observed at
many of the sites that had low elevation shrublines. Hill-slopes with talus, scree or exposed rock are
not sufficiently stable at higher elevations to support further willow range expansion. On many of
the hill-slopes with high shrublines, tall willows are already growing close to the tops of ridges.

Though these shrubline individuals were small in stature and did not make up a significant
proportion of the overall shrub cover, they had successfully established and were persisting at these
higher elevation sites.

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

Conclusions

Our findings add to the growing evidence of increases in shrub abundance in tundra ecosystems,
and provide one of the few examples of both upslope advancement and increasing rate of initiation
of largest stems of shrubs in relation to climate warming in tundra ecosystems (Fig. 1). We find that
contrasting seasons influence growth (summer) and largest stem initiation (winter) in this system. A
significant change in tall shrub canopy cover and elevational range extent will begin to alter a
variety of factors from soil temperatures and nutrients (Blok et al. 2010; Buckeridge et al. 2010;
Myers-Smith & Hik 2013) to habitat availability for tundra-dwelling animal species (Wheeler &
Hik 2013; Boelman et al. 2015), which could feedback to influence tundra ecosystem functions as a whole. If growing conditions remain the same or improve over the next 50 years, we predict that tall willow cover will increase by at least 20% and enhanced recruitment will continue to lead to further shrubline advance. However, our results highlight that with different climate drivers for growth and recruitment, variation in the rates of future climate change between summer and winter seasons could lead to different trajectories for vegetation dynamics in this high-latitude alpine tundra.

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

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Data Accessibility

Data are available at the polar data catalogue (https://www.polardata.ca Reference Number = 1647).
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Figure 1. Evidence of shrubline advance (red), increased recruitment (green) from the 60 studies of shrub change and 128 study locations at sites around the tundra biome identified in the literature. Six studies at five study sites investigated shrubline advance beyond current elevational limits of shrub species in addition to this study, and none investigated shrubline advance beyond latitudinal limits of the species. Ten studies investigated increased recruitment.
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).
Figure 3. Evidence of shrubline advance (slope of the relationship between the number of shrubs per 100 m as recruitment progresses and time in years, see Fig S5) at sites across the Kluane Region of the Southwest Yukon. Shrublines that are advancing faster (a greater increase in shrub density over time) are indicated by larger red circles (A). Shrubline advance was higher for sites with more shallow hill-slopes across the 11 alpine valleys studied (B). Hill-slope was the only measured topographic or ecological variable that explained variation in shrubline advance among the 11 study sites.
Figure 4. Age distributions indicate that shrublines are advancing in the Kluane Region of the Southwest Yukon. Age distributions of willows at (A) and below (B) shrubline are pooled for all sites at the shrubline and 50% shrub ecotones. The distribution of willows at shrubline is right skewed indicating a higher proportion of younger individuals at the shrubine ecotone (Shapiro-Wilk normality test, $W = 0.94$, $P < 0.01$).
Figure 5. Variation in willow recruitment at the elevational shrubline plotted as a detrended index from the time series analysis (green) in the Kluane Region of the Southwest Yukon is best explained by winter temperatures the year after germination (B). The red lines in plots A and B indicate the June–July mean and October–February mean temperatures and the blue lines indicate precipitation over the same periods. Climate data are CRU TS3.21 gridded temperature and precipitation data (0.5° resolution).
Figure 6. Map of climate sensitivity of growth of willows across the Kluane Region of the Southwest Yukon. Summer temperatures best explained the variation in shrub growth at most sites. The size of the circle indicates the strength of the climate sensitivity (ΔAIC value, see Figure S5 for other indices of climate sensitivity); colour indicates the type of climate model that best explained the variation in growth. Climate data are ClimateWNA v5.30 gridded temperature and precipitation data (4 x 4 km resolution).
Figure 7. Estimated current and future projected tall willow cover in alpine tundra of the Kluane Region of the Southwest Yukon. The solid line is the exponential regression between patch age and shrub cover indicating the average growth rate and the dashed line is the 95% exponential quantile regression indicating the estimated maximum growth rate (a). The error bars (b) indicate the standard error of the projections for the shrub patch cover increases from the survey data, but not the overall uncertainty of these simplified model estimates which would be much greater. These estimates suggest that shrub cover will double at lower elevations and increase 10-fold at the shrubline ecotone, if conditions remain unchanged and all the individuals surveyed continue to grow at the same rate over the next 50 years (b). New recruitment and continued improved growing conditions, which are not
incorporated into this simple projection, are likely to result in an even greater rate of increase if rates of
mortality, stem dieback and herbivory remain low. However, lack of suitable substrates further upslope
may limit shrub expansion.