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Annual ring growth of a widespread high-arctic shrub reflects past fluctuations in community-level plant biomass

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Summary

1. Long time-series of primary production are rarely available, restricting our mechanistic understanding of vegetation and ecosystem dynamics under climate change. Dendrochronological tools are increasingly used instead, particularly in the Arctic – the world's most rapidly warming biome. Yet, high-latitude plant species are subject to strong energy allocation trade-offs, and whether annual allocations to secondary growth (e.g. 'tree-rings') actually reflects primary production above-ground remains unknown. Taking advantage of a unique ground-based monitoring time-series of annual vascular plant biomass in high Arctic Svalbard (78°N), we evaluated how well retrospective ring growth of the widespread dwarf shrub *Salix polaris* represents above-ground biomass production of vascular plants.

2. Using a balanced design in permanent plots for plant biomass monitoring, we collected 30 *S. polaris* shrubs across five sites in each of two habitats. We established annual ring growth time-series using linear mixed-effects models and related them to local weather records and 13 years of above-ground biomass production in six habitats.

3. Annual ring growth was positively correlated with above-ground biomass production of both *S. polaris* ($r = 0.56$) and the vascular plant community as a whole ($r = 0.70$). As for above-ground biomass, summer temperature was the main driver of ring growth, with this ecological signal becoming particularly clear when accounting for plant, site and habitat heterogeneity. The results suggest that ring growth measurements performed on this dominating shrub can be used to track fluctuations in past vascular plant production of high-arctic tundra.

4. *Synthesis*. Dendrochronological tools are increasingly used on arctic shrubs to enhance our understanding of vegetation dynamics in the world's most rapidly warming biome. Fundamental to such applications is the assumption that annual ring growth reflects between-year variation in above-ground biomass production. Here we showed that ring growth indeed was a robust proxy for the annual above-ground productivity of both the focal shrub and the vascular plant community as a whole. Despite the challenges of constructing ring growth chronologies from irregularly growing arctic shrubs, our findings confirm that shrub dendrochronology can open new opportunities for community-dynamic studies under climate change, including in remote places where annual field sampling is difficult to achieve.

Introduction

Primary producers form the foundation of the Eltonian pyramid, fuelling higher trophic levels of the ecosystem (Elton 1927; Lindeman 1942; Field 1998). In the terrestrial Arctic, where primary productivity is low and food webs are often bottom-up controlled (Legagneux *et al.* 2014), temperatures are rising faster than anywhere else on Earth (Larsen *et al.* 2014; Nordli *et al.* 2014). Consequently, primary productivity across a large part of this biome has been increasing – a phenomenon known as 'arctic greening' (Elmendorf *et al.* 2012; Epstein *et al.* 2012; Macias-Fauria *et al.* 2012) – with potential cascading effects on the population dynamics of animals as

well as on carbon and nutrient cycling (Stenseth *et al.* 2002; Post *et al.* 2009; Wookey *et al.* 2009). Recent field observations and remote sensing also indicate a contrasting trend of declining primary productivity in some areas, known as the "browning of the Arctic" (Phoenix & Bjerke 2016), which further stresses the importance of a mechanistic and predictive understanding of climate change impacts in this realm. However, identifying mechanisms behind vegetation and ecosystem change requires long-term, high-quality and continuous data across trophic levels. Field-based monitoring time-series are still extremely rare for primary producers, particularly in the remote Arctic biome (Ims & Fuglei 2005; Van der Wal & Stien 2014). Accordingly, annual measures of secondary growth, such as tree-ring growth chronologies, have the potential to fill this knowledge gap retrospectively, if proven to represent a proxy for above-ground plant productivity.

The field of dendrochronology consists of reconstructing woody plant growth, typically through the measurement of ring-widths growth, both in trees and shrubs. Forestry studies regularly use dendrochronology to assess net primary production for the purpose of e.g. estimating stand development or carbon sequestration rates (Metsaranta & Lieffers 2009; Babst *et al.* 2014; Dye *et al.* 2016; Klesse, Etzold & Frank 2016). Such studies compare tree-ring readings to *in situ* measures of woody biomass in permanent forest plots, often sampled every five to ten years, to improve precision of primary productivity measures. Dendrochronological tools are also increasingly used on arctic shrubs for purposes such as understanding climate-ring growth relationships, carbon cycle dynamics, or even geomorphological processes (Owczarek *et al.* 2014; Myers-Smith *et al.* 2015a). These applications followed recent methodological developments which overcome the difficulties associated with high irregularity of ring growth in tundra shrubs (Wilmking *et al.* 2012; Myers-Smith *et al.* 2015b). During the last few decades,

the development of remote sensing products has been an alternative route through which measures of overall annual vegetation productivity can be obtained (Pettorelli *et al.* 2005; Vickers *et al.* 2016; Karlsen *et al.* 2018). Some studies using these tools, have related e.g. Normalized Difference Vegetation Index (NDVI) to shrub expansion and growth traits (Babst *et al.* 2010; Forbes, Macias-Fauria & Zetterberg 2010; Blok et al. 2011; Macias-Fauria *et al.* 2012; Weijers *et al.* 2018). However, especially at high latitudes, remotely sensed vegetation production maps with sufficiently high spatial resolution are relatively recent, and obtaining sufficiently cloud-free images during the plant growing season remains a major challenge (Karlsen *et al.* 2018). Moreover, soil moisture levels and extensive bryophyte and lichen cover may limit the validity of NDVI measurements as estimations of vascular plant productivity, since no effective techniques to separate their signals exist so far (Fang, Yu & Qi 2015; Raynolds & Walker 2016. Here, dendrochronological tools provide potentially much more fine-scaled and precise information, available at the individual, species or community level, which could complement restrictions of remote sensing. It remains unknown, however, to what extent shrub ring growth actually reflects above-ground vascular plant biomass, likely because long-term *in situ* biomass monitoring is rare.

A key challenge for ecological inference from arctic shrub dendrochronology is the substantial heterogeneity in growth (and associated ring growth irregularities) within and between individual, as well as across the landscape, due to a great variety of factors. Plants face trade-offs in resource allocation between e.g. stem growth, leaf production, defence against herbivores or reproductive structures, especially in harsh high-latitude environments where the growing season is just a few weeks long (Skarpe & Van der Wal 2002; Milner *et al.* 2016; Ropars *et al.* 2017). In different parts of the landscape, biotic and abiotic conditions introduce

variation in arctic plant growth and allocation patterns (Armbruster, Rae & Edwards 2007),

which include starkly differential levels of, herbivory (Babst, Esper & Parlow 2010; Speed *et al.*

2013), interspecific competition (Dormann, Van der Wal & Woodin 2004), pathogen load (Tojo

& Newsham 2012), soil movement and frost damage (Bokhorst *et al.* 2008; Crawford 2008). In

addition, individual shrubs may respond differently to environmental conditions according to

their genetic make-up or phenotypic plasticity (Albert *et al.* 2011; Housset *et al.* 2016). Arctic

woody plants can even prioritise growth investment differentially among plant parts, e.g. roots

versus branches, according to their phenological growth stage (Sloan, Fletcher & Phoenix 2016)

or with lagged responses (i.e. carry-over effects, Skarpe & Van der Wal 2002; Wu *et al.* 2015).

Some studies have investigated trade-offs in growth allocation within above-ground structures of

arctic shrubs, i.e. between primary (apical) and secondary (radial) growth (Bret-Harte, Shaver &

Chapin 2002; Campioli *et al.* 2013; Magnin, Puntieri & Villalba 2014; Berner *et al.* 2015). They

typically use retrospective measures of shoot primary growth (i.e. length and number of shoots

per year) and relates it to the secondary growth, which can be measured as basal stem diameters,

annual stem mass standardised by its length or ring growth. Nonetheless, the relationship

between above-ground primary growth (including new green biomass), and below-ground

secondary growth, on an annual basis, remains to be studied and is therefore far from clear.

Recent studies have shown high inter-annual variability in arctic plant biomass

production and a strong direct effect of summer temperatures (Gauthier *et al.* 2011; Elmendorf *et

al.* 2012; Van der Wal & Stien 2014; Karlsen *et al.* 2018). The same pattern appears to

characterise annual shrub ring growth (Myers-Smith *et al.* 2015a; Weijers *et al.* 2017). On the

archipelago of Svalbard, Van der Wal and Stien (2014) used the only continuous and long-term

monitoring location for high-arctic biomass measurements to demonstrate that summer

temperature was indeed driving above-ground vascular plant biomass production across habitats, plant functional types and species, and without strong carry-over effects from the previous year's biomass production. At another location in Svalbard, ring-widths of the polar willow *Salix polaris* Wahlenb., a common dwarf shrub with most of its biomass below-ground, was also shown to be primarily driven by the current year's summer temperature (Buchwal *et al.* 2013). Here, we take the unique opportunity of combining the existing plant biomass monitoring time-series (Van der Wal & Stien 2014) with the established methodology for dendrochronology on *S. polaris* shrubs sampled in the same permanent plots. This allows us to test whether retrospective shrub ring growth represents an adequate proxy for annual variation in above-ground biomass production of the species itself and the vascular plant community as a whole.

Methods

Study area

The study area was in Semmeldalen (77°90' N, 15°20' E, 100 m a.s.l.), central Spitsbergen, Svalbard, were a long-term above-ground plant biomass monitoring set-up was established in 1998 (Van der Wal & Stien 2014). This wide U-shaped inland valley has a relatively high primary productivity for such a northern location (bioclimatic zone C: middle arctic tundra, Jónsdóttir 2005). We focused on two widespread habitat types: dry ridge and moist heath (Fig. 1). Ridge habitat was dominated by the dwarf shrubs *Dryas octopetala* and *S. polaris,* and heath habitat by *S. polaris*, the wood rush *Luzula confusa* and the grass *Alopecurus borealis*. In Semmeldalen, the herbivore community comprises the wild and non-herding Svalbard reindeer (*Rangifer tarandus platyrhynchus*), with a doubling population size throughout the study period

(Lee *et al.* 2015), rock ptarmigan (*Lagopus muta hyperborea*) and geese. The increasingly abundant pink-footed goose (*Anser brachyrhynchus*, Madsen *et al.* 2017) notably disrupts wet habitats by pulling out moss to gain access to the extensive below-ground parts of forage species like the grass *Dupontia fisheri*, the rush *Eriophorum scheuzeri* and the forb *Bistorta vivipara* (Anderson *et al.* 2012). From 1985 to 2014 (i.e. our study period), the annual temperature recorded at Svalbard airport (78°25 N, 15°46 E, 30 km from the study area) was on average -4.7°C (min: -8.9°C in 1988, max: -1.7°C in 2006) and the annual precipitation sum was on average 192 mm (min: 92 mm in 1998, max: 265 mm in 2012).

Study species

S. polaris has a circumpolar distribution (http://www.flora.dempstercountry.org/) and is the most widespread shrub species found across Svalbard, in habitats ranging from arctic meadow to polar desert (http://svalbardflora.no/, Rønning 1996; Nakatsubo *et al.* 2010). Its abundance and high digestibility make it an important food resource for herbivores, and especially reindeer (Van der Wal *et al.* 2000; Bjørkvoll *et al.* 2009). The species has been reported to live for many decades, with a mean plant age of around 40 years (Buchwal *et al.* 2013; Owczarek & Opała 2016). The oldest known individual was 120 years old (A. Buchwal, pers. obs.). Therefore, *S. polaris* represents a potential key species for reconstructing long-term, large-scale primary productivity information relevant for studying arctic vegetation and ecosystem dynamics. The above-ground parts of *S. polaris* (i.e. branch tips, leaves and reproductive structures) grow to a height of 2-5 cm and represent a very small proportion of the plant (Fig. 1d). Overall, no more than 5-6% of Svalbard's live vascular plant biomass is above the moss layer (Bardgett *et al.* 2007). The below-ground structure of *S. polaris* can extend several decimetres into the ground and is composed of a root collar (i.e. the oldest part of the shrub) from which develop a network of branches and

roots. Generally, those roots consist of a core root with several thinner lateral roots, but in moist habitats such as meadows and snow beds much more complex or fine-rooted individuals seem to dominate. The reproductive system can be asexual (i.e. cloning through rhizomes) or sexual with both wind and insect pollination (i.e. ambophily, Rønning 1996; Dormann & Skarpe 2002).

Study design

Biomass sampling

In each of the two focal habitats, i.e. ridge and heath, above-ground biomass was sampled in early August in the years 1998-2009 and 2013. In each habitat, five replicated sites were followed over time. Sites were distributed across the landscape within an area of ca. 4.4 km^2 and did not exclude herbivory (see Van der Wal and Stien (2014) for further detail). Above-ground biomass of *S. polaris* and that of all other vascular plant species was estimated for those 10 sites (2 habitats $\times$ 5 sites) by counting shoots of all species in small permanent quadrats (25 cm $\times$ 25 cm; 10 quadrats per site) in all 13 years (Fig. S1). Shoot densities were multiplied with site-specific shoot mass estimates, obtained through destructive sampling at each site at such distance from the small squares to represent the permanent plots well whilst not impacting plant performance therein. In the current study, we used three measures of above-ground biomass: i) *S. polaris* biomass in the two focal habitats, separately and combined; ii) total community biomass, comprising all vascular plant species, in the two focal habitats combined; and iii) total community biomass on a larger scale, i.e. including four other habitats: wet moss, moist grass-dominated and dry *Luzula-Salix* tundra sampled until 2002, and *Dupontia* marsh sampled until 2013.

Shrub sampling and processing

In early August 2015, complete *S. polaris* shrubs (i.e., both above- and below-ground structures)

were carefully excavated from the soil in close vicinity to all heath and ridge biomass sampling sites (Fig. S1). Sampled individuals were separated by a minimum distance of 5 m to avoid sampling of clones. Of all sampled individuals, we selected three shrubs per site, i.e. $n = 30$ shrubs in total, suitable for dendrochronological analysis, i.e. of healthy appearance, with clearly distinguishable root collar, branches and roots, and with fairly straight plant sections appropriate for serial sectioning (Kolishchuk 1990; Myers-Smith *et al.* 2015b, Fig. S1d). We used a GLS-1 sledge microtome (Gärtner, Lucchinetti & Schweingruber 2014) to cut five to six cross-sections per individual shrub: two to three sections from the main root and/or side roots; one section from the root collar; and two sections from the branches. The sectioning was spread along the shrub's parts to avoid bias of e.g. larger ring growth in juvenile branches (Büntgen & Schweingruber 2010). The detailed laboratory preparation of the 15-20 μm thick thin-sections is described in Appendix I.

Chronology building

Ring-widths of each shrub were measured on digital images captured from the thin sections prepared. Each cross-section of a particular part of the shrub was divided into four quarters and within each quarter we randomly drew a radius, excluding injured xylem parts (Fig. S2). Along each radius, we manually measured ring-widths (i.e. the shortest distance between adjacent ring boundaries) starting from the outermost ring to the pith in ImageJ 1.48 (Schindelin *et al.* 2015). Additionally, we visually inspected the entire cross-section for irregular, partially missing rings (i.e. wedging rings, Buchwal 2014). We stopped ring-width measurements at the innermost clearly developed ring and assessed the number of the remaining (usually highly wedging) rings located close to the pith. This step allowed us to correct for an age effect (see below). Because the eccentricity of our cross-sections was moderate, we believe that our four-radii readings of

ring-widths captured individual growth of the specimen well (Buras & Wilmking 2014, Fig. S2).

Cross-dating

Arctic shrubs, and in particular *S. polaris*, are known to restrict their growth under harsh conditions, forming irregular, wedging rings that can be absent in part of the shrub or, more rarely, entirely missing (Buchwal *et al.* 2013). Given these challenges and to ensure correctly established ring growth chronologies, we adopted the serial sectioning method (Kolishchuk 1990) to allow multilevel cross-dating (Buchwal 2014; Myers-Smith *et al.* 2015b). We conducted three levels of cross-dating: 1) cross-dating between the four radial measurements within a single cross-section; 2) cross-dating between all five to six cross-sections of one shrub, to obtain a mean growth curve for an individual shrub; and 3) cross-dating between individual shrubs' mean growth curves within a site, to obtain site-specific mean growth curves (obtained with linear mixed-effects models, see below). To ensure the highest quality of cross-dating, we moved back and forth between these three levels of cross-dating to detect all missing rings. The three levels of cross-dating are detailed in Appendix I and Fig. S2.

Chronology standardisation

Tree-ring standardisation aims to remove biological trends from growth time-series that are caused by e.g. age and/or geometry. A variety of methods exists to account for age-driven mean growth variation (Fritts 1976; Cook & Kairiukstis 1990; Helama *et al.* 2004; Sullivan *et al.* 2016). We first investigated the effect of age on raw ring-widths by plotting mean growth curves of all cross-sections aligned by cambial age (i.e. biological age) in R version 3.3.2 (R Core Team 2016), package 'dplR' (Bunn 2008). The cambial age curve showed a typical juvenile effect, with higher ring-widths at a young age (Fig. S3a). This pattern was caused by geometry, i.e. the further away from the pith a ring is formed, the greater area has to be covered by the xylem, so

that, inevitably, ring widths become thinner and thus may seemingly decrease with age (Cook & Kairiukstis 1990; Biondi & Qeadan 2008). We accounted for this geometric constraint by transforming ring-width measures to basal area increments (μm^2) (Biondi & Qeadan 2008; Buras & Wilmking 2014), using the mean growth curve constructed for each cross-section. Plotting basal area increments series against cambial age, we observed a slight but constant increase with age (Fig. S3b). Therefore, the final standardisation step consisted of detrending basal area increment series using the regional curve standardisation method (Briffa & Melvin 2008) with a 20-year-windows cut-off. Combined, those standardisation approaches ensured that all possible age effects were eliminated, which in turn resulted in a dimensionless Ring-Width Index (RWI; hereafter simply called 'ring growth', Fig. S3c). We additionally ran our analyses with other standardisation methods leading to similar results (Table S1). The year of sample collection (2015), i.e. the outermost ring, was excluded from the analyses since the secondary growth of this particular year had not always completed at the time of sampling (Fig. 1e). Growth curves were also truncated to ensure a sufficient number of cross-sections for each year, resulting in maximum number of chronologies over the period 1985-2014 (Appendix I). To calculate standard dendrochronology statistics (see below), we combined all individual shrubs' mean growth curves to derive an overall mean *S. polaris* chronology for the study area. We computed this final chronology with the 'chron' function in R package 'dplR' using arithmetic means. However, note that in all other analyses (i.e. related to above-ground biomass and climate), we used mean growth curves (at the habitat or study area level) obtained from linear mixed-effects models, which enabled us to account for spatial dependency and random variation due to the nested structure of the study design (see below and Fig. S1).

Descriptive statistics, commonly used in dendrochronology, of the truncated ring growth

time-series were computed with the functions 'rwi.stats' (R package 'dplR') and 'RwlInfo' (R package 'detrendeR', Campelo, García-González & Nabais 2012). We reported the mean correlation between individual growth curves ($r_{bar.tot}$), the mean correlation between cross-sectional growth curves within individual shrub ($r_{bar.wt}$), and the mean inter-series correlation between growth curves of all shrubs ($r_{bar.bt}$). Additionally, we evaluated how closely the constructed mean *S. polaris* chronology represents a hypothetical chronology based on an infinitive number of cross-sections, with the so-called Expressed Population Signal statistic (EPS, Wigley, Briffa & Jones 1984; Cook & Kairiukstis 1990).

Statistics

Estimating ring growth and above-ground biomass

Standardised ring growth (see above) and above-ground biomass had similar (right-skewed) distributions with only a few large values (Fig. S4). To obtain normal distribution and constant variance in the model residuals, both measures were square-root transformed for analysis.

We ran linear-mixed effects models using the 'lmer' function (R package 'lme4', Bates *et al.* 2015). This modelling approach is recommended when analysing replicated data collected in a nested design (Cnaan, Laird & Slasor 1997, Grafen & Hails 2002, Zuur et al. 2009); first, to account for the non-independency of replicates within a nested level; second, to correctly partition the within- and between- variation in the different ecological levels sampled (Fig. S1); third, to give the correct weight to each observations when the sampling design is unbalanced (for instance, this applies here to sampling of total biomass across habitats, since the six habitats were not all monitored over exactly the same period). Using ordinary linear models based on all measurements would violate assumptions of measurements independence, resulting in too small standard errors. Instead, using linear mixed-effects models, we included a random intercept

structure (i.e. variation in mean between replicated units) composed of year and individual shrub (for ring growth estimations) or plot (for biomass estimations) nested within site, which in turn was nested within habitat. We used linear mixed-effects models in two types of analysis. First, to estimate mean ring growth (1985-2014) and mean biomass production (1998-2009, 2013) over the study period, both in total and by habitat, we only included the intercept and the hierarchical structure as random effect (variance partitioning reported). Second, to estimate annual ring growth and biomass time-series for the study area, we included year as a fixed factor and extracted yearly coefficient estimates. By a similar way, we added the interaction year × habitat to obtain annual estimates per habitat. Factors included as fixed effects were excluded from the random intercept structure described above. From these models, we reported mean estimates with associated 95 % confidence intervals, obtained from 1000 bootstrap iterations ('bootMer' function in R package 'lme4'). In further analyses (see below) we used the time-series estimates obtained from these linear mixed-effects models.

Trends over time were fitted with linear models, and 95 % confidence intervals were obtained from 1000 bootstrap iterations with the 'Boot' function within the R package 'car' (Fox & Weisberg 2011). Trend coefficients and annual biomass estimates were reported on the back-transformed scale (using the delta method) for ease of interpretation of effect size. However, Pearson's correlations (*r*) and *t*-tests were always calculated and reported on the square-root scale.

Estimating climate effects on ring growth

The closest weather station with long-term temperature and precipitation data is located 30 km north of the study site, at Svalbard airport (78°25 N, 15°46 E), at the coast. Daily mean temperature (°C) and total precipitation sum (mm) data for this station were obtained from the

Norwegian Meteorological institute (http://eklima.met.no). We considered the following six weather variables: onset of winter (Julian day); end of winter (Julian day); snowfall (mm); rain-on-snow (mm); summer temperature (°C); and summer precipitation (mm). We defined the onset of winter as the (Julian) day when a 10-day forward moving window averaged below 0°C for the first time in autumn (and stayed below 0°C for $\geq$ 10 days); for the end of winter (and therefore onset of spring) the opposite was used. For the winter period (i.e. from November to April), we defined snowfall (mm) and rainfall ['rain-on-snow', log(mm)] as the precipitation falling at temperatures < 1°C and ≥ 1°C, respectively (Hansen *et al.* 2013).

The model selection was performed using linear mixed-effects models to identify the main climatic variables driving shrub ring growth. The full model contained the six weather variables listed above and previous year's ring growth to detect possible carry-over effects. In addition, the interaction between the previous year's ring growth and summer temperature and precipitation was included. To test for possible habitat effects we proposed an interaction of habitat with the previous predictors presented (i.e. up to three-ways interactions, see summary of all proposed predictors in Table S2). The hierarchical study design was accounted for in the random effect structure described above.

Pearson's correlation is commonly used in climate-ring growth relationship analysis, covering climate variables for all months of the year and even including prior years. However, including numerous predictors can, by chance, select one or several as statistically significant without a priori biological support (Peres-Neto 1999). Thus, we only adopted this hypothesis based procedure (using the function 'dcc' from the R package 'treeclim', Zang & Biondi 2015) to investigate preliminarily, for temperature and precipitation, which combination of summer months (June, July, August, June-July, July-August, June-July-August) best captured ring

growth (Fig. S5). For the full period 1985-2014, June-July-August mean temperature (hereafter referred to as 'summer temperature') best explained *S. polaris* ring growth . None of the summer month combinations for precipitation sum were significantly correlated to ring growth, and in the model selection (below) we therefore decided to use the same summer month combination as for temperature (Fig. S5). For this period, the mean summer temperature was 5.2°C (min: 3.6°C in 1987, max: 6.4°C in 2007, Fig. 2) with a significantly increasing rate of 0.06 [0.03:0.08] °C per year ($t = 4.27$, $P < 0.001$). The summer precipitation sum was on average 48.7 mm (min: 14.4 mm in 1998, max: 122.7 mm in 2013) and did not change significantly over time (0.13 [-0.70:1.59] mm/year, $t = 0.26$, $P = 0.80$).

The function 'dredge' from the R package 'MuMIn' (Barton 2013) was used for model ranking based on the parsimony principle of the corrected Akaike Information Criteron (AICc, Burnham & Anderson 2002). This ranking approach utilises maximum likelihood, as opposed to hypotheses testing, and therefore is not subject to issues of multiple testing like in Pearson's correlation (see above). All predictors' pairwise correlations were relatively low ($r < 0.5$) and all proposed interactions were considered to be biologically meaningful. Estimates from the top model were obtained using restricted maximum likelihood. Residual distributions were investigated for normality and homoscedasticity.

Results

Ring growth in time and space

Robust *S. polaris* ring growth curves were constructed for the period 1985-2014 in

Semmeldalen, central Spitsbergen, Svalbard (Fig. 2). Because above-ground biomass

measurements were taken in 1998-2009 and 2013, this resulted in an overlap of 13 years for

which the two measurements could be compared for the same study area (Fig 2). The ridge

habitat tended to have younger plants (25 ± 7 years, mean ± sd) than the heath habitat (30 ± 8

years). Both ring growth and vegetation biomass time-series demonstrated high inter-annual

variation, with 1998 and 2007 standing out as highly productive years and 1999 and 2008 as

relatively unproductive years. Descriptive chronology statistics revealed limited annual growth

variability within an individual shrub ($r_{bar.wt} = 0.65$), but rather high growth variability between

shrubs ($r_{bar.bt} = 0.21$). Mean correlation between individual growth curves was relatively low

($r_{bar.tot} = 0.22$), but despite this the Expressed Population Signal for the period 1985-2014 was

high (EPS = 0.90). Thus, the chronology was considered highly applicable for reliable

comparison with above-ground biomass measures.

In line with the small stature of the species, *S. polaris* had very small root-collars,

between 1.5 and 4.1 mm in diameter (bark excluded). Annual mean raw ring-widths were

therefore likewise small (0.045 [0.035:0.053] mm, mean [95 % confidence interval], Table 1),

and there was no significant difference in annual ring growth pattern between heath and ridge

habitat ($t = 1.55$, d.f = 55, $P = 0.13$). Over the period 1985-2014 ring growth increased over time;

yet, this positive trend was only found for heath habitat (Table 1). Despite this difference in

trends between the habitats, ring growth in heath and ridge co-fluctuated over time ($r = 0.42$

[0.04:0.69], $t = 2.29$, d.f = 25, $P < 0.05$, Fig. S6), indicating shared drivers of annual growth.

Above-ground biomass in time and space

The estimated annual mean above-ground biomass production of *S. polaris* was 17.9 [10.7:27.3] g/m^2 (Table 1), and larger in heath than ridge habitat ($t = 3.58$, d.f =22, $P < 0.01$, Fig. S6). From 1998 to 2013, the overall tendency for a positive trend was non-significant; yet, biomass in ridge habitat increased over time (Table 1, Fig. S6). Ridge and heath biomass co-fluctuated during the period 1998-2009 ($r = 0.61$ [0.05:0.88], $t = 2.41$, d.f = 10, $P < 0.05$), but not significantly when also including 2013 (no biomass monitoring took place in 2010-2012, Fig. S6).

About half of the total vascular plant above-ground biomass in heath and ridge habitat was composed of *S. polaris* (Table 1). Like for *S. polaris* biomass, the annual biomass production of vascular plants differed between these two habitats ($t = -5.45$, d.f = 24, $P < 0.001$). Total biomass in ridge habitat increased over time (Table 1). Over all six habitats monitored, the mean above-ground vascular plant biomass was 37.0 [29.9:45.1] g/m^2 and showed no clear trend over time (Table 1).

Ring growth versus above-ground biomass production

When combining measurements from ridge and heath, ring growth and above-ground biomass of S. *polaris* were positively correlated (r = 0.56 [0.01:0.85]), demonstrating that variation in ring growth reflects variation in above-ground biomass in this high-arctic shrub (Figs. 3c and 4). Both measures were significantly positively related to summer temperature, suggesting this climate variable as the overall driver of *S. polaris* growth (Table 2, Figs. 3a and 3b). When inspecting patterns by habitat, the strength of these relationships dropped. The relationship between *S. polaris* above-ground biomass and summer temperature for heath habitat was no longer significant due to an outlying point (year 2013, Fig. 3h), whilst for ridge habitat this relation remained strong (Fig. 3e). The opposite was the case for the relationship between ring growth

and summer temperature, which weakened for ridge but remained strong for heath (Figs. 4d and 4g). Thus, habitat-specific correlations between ring growth and biomass of *S. polaris* were weakened (Figs. 4f and 4i).

Indeed, when partitioning variance across the different nested ecological scales (i.e. random effects, Table 3), greatest variability in ring growth and above-ground biomass measurements of *S. polaris* was found at the smallest spatial sampling scale, i.e. at individual plant and plot level, respectively. Although *S. polaris* biomass variability was still considerable at the site level, random variation (i.e. in intercept) at the habitat level was small (Table 3).

When accounting for heterogeneity emerging across these different levels, and thus moving to higher levels of the hierarchical sampling design, the relationships between *S. polaris* ring growth and above-ground biomass are clear. Interestingly, when replacing *S. polaris* above-ground biomass with that of the total vascular plant community, first for ridge and heath habitat combined (r = 0.67 [0.19:0.89]), and then for all six habitats combined (r = 0.70 [0.25:0.90]), *S. polaris* ring growth reflected vascular plant biomass increasingly well (Fig. 4). Even when removing *S. polaris* from the biomass of all habitats, the correlation remained strong (r = 0.68 [0.21:0.90]).

Climate effects on ring growth

Model selection retained summer temperature as the main weather variable (positively) associated with ring growth, being selected in all models with ΔAICc < 2 (Table S3). Additionally, the summer temperature effect interacted with last year's ring growth (Table 2, Fig. S7a). In warm summers, growth was less influenced by the previous years' ring growth compared to in cold summers. In other words, after a year of low ring growth, the positive effect

of summer temperature was more pronounced than when the previous year had a large ring growth. The top ranked model also suggested that the positive effect of previous year's ring growth was less pronounced in ridge than in heath habitat (Table 2, Fig. S7b).

Discussion:

By constructing shrub chronologies and combining those with existing long-term time-series of *in situ* plant biomass production, we were able to reveal on an annual bases, how well retrospective ring growth represents above-ground production of not only the focal shrub but also the vascular plant community as a whole (Figs. 2 and 4). By doing this, we demonstrated that, with sufficient replication across spatial scales and successful stepwise cross-dating, ring growth of the widespread and highly abundant polar willow *S. polaris* can adequately capture patterns of local above-ground primary production. Accordingly, both ring growth and above-ground biomass fluctuations of *S. polaris* were controlled by the same climate driver, i.e. summer temperature, and no evidence was found for opposing investment in secondary growth versus above-ground biomass, as could be expected under strong energy allocation trade-offs.

Multilevel sampling over successive years enabled us to partition out plant trait variation that exists at different spatiotemporal scales (Messier, McGill & Lechowicz 2010; Galván *et al.* 2014; Van der Wal & Stien 2014, Table 3). Shrub ring growth and above-ground biomass were highly variable at the smallest spatial sampling scale, i.e. among individual plants or sampling plots within sites, respectively. These levels were the sampling units and thus also included variation due to measurement error. However, with the high level of replication of ring growth measures within plants (i.e. four radii within each five to six cross-sections per shrub) and high

shoot densities of *S. polaris* within 'biomass plots', we expect the effect of measurement errors to be small. By contrast, variability due to micro-habitat conditions will be great, as large differences in plant cover in the high Arctic typically occur already within metres (Armbruster *et al.* 2007). Consequently, this likely increased the variance within a site when correlating ring growth and above-ground biomass of *S. polaris*, since a shrub sampled for dendrochronological measurements was several metres away from the plots sampled for biomass measurements. Accounting for multilevel spatial variation (i.e. plot or individual nested within site, nested within habitat) captured to a considerable extent micro- and macro-habitat variation arising from a patchy topography with different biotic and abiotic characteristics. Acknowledging such multiple sources of variation strengthens the ecological insight and inference, and allowed us to reveal a remarkably high correlation between ring growth of a single shrub species and the annual biomass production of the total vascular plant community (r = 0.70 [0.25:0.90]). Although insufficiently researched, current evidence suggests that ring growth may well be a proxy of primary production throughout the alpine and Arctic biome. For instance, in the Alps, Anadon-Rosell *et al.* (2014) reported a positive correlation between ring growth and biomass of new shoots in three shrub species, although based on a single year and single location of measurements only. Furthermore, studies utilising remotely sensed vegetation production maps found positive correlations between NDVI-based plant productivity and ring growth across the low Arctic: *Salix lanata* from the Russian Arctic (Forbes *et al.* 2010, Macias-Fauria *et al.* 2012); *Betula pubescens* from Northern Sweden (Babst *et al.* 2010); and *Salix pulchra* and *Cassiope tetragona* from Northwest Canada (Weijers *et al.* 2018).

While our results confirm dendrochronology as a promising tool to reconstruct fine-scale past vascular plant biomass of tundra ecosystems, constructing a ring growth curve from small

and highly irregularly growing shrubs in a harsh arctic environment is challenging (Wilmking *et al.* 2012; Buchwal 2014). Buchwal *et al.* (2013) estimated that in their dendrochronological study on *S. polaris* in another Svalbard location, on average 14 % of the rings were partially missing from cross-sections, while 11 % were completely missing. Despite these common irregularities, a persistent search for missing rings, which included their detection and verification during a stepwise cross-dating procedure (i.e. within and between shrubs, Fig. S2), enabled us to develop a reliable chronology with an EPS-value above the commonly accepted threshold of 0.85 (Wigley *et al.* 1984). The mean within- and between-plant correlation ($r_{bar.tot}$ = 0.22) was lower than in another Svalbard species with a more regular growth pattern such as *C. tetragona* ($r_{bar.tot}$ = 0.32, Weijers *et al.* 2012). In accordance with the variance partitioning of the linear mixed-effects models at the individual plant level, the low correlation between individual plant growth curves ($r_{bar.bt}$ = 0.21) also reflects the numerous disturbances that the shrubs have to cope with during their lives in this stressful environment located at the distributional margin of woody plants (Crawford 2008; Wilmking *et al.* 2012).

In this harsh environment for woody plants growth, we found one weather variable – summer temperature – that stands out as main driver of both the vascular plant community's above-ground biomass and *S. polaris* below-ground ring growth. This is in line with previous findings across arctic and alpine shrubs (Forbes *et al.* 2010; Elmendorf *et al.* 2012; Buchwal *et al.* 2013; Van der Wal & Stien 2014; Myers-Smith *et al.* 2015a; Weijers *et al.* 2017; Ackerman et al. 2018; Weijers *et al.* 2018). Sun exposure has also been suggested to potentially influence *S. polaris* ring growth on Svalbard (Owczarek & Opała 2016), and that of the net above-ground production of tundra vascular plants in general (Wiegolaski *et al.* 1981; Muraoka *et al.* 2008; Van der Wal & Hessen 2009). Van der Wal and Stien (2014) found a negative relationship

between cloud cover and summer temperature in our study area, suggesting that temperature could be a good index of photon flux density necessary for carbohydrate production in the photosynthetic process (Muraoka *et al.* 2008). Nonetheless, in addition to carbohydrates, favourable tissue temperature and the presence of auxin hormones trigger xylogenesis, i.e. the cambial activity that leads to the formation of annual ring growth. More specifically, temperature influences the flux of auxins, which in cold or short summers likely does not reach all parts of the shrub (Sundberg, Uggla & Tuominen 2000; Wilmking *et al.* 2012). Air temperature is thus tightly connected to the physiological processes required for ring growth, and therefore, not surprisingly, a driver of shrub growth.

More surprisingly, recent dendrochronology studies from Greenland and Svalbard report on a deviation from the aforementioned clear and positive summer temperature responses (Forchhammer 2017; Gamm *et al.* 2017; Opała-Owczarek *et al.* 2018). In a coastal site in Svalbard, with twice as high precipitation levels as our inland site, Opała-Owczarek *et al.* (2018) proposed that soil moisture and soil structure have a larger influence on *S. polaris* ring growth than temperature. Water availability through precipitation did not appear to influence *S. polaris* growth in our study, with the possible exception that the extremely rainy summer in 2013 resulted in a prominent reduction in heath habitat's above-ground biomass. Furthermore, in spite of increasing summer temperatures, Gamm *et al.* (2017) observed a temporal decline in ring growth in continental Western Greenland for *Betula nana* and *Salix glauca*. They suggested this could be due to increased defoliation from herbivory and increasing moisture limitation. Likewise, Forchhammer (2017) reported an overall decline in *B. nana* ring growth but related this to a decrease in June sea ice extent instead. While the latter study implicates summer temperature effects only indirectly through correlation with sea ice extent, the reported effects

were weak on Svalbard, possibly because of carry-over effects (i.e. previous year's growth). Accordingly, we show that ring growth was less (positively) influenced by the previous years' ring growth during warm summers, compared to cold summers. This indicates an increased likelihood of using available storage resources (i.e. from last year's growth) when conditions are unfavourable.

Secondary growth in biomass production of shrubs is often overlooked. Especially shrubs' below-ground growth – the "hidden part of the iceberg" – has received little attention so far (Bret-Harte *et al.* 2002; Iversen *et al.* 2015). However, a substantial proportion of the biomass of our study species is situated below-ground, even branches are nested into the ground (Fig. 1). Woody tissues have much higher C:N ratio than leaves, and especially in the High-Arctic, are mostly located below-ground and are represented by strong positive root-to-shoot ratio (> 4, Mokany, Raison & Prokushkin 2006; Iversen *et al.* 2015). Therefore, shrubs' below-ground growth importantly contribute to the large storage of carbon. Considering only above-ground woody structures may result in an underestimation of carbon storage in tundra soils (Iversen *et al.* 2015). According to our results, below-ground carbon storage may vary greatly annually as a function of temperature. A recent study by Berner *et al.* (2018) roughly estimated large-scale tundra below-ground biomass from above-ground measurements, but clearly, further studies are needed to establish which mechanisms control below-ground growth dynamics including both primary (length and ramification architecture) and secondary growth (but see Wang *et al.* 2016; Blume-Werry *et al.* 2018). Starting to fill up this knowledge gap, our work on secondary growth (i.e. below-ground) inform on the annual green biomass available for higher trophic levels (i.e. above-ground). Therefore, this can make the link to more extensively studied topics like plant-herbivore interaction, were robust annual vegetation production time-series are too often

missing.

Given that *S. polaris* forms a major component of the diet of Svalbard reindeer (Van der Wal *et al.* 2000; Bjørkvoll *et al.* 2009), it could well be that herbivory influences ring growth in this dwarf shrub, with possible carry-over effects. Simulated grazing was shown to reduce leaf biomass production in the following summer (Skarpe & Van der Wal 2002). Although *S. polaris* constitutes around half of the total above-ground vascular plant community biomass at our study location, the browsing impact on the sampled shrub is expected to be highly stochastic, in space and between years. Thus, when including annual reindeer numbers (Lee *et al.* 2015), corresponding to approximately 6 animals/km^2, in our model testing for climate effects (truncated to the reindeer abundance time-series 1994-2014), we found no strong evidence for a reindeer density effect on *S. polaris* ring growth (Table S4). Conversely, in this bottom up system, we do expect our measurements of *S. polaris* annual growth to represent the plane of nutrition for reindeer and other herbivores at a larger scale. In line with that expectation, Albon *et al.* (2017) found that reindeer body mass in autumn was positively related to annual total above-ground biomass estimates from our sampling sites. Accordingly, there is not only considerable potential to use *S. polaris* ring growth as a proxy for large-scale biomass production, but also to inform ecosystem ecological questions such as carbon and nutrient cycling, and energy flow through high-arctic food webs. Ring growth proxies may therefore complement other data types in community-dynamic studies but are also particularly useful in remote places where climate or vegetation data are not available.

In conclusion, while shrub dendrochronology is increasingly used across the circumpolar Arctic to compensate for the lack of local climate or vegetation productivity time-series, this

study demonstrates *in situ* that annual ring growth curves can indeed reliably track past vascular plant productivity. This opens new opportunities for ecosystem-based monitoring and retrospective studies of community dynamics under climate change, particularly in study areas where time-series are available for higher trophic levels. However, detecting ecological signals of climate (change) using shrub dendrochronology clearly requires rigorous search of wedging or missing rings, as well as sampling replication across the landscape, thereby accounting for the large habitat variation characterising high-arctic landscapes.

Author contributions:

MLM, BBH and RvdW conceived the ideas and designed methodology; MLM, RvdW and LS collected the data; MLM, LS and AB conducted the laboratory work; MLM and BBH analysed

the data; MLM wrote the manuscript, with the help of all co-authors.

Data accessibility:

Data deposited in the Dryad repository:
http://datadryad.org/resource/doi:10.5061/dryad.d7p3b40 (Le Moullec et al., 2018)

Tables & Figures

Table 1. Summary of mean ring growth and plant biomass estimates [and 95 % confidence intervals] and their trends over the time period studied; for the two focal habitats (Heath and Ridge) separately and combined, and for plant biomass of six habitats together. Mean estimates of *S. polaris* ring growth are based on (raw) ring-widths (in mm), whilst trends in *S. polaris* ring growth are based on Ring-Width Index (RWI) corrected for age and geometry effects. Reported estimates were square-root back-transformed. Trend coefficients (Trend) and their associated 95% confidence intervals (from 1000 bootstrap iterations) were calculated with linear models fitted to back-transformed mean-estimate time-series.

		Heath	Ridge	Both heath and ridge	All habitats
S. polaris ring-width 1985-2014	Mean estimates (mm)	0.04 [0.03:0.05]	0.05 [0.04:0.06]	0.05 [0.04:0.05]	-
	Trend (RWI/year)	0.03 [0.02:0.04]	<0.01 [-0.01:0.02][a]	0.02 [0.01:0.03]*	-
S. polaris biomass 1998-2013	Mean estimates (g.m^{-2})	21.3 [10.3:35.6]	14.7 [5.6:26.6]	17.9 [10.7:27.3]	17.1 [11.2:24.7]
	Trend (g.m^{-2}/year)	0.1 [-0.8:1.0]	0.6 [0.3:1.2]	0.4 [-0.3:1.1]	0.2 [-0.3:1.0]

| All vascular plants | Mean estimates (g.m^{-2}) | 36.8 [26.7:49.4] | 24.0 [15.7:33.9] | 30.1 [19.3:43.5] | 37.0 [29.9:45.1] |
| biomass 1998-2013 | Trend (g.m^{-2}/year) | 0.4 [-1.2:1.7] | 0.9 [0.2:1.6] | 0.7 [-0.4:1.7] | 0.8 [-0.6:2.1] |

[a]1988-2014

* Still increasing trend when considering the same time scale as the biomass measurements 1998-2013

Table 2. Parameter estimates β with their associated 95% confidence interval (from 1000 bootstrap iterations) and test statistics (*t* and *P* values) of the top ranked model (using restricted maximum-likelihood) from model selection, of *S. polaris* Ring-Width Index (RWI) during the period 1985-2014. The response variable RWI (and the explanatory variable RWt-1, previous years' ring growth) is on the square-root scale.

Parameter	β	*t*	*P*
Intercept (heath as reference)	-0.52 [-1.07:0.02]	-1.88	0.06
Summer temperature (°C)	0.23 [0.13:0.33]	4.52	<0.001
Habitat (ridge)	0.16 [-0.07:0.39]	1.26	0.23
RWI_{t-1}	0.67 [0.15:1.20]	2.59	<0.01
Habitat (ridge) $\times$ RWI_{t-1}	-0.17 [-0.33:-0.03]	-2.32	<0.05
Summer temperature $\times$ RWI_{t-1}	-0.08 [-0.18:0.01]	-1.82	0.07

Table 3. Variance partitioning across the different nested ecological factor (i.e. random effects) in a linear mixed-effects model where no fixed effects (other than the intercept) were included. All three response variables, *S. polaris* Ring-Width Index (RWI, 1985-2014), *S. polaris* above-ground biomass (from heath and ridge habitats combined) and total plant community above-ground biomass (1998-2009, 2013), were analysed on the square root scale. Numbers in parentheses represent the number of levels associated with each ecological factor.

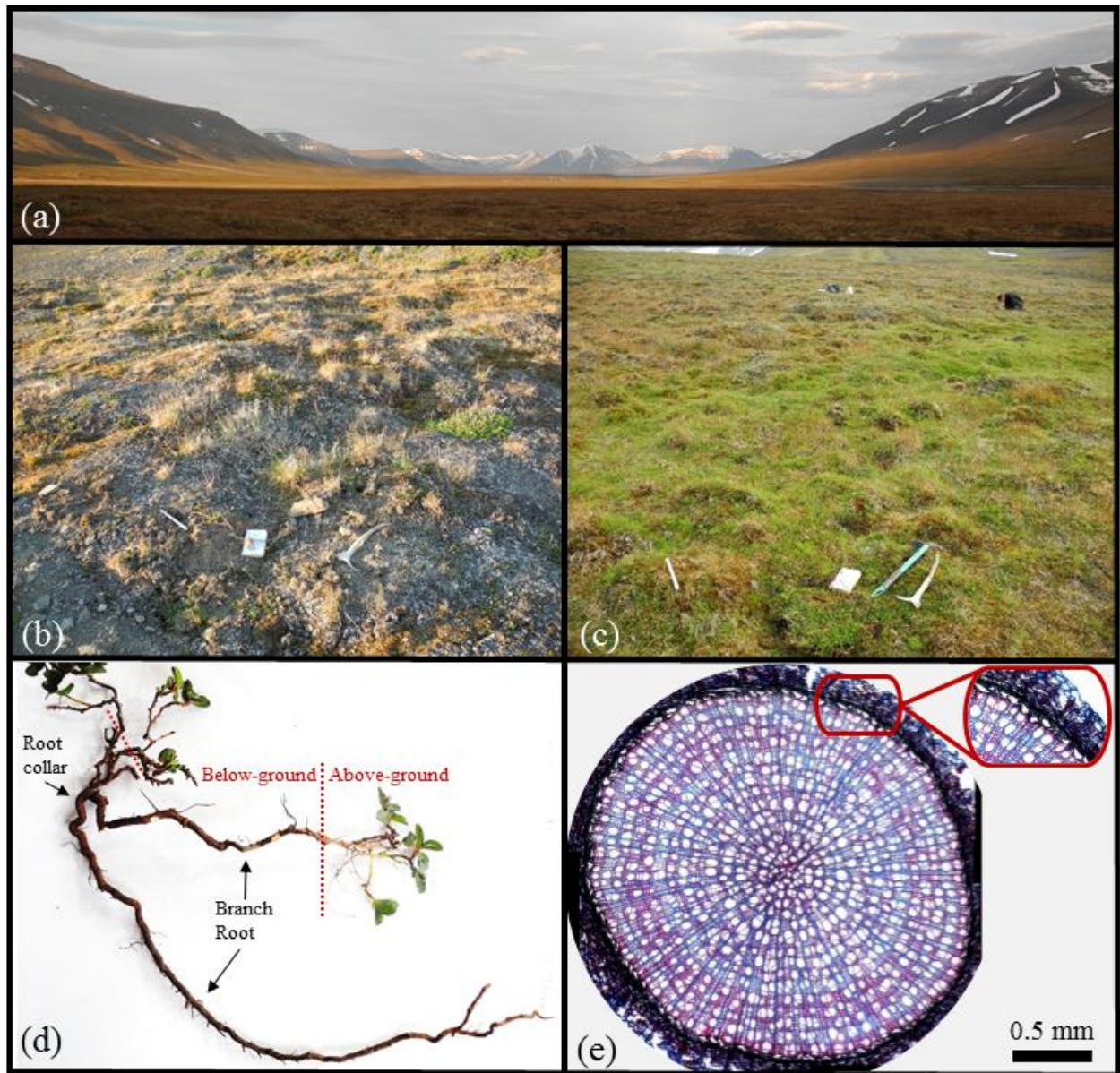| Ecological factor	Variance		
	S. polaris RWI	*S. polaris* biomass	Community biomass
Plant or Plot	0.04	0.12	0.08
	(30)	(94)	(272)
Site	0.01	0.15	0.05
	(10)	(10)	(28)
Habitat	<0.001	<0.001	0.02
	(2)	(2)	(6)
Year	0.03	0.01	0.02
	(30)	(13)	(13)
Residuals	0.09	0.08	0.04
	(673)	(1159)	(2158)

Figure 1. The study system. (a) The valley of Semmeldalen, central Spitsbergen, Svalbard, in early August 2015. (b) Ridge habitat. (c) Heath habitat. (d) An entire *S. polaris* individual extracted from the ground, illustrating the substantial below-ground part composed of a core root, a root collar and nested branches in the ground. (e) The cross-sectional view of a *S. polaris* root (stained thin-section of 20 μm thickness) with an on average radius of 1.125 mm. Note the outermost darker ring that represents mid-growing season of year 2015, where the cells are not yet fully lignified.
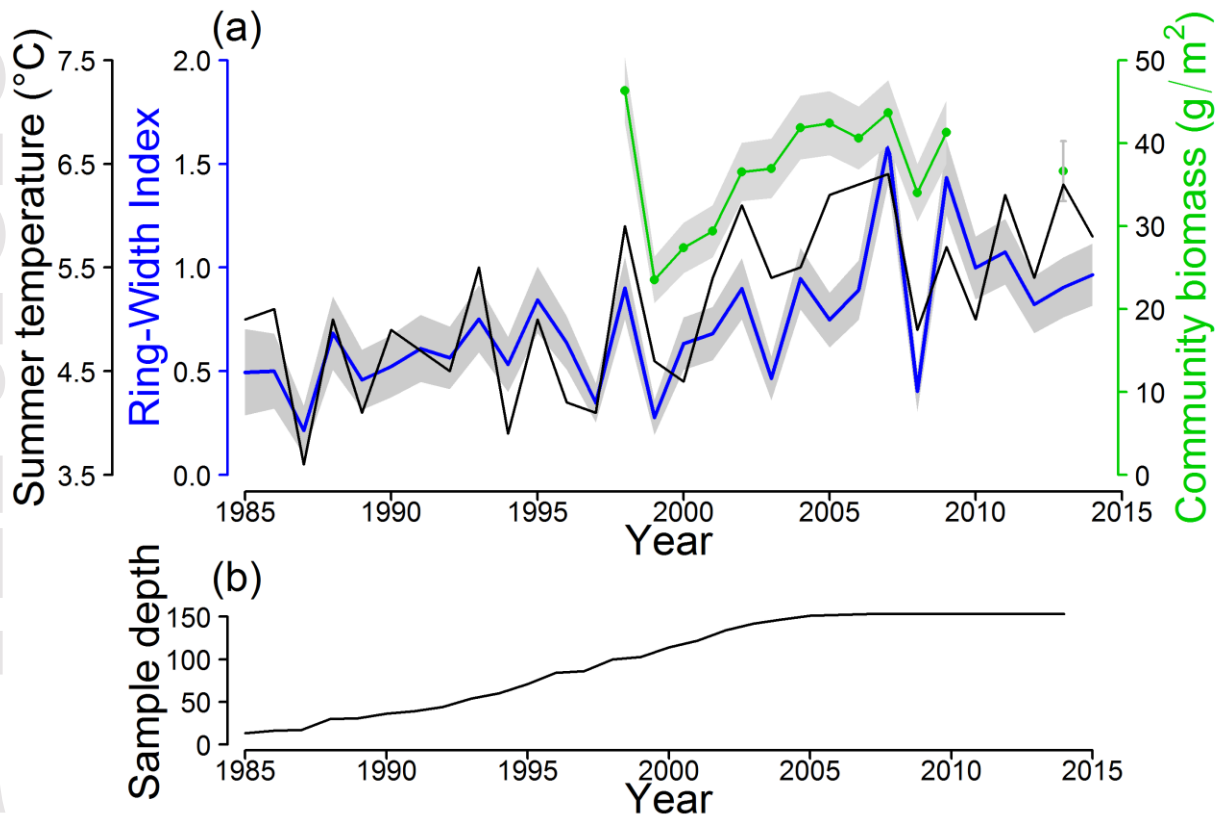
Figure 2. Time-series of (a) the mean *S. polaris* Ring-Width Index (blue line) for the Semmeldalen study location in central Spitsbergen, Svalbard, plotted together with the mean above-ground biomass of the total vascular plant community (green line) and mean summer temperature (June-July-August) (black line). The grey shades represent the standard error of the back-transformed estimates, obtained by fitting linear mixed-effects models that account for the hierarchical sampling structure. (b) The number of *S. polaris* cross-sections (i.e. sample depth) used to establish a chronology across years.
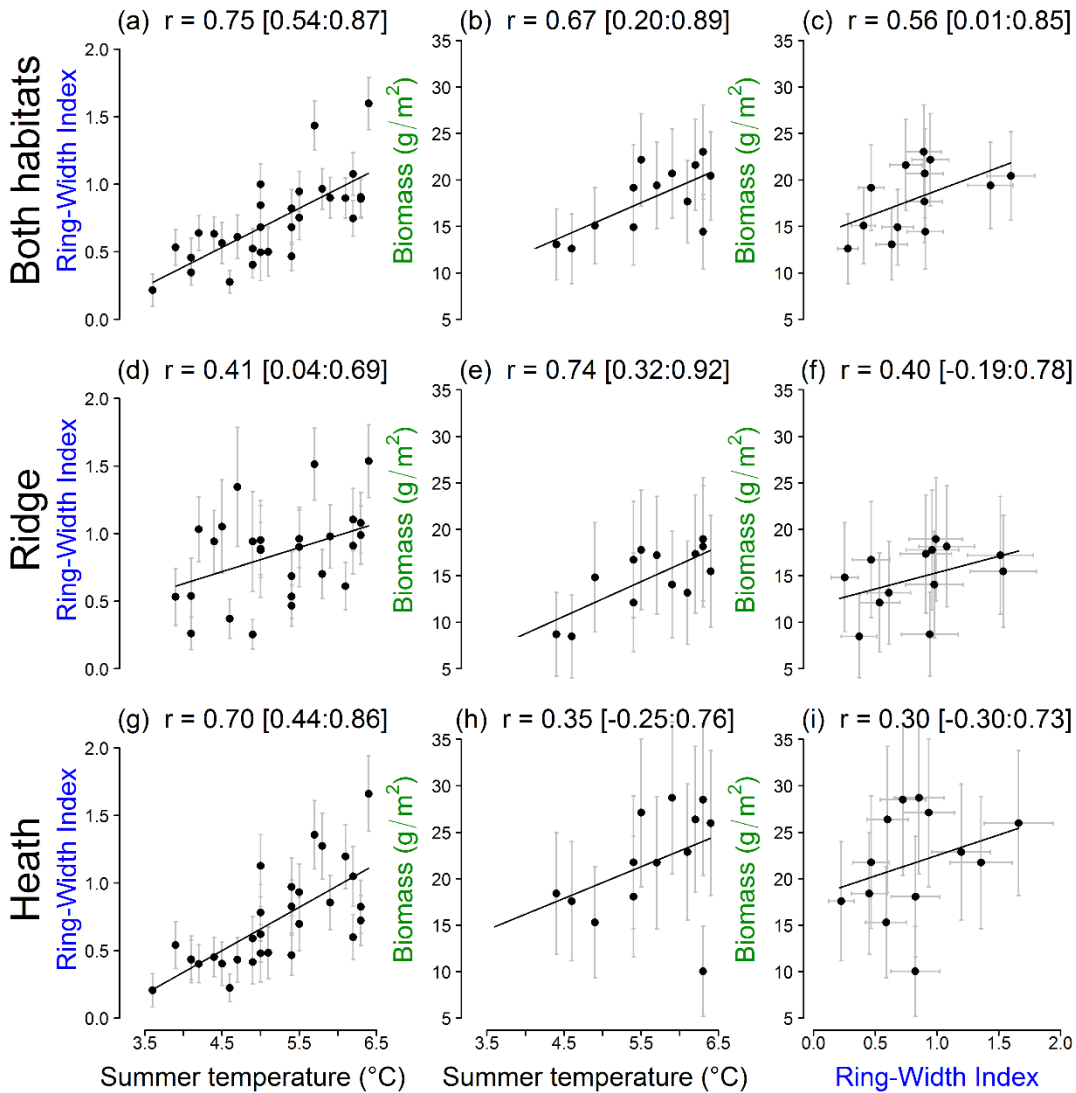
Figure 3. Pairwise relationships between Ring-Width Index of *S. polaris*, above-ground *S. polaris* biomass and summer temperature (June-July-August) for (a-c) both habitats combined and for (d-f) ridge and (g-j) heath separately. Plotted mean values (circles) and associated standard errors (whiskers) were estimates from linear mixed-effects models accounting for the nested structure of the data and back-transformed from the square-root scale. However, note that the correlation coefficients (r) and associated 95% confidence intervals given in each panel were calculated from square-root transformed values.
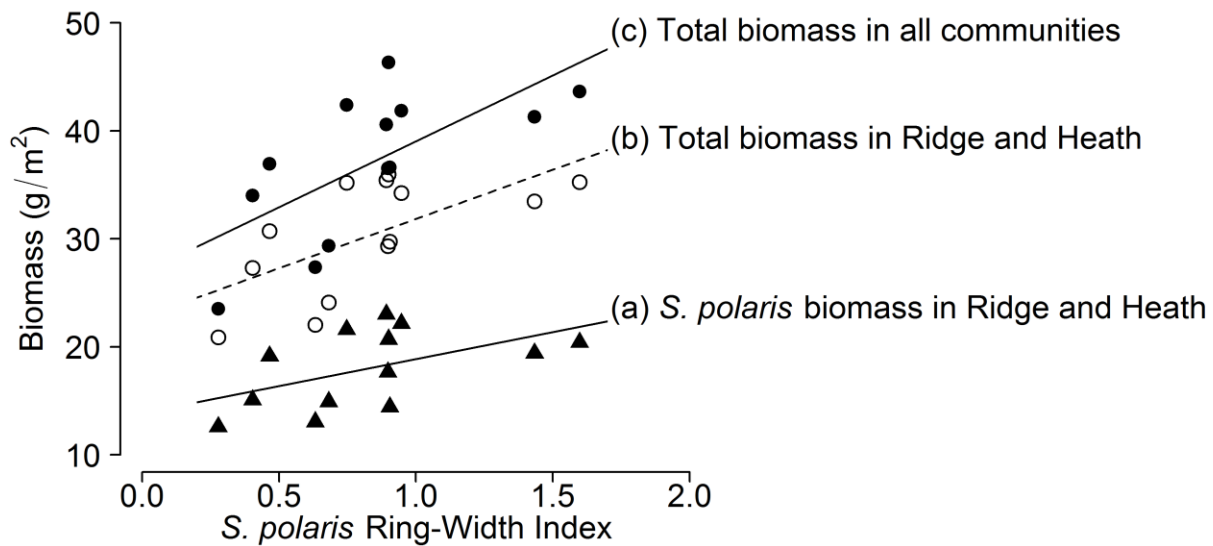
Figure 4. Relationships between *S. polaris* Ring-Width Index (RWI) and above-ground plant biomass. (a) *S. polaris* above-ground biomass versus *S. polaris* RWI in ridge and heath habitats combined (triangles): r = 0.56 [0.01:0.85]. (b) Total vascular plant above-ground biomass versus *S. polaris* RWI in ridge and heath habitats combined (open circles): r = 0.67 [0.19:0.89]. (c) Total vascular plant above-ground biomass in all six habitats versus *S. polaris* RWI: r = 0.70 [0.25:0.90]. Plotted values were estimates from linear mixed-effects models accounting for the nested structure of the data, back-transformed from the square-root scale. The correlation coefficients and 95% confidence intervals reported were calculated from square-root transformed values.

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Supporting information

Additional supporting information is provided in a separated document:

Appendix I. Building the *Salix polaris* ring growth chronology.

Table S1. Comparison of different methods of ring-width standardisation.

Table S2. List of all predictors and their interactions proposed in the model selection step

Table S3. Summary table of the top models (Δ AICc < 2) from the model selection.

Table S4. Summary table of the top ranked models (Δ AICc < 2) from the model selection including reindeer abundance.

Fig. S1. Graphical summary of the balanced sampling design.

Fig. S2. Graphical presentation of the three cross-dating steps performed on *Salix polaris*.

Fig. S3. *Salix polaris* tree-ring chronology standardisation steps.

Fig. S4. Frequency distributions of the data.

Fig. S5. Pearson's correlation coefficients between the *S. polaris* ring growth chronology and summer monthly temperature and precipitation.

Fig. S6. Time-series from the ring growth curves and above-ground biomass of *S. polaris*

estimated for the ridge and heath habitat.

Fig. S7. Graphical representation of interaction effects.