Climate change is most pronounced at high latitudes, where plant and animal populations are often strongly influenced by environmental fluctuations related to climate and weather. Environmental conditions can co-fluctuate over large distances and thereby synchronise primary production in space. However, large-scale studies of such spatio-temporal patterns remain rare in the Arctic, where short time-series and poor spatial replication have characterised the data available on both biotic and abiotic parameters. Here, we use dendrochronological tools to measure ring growth of a dominant dwarf shrub, the polar willow *Salix polaris*, previously found to reliably trace community-level vascular plant biomass production. We investigated climate drivers of vegetation growth and their role in the synchronisation of primary production across the rapidly warming archipelago of Svalbard (n = 8 sites, composed of 17 sub-sites, 0.06–293 km apart). We found contrasting effects of summer versus winter weather on ring growth and its spatial synchrony. Although an overall positive effect of summer temperature caused spatially synchronous growth, negative impacts of winter rain-on-snow events occurred only locally, potentially counteracting such synchrony. However, the anticipated increase in both summer temperature and spatial extent of rain-on-snow events, causing basal ice encapsulation of the vegetation, could change the relative importance of seasons for spatiotemporal dynamics of shrub growth. Because these shrub ring growth chronologies reflect annual fluctuations in total vascular plant biomass, fueling the bottom–up controlled food-web, these results have large implications for our understanding of how climate change shapes tundra ecosystem productivity in time and space.

Keywords: dendrochronology, rain on snow, *Salix polaris*, spatial heterogeneity, Svalbard tundra, vegetation production

Introduction

Global warming and its ecological implications are more pronounced in the Arctic than elsewhere (Post et al. 2009a, CAFF 2013, Larsen et al. 2014). Indeed, plant...
and animal populations at high latitudes are often strongly influenced by climate and year-to-year weather variations (Stenseth et al. 1999, Sæther et al. 2003, Ims and Fuglei 2005, Post et al. 2009b, Hansen et al. 2013, Van der Wal and Stien 2014, Myers-Smith et al. 2015a), making Arctic species particularly susceptible to climate change (Ims and Fuglei 2005, Post et al. 2009b, Ims and Ehrich 2013, Descamps et al. 2017). Climate-induced environmental changes have already altered tundra ecosystems, with potential reinforcing feedbacks on global warming (Zhang et al. 2013). In particular, in spite of a considerable spatial heterogeneity in climate change impacts (Elmendorf et al. 2012a), studies from across the Arctic report overall positive effects of warmer summers on plant growth (Forbes et al. 2010, Van der Wal and Stien 2014, Myers-Smith et al. 2015a, Weijers et al. 2017, Ackerman et al. 2018, Bjorkman et al. 2018). Accordingly, increased vegetation productivity and shrub expansion (i.e. ‘shrubification’) have led to ‘Arctic greening’ (Elmendorf et al. 2012b, Macias-Fauria et al. 2012, Ju and Masek 2016, Vickers et al. 2016). Recently, however, large-scale vegetation damage (‘Arctic browning’) has also been observed and might among other reasons be related to extreme warm spells in winter, which can be accompanied by rain-on-snow events (ROS) (AMAP 2017, Pan et al. 2018, Peeters et al. 2019). In the Arctic where the snow cover is often thin, ROS events can lead to an encasement of plants in basal ice instead of snow (Bokhorst et al. 2008, Phoenix and Bjerke 2016, Bjerke et al. 2017). How such events affect variation in Arctic plants’ growth, as well as vital rates such as recruitment or mortality, spatially and temporally, is still far from understood, and has not been investigated based on long-term time-series data. Climate projections forecast not only warmer summers, but also rainier winters throughout arctic regions (Hansen et al. 2014, Bintanja and Andry 2017). Therefore, disentangling the effects of such contrasting environmental drivers on spatiotemporal patterns of plant growth is crucial for our understanding of large-scale and long-term climate change effects. This is particularly important for ecosystem dynamics, since changes in plant growth could potentially trigger trophic cascades (Wooley et al. 2009).

Fluctuations in weather and climate are often correlated over large distances (Koenig 1999, Koenig 2002, Stenseth et al. 2003). Moran (1953) suggested that the dynamics of animal populations may be synchronised over similarly large spatial scales if they are strongly influenced by these environmental variables (the ‘Moran effect’), Royama (1992, Ranta et al. 1997). This phenomenon is seen in a large variety of taxa, ranging from large herbivores (Stenseth et al. 1999) to viruses (Pitzer et al. 2015), and has been reported for example in rodents (Bjørnstad et al. 1995, Krebs et al. 2002, Ims and Andreassen 2005), herbivores (Grenfell et al. 1998, Groten et al. 2005), insects (Peltonen et al. 2002, Ims et al. 2004, Sheppard et al. 2015), birds (Engen et al. 2005, Sæther et al. 2007, Koenig and Liebhold 2016), fish (Østman et al. 2017) and plankton (Massie et al. 2015, Defries et al. 2016). The concept has also been applied to and observed in plants, noticeable as a synchrony in e.g. recruitment, primary or secondary growth (i.e. radial growth) (Post 2003, Defries and Reuman 2017, Shestakova et al. 2017). Although relatively few studies have so far examined the synchronising role of environmental fluctuations on the dynamics of plant growth, it is a rapidly expanding research area in tree species (Läänelaid et al. 2012, Koenig and Knops 2013, Shestakova et al. 2017). In many plant species, strong direct influence of climatic drivers, such as temperature, on growth can often be expected. This is especially the case in the Arctic (Elmendorf et al. 2012b, Myers-Smith et al. 2015a, Bjorkman et al. 2018), where fluctuations in primary production play an important role in shaping the dynamics of many bottom–up ecosystems i.e. primary producer-controlled ecosystems (Power 1992, Ims and Fuglei 2005, Post et al. 2009b, Wooley et al. 2009). In this biome, on the other hand, in situ time-series of annual plant biomass production covering a large spatial range are rare, because of difficult logistics associated with long-term, large-scale monitoring programs. However, this is now changing due to the rapid development of dendrochronology applicable to shrubs (Myers-Smith et al. 2015b), as well as of proxy for vegetation productivity maps from remote sensing, such as normalized difference vegetation index (NDVI) (Forbes et al. 2010, Blok et al. 2011, Macias-Fauria et al. 2012, Tape et al. 2012, Weijers et al. 2018b).

Recently, in a study from central Svalbard, Le Moullec et al. (2019) showed that annual secondary growth in the polar willow Salix polaris, a widespread dwarf shrub and important food resource for herbivores in the high-arctic tundra ecosystem of Svalbard (Rønning 1996, Bjørkvell et al. 2009), can be used as a proxy for above-ground biomass productivity of the entire vascular plant community. Single-site studies from central parts of Svalbard have indicated that annual fluctuations in summer temperature largely determine the year-to-year variation in S. polaris secondary growth (Buchwal et al. 2013, Le Moullec et al. 2019), as well as the above-ground biomass production of vascular plants (Van der Wal and Stien 2014), i.e. the major plane of nutrition for herbivores (Bjørkvell et al. 2009). The Svalbard tundra hosts a relatively simple, bottom-up controlled food web (Descamps et al. 2017). Here the fluctuations in population size of the only large ungulate, the Svalbard reindeer Rangifer tarandus platyrhynchus, are mainly shaped by forage availability during winter (notably density-dependent effects of ROS events) and productivity during summer (regulated by summer temperature, Hansen et al. 2013, 2019, Albon et al. 2017). Recent field observations and experiments also indicate that such ice encapsulation following ROS events negatively impact the growth patterns of shrubs, as well as their mortality and reproduction (Milner et al. 2016, Bjerke et al. 2017). On Svalbard, effects of climate warming are more pronounced in winter than in summer and a strong change in the winter precipitation pattern has been observed, with an increase in rainfall that is most pronounced on the west coast (Nordli et al. 2014, Peeters et al. 2019). The role of spatial heterogeneity
and the geographical scale at which these contrasting climate drivers act on primary production in the Arctic, as well as their implications for the spatial synchrony of primary production, remain unexplored.

Here, we take advantage of the dendrochronological tools developed for shrub species (Kolishchuk 1990) and a rare network of long-term Arctic weather station data to investigate climate–shrub growth relationships in time and space across Svalbard. First, we explore the main climate drivers of secondary growth in *S. polaris*, asking how and why their effects may vary across the archipelago. Second, we assess to what extent fluctuations in this proxy for annual primary production (Le Moullec et al. 2019) are spatially synchronised, and how climate and weather fluctuations contribute to this synchrony.

**Methods**

**Study area and species**

Around 60% of the land area of Svalbard (ca 74–81°N, 10–35°E) is covered by glaciers, while only ca 13% is vegetated (Johansen et al. 2012, Fig. 1). The archipelago has a relatively mild climate for its latitude and shows high inter-annual variability in temperature and precipitation (Johansen et al. 2012, Nordli et al. 2014, Van Pelt et al. 2016). Both temperature and precipitation show a negative gradient from southwest to northeast with milder climates inland of deep fjords (Van Pelt et al. 2016). These climatic gradients are strongly influenced by the West Spitsbergen Current, which delivers warm North Atlantic water along the west coast and, the colder currents of the Arctic Ocean on the east coast (Van Pelt et al. 2016). During 1962–2014, the mean annual temperature across Svalbard was $-5.8 \pm 0.6$ (SE)°C, with winter (November–April) temperatures of $-12.0 \pm 2.6$°C and summer (June–August) temperatures of $3.0 \pm 0.8$°C (Supplementary material Appendix 2 Fig. A1). The annual precipitation was 372 ± 56 mm (winter = 196 ± 44 mm, summer = 81 ± 32 mm, the calculations of these summary statistics follow the same method described below). In this period, annual mean temperature increased with a rate of 0.8°C per decade, the increase in winter temperature being stronger than that in summer temperature (1.1 ± 0.2 and 0.4 ± 0.04 respectively, Supplementary material Appendix 2 Fig. A1), while annual precipitation did not show significant temporal trends (Nordli et al. 2014).

The focal species in this study, *Salix polaris*, has a nearly circumpolar distribution (absent on Greenland) (<www.flora.dempstercountry.org>) and is the only widespread and abundant shrub found in most habitats across the Svalbard archipelago, including in polar deserts (<http://svalbardflora.no>, Rønning 1996). The circumarctic dwarf shrub *Cassiope tetragona* is also of great value to dendrochronological studies at high latitudes (Callaghan et al. 1989, Rayback and Henry 2005, 2006, Rozema et al. 2009, Weijers et al. 2010, 2012, 2013, 2017, 2018a, Rayback et al. 2011, 2012, Milner et al. 2018) but this species is dependent on dry soils with some...
snow-cover (Rønning 1996) and is hence found in a more restricted area on Svalbard than *S. polaris*. Also, contrary to *C. tetragona*, *S. polaris* is an important food resource for resident herbivores, i.e. the wild Svalbard reindeer and Svalbard rock ptarmigan *Lagopus muta hyperborea*, as well as for migratory geese *Branta* spp. (Van der Wal et al. 2000, Bjørkvoll et al. 2009). A particularity of the High Arctic Svalbard ecosystem is the low biomass of lichens, which therefore compose only a marginal part of the reindeer diet in winter (< 2%, Bjørkvoll et al. 2009). Instead, Svalbard reindeer graze on *S. polaris* year-round, with highest grazing pressure in late winter (~25%, Bjørkvoll et al. 2009).

This prostrate shrub has often only shoot tips, leaves and reproductive structures visible above-ground. The reproduction can be sexual or clonal through rhizomes (Rønning 1996). The below-ground structure usually consists of one main root which can extend several decimetres into the ground, and several thin secondary roots and shoots nested into the ground (Le Moullec et al. 2019, Fig. 2). The shoots usually emerge from the root collar complex, i.e. the oldest part of the plant, which is situated on top of the central root. Both primary and secondary growth of this species are found to be mainly driven by a positive effect of summer temperature (Buchwal et al. 2013, Van der Wal and Stien 2014, Le Moullec et al. 2019). *Salix polaris* shrubs usually form well-defined, however, often incomplete, annual ring growth (Buchwal et al. 2013). Ring growth in arctic shrubs is often irregular, because they are adapted to tolerate high variability in their physical environment (Crawford 2008, Wilmking et al. 2012). Nevertheless, dendrochronological tools have previously successfully been used on *S. polaris* at three sites in Svalbard, i.e. Hornsund (Owczarek and Opała 2016), Petuniabukta (Buchwal et al. 2013) and Semmeldalen (Le Moullec et al. 2019). The average age of analysed samples from these studies was 40 years. The oldest shrub of the study was 70 years old, from Petuniabukta.

![Figure 2. (a) Overview of *Salix polaris* shrub extracted from the ground with a main root indicated by a white arrow. (b) The digital image of its stained root's cross-section. Note that the outermost blue belt indicates the cambial zone, i.e. the part of the ring that was still in formation at the time of sampling (i.e. mid July 2015). (c) Landscape image from eastern Svalbard, Barentsøya.](image)
Table 1. Description of sampling sites and *Salix polaris* ring growth chronology statistics. Vegetation type is extracted from Johansen et al. (2012). The chronologies contain a minimum of 10 cross-sections for the given time-span. Number of plants, cross-sections and radii measured are given, as well as the standard descriptive statistics for within-, between- and total plant inter-series correlation (i.e. $r_{wnt}$, $r_{bnt}$ and $r_{nt}$, respectively), as well as expressed population signal (EPS).

| Coordinates | Ny-Ålesund | Petuniabukta | Kapp Linné | Semmeldalen | Hornsund | Sorkapp | Edgeoya | Barentsøya |
|-------------|------------|--------------|------------|-------------|-----------|---------|---------|-----------|
| Sampling date | 28 Jul 2015 | 4–15 Aug 2010 | 22 Jul 2015 | 2 Aug 2015 | 20 Jul 2015 | 4 Jul 2015 | 10 Jul 2015 | 15 Jul 2015 |
| Vegetation type | Exposed Dryas tundra | Exposed Dryas tundra | Established Dryas tundra | Arctic meadow | Established Dryas tundra | Gravel snowbed | Exposed Dryas tundra | Exposed Dryas tundra |
| Chronology | 1986–2014 | 1941–2010 | 1977–2014 | 1985–2014 | 1962–2014 | 1989–2014 | 1976–2014 | 1974–2014 |
| Total plants | 5 | 10 | 5 | 30 | 5 | 5 | 5 | 5 |
| Total sections | 24 | 142 | 27 | 153 | 23 | 25 | 28 | 25 |
| Total radii | 96 | 471 | 108 | 612 | 92 | 100 | 112 | 100 |
| $r_{wnt}$ | 0.67 | 0.66 | 0.64 | 0.64 | 0.72 | 0.57 | 0.68 | 0.58 |
| $r_{bnt}$ | 0.33 | 0.32 | 0.19 | 0.18 | 0.31 | 0.32 | 0.36 | 0.32 |
| $r_{nt}$ | 0.39 | 0.36 | 0.27 | 0.19 | 0.38 | 0.37 | 0.41 | 0.36 |
| EPS | 0.80 | 0.89 | 0.65 | 0.90 | 0.76 | 0.82 | 0.82 | 0.81 |

* S. polaris ring growth data obtained from Buchwal et al. (2013). The period used in this study was 1962–2010. }
Le Moullec et al. 2019): 1) between radial measurements within cross-sections; 2) between cross-sections within a single shrub to obtain individual mean growth curves (i.e. time-series) and 3) between shrubs (minimum of five) within a site, to obtain site-specific mean growth curves (using linear mixed-effects models). After cross-dating, we truncated the mean site chronologies to contain a minimum sample depth of 10 cross-sections. No cross-dating was conducted between sites to respect spatial independency of temporal variation across Svalbard. We did not consider tree-ring measurements from the sampling year, 2015, because not all shrubs at all localities had fully completed that year’s ring formation at the time of sampling. Accordingly, growth curves end in 2014.

A major challenge in dendrochronology is to successfully disentangle the effect of weather from other factors, such as age-related processes, which affect trees’ and shrubs’ growth simultaneously. Chronology standardisation can help to account for some of these factors, and we followed the steps applied in Le Moullec et al. (2019). As trees become older, stem and root diameter increases so that inevitably, ring-width becomes thinner with increasing age for a similar amount of xylem produced (Biondi and Qeadan 2008, Buras and Wilming 2014). Hence, the first standardisation step involved transforming the cross-sections’ ring-width measurements to basal area increments (BAI, µm²) using R-ver. 3.3.2 (<www.r-project.org>), package ‘dplR’ (Bunn 2008), which can correct for changes in stem diameter with an increasing age (Visser 1995, Biondi and Qeadan 2008). This approach assumes circular cross-sections, which is often not the case for shrubs. However, Buras and Wilming (2014) showed that moderate eccentricity is reasonably well accounted for by averaging four radial measurements, as was done in this study. Secondly, trees and shrubs often exhibit increased ring-width development in their juvenile phase compared to in their adult phase (Briffa and Melvin 2011, Bowman et al. 2013). To account for such age effects, we standardised the cross-sectional growth curves by the trend in the BAI found when aligning all cross-sectional growth curves from all sites by cambial age, i.e. regional curve standardization (RCS, Briffa and Melvin 2011), again using the R-package ‘dplR’. RCS was applied to remove the (minor) age-related trends observed in our shrubs (Supplementary material Appendix 2 Fig. A2). Applying RCS transforms the growth curves into deviations from a mean growth trend representative of expected growth changes arising as a consequence of general shrub ageing (Helama et al. 2016), a process which also stabilizes the variances across ages. These standardisation steps resulted in dimensionless ring-width indices (RWI). Hereafter, we refer to ‘ring growth’ as a simplification of RWI.

As a standard quality check for ring growth data we used the following selected descriptive statistics: average correlation between growth series of all cross-sections from the same shrub (\(r_{bars}\)), the average inter-series correlation between growth series from different shrubs within a site (\(r_{bars}\)), the total average correlation between all cross-sections within a site (\(r_{bars}\)), as well as the expressed population signal (EPS) for the standardised ring growth chronologies established for each study site (Table 1). EPS is an evaluation of how closely the observed mean chronology (based on the finite sample collection) represents a hypothetical mean based on an infinitive number of cross-sections (Wigley et al. 1984). These descriptive statistics were obtained using the R-packages ‘dplR’ (Bunn 2008) and ‘detrendR’ (Campelo et al. 2012). In addition, we reported the average Gini-coefficient and first-order autocorrelation coefficient, calculated at the shrub level with the R-functions ‘gini’ and ‘acf’.

Annual ring growth was first averaged (i.e. arithmetic mean) over radial measurements obtained from within each cross-section, and then between the cross-sections of a shrub, to obtain a growth curve for the individual shrub. This resulted in the construction of growth curves from 30 individuals from these six sites. Additionally, the previously published studies from Petuniabukta (Buchwal et al. 2013) and Semmeldalen (Le Moullec et al. 2019) contained 10 and 30 individual growth curves respectively. The S. polaris chronology for Petuniabukta was published as non-standardised, i.e. raw ring-width chronology (Buchwal et al. 2013). Therefore, to obtain comparable scales, we mean centred time-series of all individual shrubs from all sites by dividing their annual growth by the shrub’s overall mean growth. Finally, to minimize the risk of detecting spurious correlations with climatic variables due to common trends, linear detrending across years was applied to the climate data (see below) and to all ring growth time-series of each individual shrub by extracting the residuals from a linear model of growth as a function of years.

As a summary, we used 70 individual growth curves from eight sites (Fig. 1), spread along a gradient of distances from 60 m (sub-sites within Semmeldalen) to 292 km (between Sørkapp and Ny-Ålesund). The maximum and minimum length of ring growth time-series was 66 (i.e. Petuniabukta and Hornsund) and 26 years (i.e. Sørkapp), respectively (Table 1).

Climate variables

A set of climate variables likely to influence S. polaris growth on Svalbard were selected a priori (see Supplementary material Appendix 2 Table A1 for detailed information on weather station data). Summer temperature was previously documented as an important driver of S. polaris growth at two sites in central Svalbard (i.e. Petuniabukta and Semmeldalen, Buchwal et al. 2013, 2019, Le Moullec et al. 2019), and summer precipitation seems to promote ring growth in southern regions (i.e. Hornsund, Opała-Owczarek et al. 2018). Amount and type of winter precipitation likely also affect shrub growth in the Arctic: snow, often redistributed by wind, may be beneficial to plants in terms of increased insulation (Hallinger et al. 2010) and increased mineralization rates (Blok et al. 2015), but may shorten the growing season by
Spring onset, which is also temperature-dependent, may influence plant performance at high latitudes (Karlsen et al. 2014). Furthermore, ROS may lead to basal ice formation that can injure plants by inducing cell death due to frost damage or because of stress- and anoxia induced metabolite accumulations (Crawford et al. 1994, Bokhorst et al. 2010, Bjerke et al. 2017). Accordingly, we calculated monthly mean air temperature (°C, from 17 weather stations, Supplementary material Appendix 2 Table A1) and total precipitation (mm, from eight weather stations, Supplementary material Appendix 2 Table A1) during summer, as well as total precipitation (mm) falling as snow (i.e. at a temperature < 1°C) or rain (i.e. ROS, at a temperature ≥ 1°C) during winter (November–April, extracted as daily data from <www.eklima.met.no>). ROS was on the natural logarithmic scale after adding one unit to avoid transforming values of 0. A proxy for spring onset was calculated as the Julian day when the smoothed daily temperature (over 10 days) crossed 0°C and stayed above 0°C for ≥ 10 days (Le Moullec et al. 2019). Summer was here defined as July, the month reflecting the peak growing season across the whole archipelago (Supplementary material Appendix 2 Fig. A3). Climate variables’ time-series from all weather stations are presented in Supplementary material Appendix 2 Fig. A4, starting from year 1962, which corresponded to the year when Petunibukta and Hornsund’s time-series start to overlap.

We also examined whether large-scale climatic patterns impacted plant growth by using summer and winter Arctic Oscillation (AO, 1950–2014) indices (available on <www.ncdc.noaa.gov/teleconnections/ao/>, Aanes et al. 2002, Stenseth et al. 2003). The AO is an index measuring a difference in atmospheric pressure measured at sea-level between 20°N and arctic regions (Thompson and Wallace 1998). When atmospheric pressure in the Arctic is low, but high pressure dominates temperate regions, this characterizes positive AO phases. In parts of the Arctic, positive AO index generally results in warm, but stormy, winters with early snowmelt, while summers are often cold, rainy and cloudy (Aanes et al. 2002). Such weather conditions are expected to reduce shrub growth (Aanes et al. 2002, Welker et al. 2005, Weijers et al. 2017). However, large-scale AO does not result in uniform changes of local weather conditions across the Arctic and can result in opposite weather conditions between, e.g. Greenland and Fennoscandia (Stenseth et al. 2003, Wang and Key 2003). Since Svalbard is situated at the interface between these regions, there is limited correlation between air temperature and AO (Wang and Key 2003). Additionally, sea ice can influence coastal vegetation productivity by cold air breeze from the sea, we investigated the relation between shrub secondary growth and sea ice cover time-series at the onset of growing season, i.e. June (Forchhammer 2017, Macias-Fauria et al. 2017). We used sea ice on a regional scale (instead of on an arctic-wide scale), from five coastal areas of Svalbard during 1979–2014, extracted from Prop et al. (2015).

Statistics

**Climate effect analysis**

We used the available weather data in Svalbard (Supplementary material Appendix 2 Table A1) to estimate weather variables across Svalbard for each year, using a linear mixed-effects model with year as fixed effect and weather station as random effect on intercept (Supplementary material Appendix 2 Fig. A4). The same approach was used for June sea ice extent from five areas around Svalbard, providing a general estimate at the Svalbard scale. All climate variables were linearly detrended for the time-span of each individual shrub’s time-series to avoid correlations due to common trend. For this climate-growth analysis, the 10 sub-sites in the Semmeldalen valley were treated as one site, resulting in a total of eight sites across Svalbard (Fig. 1).

We performed three different model selection procedures, in which we fitted linear mixed-effect models in the R package ‘lmer’ (function ’lme4’, Bates et al. 2015). Advantages of using linear mixed-effects models in dendrochronological studies following a hierarchical sampling design are detailed in Le Moullec et al. (2019). In the first model selection (‘Svalbard scale’), we explored which weather variables explain S. polaris ring growth the best at a Svalbard scale. The full model was composed of additive effects of the weather variables and the previous year’s ring growth (i.e. taking into account a possible first-order autocorrelation at the shrub level) (Supplementary material Appendix 2 Table A2). This first step enabled us to identify important environmental variables acting at large spatial scales, and thus potentially acting as synchronising variables. Second, we performed a model selection (‘regional scale’), where, opposed to at the ‘Svalbard scale’, we tested for differences in ring growth responses between sites. In this model selection, site was included as an interaction term with the different weather variables and the previous year’s ring growth (Supplementary material Appendix 2 Table A3). To avoid overparameterization, a maximum of six terms (excluding intercept) were allowed in the candidate models. The third model selection (‘climate proxy’) investigated the potential influence of summer and winter AO indices and fluctuations in June sea ice extent on ring growth across Svalbard (Supplementary material Appendix 2 Table A4). Because these variables are assumed to reflect weather conditions (Stenseth et al. 2002, Macias-Fauria et al. 2017), the investigation of these climate proxies was conducted in a separate model selection to avoid possible collinearity with the weather variables.

For all three model selection procedures described above, the full model and all of its possible subsets were fitted as candidate models (see all proposed models at the ‘Svalbard scale’ Supplementary material Appendix 2 Table A2, at the ‘regional scale’ Supplementary material Appendix 2 Table A3 and for the ‘climate proxy’ Supplementary material Appendix 2 Table A4). Year was always included as random effect on the intercept to account for dependency in the response variable due to spatially correlated annual environmental conditions not captured by the fixed effects. Shrubs within each site...
cannot be viewed as being independent (due to shared environment and through cross-dating), but since growth data were detrended (i.e. mean of zero for all plants), the effect of plant on the intercept was zero, and shrub ID was therefore not included as random intercept effect. No signs of a substantial random slope effect of plant were found (analysis not presented). There was no serious colinearity between weather variables ($r < 0.5$, Supplementary material Appendix 2 Table A5) and climate proxies ($r < 0.3$, Supplementary material Appendix 2 Table A6). Candidate models were compared using the Akaike information criterion corrected for sample size (AICc, Burnham and Anderson 2002), obtained from models fitted using maximum likelihood (ML), facilitated by the ‘dredge’ function from the R package MuMIn (Barton 2013). Parameter estimates were subsequently obtained for the top models (i.e. models with the lowest AICc), fitted with restricted maximum likelihood and corresponding 95% confidence intervals were associated to the mean estimates from 1000 bootstrap iterations (‘bootMer’ function in r package ‘lme4’, Table 2). Residual distributions were investigated for normality and homoscedasticity.

**Spatial synchrony analysis**

Environmental conditions can co-fluctuate over large distances and thereby synchronise primary production. Thus, we analysed spatial synchrony of shrub secondary growth and the contribution of climate to this synchrony. The correlation function ‘Sncf’ for spatiotemporal data from the R package ‘ncf’ (Bjørnstad 2019) was used to visualize the synchrony in average ring growth chronologies for all independently cross-dated sites ($n=18$ sub-sites, since the 10 sub-sites from Semmeldalen were treated separately in this analysis) as a function of distance between them. The ‘Sncf’ function uses a non-parametric smoothing spline to continuously model synchrony as a function of distance between sites (formulae in Bjørnstad et al. 1999) with associated 95% bootstrapped confidence envelopes (using 1000 resamples and two degrees of freedom). According to Bjørnstad et al. (1999), the spatial scale of synchrony can be defined as the distance at which the synchrony is no longer significantly different from zero, for example, the distance at which the lower confidence interval of the ‘Sncf’ smoothing spline crosses zero (Nieminen 2015, Eberhart-Phillips et al. 2016). The regional average synchrony ($\rho$), i.e. the average of the pairwise correlations across all distances, was calculated using a non-parametric bootstrap also providing the associated 95% confidence interval (i.e. 2.5% and 97.5% quantiles, Supplementary material Appendix 1). Compared with the non-parametric bootstrap implemented in the ‘Sncf’ function, the estimates were similar, but with higher precision (Supplementary material Appendix 2 Table A7).

We calculated the contribution to the average regional synchrony of the main climatic drivers by first accounting for their effect on ring growth using ordinary linear models, for their maximum overlapping time-span in each site. We calculated the spatial scale of synchrony and regional average synchrony ($\rho_{av}$, Supplementary material Appendix 1) using the residuals from these linear models. Note that since we are using residuals, adding year as random effect in the linear models described above would remove the very thing we are interested in, i.e. the remaining synchrony in these. To evaluate the statistical significance of contribution of the climate variables to the regional average synchrony, we used the 95% confidence interval of the difference in non-parametric bootstrapped replicates (Supplementary material Appendix 1) of average regional synchrony ($n=1000$) before ($\rho$) and after ($\rho_{av}$) accounting for the climate variable. We also computed the spatial synchrony of the most important climate variable, based on the six most complete weather station time-series from 1979 to 2014 (Svalbard airport, Barentsburg, Svea, Ny-Ålesund, Hornsund and Hopen, Supplementary material Appendix 2 Table A1), and fitted a linear regression across distances. Similar analyses of regional spatial synchrony and the contribution of climate variables to this synchrony across Svalbard have been applied in Hansen et al. (2019) [reindeer synchrony] and Peeters et al. (2019) [rain-on-snow synchrony].

**Results**

**Ring growth variation in time and space**

All *Salix polaris* site time-series’ overlapped for the period 1989–2014 (except Petuniabukta which overlapped until 2010), and for this period the largest and lowest average ring

| Scale     | Site            | July temperature (°C) | log(ROS)       | Growth (t – 1) |
|-----------|-----------------|-----------------------|----------------|---------------|
| Svalbard  | Barentsøya      | 0.20 [0.10:0.32]      | –              | −0.15 [−0.19:−0.11] |
| Regional  | Edgeøya         | 0.20 [0.10:0.31]      | 0.07 [−0.03:0.17] | −0.23 [−0.37:−0.10] |
|           | Hornsund        | 0.20 [0.10:0.31]      | −0.09 [−0.19:0.01] | 0.16 [0.01:0.30] |
|           | Kapp Linné      | 0.20 [0.10:0.31]      | −0.09 [−0.19:0.02] | −0.25 [−0.36:−0.16] |
|           | Ny-Álesund      | 0.20 [0.10:0.31]      | −0.10 [−0.22:0.02] | −0.37 [−0.51:−0.23] |
|           | Petuniabukta    | 0.20 [0.10:0.31]      | −0.04 [−0.08:0.07] | −0.06 [−0.17:0.05] |
|           | Semmeldalen     | 0.20 [0.10:0.31]      | −0.02 [−0.10:0.05] | −0.09 [−0.18:−0.01] |
|           | Sorkapp         | 0.20 [0.10:0.31]      | 0.04 [−0.09:0.17] | −0.35 [−0.51:−0.19] |
growth occurred in 1998 and 2008, respectively. Generally, the year-to-year variation in growth was substantial with an average Gini-coefficient of 0.37 [0.28:0.48] [95% CI] (ranging from 0.27 to 0.45) (Fig. 1, 3), and average first-order autocorrelated of −0.08 [−0.47:0.31] (ranging from −0.5 to 0.4), both calculated at the shrub level. The average raw-ring width of an individual shrub was 49 ± 37 SE, with a maximum value of 220 μm for a shrub from Edgeøya in 2002. Descriptive chronology statistics showed a low within shrub variation (r_{\text{within}}), but a relatively high between-shrub variation (r_{\text{between}}, Table 1). The EPS-value for sites with limited shrub replication had relatively low values, such as Kapp Linné, yet, no consistent mismatch in alignment with the other Svalbard sites’ mean growth time-series was observed (Supplementary material Appendix 2 Table A8). We considered all eight chronologies, obtained after our elaborated cross-dating procedure, as sufficiently reliable for climate effect analyses. Nevertheless, while the overall pattern of high- and low-growth years may have been captured quite well even for sites with low EPS values, the results, especially from such low-replicate sites, must still be interpreted with care, as the shrubs sampled may not represent the mean growth rate of these sites sufficiently.

Climate effects on ring growth

The correlation between the mean ring growth and mean July temperature over Svalbard was fairly high (1962–2014: r = 0.40 [0.15:0.61]; 1989–2014: r = 0.53 [0.19:0.76], Fig. 3 and for a comparison with non-detrended data, Supplementary material Appendix 2 Table A8). Accordingly, the linear mixed-effect model showed that July temperature positively influenced ring growth at the ‘Svalbard scale’ (for a comparison with non-detrended data, Supplementary material Appendix 2 Table A9) and similarly at the ‘regional scale’ (i.e. no interaction with site, Table 2). Moreover, all models with ΔAICc < 2 included July temperature (Supplementary material Appendix 2 Table A10).

The top model of the ‘regional scale’ model selection also contained ROS in interaction with site, meaning that this variable influenced ring growth differently among sites (Table 2). Results from the analysis at the ‘local scale’ supported that two (i.e. Ny-Ålesund and Kapp Linné) out of four sites with an established weather station close by showed a negative effect of ROS (Supplementary material Appendix 2 Table A11, Fig. A6). The effect of the previous year’s growth differed among sites both in strength and sign (Table 2). Overall in Svalbard, the effect of growth of the previous year was negative (Table 2). Note that this effect was masked by the autocorrelation in time-series, before temporal linear detrending was performed (Supplementary material Appendix 2 Table A9). Year explained 9% of the total random variation (number of years n = 52) in both the top model at the ‘Svalbard scale’ and the ‘regional scale’.

Ring growth did not show any consistent response to the detrended large-scale climate proxies. The top-ranked model only included previous year’s ring growth, without any of these variables (intercept = −1.68 × 10^{−03} ± 0.04, slope = −0.14 ± 0.02, t = −5.91, p ≤ 0.001). Additionally, including any of the climate proxies did not enhance model fit (ΔAICc > 2 for all models). Note also that none of the large-scale climate proxy variables were significantly correlated with July temperature or ROS. Hence, the correlation between summer AO and July temperature (linearly detrended) was r = −0.04 [−0.23:0.31]; the correlation between June sea-ice and July temperature was r = −0.33 [−0.60:0.01]; and the correlation between winter AO and ROS was r = −0.20 [−0.45:0.08].

Synchrony analysis

From the climate effect analysis, July temperature was considered the main potentially synchronising climate variable (Table 2, Fig. 3). July temperature was highly synchronised over large scales, linearly decreasing with distance (intercept = 0.88 [0.77:0.99], slope = −0.22 [−0.28:−0.17] per 100 km, R^2 = 0.81, Supplementary material Appendix 2 Figure A5). We considered the main potentially synchronising climate variable (Table 2, Fig. 3). July temperature was highly synchronised over large scales, linearly decreasing with distance (intercept = 0.88 [0.77:0.99], slope = −0.22 [−0.28:−0.17] per 100 km, R^2 = 0.81, Supplementary material Appendix 2 Figure A5).

Figure 3. Annual mean ring growth (blue line) of Salix polaris and mean July temperature (red line) across Svalbard. Time-series were linearly detrended and for graphical visualisation they were standardised (std; annual mean divided by the standard deviation). Both time-series are presented with their approximate 95% confidence intervals (light blue [ring growth] and light red [July temperature] shades, ± 1.96×SE). The correlation between ring growth and July temperature was r = 0.40 [0.15:0.61] for the period 1962–2014 and r = 0.53 [0.19:0.76] from 1989 to 2014 (when all eight sites were represented).
The average regional synchrony was $\rho_T = 0.49 [0.42:0.56]$ (mean [95% CI], non-parametric bootstrap, Supplementary material Appendix 1) and the spatial scale of synchrony was estimated to 350 km (Supplementary material Appendix 2 Fig. A7). Ring growth also showed significant spatial synchrony across large distances: the average regional synchrony was $\rho = 0.24 [0.21:0.27]$ (Supplementary material Appendix 1), and the spatial scale of synchrony was estimated to be 183 km (Fig. 4a). Average regional synchrony in model residuals when accounting for the effect of July temperature remained significant but was reduced to $\rho_{res} = 0.18 [0.15:0.22]$ (Supplementary material Appendix 1), and the spatial scale of synchrony was estimated to 159 km (Fig. 4b). Hence, the average regional synchrony after accounting for July temperature was significantly reduced by 0.054 [0.039:0.069] (Fig. 4c). ROS average regional synchrony was $\rho_{ROS} = 0.62 [0.48:0.76]$ (see also Peeters et al. 2019). However, accounting for the effect of ROS (instead of July temperature) did not reduce the regional average synchrony ($\rho_{res} = 0.24 [0.21:0.27]$, i.e. similar estimates as $\rho$).

Discussion

By applying dendrochronological tools to the high-arctic dwarf shrub Salix polaris, this study has demonstrated how spatial autocorrelation in weather fluctuations synchronises shrub secondary growth over large distances in a hotspot for climate change. We found contrasting effects of different weather variables associated with climate warming during summer versus winter. Summer temperature had an overall strong positive effect on ring growth (Table 2, Fig. 3) and, hence, explained a significant part of the spatial synchrony in secondary growth (Fig. 4). On the contrary, ROS events associated with winter warming caused reduced ring growth, yet only in some relatively wet and mild coastal sites (Table 2).

The archipelago-wide positive summer temperature effect was expected, since it has been previously indicated to be the major driver of biomass and secondary growth of other vascular plants in several sites across the Arctic, both from field based and remote sensing studies (Forbes et al. 2010, Blok et al. 2011, Macias-Fauria et al. 2012, Van der Wal and Stien 2014, Myers-Smith et al. 2015a, Weijers et al. 2017, 2018a, b, Ackerman et al. 2018). While it is the temperature of a plant’s tissue that regulates the plant hormone triggering xylogenesis and ring formation (i.e. auxin) (Wilmking et al. 2012), summer air temperature is one of many proxies for plant temperature that can be used (Körner and Hiltbrunner 2018). The dwarf shrub S. polaris’ secondary growth has previously been demonstrated to be strongly influenced by summer temperature in two single sites (i.e. Petuniabukta and Slemmeldalen, Buchwal et al. 2013, Le Moulec et al. 2019), and in the current study we found supporting evidence for its summer temperature sensitivity across Svalbard.

Furthermore, dendrochronological studies performed on another dwarf shrub, Cassiope tetragona, also found a close relationship between growth and summer temperature in several sites located in central and western Spitsbergen (Callaghan et al. 1989, Aanes et al. 2002, Rozema et al. 2009, Weijers et al. 2010, 2012, 2013, Blok et al. 2015, Milner et al. 2018). Although the correlation between shrub growth and July temperature in our study was fairly high, it was lower
than correlations reported in some local studies conducted on *C. tetragona* on Svalbard (Weijers et al. 2010, 2012). This is possibly because of the high individual variation in *S. polaris* secondary growth (as will be discussed more in-depth later). Also, this study is conducted at an archipelago-wide scale and the weather data across Svalbard cannot capture microclimatic variations in the same way as local studies can (Armbruster et al. 2007, Körner and Hilbrunner 2018).

The Arctic climate is rapidly changing, particularly during the winter season, and weather events such as warm spells and ROS are already increasing in frequency (Rennert et al. 2009, Hansen et al. 2014, Larsen et al. 2014, Moore 2016, AMAP 2017, Bintanja and Andry 2017, Pan et al. 2018, Peeters et al. 2019). Although the most dramatic effects of ROS have been found in large herbivores (Rennert et al. 2009, Hansen et al. 2011, Forbes et al. 2016, Berger et al. 2018), the consequences of ROS for primary production are still not well understood. Weijers et al. (2010) noted that the relation between July temperature and shrub growth was reduced following winters with numerous thawing days (temperature > 0°C, January–April), and Milner et al. (2016) found that basal ice due to experimental ROS had negative effects on shoot survival and flowering in *C. tetragona*, thereby indirectly promoting growth in surviving shoots. Other field observations and remote sensing indicate broader plant community-level effects of ROS, possibly explaining part of the recently observed ‘browning of the Arctic’ (Bojkhorst et al. 2011, Phoenix and Bjerke 2016, Bjerke et al. 2017). This could result in a reduced positive effect of increasing summer temperatures on primary production (Vickers et al. 2016).

A negative effect of ROS-events on primary production was found at some, but not all, sites. Two of these sites are located along the west coast, on flat plains close to the sea, exposed to milder and rainier winter climate. Such locations facilitate the conditions that frequently cause formation of thick and continuous basal ice after ROS events (Supplementary material Appendix 1 Fig. A8) (Van Pelt et al. 2016, Peeters et al. 2019). Basal ice occurrence and thickness vary according to the small-scale topography and its accumulated snow amount, which can impact individual shrubs differently. Large rain-on-snow amounts could even lead to total ablation of snow/ice cover, although this will mainly occur on very exposed ridges with negligible snow cover. However, Peeters et al. (2019) showed, using similar weather records as used in our study, that these records predicted field-based basal ice measurements well. These site differences and possibly individual differences to ROS exposure potentially introduces spatial heterogeneity that influences the co-fluctuations of primary production. Accordingly, ROS did not contribute to the observed regional synchrony in ring growth in the past. The magnitude and spatial extent of ROS is forecasted to increase (Bintanja and Andry 2017), so that these sites could represent future conditions across larger areas on Svalbard and the Arctic in general, potentially changing the relative importance of different seasons in their influence on spatio-temporal dynamics of shrub growth. However, note that one of the two coastal sites where we detected adverse effects of ROS at the local scale had a fairly low EPS-value and hence we encourage further in-depth investigations into this matter.

The synchronising effect of summer temperature on primary production represents an analogy to the theoretically expected (Moran 1953) and observed (Grenfell et al. 1998, Sæther et al. 2007) ‘Moran effect’ in animal population dynamics. Although this study is the first to conduct such spatial synchrony analysis from dendrochronological data on a relatively large spatial scale in the high-Arctic, a recent study on *C. tetragona* (Milner et al. 2018) correlated retrospective shrub growth in neighboring valleys (including Semmeldalen), but at a smaller spatial scale. The correlation at the maximum distance (~30 km) corresponded approximately to our findings at similar distances for *S. polaris*. At much larger scales, using estimates from NDVI, Defriez and Reuman (2017) demonstrated an effect of temperature on spatial synchrony in vegetation productivity across large parts of the globe, yet excluding high latitudes. Together, these studies strongly indicate a generalizable pattern that fluctuations in weather, notably summer temperature, cause large-scale synchronisation of plant growth dynamics across biomes. To our knowledge, this study is the first to quantify, in situ, the role of weather in generating archipelago-wide spatial synchrony in plant growth in the high-Arctic. Important insights from remote sensing studies have previously been gained from analysing spatiotemporal gradients of arctic primary production driven by weather (e.g. land surface temperature) (Raynolds et al. 2008, Forbes et al. 2010, Walker et al. 2012), but no studies exist on spatial synchrony per se. The lack of such studies is likely due to few in situ plant growth time-series at large spatial scales combined with the low resolution of available weather station records at high latitudes. Svalbard is unique within the High Arctic with respect to availability of such data (Nordli et al. 2014, Supplementary material Appendix 2 Table A1). This, combined with the recent development of dendrochronological tools applied to shrubs (Schweingruber and Poschold 2005, Buchwal 2014, Myers-Smith et al. 2015b), enabled us to detect the synchronising role of a single-month weather variable (July temperature). When such in situ weather data are missing, regional weather proxies can be used as an alternative to detect important large-scale patterns of biotic dynamics on the tundra (Aanes et al. 2002, Forchhammer 2017, Macias-Fauria et al. 2017, Weijers et al. 2017, Buchwal et al. 2019). However, it seems that these regional variables were not able to capture the mechanistically important weather variables for ring growth in Svalbard well (Polyakov et al. 2003, Stenseth et al. 2003, Wang and Key 2003).

Population synchrony is expected to be lower than that of the environmental drivers (Sæther et al. 2007) due to the wide array of microclimates, habitats and associated individual variation. In our case, July temperature had a stronger spatial autocorrelation across Svalbard (*p* = 0.49) than ring growth in *S. polaris* (*p* = 0.24). One reason for this is the high heterogeneity in individual growth (Crawford 2008),
caused in part by substantial irregularities such as missing and wedging rings (Buchwal et al. 2013) and measurable as high between-plant variation (\( r_{\text{between}} \)). The observed individual heterogeneity was likely amplified by our restricted sample sizes and possible exposure to grazing. Furthermore, temperature effects at the microhabitat level are important (Scherrer and Körner 2011) and snow cover and soil moisture at such small scales can interact with the effect of summer air temperature on individual growth (Hallinger et al. 2010, Ackerman et al. 2017, Weijers et al. 2017). We also observed heterogeneity in the strength and even sign of delayed growth effects, both between sites and between individuals. This likely reflects different tradeoffs in resource allocation between growth and e.g. damage repair or reproduction, which is a highly individual process (Dormann and Skarpe 2002, Skarpe and Van der Wal 2002).

Nonetheless, the synchronising effect of summer temperature was still clearly detectable, explaining one fourth of the observed regional synchrony of ring growth. The remaining observed synchrony is likely a combination of different climatic variables affecting growth simultaneously (Supplementary material Appendix 2 Table A10, A11), and during other parts of spring and summer than July (Weijers et al. 2018b). Furthermore, the temporal linear detrending we performed is a conservative approach, increasing the confidence with which the results from this work can be reported but may have reduced the strength of the detected climate–growth relationships (Supplementary material Appendix 2 Table A9). Other factors that can influence population synchrony include trophic interactions (Bjornstad et al. 1999, Liebhold et al. 2004). However, the single most abundant herbivore (in terms of biomass), the Svalbard reindeer, is highly sedentary, and does not migrate between sites (Tyler and Øritsland 1989) and a significant effects of top–down regulation on annual plant growth in this system is not expected (Ims et al. 2013, Descamps et al. 2017, Le Moullec et al. 2019).

Bottom–up effects of spatial synchrony in primary production are expected to have large implications for ecosystem-level dynamics through cascading effects (Haynes et al. 2009, Post et al. 2009b, Wookey et al. 2009). The evidence of climate-driven spatial synchrony in *S. polaris* secondary growth found in the present study, calls for large-scale investigations of spatial synchrony in tundra community dynamics. Secondary growth dynamics of *S. polaris* from multiple sites also contain valuable information on the spatial synchrony in wood deposited below-ground (shoots are nested into the ground, Le Moullec et al. 2019) and, hence, their contribution to the carbon pool size contained therein (Buchwal et al. 2013, Babst et al. 2014, Iversen et al. 2015). Regionally replicated plot-design experiments, similar to the International Tundra Experiment (ITEX) project (Henry and Molau 1997, Elmendorf et al. 2012a, b), could test how different vascular plant species cope with rainy winters (i.e. experimentally encapsulated in basal ice), in addition to, and in interaction with, simulated summer warming. Such experiments simulating ROS and basal ice encasement found species-specific effects on some growth and reproductive traits, however, there was also an overall high tolerance to experimental icing (Preece and Phoenix 2014, Milner et al. 2016, Bjerke et al. 2018). To expand our spatial synchrony study to larger parts of the Arctic, in situ dendrochronological data from multiple species can be combined with experimental icing data and remote-sensing vegetation productivity index maps (Forbes et al. 2010, Blok et al. 2011, Macias-Fauria et al. 2012, Weijers et al. 2018b). Furthermore, in areas with ROS data available from local weather stations, alternatively down-scaled climate models, the larger-scale implications of (potentially negative) effects of ROS on secondary shrub growth, and how this influences spatial synchrony across environmental gradients (e.g. coast versus inland), could be tested through remote sensing (e.g. observed as ‘browning’, Phoenix and Bjerke 2016, Bjerke et al. 2017). We believe that such large-scale studies may contribute to a holistic understanding of the role of spatial synchrony in primary production in arctic community-level dynamics in both time and space.

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k3j9kd54c> (Le Moullec et al. 2020).

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### References

Aanes, R. et al. 2002. The Arctic Oscillation predicts effects of climate change in two trophic levels in a high-arctic ecosystem. – Ecol. Lett. 5: 445–453.

Ackerman, D et al. 2017. Arctic shrub growth trajectories differ across soil moisture levels. – Global Change Biol. 23: 4294–4302.
Ackerman, D. et al. 2018. Uniform shrub growth response to June temperature across the North Slope of Alaska. – Environ. Res. Lett. 13: 044013.

Albon, S. D. et al. 2017. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited arctic herbivore. – Global Change Biol. 23: 1374–1389.

AMAP 2017. Snow, water, ice and permafrost in the arctic (SWIPA). – Arctic Monitoring and Assessment Programme (AMAP).

Armbruster, W. S. et al. 2007. Topographic complexity and terrestrial biotic response to high-latitude climate change: variance is as important as the mean. – In Ørberg, J. B. et al. (eds), Arctic–Alpine ecosystems and peoples in a changing environment. Springer. pp. 105–122.

Babst, F. et al. 2014. A tree-ring perspective on the terrestrial carbon cycle. – Oecologia 176: 307–322.

Barton, K. 2013. MuMIn: multi-model inference. – R package ver. 1.9.0. <https://cran.r-project.org/web/packages/MuMIn/index.html>.

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Berger, J. et al. 2018. Climate degradation and extreme icing events constrain life in cold-adapted mammals. – Sci. Rep. 8: 1156.

Bintanja, R. and Andry, O. 2017. Towards a rain-dominated Arctic. – Nat. Clim. Change 7: 263–267.

Biondi, F. and Qeadan, F. 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. – Tree-Ring Res. 64: 81–96.

Bjerke, J. W. et al. 2017. Understanding the drivers of extensive plant damage in boreal and arctic ecosystems: insights from field surveys in the aftermath of damage. – Sci. Total Environ. 599–600: 1965–1976.

Bjerke, J. W. et al. 2018. High tolerance of a high-arctic willow and graminoid to simulated ice encasement. – Boreal Environ. Res. 23: 329–338.

Bjorkman, A. D. et al. 2012a. Global assessment of experimental climate warming impacts on sub-Arctic heathland: phenology, reproduction, growth and CO2 flux responses. – Global Change Biol. 17: 2817–2830.

Bokhorst, S. et al. 2011. Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth and CO2 flux responses. – Global Change Biol. 17: 2817–2830.

Bowman, D. M. et al. 2013. Detecting trends in tree growth: not so simple. – Trends Plant Sci. 18: 11–17.

Braña, K. R. and Melvin, T. M. 2011. A closer look at regional curve standardization of tree-ring records: justification of the need, a warning of some pitfalls, and suggested improvements in its application. – In: Hughes, M. K. et al. (eds), Dendroclimatology: progress and prospects. Springer, pp. 113–145.

Buchwal, A. 2014. Constraints on dendrochronological dating of Salix polaris from central Spitsbergen. – Czech Polar Rep. 4: 73–79.

Buchwal, A. et al. 2013. Temperature modulates intra-plant growth of Salix polaris from a high arctic site (Svalbard). – Polar Biol. 36: 1305–1318.

Buchwal, A. et al. 2019. Temperature sensitivity of willow dwarf shrub growth from two distinct High Arctic sites. – Int. J. Biometeorol. 63: 167–181.

Bunn, A. G. 2008. A dendrochronology program library in R (dplR). – Dendrochronologia 26: 115–124.

Buras, A. and Wilmking, M. 2014. Straight lines or eccentric eggs? A comparison of radial and spatial ring width measurements and its implications for climate transfer functions. – Dendrochronologia 32: 313–326.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and inference: a practical information-theoretic approach. – Springer.

CAFF. 2013. Arctic biodiversity assessment. status and trends in arctic biodiversity. – Conservation of Arctic Flora and Fauna.

Callaghan, T. V. et al. 1989. Historical records of climate-related growth in Cassiope tetragona from the Arctic. – J. Ecol. 77: 823–837.

Campelo, F. et al. 2012. detrendR – a graphical user interface to process and visualize tree-ring data using R. – Dendrochronologia 30: 57–60.

Crawford, R. M. M. 2008. Plants at the margin: ecological limits and climate change. – Cambridge Univ. Press.

Crawford, R. M. M. et al. 1994. Anoxia tolerance in high arctic vegetation. – Arct. Antarct. Alp. Res. 26: 308–312.

Defriese, E. J. and Reuman, D. C. 2017. A global geography of synchrony for terrestrial vegetation. – Global Ecol. Biogeogr. 26: 887–888.

Defriese, E. J. et al. 2016. Climate change-related regime shifts have altered spatial synchrony of plankton dynamics in the North Sea. – Global Change Biol. 22: 2069–2080.

Descamps, S. et al. 2017. Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. – Global Change Biol. 23: 490–502.

Dormann, C. F. and Skarpe, C. 2002. Flowering, growth and defence in the two sexes: consequences of herbivore exclusion for Salix polaris. – Ecology 16: 649–656.

Douglas, A. E. 1941. Crossdating in dendrochronology. – J. For. 39: 825–831.

Eberhart-Phillips, L. J. et al. 2016. Spatial synchrony of a threatened shorebird: regional roles of climate, dispersal and management. – Bird Conserv. Int. 26: 119–135.

Elmendorf, S. C. et al. 2012a. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. – Ecol. Lett. 15: 164–175.
Elmendorf, S. C. et al. 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. – Nat. Clim. Change 2: 453–457.

Engen, S. et al. 2005. Estimating the pattern of synchrony in fluctuating populations. – J. Anim. Ecol. 74: 601–611.

Forbes, B. C. et al. 2010. Russian arctic warming and ‘greening’ are closely tracked by tundra shrub willows. – Global Change Biol. 16: 1542–1554.

Forbes, B. C. et al. 2016. Sea ice, rain-on-snow and tundra reindeer nomadism in Arctic Russia. – Biol. Lett. 12: 20160466.

Forchhammer, M. 2017. Sea-ice induced growth decline in arctic shrubs. – Biol. Lett. 13: 20170122.

Fritts, H. C. 1976. Tree rings and climate. – Academic Press.

Gärtner, H. and Schweingruber, F. H. 2013. Microscopic preparation techniques for plant stem analysis. – Verlag Dr. Kessel.

Gärtner, H. et al. 2014. New perspectives for wood anatomical analysis in dendrochronology: the GSL1-microtome. – Dendrochronologia 32: 47–51.

Grenfell, B. et al. 1998. Noise and determinism in synchronized sheep dynamics. – Nature 394: 674–677.

Grotan, V. et al. 2005. Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. – Ecology 86: 1472–1482.

Hallinger, M. et al. 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. – New Phytol. 186: 890–899.

Hansen, B. B. et al. 2011. Climate, icing and wild arctic reindeer: past relationships and future prospects. – Ecology 92: 1917–1923.

Hansen, B. B. et al. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. – Science 339: 313–315.

Hansen, B. B. et al. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. – Environ. Res. Lett. 9: 114021.

Hansen, B. B. et al. 2019. Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic. – Global Change Biol. 25: 3556–3668.

Haynes, K. J. et al. 2009. Spatial synchrony propagates through a forest food web via consumer-resource interactions. – Ecology 90: 2974–2983.

Helama, S. et al. 2016. Regional curve standardization: state of the art. – Holocene 27: 172–177.

Henry, G. H. R. and Molau, U. 1997. Tundra plants and climate change: The International Tundra Experiment (ITEX). – Global Change Biol. 3: S1–S9.

Ims, R. A. and Andreassen, H. P. 2005. Density-dependent dispersal and spatial population dynamics. – Proc. R. Soc. B 272: 913–918.

Ims, R. A. and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. – Bioscience 55: 311–322.

Ims, R. A. and Ehrlich, D. 2013. Chapter 12. Terrestrial ecosystems. – In: Arctic biodiversity assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna (CAFF), pp. 384–441.

Ims, R. A. et al. 2004. Do sub-Arctic winter moth populations in coastal birch forest exhibit spatially synchronous dynamics? – J. Anim. Ecol. 73: 1129–1136.

Ims, R. A. et al. 2013. Science plan for COAT: climate-ecological observatory for Arctic Tundra. – Fram Centre Report Series No. 1.

Iversen, C. M. et al. 2015. The unseen iceberg: plant roots in arctic tundra. – New Phytol. 205: 34–58.

Johansen, B. E. et al. 2012. Vegetation mapping of Svalbard utilising Landsat TM/ETM+ data. – Polar Rec. 48: 47–63.

Ju, J. and Masek, J. G. 2016. The vegetation greenness trend in Canada and US Alaska from 1984–2012 Landsat data. – Remote Sens. Environ. 176: 1–16.

Karlsen, S. et al. 2014. Spatial and temporal variability in the onset of the growing season on Svalbard, Arctic Norway – measured by MODIS-NDVI satellite data. – Remote Sens. 6: 8088–8106.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. – Trends Ecol. Evol. 14: 22–26.

Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. – Ecography 25: 283–288.

Koenig, W. D. and Knops, J. M. 2013. Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. – Ecology 94: 83–93.

Koenig, W. D. and Liebhold, A. M. 2016. Temporally increasing spatial synchrony of north american temperature and bird populations. – Nat. Clim. Change 6: 614–617.

Kolischuk, V. 1990. Dendroclimatological study of prostrate woody plants. – In: Cook, E. and Kairiukstis, L. (eds), Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, pp. 394.

Körner, C. and Hilbertbrunner, E. 2018. The 90 ways to describe plant temperature. – Perspect. Plant Ecol. Evol. Syst. 30: 16–21.

Krebs, C. J. et al. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. – Can. J. Zool. 80: 1323–1333.

Länelaid, A. et al. 2012. Common growth signal and spatial synchrony of the chronologies of tree-rings from pines in the Baltic Sea region over the last nine centuries. – Dendrochronologia 30: 147–155.

Larsen, J. N. et al. 2014. Polar regions. – In: Barros, V. R. et al. (eds), Climate Change 2014: impacts, adaptation and vulnerability. Part B: regional aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge Univ. Press, pp. 1567–1612.

Le Mouillet, M. et al. 2019. Annual ring growth of a widespread high-arctic shrub reflects past fluctuations in community-level plant biomass. – J. Ecol. 107: 436–451.

Le Mouillet, M. et al. 2020. Data from: Climate synchronises shrub growth across a high-arctic archipelago: contrasting implications of summer and winter warming. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.k3j9kd54c>.

Liebhold, A. et al. 2004. Spatial synchrony in population dynamics. – Annu. Rev. Ecol. Evol. Syst. 35: 467–490.

Macias-Fauria, M. et al. 2012. Eurasian arctic greening reveals telecommunications and the potential for structurally novel ecosystems. – Nat. Clim. Change 2: 613–618.

Macias-Fauria, M. et al. 2017. Disentangling the coupling between sea ice and tundra productivity in Svalbard. – Sci. Rep. 7: 8586.

Massie, T. M. et al. 2015. Enhanced Moran effect by spatial variation in environmental autocorrelation. – Nat. Commun. 6: 5993.

Milner, J. M. et al. 2016. Experimental icing affects growth, mortality and flowering in a high arctic dwarf shrub. – Ecol. Evol. 6: 2139–2148.
Milner, J. M. et al. 2018. Retrospective growth analysis of the dwarf shrub *Cassiope tetragona* allows local estimation of vascular plant productivity in high arctic Svalbard. – J. Veg. Sci. 00: 1–29.

Moore, G. W. K. 2016. The December 2015 North Pole warming event and the increasing occurrence of such events. – Sci. Rep. 6: 39084.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. – Aust. J. Zool. 1: 291–298.

Myers-Smith, I. H. et al. 2015a. Climate sensitivity of shrub growth across the tundra biome. – Nat. Clim. Change 5: 887–891.

Myers-Smith, I. H. et al. 2015b. Methods for measuring arctic and alpine shrub growth: a review. – Earth-Sci. Rev. 140: 1–13.

Nieminen, M. 2015. Distance decay is uncommon in large-scale population synchrony of common moths: does it promote vulnerability to climate change? – Insect Conserv. Divers. 8: 438–447.

Nordli, Ø. et al. 2014. Long-term temperature trends and variability on Spitsbergen: the extended Svalbard Airport temperature series, 1898–2012. – Polar Res. 33: 21349.

Opala-Owczarek, M. et al. 2018. The influence of abiotic factors on the growth of two vascular plant species (*Saxifraga oppositifolia* and *Salix polaris*) in the High Arctic. – Catena 163: 219–232.

Östman, Ö. et al. 2017. Inferring spatial structure from population genetics and spatial synchrony in demography of Baltic Sea fishes: implications for management. – Fish Fish. 18: 324–339.

Owczarek, P. and Opala, M. 2016. Dendrochronology and extreme pointer years in the tree-ring record (AD 1951–2011) of polar willow from southwestern Spitsbergen (Svalbard, Norway). – Geochronometria 43: 84–95.

Pan, C. G. et al. 2018. Rain-on-snow events in Alaska, their frequency and distribution from satellite observations. – Environ. Res. Lett. 13: 075004.

Peeters, B. et al. 2019. Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift. – Environ. Res. Lett. 14: 015002.

Peltonen, M. et al. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. – Ecology 83: 3120–3129.

Phoenix, G. K. and Bjerke, J. W. 2016. Arctic browning: extreme events and trends reversing arctic greening. – Global Change Biol. 22: 2960–2962.

Pilcher, J. R. 1990. Sample preparation, cross-dating and measurement. – In: Cook, E. and Kairiukstis, L. (eds), Methods of dendrochronology: applications in the environmental sciences. Academic Publishers, pp. 394.

Pitzurra, V. E. et al. 2015. Environmental drivers of the spatiotemporal dynamics of respiratory syncytial virus in the United States. – PLoS Pathol. 11: e1004591.

Polyakov, I. V. et al. 2003. Variability and trends of air temperature and pressure in the maritime Arctic, 1875–2000. – J. Clim. 16: 2067–2077.

Post, E. 2003. Large-scale climate synchronizes the timing of flowering by multiple species. – Ecology 84: 277–281.

Post, E. et al. 2009a. Global population dynamics and hot spots of response to climate change. – Bioscience 59: 489–497.

Post, E. et al. 2009b. Ecological dynamics across the Arctic associated with recent climate change. – Science 325: 1355–1358.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. – Ecology 73: 733–746.

Preece, C. and Phoenix, G. K. 2014. Impact of early and late winter icing events on sub-arctic dwarf shrubs. – Plant Biol. 16: 125–132.

Prop, J. et al. 2015. Climate change and the increasing impact of polar bears on bird populations. – Front. Ecol. Evol. 3: 33.

Ranta, E. et al. 1997. The Moran effect and synchrony in population dynamics. – Oikos 78: 136–142.

Rayback, S. A. and Henry, G. H. R. 2005. Dendrochronological potential of the Arctic dwarf-shrub *Cassiope tetragona*. – Tree-Ring Res. 61: 43–53.

Rayback, S. A. and Henry, G. H. R. 2006. Reconstruction of summer temperature for a Canadian High Arctic site from retrospective analysis of the dwarf shrub, *Cassiope tetragona*. – Arct. Antarct. Alp. Res. 38: 228–238.

Rayback, S. A. et al. 2011. Spatial variability of the dominant climate signal in *Cassiope tetragona* from sites in Arctic Canada. – Arctic 64: 98–114.

Rayback, S. A. et al. 2012. Multiproxy reconstructions of climate for three sites in the Canadian High Arctic using *Cassiope tetragona*. – Clim. Change 114: 593–619.

Raynolds, M. K. et al. 2008. Relationship between satellite-derived land surface temperatures, arctic vegetation types and NDVI. – Remote Sens. Environ. 112: 1884–1894.

Rennert, K. J. et al. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar Arctic. – J. Clim. 22: 2302–2315.

Ronning, O. I. 1996. The flora of Svalbard. – Norsk Polarinstitutt.

Royama, T. 1992. Analytical population dynamics (Vol. 10). – Springer Science and Business Media.

Rozema, J. et al. 2009. Annual growth of *Cassiope tetragona* as a proxy for Arctic climate: developing correlative and experimental transfer functions to reconstruct past summer temperature on a millennial time scale. – Global Change Biol. 15: 1703–1715.

Saether, B.-E. et al. 2003. Climate variation and regional gradients in population dynamics of two hole-nesting passerines. – Proc. R. Soc. B 270: 2397–2404.

Saether, B. E. et al. 2007. The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. – J. Anim. Ecol. 76: 315–325.

Scherrer, D. and Körner, C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. – J. Biogeogr. 38: 406–416.

Schindelin, J. et al. 2015. The ImageJ ecosystem: an open platform for biomedical image analysis. – Mol. Reprod. Dev. 82: 518–529.

Schmidt, N. M. et al. 2006. Reconstructing century-long snow regimes using estimates of high arctic *Salix arctica* radial growth. – Arct. Antarct. Alp. Res. 38: 257–262.

Schweingruber, F. H. and Poschold, P. 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. – For. Snow Landsc. Res. 79: 195–415.

Semenchuk, P. R. et al. 2016. High Arctic plant phenology is determined by net primary productivity but duration of phenological periods is fixed: an example of periodicity. – Environ. Res. Lett. 11: 125006.

Sheppard, L. W. et al. 2015. Changes in large-scale climate alter spatial synchrony of aphid pests. – Nat. Clim. Change 6: 610–613.

Shestakova, T. A. et al. 2017. A roadmap to disentangling eco-geographical patterns of spatial synchrony in dendrosciences. – Trees 32: 359–370.
Skarpe, C. and Van der Wal, R. 2002. Effects of simulated browsing and length of growing season on leaf characteristics and flowering in a deciduous arctic shrub, *Salix polaris*. – Arct. Antarct. Alp. Res. 34: 282–286.

Stenseth, N. C. et al. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. – Science 285: 1071–1073.

Stenseth, N. C. et al. 2002. Ecological effects of climate fluctuations. – Science 297: 1292–1296.

Stenseth, N. C. et al. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Nino Southern Oscillation and beyond. – Proc. R. Soc. B 270: 2087–2096.

Tape, K. D. et al. 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. – Ecosystems 15: 711–724.

Tardif, J. C. and Conciatori, F. 2015. Microscopic examination of wood: sample preparation and techniques for light microscopy. – In: Yeunges, E. C. T. et al. (eds), Plant microtechniques and protocols. Springer, pp. 373–415.

Thompson, D. W. J. and Wallace, J. M. 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. – Geophys. Res. Lett. 25: 1297–1300.

Tyler, N. J. C. and Øritsland, N. A. 1989. Why don’t Svalbard reindeer migrate? – Ecography 12: 369–376.

Van der Wal, R. and Stien, A. 2014. High-arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. – Ecology 95: 3414–3427.

Van der Wal, R. et al. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. – Oecologia 123: 108–115.

Van Pelt, W. J. J. et al. 2016. Multidecadal climate and seasonal snow conditions in Svalbard. – J. Geophys. Res. Earth Surface 121: 2100–2117.

Vickers, H. et al. 2016. Changes in greening in the high arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. – Environ. Res. Lett. 11: 105004.

Visser, H. 1995. Note on the relation between ring widths and basal area increments. – For. Sci. 41: 297–304.

Welker, J. M. et al. 2005. Arctic and North Atlantic Oscillation phase changes are recorded in the isotopes (δ18O and δ13C) of *Cassiope tetragona* plants. – Global Change Biol. 11: 997–1002.

Wigley, T. M. et al. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. – J. Clim. Appl. Meteorol. 23: 201–213.

Wilmking, M. et al. 2012. Continuously missing outer rings in woody plants at their distributional margins. – Dendrochronologia 30: 213–222.

Wookey, P. A. et al. 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of arctic and alpine ecosystems to environmental change. – Global Change Biol. 15: 1153–1172.

Zhang, W. et al. 2013. Tundra shrubification and tree-line advance amplify arctic climate warming: results from an individual-based dynamic vegetation model. – Environ. Res. Lett. 8: 034023.

Supplementary material (available online as Appendix oik-07059 at <www.oikosjournal.org/appendix/oik-07059>). Appendix 1–2.