ISBN 978-82-326-3652-5 (printed ver.)
ISBN 978-82-326-3653-2 (electronic ver.)
ISSN 1503-8181

NTNU
Norwegian University of
Science and Technology

Le Moullec Mathilde

Doctoral thesis

Doctoral theses at NTNU, 2019:20

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Norwegian University of Science and Technology
Thesis for the Degree of
Philosophiae Doctor
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Printed by NTNU Grafisk senter

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I. Le Moullec, M., Pedersen, Å.Ø., Yoccoz, N.G., Aanes, R., Tufto, J. & Hansen, B.B. (2017) Ungulate population monitoring in an open tundra landscape: distance sampling versus total counts. Wildlife Biology, 1, wlb.00299. DOI: 10.2981/wlb.00299.

II. Le Moullec, M., Buchwal, A., van der Wal, R., Sandal, L. & Hansen, B.B. (2018) Annual ring growth of a widespread high-arctic shrub reflects past fluctuations in community-level plant biomass. Journal of Ecology, 00, 1-16. DOI: 10.1111/1365-2745.13036

III. Le Moullec, M., Pedersen, Å.Ø., Stien, A., Rosvold, J. & Hansen, B.B. A century of recovery from overharvest in a warming high-arctic: the successful conservation story of endemic Svalbard reindeer. Submitted Manuscript.

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Declaration of contributions:

Paper I. BBH, RA and ÅØP conceived the ideas; MLM designed the study and conducted the field work; MLM analyzed the data with input from NGY, BBH, ÅØP and JT. MLM wrote the manuscript with help of all co-authors.
Paper II. M.L.M., B.B.H. and R.vd.W. conceived the ideas and designed methodology; M.L.M., R.vd.W. and L.S. collected the data; M.L.M., L.S. and A.B. conducted the laboratory work; M.L.M. and B.B.H. analyzed the data; M.L.M. wrote the manuscript, with the help of all co-authors.
Paper III. MLM, BBH and ÅØP designed the study; MLM conducted the field work with help of BBH, ÅØP and AS; MLM analyzed the data with input from BBH and AS; MLM wrote the manuscript with help of all co-authors.
Paper IV. BBH designed the study; RA and ÅØP conducted field work with help from BBH, BP and MLM; BBH and BP analyzed the data with input from MLM and VG; BBH wrote the manuscript with help of all co-authors.
Paper V. MLM and BBH designed the study; MLM and LS conducted the field work and the laboratory work, with help from AB on the cross-dating; MLM and LS analyzed the data with input from VG and BBH; LS and MLM wrote the manuscript with help of all co-authors.

INTRODUCTION

Spatiotemporal variation in abundance

'The hope of the future lies not in curbing the influence of human occupancy – it is already too late for that – but in creating a better understanding of the extent of that influence' (Leopold, 1933)

The estimation of abundance in order to manage wild populations lies at the origin of the field of wildlife ecology (Leopold, 1933). In wildlife studies, abundance is usually quantified as population size, i.e. the number of individuals in the population. Alternatively, one can monitor demographic rates (i.e. reproduction, survival, immigration and emigration), which will determine the population size at the next reproductive cycle (Williams et al., 2002). In some cases, individuals are not clearly identifiable units and instead, a measure of productivity, such as vegetation productivity, is more relevant to ecosystem functioning. For instance, the role of a plant community in fuelling higher trophic levels of the Eltonian pyramid relates more to its productivity than to the number of individuals (Elton, 1927). I hereafter include 'productivity' within the concept of abundance.

Individuals are often unevenly distributed within the geographical range of a species, and divided into subpopulations semi-isolated from each other by, for example, fragmentation of the landscape. Various biotic and abiotic drivers, as well as stochastic events, may influence subpopulations' abundance dynamics differently in time and space (MacArthur & Wilson, 1967; May, 1974; Lundberg et al., 2000; Lande et al., 2003). Understanding these heterogeneous spatiotemporal dynamics within a metapopulation (i.e. composed of subpopulations) is fundamental in order to take appropriate measures for the species' conservation (Hanski & Simberloff, 1997; Yoccoz et al., 2001). As ecosystem functioning depends on interacting species and feedback loops, the spatiotemporal dynamics of a single species can have implications for the dynamics of an entire ecosystem through trophic cascades (Polis et al., 2000; Wookey et al., 2009; Peterson et al., 2014). Herbivores are often ecosystem engineers that manipulate their food resource through successional states by depleting or improving it (i.e. modification of soil nutrient processes, Van Wieren, 1998). Additionally, they are competitors/mutualists with other secondary producers and they are prey for secondary consumers i.e. predators and scavengers.

Any mechanistic understanding of ecosystem dynamics requires accurate (i.e. unbiased and precise) estimates of abundance (Williams et al., 2002). Under- or over-estimation of abundance can have fundamental implications for management and conservation decisions, when determining a species conservation status and when making inferences about population drivers such as climate change or harvest impacts (Thompson et al., 1998; Yokomizo et al., 2014). Local evaluation of methodological uncertainty is thus a crucial first step before expanding studies spatially. In turn, spatially extensive studies of abundance allow spatial patterns of densities to be studied, and when compared with past extent (or future predictions), inform on a species capability to expand or its vulnerability to decline (Brown, 1984; Acevedo et al., 2011).

The co-fluctuation of subpopulation dynamics across large geographical distances, (i.e. spatial synchrony) has interested ecologists since the early 1950s (Elton & Nicholson, 1942; Moran, 1953). The associated search for a common driver, biotic (i.e. trophic interaction and dispersal) or abiotic (i.e. weather and climate), controlling several subpopulations' dynamics simultaneously is still an active field of research (Ranta et al., 1997; Bjørnstad et al., 1999; Liebhold et al., 2004; Krebs, 2013; Walter et al., 2017). This is because spatial synchrony has implications for the viability of metapopulations and therefore for species conservation. High synchrony in population fluctuations over large distances can result in regional mass extinction, for instance following extreme events (Heino et al., 1997; Elmhagen & Angerbjörn, 2001; Engen et al., 2002). On the contrary, spatial heterogeneity can buffer regional extinction as metapopulations can be maintained in a dynamic landscape by the counteracting processes of local extinctions and recolonizations (Levins, 1970). A main mechanism that may cause spatial synchrony in populations, is the spatial correlation of environmental fluctuations in space – a phenomenon commonly called 'the Moran effect' (Moran, 1953; Grenfell et al., 1998; Koenig, 1999, 2002; Stenseth et al., 2003; Sæther et al., 2007).

The Moran effect is one of three main groups of mechanisms proposed to explain synchronous responses among populations (Bjørnstad et al., 1999; Liebhold et al., 2004). Dispersal of individuals between subpopulations or trophic interactions can also cause spatially correlated fluctuations in abundance (Lande et al., 1999; Engen et al., 2002; Ims & Andreassen, 2005; Vasseur & Fox, 2009). Dispersal ability of an animal often depends of the behavioral characteristics intrinsic to the species and landscape fragmentation, while in many plants species, particularly perennial plants, dispersal is negligible. Trophic interaction can, for instance, happen through nomadic predators (or herbivores) focusing on prey hotspots (Ims & Andreassen, 2000).

There are several assumptions underlying Moran's original theorem which assumes no migration between populations, identical (log-)linear density regulation and homogeneity in population responses to climate, so that spatial synchrony among populations is found to generally be much lower than that of the environmental drivers (Moran, 1953; Royama, 1992; Sæther et al., 2007). Although these assumptions are rarely met, the term 'Moran effect' is commonly used to describe population synchrony patterns resulting from spatial auto-correlation in environmental noise. In the light of recent and on-going climate change, understanding the level of spatial synchrony *versus* heterogeneity, and the climatic contribution to it, is more important than ever, particularly at northern latitudes, where direct climate effects on species dynamics often are strong.

The Arctic: a laboratory for human kind

'For human civilization, the Arctic stands both as a laboratory and a warning for human kind.'
Matthias Finger (2018)

Despite its isolation from industrial lands, climate change is transforming the Arctic at the most rapid rate on Earth (IPCC, 2014). In addition to background warming, the 'Arctic amplification' is the result of several phenomena including sea-ice extent retreat, increased oceanic and atmospheric heat transport and anomalies in atmospheric circulations (Serreze & Barry, 2011; Isaksen et al., 2016). These pronounced changes have already altered tundra ecosystems with potentially increased positive feedbacks on global climate warming (Zhang et al., 2013). One major change is increased vegetation productivity and shrub expansion (i.e. 'shrubification') leading to Arctic 'greening' (Myers-Smith et al., 2011; Elmendorf et al., 2012b; Ju & Masek, 2016). However, recent vegetation damage has been documented, namely Arctic 'browning', which may result from plants encased in ice instead of snow (Bokhorst et al., 2008; Phoenix & Bjerke, 2016; Bjerke et al., 2017). This phenomenon can occur when precipitation in winter falls as rain on snow-covered ground (i.e. rain-on-snow, Peeters et al., 2018). Such ice formation on vegetation also have direct effects on the availability of vegetation for herbivores and have triggered massive die-offs of arctic ungulates (Miller & Gunn, 2003; Kohler & Aanes, 2004; Rennert et al., 2009; Forbes et al., 2016). Alarming climate change predictions forecast a rain-dominated Arctic winter in the near future (Hansen et al., 2014; AMAP, 2017; Bintanja & Andry, 2017; Pan et al., 2018). Nevertheless, habitat fragmentation through increased industrialization, but also loss of sea-ice, is ranked as the major threat for several arctic ungulates, including reindeer and caribou *Rangifer tarandus* (hereafter collectively referred as reindeer, Gunn et al., 2009; Festa-Bianchet et al., 2011; Lorenzen et al., 2011; Post et al., 2013).

Arctic ecosystems provide unique opportunities for understanding the effects of climate change on ecosystems. Plant and animal populations at their distribution margins, such as at high latitudes, are often strongly influenced by year to year environmental fluctuations (Forchhammer et al., 2002; Sæther et al., 2003; Ims & Fuglei, 2005; Post et al., 2009). Furthermore, because arctic food webs are composed of relatively few interacting species, indirect climate effects through trophic interactions may be easier to tease apart from direct climate effects in arctic ecosystem dynamics (Ims & Ehrich, 2013). Surprisingly, the geographical scale at which direct climate drivers, such as temperature and rain-on-snow events, act on arctic primary producers and secondary consumers' spatial synchrony remains largely unexplored (but for reindeer see Post & Forchhammer, 2002; Post & Forchhammer, 2004; Uboni et al., 2016). Reindeer is a targeted model species because they are key components of tundra ecosystems and their population dynamics can trigger trophic cascades (Ims et al., 2007; CAFF, 2013). The main limitation to synchrony studies is the high resolution of spatiotemporal data required. Such data do not exist for *in situ* measurements of arctic vascular plant production. In forestry, the use of tree-ring growth to model forest growth synchrony patterns has increased (Shestakova et al., 2017). These dendrochronological methods – reconstructing woody plant growth – have also been adapted to arctic shrubs (Myers-Smith et al., 2015b). This method is a potential road to filling the gap of spatially replicated primary production time-series. Implications for the understanding of ecosystem dynamics would be particularly significant if shrub ring growth accurately traced past vascular plant production, which remains to be documented.

Enhancing our understanding of how environmental drivers shape spatial and temporal arctic ecosystem dynamics is of major importance for anticipating adverse effects on global biodiversity, including on humans (IPCC, 2014). To seek this pathway, Post et al. (2009) identified seven gaps of knowledge listed as: 1) 'conservation' of arctic species including range extirpation or shift; 2) dynamics 'outside the growing season'; 3) 'trophic interactions'; 4) 'heterogeneity' as a buffer against climate change; 5) the 'scale dependence' of climate responses; 6) 'extreme events'; 7) 'baseline studies' as reference for predicted changes. However, identifying these mechanisms requires long-term, large-scale and high-quality data across trophic levels, which is a challenge, especially in the remote Arctic. Candidate model systems with long-term ecological research sites such as Zackenberg on Greenland, Bylot Island in Canada, Wrangel Island in Russia and the Svalbard archipelago are particularly well-suited for such an undertaking (Ims & Ehrich, 2013).

Monitoring wildlife

Imperfect detection in animal surveys

'I just want to count them!' (Amos et al., 2014)

The ultimate goal of many wildlife monitoring programs is to estimate how many there are. However, as a general problem when assessing ecological this state variable, uncertainties emerge both from the state process itself (through demographic and environmental stochasticity) and from observation errors (i.e. detection probability, Kery & Schaub, 2012; Ahrestani et al., 2013), Figure 1). Imperfect detection is a major concern when conducting a population survey, but is currently integrated in only 23% of studies (Kellner & Swihart, 2014). Since it is in our ability to reduce these errors, it is important to identify their different sources.

First, individuals can be missed although they were present at the site (i.e. false negative), or counted more than once (i.e. false positive, Miller et al., 2011). When present at the site, they first have to be in sight of the observer i.e. available, and second, the observer has to detect them (Buckland et al., 2004). Together these form the detection probability which is influenced by characteristics (not mutually exclusive) of the species, spatial variation, temporal variation and the survey (Yoccoz et al., 2001; Sutherland, 2006; Guillera-Arroita, 2017, Figure 1). The survey characteristics include the monitoring method, sampling design (Marques et al., 2012; Sillett et al., 2012), and modelling method chosen. Different methodologies are adapted for different systems. For example, sign counts (i.e. indirect methods such as pellet counts) may be adopted for rare or nocturnal species, those inhabiting landscapes with low visibility, and be cost-effective for large-scale studies. Ideally, managers would perform animal counts using direct methods such as mark-recapture, distance sampling, or total counts) but it is often logistically costly to reach a sufficiently high sample size for robust abundance estimation. Furthermore, direct monitoring at large spatial scales is difficult to achieve, but is possible, particularly when combining methodologies (Pollock et al., 2002; Jones, 2011; Putman et al., 2011; Martin et al., 2015).

Imperfect detection in vegetation surveys: the use of dendrochronological tools

Imperfect detection does not only apply to animal surveys, but to most (if not all) ecological observations. In the field of dendrochronology, the state variable being estimated, for instance annual ring growth, is also subject to observation errors in much the same way as in abundance monitoring (Cook & Pederson, 2011, Figure 1). A key advantage of dendrochronological tools is that decadal time-series of plant growth traits can be collected from a single visit to the field – a method well-suited to remote regions. Chronology construction of ring growth is widely used in trees (Douglass, 1941; Fritts, 1976; Cook & Kairiukstis, 1990) and recently in shrubs (Schweingruber & Poschold, 2005; Myers-Smith et al., 2015b). Dendrochronology applied to shrubs has advanced several ecological topics such as climate-ring growth relationships (Weijers et al., 2010; Myers-Smith et al., 2015a), assessment of land-use history (e.g. grazing pressure, Speed et al., 2013), and understanding of geomorphological processes (Owczarek, 2010). Arctic shrubs face the full array of environmental conditions they live in, at the margin of woody plant growth (Crawford, 2008). This has two main consequences: first climate drives their growth to a large extent and second their growth is highly irregular, often resulting in partially missing rings (Wilmking et al., 2012; Buchwal et al., 2013; Myers-Smith et al., 2015b). To disentangle the ecological mechanisms behind climate effects, one needs to account for this spatiotemporal heterogeneity within and between shrubs, and across time. Therefore, the study design requires sampling across hierarchical levels: from serial sectioning along different shrub parts (Kolishchuk, 1990; Ropars et al., 2017), to replication across the landscape (Myers-Smith et al., 2015b, Figure 1). The detection of partially missing rings and assessment of calendar years have to be accurate for dendrochronology to 'exist as a legitimate science'(Cook & Pederson, 2011), and are possible to achieve with multi-level cross-dating techniques (Douglass, 1941; Buchwal, 2014; Myers-Smith et al., 2015b). Climate trends should be disentangled from trends due to geometry (i.e. rings grow in circles) and age (i.e. different growth rates in the juvenile phase, Cook & Kairiukstis, 1990; Biondi & Qeadan, 2008). This step is particularly important because different standardization methods can lead to different results (Helama et al., 2004; Sullivan et al., 2016) and no 'recipes' exist since the mechanisms of ring growth (e.g. aging of shrubs) are not yet fully understood (Schweingruber & Poschold, 2005). Even so, a well-documented mechanism of shrub ring growth is its relationship with temperature.

Tissue temperature determines the production and flow of auxin hormones triggering xylogenesis i.e. the cambial activity forming ring growth (Sundberg et al., 2000; Wilmking et al., 2012). Accordingly, summer temperature has been widely found to influence arctic and alpine shrub ring growth (Myers-Smith et al., 2015a; Ackerman et al., 2018; Weijers et al., 2018a; Weijers et al., 2018b). However, other environmental characteristics, such as soil moisture (Ackerman et al., 2017; Weijers et al., 2017), snow cover (Hallinger et al., 2010; Schmidt et al., 2010), or freezing (Bokhorst et al., 2008; Milner et al., 2016; Bjerke et al., 2017) can interfere with the strength of the summer temperature-shrub growth relationship. Delayed growth effects can also interfere with the strength of climate effects on the current year's growth (Forchhammer, 2017). Vegetation monitoring using recently developed remote sensing products such as Normalized Difference Vegetation Index (NDVI) has also detected these most important climate drivers of shrub growth (Forbes et al., 2010; Ju & Masek, 2016; Phoenix & Bjerke, 2016; Vickers et al., 2016), despite the relatively short time-series and low resolution available in high-arctic regions (Karlsen et al., 2018). Furthermore, dendrochronological tools provide detail information at the individual, site or species hierarchical sampling level, so complementing information from remote sensing and enabling a detailed understanding of the mechanisms by which climate change affects primary production.

'Individual trees, not forests, respond to climate' (Galván et al., 2014).

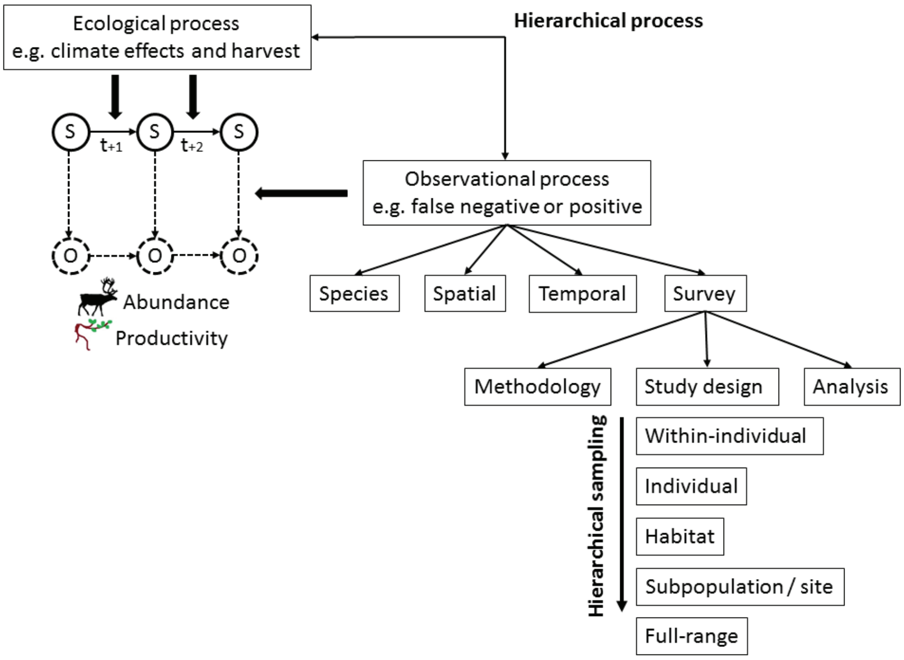

Figure 1. Hierarchical organization of imperfect detection in wildlife systems inspired by Royle and Dorazio (2008); Zuur et al. (2009); Kery and Schaub (2012); Guillera-Arroita (2017). The true abundance is a latent state (S) changing from year to year (t_{+1}) according to the **ecological processes**' demographic rates. Each annual monitoring results in an observed abundance (O) subject to the **observational process**. The complexity of this processes can be decomposed and hierarchically organized in distinct components. Observation errors can arise from intrinsic characteristics of the **species** (e.g. herding or sedentary behavior [ungulate], eccentricity of shoot growth [shrub]), **spatial** and **temporal** variation (e.g. migratory behavior [ungulate], grazing/icing plant damage [shrub]) and the different components of a **survey**. First, adequate **methodology** needs to be chosen for the study species (e.g. distance sampling [ungulate], dendrochronology [shrub]). Then the **study design** can be adapted in hierarchical sampling steps to account for spatiotemporal heterogeneity ranging from local **within-individual** variation (i.e. daily-rhythm [ungulate], partially missing rings [shrub]) to **between-site** variation (i.e. terrain ruggedness [ungulate], collection date [shrub]). Finally, adequate **analytical** methods should account for these imperfect detections (e.g. linear mixed-effects models, ring growth standardization). Only then can ecological processes be decoupled from observation errors, thus allowing accurate **full-range** estimation of species abundance or productivity.

AIMS

Enhancing our predictive understanding of large-scale effects of climate change on arctic tundra ecosystems is of major importance to anticipate adverse global consequences for biodiversity. A crucial step to achieving this is to study how weather and climate act across the hierarchy of ecological scales, and the roles of local heterogeneity *versus* large-scale common drivers of population processes. This is the overarching objective of my thesis. Disentangling the mechanisms behind changes in ecosystem dynamics, including mechanisms triggering co-fluctuation between subpopulations' abundance, requires long-term, large-scale, high-quality data across trophic levels. Therefore, I started with local-scale methodological investigations and progressed towards the large-scale application of these methodologies. This enabled me to study variation in climate effects on local population abundance and on large-scale patterns of population synchrony of two key tundra species from different trophic level: the Svalbard reindeer *Rangifer tarandus platyrhynchus* and the polar willow *Salix polaris*, living at the edge of their species' distributional ranges. This thesis has three main aims subdivided into several questions.

I. *Local-scale methodological investigations* – Which monitoring methods are best suited for accurate assessments of reindeer abundance and vascular plant productivity in tundra landscapes? (Papers I & II)

Annual population counts have been performed in two subpopulations on Svalbard for 40 years using a total count methodology. In Paper I, I asked: **(1)** is this methodology accurate (i.e. unbiased and precise)? **(2)** How does distance sampling – the most commonly used methodology for wild ungulates surveys – perform compared with total counts? Above-ground plant biomass has been monitored for 13 years at one unique site in central Svalbard. From this site, I collected dwarf shrubs of *Salix polaris* and used dendrochronological tools to reconstruct time-series of annual shrub ring growth. Ring growth represents a secondary growth trait, while above-ground biomass represents a primary growth trait. In Paper II, I asked: **(3)** does the reconstructed annual secondary growth of *S. polaris* shed light on the past above-ground biomass available for higher trophic levels? Expanding my work into large-scale and long-term variation in abundance, the second aim was:

II. *Large-scale abundance surveys and climate effects* – What are the drivers of spatial and temporal variation in reindeer and *S. polaris* abundance across Svalbard? (Papers III, IV & V)

The Svalbard reindeer, as with most arctic mammals, has suffered from past overharvesting and is now under the threat of a rapidly warming Arctic. By expanding the previously developed methodologies to all of Svalbard, I addressed the following questions in Paper III: **(1)** what drivers control Svalbard reindeer spatial distribution and abundance across their full-range? **(2)** Have reindeer recovered from past overharvesting? **(3)** What is the conservation status of Svalbard reindeer today? Understanding the climatic drivers of temporal population dynamics requires long-term annual time-series, only available from a few localities when I started my work. To improve this situation, I reconstructed *S. polaris* ring growth time-series across Svalbard. Using existing spatially replicated reindeer and weather time-series, investigated: **(4)** what are the main climate drivers of reindeer and *S. polaris* population dynamics across Svalbard, and how do they vary spatially? (Papers IV and V).

III. *Spatial synchrony and climate effects* – To what extent are the respective population dynamics of *S. polaris* growth and reindeer synchronized across Svalbard, and what is the climatic contribution to this synchrony? (Papers IV & V)

Population sizes may co-fluctuate with their environmental drivers over a large spatial scale (commonly named 'the Moran effect'). Studying this phenomenon in 10 reindeer and 18 *S. polaris* subpopulations/sites, and taking advantage of the climate data recorded by six weather stations from across Svalbard, I answered the questions: **(1)** how strongly are climatic variables synchronized over a large spatial scale? **(2)** Are the reindeer populations and *S. polaris* growth spatially synchronized in their fluctuations? **(3)** How much of the synchrony pattern can be attributed to climatic drivers? (Papers IV and V).

METHODS

The environment of the high-arctic Svalbard

The Svalbard archipelago (76-81°N and 10-34°E, 59 793 km^2) is located in the high Arctic, between the Barents Sea and the Greenland Sea, and comprises approximately 500 islands. The four principal islands are Spitsbergen, Nordaustlandet, Edgeøya and Barentsøya (Figure 1). Glaciers cover 62 % of the land surface, while only 16 % is vegetated (Johansen et al., 2012). The vegetated landscape is highly fragmented and characterized by peninsulas separated by tidewater glaciers on the coast and U-shaped valleys inland. The bioclimatic zones of Svalbard comprise: polar deserts with plant species such as *Papaver dahlianum, Saxifraga spp.* and *Draba spp.*; Northern Arctic tundra with *Salix polaris* and *Saxifraga oppositifolia*; and Middle Arctic tundra with *Cassiope tetragona* on acidic substrate and *Dryas octopetala* on alkaline substrate (Elvebakk, 1997; Jónsdóttir, 2005). The plant growing season lasts for two-three months. The western and central parts of Svalbard are influenced by the Atlantic warm water current giving a relatively mild oceanic climate for its latitude (Nordli et al., 2014). Both temperature and precipitation follow a negative gradient from Southwest to the Northeast (Van Pelt et al., 2016). Across Svalbard over the period 1962-2014, the mean annual temperature was -5.8 ± 0.57 °C (winter [November to April] = -12.0 ± 2.6, summer [June to August] = 3.0 ± 0.8) and the annual precipitation was 372 ± 56 mm (winter = 196 ± 44, summer = 81 ± 32, Paper V). Over the last century, mean temperature increased at a rate of ~ 0.2°C per decade (stronger increase in winter than in summer). However, precipitation did not exhibit a significant temporal trend (Nordli et al., 2014; Van Pelt et al., 2016). Svalbard is among the regions with the strongest temperature increase on Earth (Nordli et al., 2014; Isaksen et al., 2016).

Key species: the Svalbard reindeer and the polar willow

The Svalbard reindeer is an endemic subspecies living at the edge of the circumpolar distribution of *Rangifer*. Contrary to other *Rangifer* subspecies, the Svalbard reindeer do not perform long-distance migrations (Tyler & Øritsland, 1989), although short-distance displacement can occur under poor climatic conditions (Hansen et al., 2010; Stien et al., 2010; Loe et al., 2016). The most recent phylogeny supports a Eurasian origin of the subspecies (Kvie et al., 2016). Since the 17th century hunting had led to local extinction across 60% of the land (Lønø, 1959) by the time the species became protected in 1925. Reindeer seem to have recolonized most of the archipelago, both naturally and by translocation (Øritsland, 1986; Aanes et al., 2000). For instance, some individuals (n = 12) were reintroduced for scientific purposes from central Svalbard (i.e. Nordenskiöld land) to the northwest coast in 1978 (i.e. Ny-Ålesund area). Over the 40 years since, the founded and founder subpopulations have been monitored annually, yielding important knowledge of the population dynamics at these localities (Solberg et al., 2001; Aanes et al., 2003; Kohler & Aanes, 2004; Tyler et al., 2008). These studies suggest that winter rain-on-snow events limits winter-forage accessibility by enclosing vegetation in ice. Consequently, individuals may starve to death in late winter (Albon et al., 2016), especially when they are numerous (i.e. density dependence). Calves and individuals older than 9 years old are the most vulnerable age classes (documented for females, Lee et al., 2015). Vital rates (i.e. mortality and fecundity) are driven by body mass, which is highly variable between winters depending on the environmental conditions (Albon et al., 2016; Veiberg et al., 2017). In winter, reindeer can be found at high altitude, reaching non ice-encased vegetation patches. In summer, however, reindeer occupy lowlands, on open planes and valley bottoms where their detectability is high. The reindeer is a keystone species of the tundra ecosystem. Reindeer carcasses are a major food supply for Arctic foxes and drive their population dynamics (Fuglei et al., 2003; Hansen et al., 2013). They can affect both above- and below-ground tundra through grazing and input of nitrogen (i.e. feces and carcasses), resulting in a predictable vegetation succession: from lichen, to moss, and to graminoid dominated tundra (Van der wal et al., 2004; Van der Wal, 2006). Reindeer are generalist grazers and the dwarf shrub *S. polaris* composes a major part of their diet year round (Bjørkvoll et al., 2009).

The polar willow, *S. polaris*, is a long-lived dwarf shrub with a circumpolar distribution, and Svalbard is located at its northenmost distribution margin (https://www.flora.dempstercountry.org/). *S. polaris* commonly dominates arctic communities, from polar deserts to arctic meadows and is the only widespread shrub on Svalbard (https://svalbardflora.no/, Rønning, 1996). The major part of the individual is located below-ground and often only shoot tips, leaves and reproductive structures (about 2-5 cm high) compose the above-ground part (Paper II, Fig. 1). Reproduction can be asexual (i.e. clonal) or sexual through both wind and insect pollination (Rønning, 1996; Dormann & Skarpe, 2002). In common with other arctic shrubs, the secondary growth of *S. polaris* forms annual rings, yet ring growth is particularly irregular, reflecting the large fluctuations in high arctic climatic conditions (Wilmking et al., 2012; Buchwal, 2014; Owczarek & Opała, 2016). Hence, both annual primary and secondary growth are highly variable among years, and this variation seems mainly driven by summer temperatures (Buchwal et al., 2013; Van der Wal & Stien, 2014).

From expeditions, to the laboratory, to the data

The data reported in this thesis (Figure 2) were collected during field campaigns from remote base camps, a sailing boat or research vessels during the summers 2013-2016 (Paper I, II, III & V). A typical field day started with reindeer monitoring, allowing the identification of suitable locations for *S. polaris* collection (Papers III & V). In addition, I opportunistically collected ancient bones and antlers, well preserved in the cold and dry high arctic climate (Van der Knaap, 1989), for ^{14}C dating (n = 46 bones from before 1800 AD, Paper III). I supplemented these data with existing time-series from 10 reindeer subpopulations censused by total counts (four of them by foot and six of them by helicopter, Paper IV), vascular plant growth time-series from one site in central Spitsbergen (Paper III) and data from 17 weather stations spread across Svalbard (Paper IV & V).

Distance sampling and total counts are monitoring methodologies that provide direct measures of reindeer abundance. Distance sampling was conducted along line transects, with reindeer detectability decreasing as distance from the transect line increased. We recorded the distance and angle from the observer to the animal, and the coordinates of the observer's position, to calculate the reindeer's location. One independent observation was either a reindeer or a group (i.e. cluster) of known size. The open tundra landscape, with high reindeer detectability, enabled us to fulfil the fundamental assumptions and minimum sample size (> 80 observations) required by distance sampling methodology (Buckland et al., 2001; Buckland, 2015, Papers I & II). Total counts assume that all animals within a defined area are detected with certitude, thus no false positive or negative counts should occur. Observers (1 to 5 depending on the area's size) walked parallel routes ~ 1 km apart. However, the observers were expected to deviate from their route to get the best view for binocular scanning of the landscape and they could communicate by VHF-radio with other observers to avoid double counts. We recorded the animal or cluster's position together with group size on a topographic map (1:100 000, except for helicopter counts in paper IV). No measure of imperfect detection can be associated with the counts, except if total counts are repeated over exactly the same closed population (Paper I), if insight can be gained from marked animals resighted during the census (Paper I), or if the frequency of detection and their associated spatial covariates can be extrapolated across space (Paper III).

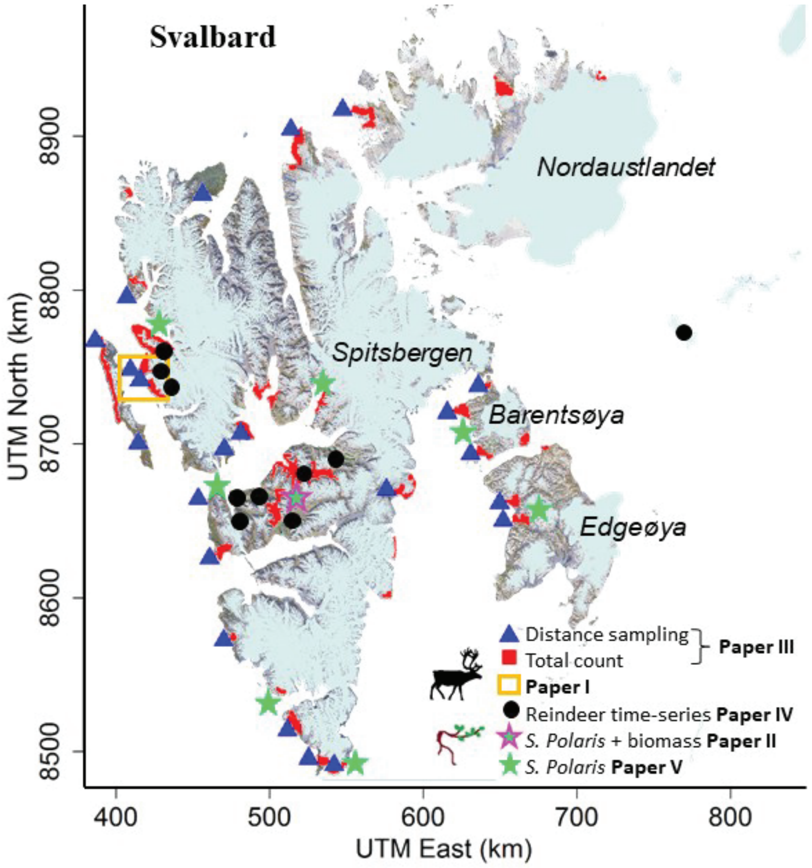

Figure 2. Overview of the sampling sites included in this thesis. In total, 300 km of distance sampling line transects and 1350 km^2 of total counts were surveyed on foot (2013-2016), amounting to ~ 5000 reindeer observed (~ 1850 clusters). Two sites were repeatedly surveyed within summer 2013, both with distance sampling and total counts (orange square). Ten reindeer populations were counted annually with an overlapping timespan from 1997-2015. A total of 70 *Salix polaris* shrubs, collected in 8 sites, were used for dendrochronological readings of ring growth covering the period 1962-2014. The site from central Spitsbergen (purple star) contained 10 subsites from which both ring growth (1985-2014, 30 individual shrubs) and above-ground biomass (1998-2009, 2013, 272 plots) time-series were acquired. The background map is a vegetation map from Johansen et al. (2012), and the light blue represent glaciers. For visual clarity, symbol locations are not always at their exact position.

Sampling of *S. polaris* was non-random because only the largest individuals without visible injuries are suitable for dendrochronological studies (Myers-Smith et al., 2015b). We carefully extracted entire individuals from the ground, each separated by a minimum distance of 5 m to avoid repeated sampling of the same individuals (i.e. underground rhizomes). In the laboratory, we applied serial sectioning with a GLS-1 sledge microtome (Gärtner et al., 2014) along the root collar, shoots and roots to measure growth variation over years within an individual (Kolishchuk, 1990). Cross-sections of 20 µm thick and ~ 3 mm diameter were stained, dehydrated, permanently fixed and digitalized for measurement of ring-width in imageJ 1.48 (Schindelin et al., 2015, Paper II). Ring growth is heterogeneous within and between individuals so a key challenge to correctly reconstruct chronologies is to detect partially or locally missing rings (Buchwal et al., 2013). This was possible by extensive and fervent cross-dating at multiple levels (Buchwal, 2014, Paper II).

Statistical analyses

Spatial density modelling of reindeer

Assessing how reindeer positions depend on local environmental conditions is central to making inferences on densities across space (i.e. spatial density modelling, Aarts et al., 2012; Miller et al., 2013). In discrete space, the true density parameter λ can vary with environmental predictors Z_i within an area i of the landscape, which can be decomposed in a suite of hierarchical generalized linear models to focus on distinct components of the system (Royle & Dorazio, 2008). A general equation with a link function f can be expressed as:

$$f(p_i) = \alpha_0 + \alpha_1 Z_i$$

where p_i can be one of the four parameters of interest σ_i, λ_i, π_i, or μ_i (see below), with respective coefficient estimates (α_0 and α_1).

For distance sampling, this implies that the detection parameter (σ_i) and the density parameter (λ_i) are expressed as linear functions of environmental predictors on the log-link scale (Papers I & III). For relatively small study sites of which a large area is covered, the detection and density processes may not be independent of each other, and it is advised to model both processes simultaneously (Royle et al., 2004; Miller et al., 2013, Paper I). For total counts, the presence parameter (π_i) and, the count parameter (μ_i, conditional on reindeer presence) can also be expressed as functions of environmental predictors on the logit- and log-link scale respectively.

Both the presence probability and count model were combined in a hurdle model (Zuur et al., 2009), accounting for zero-altered and overdispersed data, for the estimation of λ_i (paper III). Note that in Paper I, total counts were repeated within a site and uncertainty measures were not modelled with spatial density models, but with a generalized linear model in which only sites and years were predictors on the log-link scale. From the above spatial density models and the available spatial covariates from across Svalbard, we could predict abundance and its associated variance in any region of interest (i.e. entire Svalbard or specific management areas).

Time-series standardization and climate effects analyses

An important aspect of dendrochronology is standardizing ring-width chronologies to remove trends due to geometry (i.e. rings grow in circles) and age (i.e. different growth rates in the juvenile phase, Cook & Kairiukstis, 1990; Sullivan et al., 2016). Accordingly, we standardized *S. polaris* cross-section chronologies by first transforming ring-width (μm) to basal increment area (μm^2) (Biondi & Qeadan, 2008), and we subsequently aligned cross-section growth curves by biological age (i.e. cambial age). The age trend was removed by a regional curve standardization method (Briffa & Melvin, 2011) which resulted in a dimensionless Ring-Width Index (RWI, hereafter referred to as 'ring growth').

Replicated data in time and space, typically collected within a nested design (Figure 1), require the use of linear mixed-effects models to: first, account for the non-independency of replicates within a nested level; second, correctly partition the within- and between- variation in the different ecological levels sampled; third, give the correct weight to each observation when the sampling design is unbalanced (Cnaan et al., 1997; Zuur et al., 2009). Thereafter, before conducting correlation tests (i.e. between primary and secondary *S. polaris* growth, Paper II) and climate effect analyses, annual estimates were obtained from a linear mixed-effects model accounting for the hierarchical structure of the data as random effect and by setting year as a fixed factor. For example, the random effects used to obtain annual ring growth time-series were shrub individual nested within habitat, nested within sites (Paper II), while to estimate annual weather variables across Svalbard they were weather station IDs (Papers IV & V).

Climate effects were analyzed with linear mixed-effects models, where 'growth' (i.e. reindeer population growth or rate of *S. polaris* ring growth) was the response variable, the potential climate predictors were the fixed effects, and the replicated units (e.g. years) were the random effects (Papers II, IV & V). The reindeer population growth rate was defined as the ratio between population size at year *t* and population size at year *t-1*. To select the best model among competing models, we used the Akaike information criterion (Burnham & Anderson, 2002).

Spatial synchrony

We studied spatiotemporal patterns of reindeer population growth rate, *S. polaris* ring growth and weather data across Svalbard. To do so, we calculated Pearson's correlation coefficients between pairs of sites and subsequently plotted the sites' pairwise correlations as a function of the geographical distances separating these sites. The average pairwise correlations across all distances defined the regional average synchrony (ρ). To quantify the contribution of climate to ρ, we first accounted for its effect on either reindeer growth rate or *S. polaris* ring growth using ordinary linear models. Using residuals from these linear models, we re-calculated the regional average synchrony (ρ_{res}). Associated 95% confidence intervals (i.e. 2.5% and 97.5% quantiles) for ρ and ρ_{res} were obtained from non-parametric bootstraps (Paper V, appendix X). The difference in non-parametric bootstrapped replicates ($\rho_{diff} = \rho - \rho_{res}$) and 2.5% and 97.5% quantiles assessed the statistical significance of the climate variable's contribution to the regional average synchrony ρ.

All analyses were conducted with R software version 3.3.1 (R Core team, 2016).

MAIN RESULTS AND DISCUSSION

I. *Local-scale methodological investigations* – Which monitoring methods are best suited for accurate assessments of reindeer abundance and vascular plant productivity in tundra landscapes? (Papers I & II)

The most commonly used monitoring method to estimate Svalbard reindeer abundance on Svalbard is total counts (Aanes et al., 2003), and I assessed its accuracy on two peninsulas enclosing two subpopulations in the Ny-Ålesund area (Figure 2). Based on repeated total counts within a single summer, total counts abundance estimates appeared to be both precise and unbiased, based on the resighting of marked animals. Hence, marked females known to be present in the area before the survey were all resighted (i.e. no false negatives) and only 1.9 % of marked animals were double counted (i.e. false positives). Under the conditions in which we conducted the census (i.e. equal sampling effort across a clearly defined area that we covered in one day), the total count was a suitable method for estimating reindeer abundance, even though detection probability could not be assessed. In comparison, I repeated distance sampling line transects, the most widely used methodology for wildlife surveying (Buckland et al., 2004). Spatial density was positively, but non-linearly, related to vegetation cover, with a threshold at 50% vegetation cover. Distance sampling abundance estimates were unbiased because they did not differ significantly from total counts. However, the precision was lower despite the high sample size (n = 143 reindeer clusters). The recommendations of a minimum of 60-80 observations to estimate detection probability and hence density (Buckland et al., 2001) are thus likely to be insufficient to capture the ecological processes driving population dynamics. However, distance sampling is a cost-effective method for large-scale population-state assessment in open landscapes. In the case of Svalbard reindeer, large sample sizes can be relatively easily reached given their high detectability (~ 50 % detection at 500 m with the naked eye), relatively high density (~ 4 reindeer/km^2) and their non-herding behavior (mean group size = 1.6 ± 0.1). By choosing the appropriate monitoring method and analytical tools depending on landscape characteristics, it is thus possible to carry out large-scale monitoring in open tundra (Paper I).

I constructed a local chronology of below-ground secondary growth (i.e. ring growth) of *S. polaris* sampled from 10 independent subsites (n = 30 individuals, 1985-2014). During this period, 13 years overlapped with *in situ* measurements of primary growth (i.e. above-ground plant biomass production), from similar subsites (Van der Wal & Stien, 2014). Accounting for levels of variation inherent to the hierarchical sampling design (i.e. plot/shrub, site, habitat, and year) enabled us to clearly disentangle the relationship between primary and secondary growth, despite the substantial growth heterogeneity within and between individuals. I found that my measures of *S. polaris* secondary growth reliably reflected annual primary growth ($r = 0.56$) – a relationship that became even stronger at higher hierarchical sampling levels. Consequently, ring growth represented the annual production of the vascular plant community, comprising six habitat types ($r = 0.70$). In common with above-ground primary growth (Van der Wal & Stien, 2014), below-ground secondary growth of *S. polaris* was primarily driven by mean summer temperature from 1985 to 2014. This is in accordance with the majority of circumpolar and alpine studies on shrub growth (Myers-Smith et al., 2015a; Ackerman et al., 2018; Bjorkman et al., 2018; Weijers et al., 2018a). Additionally, I found an interaction between the previous year's ring growth and summer temperature, suggesting a higher use of available resources stored in the previous year, when summers were cold. I did not detect any effect of annual reindeer abundance on secondary plant growth. I expected browsing effects to be highly stochastic in space and time, considering the ranging area of this reindeer subpopulation (~ 150 km^2), while our vegetation study was only conducted in one site of this range. Our study bridges the gap between below-ground shrub growth dynamics, which belong to the 'hidden part of the iceberg', and above-ground growth dynamics (Iversen et al., 2015). Furthermore, comparative studies between shrub growth and remotely sensed vegetation maps (Babst et al., 2010; Forbes et al., 2010; Macias-Fauria et al., 2012; Weijers et al., 2018b), support the potential applicability of shrub ring growth as a proxy for primary production throughout the arctic biome. My work confirms the potentially high applicability of dendrochronological tools, thereby opening new opportunities for studies of large-scale vascular plant community dynamics under climate change, including in remote areas of the high Arctic (Paper II).

II. *Large-scale abundance surveys and climate effects* – What are the drivers of spatial and temporal variation in reindeer and *S. polaris* abundance across Svalbard?

To answer this question, I applied the methodologies developed in Paper I and II across the Svalbard archipelago. I found that Svalbard reindeer abundance has increased as an outcome of range expansion and population density increase (paper III). This is consistent with several deer species across Europe and North America (Côté et al., 2004; Milner et al., 2006; Putman et al., 2011), but differs from many other *Rangifer* subspecies (Vors & Boyce, 2009; Festa-Bianchet et al., 2011; Gunn et al., 2011) with receding ranges and decreasing density. This resulted in an assessment of the species status as vulnerable by the IUCN (Gunn, 2016). In paper III, the abundance increase was inferred from distribution maps, opportunistic counts over the past century and from the field surveys included in this thesis. Furthermore, in paper IV, the trend of the mean abundance estimates from 10 subpopulations (each on them weighted by their total population size) also increased (1997-2015). Reindeer detectability was similar to that of our distance sampling surveys from Paper I and the precision of abundance estimates was improved due to our extensive sampling effort (n = 443 independent reindeer clusters). Vegetation productivity was still the main driver of reindeer spatial density but, for the same 'greenness' level, fewer reindeer were found on the east than on the west side of Svalbard (Paper III). This longitudinal gradient likely reflects the longer snow-cover season for plants on the east side due to the colder climate there (Macias-Fauria et al., 2017). The history of Svalbard reindeer prior to protection a century ago (1925), when overharvesting extirpated 60 % of the historical and actual reindeer range, was still detected today. Reindeer densities were lower in recently recolonized regions (with total count methodology that appropriately covered this covariate's range, Sillett et al., 2012). Hence, full recolonization over the historical range does not imply population recovery to its 'baseline'. This long legacy effect of hunting constraining the population reaching its carrying capacity again was to not only be because recovery takes time, but because reindeer dispersal ability is low. Low dispersal ability was supported empirically by evidence of reindeer behavior and landscape barriers (Tyler, 1987) as well as genetically (Côté et al., 2002; Peeters et al., in prep).

Demographic fluctuations characterize the temporal dynamics of Svalbard reindeer populations (Albon et al., 2016), with linear trends in population size ranging from increasing to decreasing (Paper IV). Even within a population, linear trends can vary from positive to negative according to the starting year chosen for calculation, as illustrated by the Brøggerhalvøya population in paper IV (fig. 5d). This population is an example of a recovery trajectory after 100 years of absence, shifting from an eruptive to a post-crash phase (Hansen et al., 2007). Despite the possibility of subpopulations being in different phases of recovery, distance sampling and total counts predicted similar abundance across Svalbard, facilitated by extensive spatial replication capturing local heterogeneity (Paper III). The estimated total abundance of Svalbard reindeer was 22000 [21000-23000] individuals. Spatially, the largest populations occurred in wide inland valleys that had not suffered from past extinctions, had the highest genetic diversity (Peeters et al., in prep) and were thus likely to be more resilient to stochastic events (Lande et al., 2003). Additionally, the increase in inland summer temperature was stronger than on the coast (Paper IV). In contrast, coastal populations had the lowest abundances, had recently recolonized after overharvesting, and had the lowest genetic diversity as well as increasing isolation due to sea-ice loss (Peeters et al., in prep). These coastal areas also experienced a regime shift in increased frequency of rain-on-snow events (Peeters et al., 2018, Paper IV) and thus have the greatest vulnerability to stochastic extinctions. Temporally, reindeer dynamics across Svalbard were mainly driven by negative effects of winter rain-on-snow events (interacting with density dependence) and to a lesser degree by positive indirect effects of summer temperature on plant production (Paper IV). Interestingly, different strengths in the effect of these antagonist climate drivers, resulted in differing reindeer population trends in a coastal *versus* inland population. Contrasting effects of climate during summer *versus* winter were also found in *S. polaris* ring growth, and thus vascular plant biomass dynamics (Paper II). Summer temperature influenced plant growth positively across Svalbard (Paper V), while in some coastal areas, we reported the first evidence of a negative effect of rain-on-snow on plant growth based on longitudinal data analysis. To summarize, winter and summer warming have opposite effects on forage abundance and availability, directly controlling a key species with potential cascading effects on the ecosystem (Ims et al., 2007, Papers IV and V). How these climate drivers potentially control population co-fluctuations across large spatial scale is of major concern for the conservation of high arctic ecosystems.

III. *Spatial synchrony and climate effects* – To what extent are the respective population dynamics of *S. polaris* growth and reindeer synchronized across Svalbard, and what is the climatic contribution to this synchrony?

Summer temperature and rain-on-snow were synchronized over a large spatial scale across Svalbard (average spatial synchrony $\rho = 0.5$ and $\rho = 0.6$ respectively, Papers IV & V, Peeters et al., 2018). Accordingly, reindeer population growth rate and *S. polaris* ring growth were also spatially synchronized but to a lesser extent than their respective climatic drivers ($\rho = 0.2$ in both species). A significant part of the regional average synchrony in *S. polaris* was generated by summer temperature. For reindeer, the interaction between rain-on-snow and density dependence explained a large part of the spatial synchrony in mortality rates, but not fecundity rates, which resulted in a nearly significant effect on population growth rates.

Generally, it is a real challenge to gain sufficient spatiotemporal replicate measurements, at multiple ecological levels, to successfully detect drivers. In this highly heterogeneous system, we managed to partition variances to detect synchronizing forces. A part of the heterogeneity in the reindeer study arose from the methodology with relatively short, sometimes incomplete, time-series from helicopter counts (1997-2015), without an assessment of count uncertainty. Nevertheless, most of the observed heterogeneity in reindeer and *S. polaris* populations had a biological meaning. It represented the wide array of local climates, habitats, and associated individual variation (Messier et al., 2010; Elmendorf et al., 2012a; Fryxell & Lundberg, 2012; Galván et al., 2014), which had the potential to buffer risks of mass extinction events.

The observed regime shift in the frequency of rain-on-snow events in coastal areas of Svalbard is of major importance (Peeters et al., 2018). Depending on the future spatial extent of such events, this may result in increased spatial heterogeneity or, conversely, increased spatial synchrony. Hence, if an inland/coastal gradient persists, spatial heterogeneity may increase both in reindeer and plant population dynamics. However, if the spatial extent of rain-on-snow events expand more uniformly throughout inland Svalbard and across the entire Arctic in general (Bintanja & Andry, 2017), reindeer spatial synchrony levels may increase and possibly become a new synchronizing agent of plant growth. Unfortunately, spatial synchrony studies on rare plant species, the most at conservation risk, are nearly impossible to achieve due to the lack of long-term and large-scale data. Thus, spatial synchrony in *S. polaris* ring growth could serve as an indicator for conservation decisions regarding rarer species. Obtaining robust chronologies was probably the most innovative, but also most challenging accomplishment of my thesis.

SUMMARY AND CONCLUSION

In this thesis, I have built a framework to study spatiotemporal patterns in two key species from the high-arctic tundra ecosystem, each belonging to a different trophic level: the Svalbard reindeer *Rangifer tarandus platyrhynchus* and the polar willow *Salix polaris* (see summary Figure 3). The hierarchical approach adopted in my thesis first enabled me to identify heterogeneity emerging from the observational process (Figure 1). In the methodological investigation of reindeer abundance estimation accuracy, I found that the total count was a precise and unbiased method, even though detection probability could not be estimated. By comparison, distance sampling was less precise, but may be better suited to large-scale open landscapes than total counts. The methodological investigations of vegetation monitoring showed that time-series of vascular plant biomass production were accurately reconstructed from dendrochronological tools applied to *S. polaris*. The accuracy was greater at the total vascular plant community level than at the habitat level within our focal shrub species. Subsequently, monitoring of reindeer abundance and vascular plant productivity (through *S. polaris* ring growth) was applied across Svalbard (Figure 2). Spatial density modelling showed that vegetation productivity largely explained local reindeer abundance, but independently of that, population recovery from overharvesting a century ago is still ongoing. Predictions of reindeer abundance at the Svalbard scale were similar using the two methodologies, due to sufficient spatial replication capturing local heterogeneity (i.e. subpopulations possibly in different phases of recovery).

For the spatiotemporal analysis, I partitioned variation at different hierarchical ecological scales for climate effect analyses (Figure 1). This revealed a substantial heterogeneity in climate responses from individual, to subpopulation, to metapopulation at the Svalbard-scale. Resource allocation to primary growth [*S. polaris*] or vital rates [reindeer] is a highly individual process, affected by a wide array of abiotic and biotic disturbances, including delayed growth [*S. polaris*] and density dependence effects [reindeer]. At the subpopulation scale of both reindeer abundance and plant growth, we found contrasting effects of climate warming during summer (positive) *versus* winter (negative). Differences in the strengths of the effect of the main climate drivers, i.e. rain-on snow (interacting with density) and summer temperature, resulted in differing reindeer population trends in a coastal *versus* an inland population. Furthermore, at the subpopulation/site level, plant growth was also negatively affected by rain-on-snow events (plant ice encasement) in some coastal sites. At the Svalbard-scale, summer temperature had a strong positive effect on plant growth and, hence, explained a significant part of the spatial synchrony in growth. Likewise, a part of the spatial synchrony of reindeer population growth rates was explained by its respective major dynamic driver: rain-on-snow. Still, overall spatial heterogeneity dominated. The future direction of Svalbard's ecosystem dynamics will likely depend on the increase in frequency and spatial extent of rain-on-snow events. If spatial gradients (e.g. coastal/inland) of rain-on-snow persist, spatial heterogeneity in both reindeer populations and vascular plant production may increase. Conversely, an increase in spatial extent of rain-on-snow may promote reindeer population spatial synchrony and become a new synchronizing agent of plant growth, with potentially cascading effects on this bottom-up controlled tundra ecosystem. This work has implications far beyond my study system, as the Arctic stands as 'an experiment of human kind'. The approach adopted in this thesis could disentangle large-scale climatic phenomena across trophic levels, taking one more step towards a overarching goal of Ecology: understanding mechanisms of environmental influences on community dynamics across large parts of the globe.

To varying extents, all seven knowledge gaps of climate change effects on arctic ecological dynamics stressed by Post et al. (2009), have been addressed in this thesis. Important contributions were made in the study of heterogeneity as a potential buffer to climate changes and the spatial scale of these changes (gap 4 'heterogeneity' and 5 'spatial scale', see Introduction). Environmental change during the snow-cover season, through rain-on-snow events, is indeed important across trophic levels, including primary production (gap 2 'outside the growing season' and 6 'extreme events'). I reported a successful conservation study (gap 1 'conservation') of a *Rangifer* subspecies, despite critically declining herds in other parts of the Arctic. Although I have only discussed possible cascading effects of reindeer and primary production dynamics (gap 3 'trophic interaction'), the framework developed in my thesis has great potential to expand the study of responses of trophic dynamics to climate warming.

FUTURE PROSPECTS

The natural next step of my work is to relate spatial synchrony patterns across species, trying to identify common driving forces across trophic levels (Smith, 1983; Haynes et al., 2009). For this, one could estimate average regional synchrony over smaller time-intervals (e.g. moving average with a 3-10 year window) or on an annual basis (e.g. likelihood maximization of the z-standardized multivariate normal distribution's covariance matrix). Thereafter, one could compare patterns of annual average regional synchrony between reindeer abundance/growth rate and *S. polaris* ring growth. Spatial synchrony is a dynamic process that also changes through time (Post & Forchhammer, 2004; Allstadt et al., 2015; Defriez et al., 2016; Koenig & Liebhold, 2016; Shestakova et al., 2017; Walter et al., 2017; Kahilainen et al., 2018). Three possible patterns could emerge: 1) absence of co-fluctuation because different forces drive reindeer and *S. polaris* spatial synchrony; 2) a time-lag, which would indicate an interaction between species, where the spatial synchrony pattern of one species diffuses on the other species (May, 1973; Hansen et al., 2013); 3) co-fluctuation, which would indicate common driving forces. Within the limits of the spatiotemporal resolution of data available for other Svalbard species, one could attempt to include data on other key species such as the Arctic fox or migratory geese to this potential community-wide spatial synchrony study.

To continue the road towards a holistic understanding of spatial synchrony on arctic ecosystems, the spatial scale could be extended across the Arctic. One could also compare reindeer/caribou and shrub ring growth annual synchrony pattern from time-series gathered in databases, such as CARMA or ITRDB (https://carma.caff.is, https://www.ncdc.noaa.gov), and the literature (Vors & Boyce, 2009; Ahrestani et al., 2013; Myers-Smith et al., 2015a; Uboni et al., 2016) at the circumpolar scale. According to the empirical pattern found and mechanisms identified, one could simulate possible changes in spatial synchrony (i.e. extent of extinction risk) under different scenarios of climate change, including spatiotemporal rain-on-snow increase.

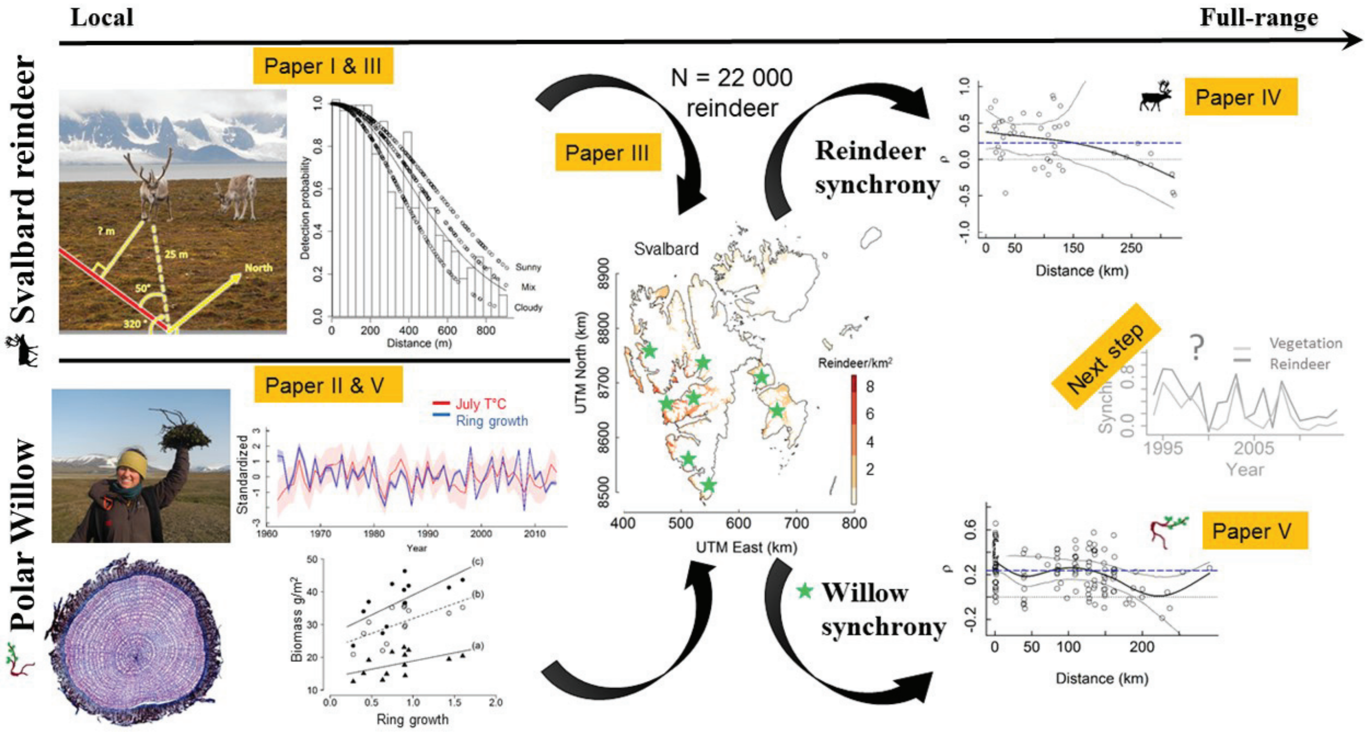

Figure 3. Summary figure of my thesis findings. The framework progressed from local-scale to full-range study of spatial synchrony across Svalbard (left to right). I monitored an endemic subspecies, the Svalbard reindeer (upper half), and its dominant food supply, the polar willow (lower half). A hypothetical graph of a potential 'next step' could relate reindeer and polar willow patterns of annual average regional synchrony.

BY WAY OF THANKS

This thesis is the output of a call for adventure and my desire to seek an understanding of the perfect things that life shaped along endless frozen peaks. On this adventure, there was the one person constantly steering the sails and pointing out the right direction, teaching me how to become an ecologist and an independent thinker. Brage, I am endlessly thankful for your total dedication as a supervisor. Åshild, thank you for all the fantastic field seasons and supervision, often sitting with you at the Norwegian Polar Institute. Bart, it has been 7.5 years that we have been studying together, day after day. How could you always stay so patient and ready to help? All three of you formed my 'reindeer family' and have supported me through my joy and struggles. I was surrounded by inspiring supervisors, including Audun S. and Bernt-Erik. Vidar and René, you were not on the official supervisor list, but I would like to thank you as if you were. In that class during my bachelor's degree, I met not only Bart, but also Morgan and Martin, who counted many reindeer with me. Morgan, I would not even have thought of starting this archipelago-wide sampling scale if I did not have my expedition buddy. Thanks for never giving up extracting shrubs from the ground with bloody hands and after so many hours (days) in the swamps, even for reporting a very important result: 0. Thanks to Marie-Diane and Christophe for their sampling help and to welcome us on onboard Sillage, even when covered in mud: we HAD to follow the randomly drawn transect line! Morgan, I think we discovered Svalbard in a unique way. A warm thanks to Lisa (Lisom!): we have learned so much together. Agata, thanks for teaching your passion of dendrochronology on the 'most difficult shrub on Earth'. This statement was floating around in those moments of wondering whether the adventure would be stranded… but you made sure this was not the case. Jørgen and Erik, thanks for transmitting me your respective passions. I would also love to be an archeologist or a wildlife veterinarian, but with you, my thesis (side thesis) could allow me to be all of these at once! Thanks to all the people I have been in the field with or helped with the logistic. There are so many wonderful colleagues at CBD and elsewhere, who have helped me make this thesis concrete, correcting my Frenchie-English, inspiring discussions, and great fun to be with. In particular my right-hand man/women Øystein, Kate, Lara, Jos and Marlène. I want to thank all, but to name a few: Endre, Thomas, Ivar, Henrik (great field help!), Joost ('counting reindeer is not just counting the number of legs and dividing by four'), Emma, Aline, Irja (Milo & Xaia also!), Stine, Elena, Michael, Eirin and Julie. The best was that your help was not only in the office, but often from the cabin, skiing, climbing and paddling. Christophe, thanks for making sure I would not lose my French identity! Sandra, you are the strongest woman I know on all sides of life. Matteo, my Italian n°1, we have re-made the world of science so many times! I thank my financing sources: my employer the NTNU faculty, the center of excellence CBD and research funding from the Research council (including AFG grants) and Svalbards Miljøvernfond.

There are the ones that 'shaped-me ready' to undertake this four-year adventure, and/or supported me all along. Papa, you taught me how to observe nature, not only how to reach the top of the mountain. Maman, you are the one who has supported me every day, without waiting for anything in return other than to listen to me. The way my parents raised my brother and me in the mountains determined who we are. I have never sat through a full day of lectures at high school (or I would still be making Raclette cheese, I loved it though!) because Nicholas created a mountaineering high-school section and showed me that maths can be learned in a harness. Following my own azimuth from Kirkenes (randomly drawn coordinate) to Tromsø, I met Nigel. You told me 'UNIS is where you should go'. I went. Sadly, I had to shorten this first travel on the tundra to reach the last breath of my Grand Pa. He was the one closely following my academic education from my first day at school. He probably had dream to see me defending my PhD on day. Grand-Père this thesis is dedicated to you. Grand-Mère, Pierre, I wish you were closer, and the rest of the family: thank you. Wam, you have taught me how to pass obstacles in my studies and let me fly away in the northern winds. Paloma, Sarah and your families, Calle, Johan and so many other friends, you all supported me. Thanks to the Chamonix Guide Company who encouraged me to take this PhD position, giving me four years' leave. There is one real polar explorer in my life… Audun T. you have been so patient (of course, or you would not be a 'real' one) in this last stretch of my thesis, 90% of the time on my PC. Your fascination for every snow –crystal and –bunting flying by, kept me reminded of the essence of my love for Ecology. In town , the family Lervik and Zweigel welcomed me with open arms. My office was often in the most inspiring corner of the Norwegian woods – at my cabin with my chickens Pretty & Ugly. Solitude has never passed the door mainly because the four farms of the 5 km^2 surrounding took good care of me. Thanks to the family Simonsen, Slupphaugen (Vibeke du er den beste hønse mor!), Lysevoll and Nils V. This cabin has gathered 79 different colleagues, friends and family during my thesis (hytte book statistics), sharing unique moments to always remind us:

'*Nature is not a place to visit. It is home.*' Gary Snyder (1990)

MERCI BEAUCOUP

Cette thèse est le fruit de l'appel de l'aventure et de la soif de comprendre comment la vie sait parfaitement bien aligner les choses tout le long de ces cimes gelées. Dans cette aventure, il y a une personne qui constamment ajuste les voiles, les pointe dans la bonne direction, m'enseigne comment devenir une écologiste avertie avec une pensée indépendante. Brage, je suis infiniment reconnaissante de t'être dévoué totalement à ton rôle de superviseur. Åshild, merci pour ces saisons de terrain fantastique et pour ta supervision, souvent assise auprès de toi à l'Institut Polaire Norvégien. Bart, cela fait 7.5 années que l'on étudie ensemble, jour après jour. Comment peux-tu être toujours aussi patient et près à m'aider ? Vous trois formiez ma 'famille de rennes' et vous m'avez soutenu tout au long du périple, dans mes joies et mes difficultés. J'ai eu la chance d'être entourée par d'autres superviseurs: Audun S. et Bernt-Erik. Vidar et René, vous n'étiez pas sur la liste officielle de superviseurs, mais je vous remercie tout autant. Dans cette classe de licence, je n'ai pas seulement rencontré Bart, mais aussi Morgan et Martin qui ont compté beaucoup de rennes avec moi. Morgan, je n'aurais même pas pensé à débuter ces échantillonnages à l'échelle de l'archipel du Svalbard si je n'avais pas eu ma coéquipière. Merci de ne jamais abandonner, d'avoir creuser les mains en sang pour ramasser ces Salix, d'avoir marcher des heures dans les marais, pour rapporter un résultat très important: 0. Merci à Marie-Diane et Christophe pour votre aide à échantillonner et pour nous avoir accueilli à bord de Sillage, même couvertes de boue: on DOIT suivre le transect aléatoirement positionné. Morgan je pense que nous avons découvert le Svalbard de manière unique. De chaleureux remerciements à Lisa (Lisom !) : nous avons appris tellement ensemble. Agata, merci pour l'enseignement de ta passion, la dendrochronologie sur 'l'arbuste le plus difficile du monde !'. Cette exclamation flottait dans les alentours dans ces moments de doute si l'aventure venait à échouer… Mais tu as fait en sorte que non. Jørgen et Erik, merci pour la transmission de votre passion respective. J'aurais rêvé aussi d'être archéologue où vétérinaire de terrain, mais grâce à vous, ma thèse a pu rassembler tout cela! Merci à tous ceux avec qui j'ai été sur le terrain. Il y a tellement de collègues fabuleux du CBD et d'ailleurs, qui m'ont aidée à concrétiser cette thèse, corrigeant mon Frenchie-English, inspirant de bonnes discussions et simplement super d'être ensemble. En particulier, il y a mes bras-droits: Øystein, Kate, Lara, Jos et Marlène. Je veux tous vous remercier, et pour en nommer que certains : Endre, Thomas, Ivar, Henrik (super aide de terrain!), Joost ('compter les rennes, ce n'est pas seulement compter le nombre le jambes et diviser par quatre !'), Emma, Aline, Irja (Milo & Xaia aussi!), Stine, Elena, Michael, Eirin Julie… Le meilleur était que votre aide n'était pas seulement au bureau, mais souvent depuis la cabane, en skiant, grimpant, pagayant… Christophe, merci de t'assurer que je ne perde pas mon identité française ! Sandra, tu es la nana la plus forte que je connaisse, sur tous les plans ! Matteo, mon italien n°1, on a refait le monde de la science tellement de fois ! Je remercie également mes financements: mon employeur à la faculté de NTNU, le centre d'excellence CBD mais encore les bourses du Council de recherche Norvégien (incluant les bourses AFG) et Svalbards Miljøvernfond.

Il y a ceux qui m'ont préparée à entreprendre une telle aventure et/ou me soutenant tout le temps. Papa, tu m'as appris à observer la nature, non seulement à trouver mon chemin vers le sommet de la montagne. Maman, tu es celle qui m'a supporté tous les jours, sans ne rien attendre en retour, juste naturellement à m'écouter. La manière dont mes parents nous ont élevés, mon frère et moi, dans les montagnes, a déterminé qui nous sommes. Je n'ai jamais été assise en cours une journée entière au Lycée (sinon je ferais encore du fromage à raclette, j'adorais ça !) grâce à Nicolas qui a crée une section BE-montagne, me montrant que l'on peut apprendre les maths depuis un baudrier. Suivant mon azimut depuis Kirkenes (coordonnée aléatoire) à Tromsø, j'ai rencontré Gilles (Nigel). Tu m'as dit 'UNIS c'est là que tu dois aller', j'y suis allée. Tristement, mon premier voyage sur la toundra s'est écourté rapidement pour aller recueillir le dernier souffle de mon Grand-Père. Il était celui qui à suivi mon éducation académique de près, dès mon 1er jour d'école. Il aurait rêvé de me voir soutenir ma thèse de doctorante. Grand-Père, je te dédie cette thèse. Grand-Mère, Pierre, si seulement vous étiez plus près, et le reste de la famille : Merci. Wam, tu m'as appris comment défier des obstacles dans mes études et tu m'as laissé m'envoler avec les vents du Nord. Paloma, Sarah et vos familles, Calle, Johan et tellement d'autre amis, merci pour votre soutien. Merci à la Compagnie des Guides de Chamonix de m'avoir encouragée à prendre cette place en doctorat en me donnant quatre années d'absence autorisée. Il y a un vrai explorateur polaire dans ma vie…Audun, tu as été si patient (bien sûr, sinon tu ne serais pas un 'vrai' exploreur) dans la dernière partie de ma thèse, où je restais 90% du temps sur mon ordi. Ta fascination pour chaque flocon- et bruant- de(s) neige m'a gardée connectée à la source de mon amour pour l'Écologie. En ville, les familles Lervik et Zweigel m'ont accueillie à bras ouvert. Mon bureau était bien souvent dans le coin le plus inspirant des bois norvégiens: à ma cabane avec mes poulettes Pretty&Ugly. La solitude n'a jamais passé le seuil de ma porte grâce aux quatre familles des fermes alentours qui ont pris soin de moi. Merci aux familles Simonsen, Slupphaugen, Lysevoll et Nils V. Cette cabane a rassemblé 79 différents collègues, amis et membres de la famille (statistiques du livre de la hytte), qui ont partagé des moments uniques pour toujours nous rappeler: ‘La Nature n’est pas une place à visiter, c’est notre maison’.

‘*Nature is not a place to visit. It is home.*’ Gary Snyder (1990)

Svalbard reindeer grazing on Salix polaris

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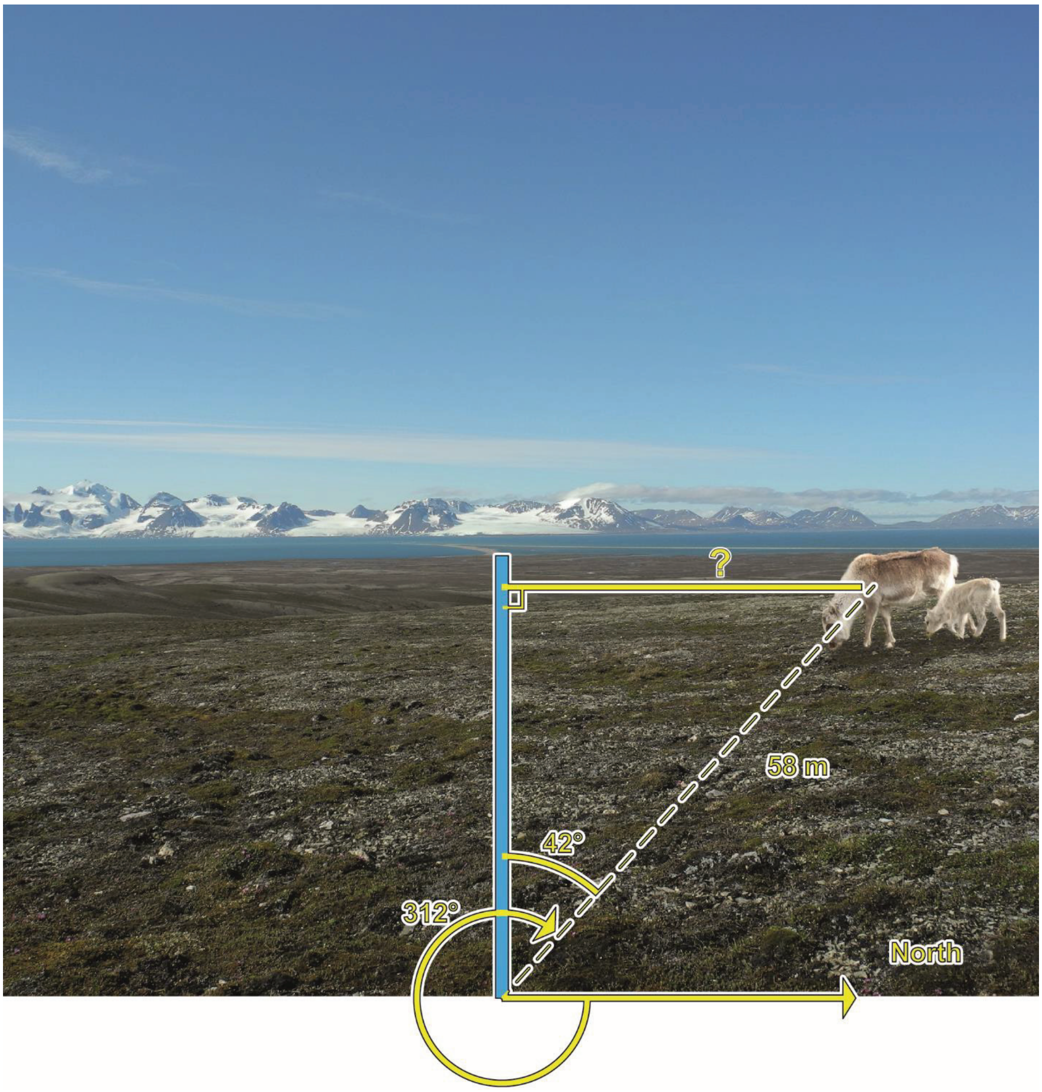
Paper I



Wildlife Biology 2017: wlb.00299
doi: 10.2981/wlb.00299

Subject Editor: Simone Ciuti. Editor-in-Chief: Ilse Storch. Accepted 29 March 2017

Ungulate population monitoring in an open tundra landscape: distance sampling versus total counts

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Researchers and wildlife managers strive for low bias and high precision (i.e. high accuracy) when estimating animal population sizes. Distance sampling is currently one of the most widely used monitoring methods. However, it relies on strict sampling designs and modeling assumptions that can be difficult to meet in the field. Here, we use data from two sub-populations of non-migratory wild Svalbard reindeer *Rangifer tarandus platyrhynchus* inhabiting flat, open and isolated coastal tundra plains, to demonstrate some challenges related to the distance sampling methodology. To achieve this, we compared distance sampling line transect estimates with repeated total population counts and combined available software tools (R packages *unmarked*, *Distance* and *dsm*) to fulfill the analytical requirements of small study sites in which large areas are surveyed relative to the study area size. Based on low variation among repeated total counts (CV = 0.02 – 0.06) and the virtual absence of false negatives and positives of marked animals, the total counts could be used as reference population sizes. Distance sampling estimates were not statistically different from the total count estimates. Our relatively large sample size of 143 observations enabled precise distance sampling abundance estimates (CV = 0.16 – 0.26) compared with other studies in the wild. However, capturing the processes shaping population dynamics would likely require even higher sampling effort or other, more resource demanding monitoring tools, such as total counts or mark-recapture. In this type of ecosystem, distance sampling nevertheless represents a cost-effective tool suitable for 'population state' assessment and studies of large-scale spatial distribution patterns. Our study stresses the importance of choosing the appropriate analytical tools and estimating the accuracy of the monitoring methods that are used to achieve specific scientific, management or conservation goals.

Population size estimates with low bias and high precision (i.e. accuracy, Williams et al. 2002, p. 45) are important to understand spatiotemporal patterns of wildlife populations, thereby informing management and conservation decisions. While there are numerous challenges associated with obtaining unbiased and precise estimates of population size and demographic rates in space and time (Williams et al. 2002), such estimates are essential to understand population fluctuations and their causes (Abadi et al. 2010, Zipkin et al. 2014). Bias and imprecision originate from sources of errors that can occur at multiple levels in the measurement of population size and vital rates (Cressie et al. 2009, Lebreton and Gimenez 2013). These uncertainties are related to process variation (i.e. demographic and environmental stochasticity) and observational error (Clark and Bjørnstad 2004, Buckland et al. 2007, Sæther et al. 2007). Because observational error is not part of the process variation, but inherent to the sampling methodology used, it is important to identify its different sources (Ahrestani et al. 2013).

Worldwide, the most common method to estimate population abundance of wild animals is distance sampling (hereafter referred to as DS) (Buckland et al. 2004). Surveys are conducted along transect lines or at transect points where the detection probability is a function of the perpendicular distance from the line or radial distance from the point to the object of interest (reviewed by Buckland et al. 2015). DS relies on four key assumptions related to study design and statistical analysis of the data (Buckland et al. 2015): 1) animals are distributed independently of the transects; 2) objects on or close to the transects are always detected; 3) distances are measured without error; and 4) objects are detected at their original position. However, the degree to which the assumptions of DS are violated in wild populations is largely unknown (Morellet et al. 2007, 2011). Comparisons of

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bias and precision have been made between DS and other sampling methods. Some examples are comparisons with capture–mark–recapture, total counts (hereafter referred to as TC) and strip transects, in different environments (e.g. forest: Focardi et al. 2005, Wegge and Storaas 2009, Amos et al. 2014, grassland: Kruger et al. 2008, Amos et al. 2014 and steppe: Seddon et al. 2003, Bårdsen and Fox 2006). Even for similar types of DS, bias can vary greatly depending on how the field sampling is conducted (e.g. foot versus road line transects; Wegge and Storaas 2009, Marques et al. 2013). Overall, few studies have assessed the performance of DS by comparing estimates to populations of known size (but see Wegge and Storaas 2009, Porteus et al. 2011 for ungulates and Glass et al. 2015 for kangaroos).

Recent spatial modeling developments have been incorporated into the DISTANCE interface (Thomas et al. 2010), whereby a two-stage approach analyzes detection and density separately. This is particularly suitable for large-scale study areas. By contrast, in small study areas, the transect width will often cover most or all of the study area. Thus, there could be information about the spatial distribution of animals in the observed distances, as well as their detectability (Miller et al. 2013). Therefore, in small study areas, the detection and density functions should be estimated simultaneously (i.e. a one-stage approach, Miller et al. 2013; see Glass et al. 2015 for a counter-example of a two-stage approach where the search area of all transects combined included the entire 76 ha study area). Hence, in line transect studies, different analytical approaches may be required depending on the type of study area (Miller et al. 2013).

In this study, we use monitoring data from a high-Arctic wild subspecies of reindeer, the Svalbard reindeer *Rangifer tarandus platyrhynchus*, which inhabits tundra with sparse vegetation of low stature. The distinctive landscape characteristics of Svalbard are highly suitable to evaluate the precision and sources of error in two methods of estimating animal abundance; DS and TC. In this open tundra landscape, the detection of reindeer should in principle only vary with distance from the transect line as visibility is good. Additionally, many coastal sub-populations are isolated in small areas by glaciers, steep mountains and the sea and so are possible to census on foot by TC. Although never assessed quantitatively, it is assumed that TCs of Svalbard reindeer give precise and unbiased population size estimates, partly due to the open habitat and partly because of the restricted ranging and solitary behavior of the reindeer (Aanes et al. 2000, Kohler and Aanes 2004, Tyler et al. 2008, Hansen et al. 2011). Recent studies suggest that the rapidly changing climate in Polar regions (Larsen et al. 2014, Nordli et al. 2014) will strongly impact ungulate population dynamics (Rennert et al. 2009, Hansen et al. 2011, 2013). This underlines the need for robust estimates of population abundance. Here we take advantage of the characteristics of this simple, high-Arctic model system to compare reindeer abundance estimates made using DS and TC methodologies. In particular, we show that TC estimates are accurate and therefore usable as reference points (i.e. 'known' population sizes). We are then able to assess whether estimates based on DS analysis, using a combination of R packages (*unmarked*, *Distance* and *dsm*), are different from TCs. We further evaluate some sources of error and imprecision.

Methods

Study system

The study was conducted in two sites, the Sarsøyra (40 km^2) and Kaffiøyra (35 km^2) peninsulas, close to the Ny-Ålesund scientific base (78°55′N, 11°55′E; Fig. 1), on Svalbard. The study sites lie in the northern Arctic tundra zone (Elvebakk 2005) which is characterized by graminoid and

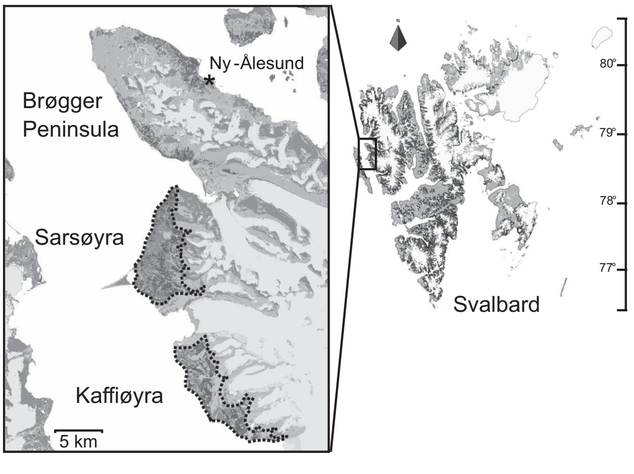

Figure 1. Map of the Svalbard archipelago including the two study sites (Sarsøyra and Kaffiøyra) where total counts and distance sampling surveys of Svalbard reindeer were conducted. The vegetation map from Johansen et al. (2012) was plotted as background of the inset map (the darker the grey, the more of the area is vegetated).

dwarf-shrub tundra. Reindeer summer habitat is generally confined to areas below 200 m elevation, excluding large moraines and glaciers. Natural barriers to reindeer movement include tidewater glaciers, steep mountains and more recently, year-round open water fjords. Both peninsulas are dominated by 'pioneer vegetation' (41% of the total coverage) and 'established Dryas tundra' (39%). The 'pioneer vegetation' is characterized by vegetation communities with low vascular plant diversity and mosses, highly affected by erosion and flooding. 'Established Dryas tundra' is dominated by *Saxifraga oppositifolia* and short-growing graminoids on coastal plains (Johansen et al. 2012). With the exception of some graminoids, plant height rarely reaches more than 5 cm above the ground.

The Svalbard reindeer is an endemic resident key herbivore that lives in a predator-free environment (but see Derocher 2000 for predation events by polar bear *Ursus maritimus*). This sub-species is tame compared to most other wild *Rangifer,* and individuals in our study sites can typically be approached by humans in summer to within 100 m before their behavior is affected (Hansen and Aanes 2015). Their space use during summer is relatively limited (Tyler and Øritsland 1989), although dispersal events can occur during winter (Hansen et al. 2010). Reindeer were absent from our study sites for a century before the sub-populations reestablished after a major dispersal event from Brøgger Peninsula to Sarsøyra in 1994 (Kohler and Aanes 2004), with onward dispersion to Kaffiøyra in 1996 (Fig. 1). Fluctuations in the reindeer population sizes are large and typically associated with 'rain-on-snow' events, which cause high mortality and reduced population growth rates (Kohler and Aanes 2004, Hansen et al. 2011).

Reindeer data collection

Total counts and marked individuals

We conducted repeated TCs of Svalbard reindeer in 2009 and 2013 (July to August) in the two study sites (Table 1). The natural barriers, limited ranging behavior (Tyler and Øritsland 1989) and negligible summer mortality rates (Reimers 1983) mean that the assumption of constant population size within the area and field season (i.e. closed population) is likely met. This also means that the same population was counted during each repeated TC. Four predefined routes from south to north, always less than 1 km apart, allowed each of the study sites to be covered in one day by four observers walking simultaneously. Observers were not strictly confined to stay on their route, but expected to deviate from the line to utilize terrain features (e.g. small mounds) to get the best possible overview, and keep visual contact with other observers (e.g. to avoid double counts). Observers scanned the area along their route with binoculars (10 × 42 mm, allowing reindeer detection up to 2–3 km distance) and communicated by VHF-radio to reduce the potential for double counts. Routes were switched between observers to reduce bias related to observer heterogeneity (Field et al. 2005). All reindeer positions (i.e. of single individuals or groups) were marked on a topographic map (1:50 000). Repeated TCs were always separated by a minimum of four days. All TCs had similar weather conditions with good visibility and little wind.

Table 1. Overview and summary statistics of the repeated total counts (TCs) of reindeer in the two study sites, Sarsøyra and Kaffiøyra, Svalbard, Norway. TC values = reindeer abundance from each TC, TC estimates = mean reindeer abundance and 95% confidence intervals, SE = standard error and CV = coefficient of variation.

Study area	Year	Dates	TC values	TC estimates
Sarsøyra	2009	1 July	143	146 [137:155] CV = 0.03
		13 July	146	
		23 July	142	
		4 Aug	153	
	2013	7 July	241	221 [212:230] CV = 0.02
		11 July	218	
		23 July	215	
		27 July	210	
Kaffiøyra	2009	31 July	142	144 [131:157] CV = 0.04
		23 Aug	146	
	2013	24 July	144	144 [125:163] CV = 0.06

In addition, we used data from TC and marked animals in previous years (1999 and 2000) to evaluate 1) the closure assumption based on data from regularly (every 2–3 days) tracked VHF-equipped females (19 in 1999 and 23 in 2000, Hansen et al. 2009); 2) the probability of missing animals in the TC based on the number of VHF-collared females known to be present in the study site immediately before the TC (27 individuals in 2000, which includes the 23 females followed every second-third day); and 3) the probability of double counting based on re-sightings of the VHF-marked animals (27 individuals) as well as other marked animals (26 individuals) during the TC in 2000.

Distance sampling

One single observer conducted line transect DS twice in each of the two study sites in 2013 (12 and 19 July in Sarsøyra and 26 and 27 July in Kaffiøyra). We chose one random latitude for each of the two DS surveys and placed additional parallel transect lines systematically 3 km away either north or south from this latitude so as to avoid overlapping reindeer observations and violation of the assumption of independence (Hammond et al. 2014, Buckland et al. 2015). Lines were orientated east/west from the sea-shore to the mountain foothills. We chose this systematic orientation to reduce any potential bias from parallel animal density gradients along the line (e.g. due to plant phenology gradients; Marques et al. 2013, Barabesi and Fattorini 2013). In total, 11 transect lines were walked in the study sites (Sarsøyra, total length 19 029 m, three transect lines in first survey and two in second survey; Kaffiøyra, 14 937 m, four transect lines first survey and two in second survey). Because of the random placements of lines in the small study locations and because two transect lines (one in each study site) were not completed due to bad weather, the surveys had different total numbers of transects.

The line transects were walked by the observer at a constant speed (2–3 km h^{-1}) without stops, except during measurements. A handheld GPS was used to keep the line direction. Reindeer were detected on both sides of the transect line with the naked eye. When a reindeer or reindeer group was spotted, the observer looked only in its direction until measurements were taken. Each observation is hereafter referred to as a cluster, regardless of whether it is an individual or a group to meet the assumption of independent detection between observations (Buckland et al. 2001, Guillera-Arroita et al. 2012). The geographic position of the observer was recorded. We used laser binocular and compass to measure the distance and angle from the observer to the reindeer. For practical reasons using the laser, measurements were taken to the largest reindeer (e.g. a mother rather than her calf), or the left-most individual of a group of adults. We acknowledge this as sub-optimal to measuring the center animal but considered the associated potential positioning bias as negligible (reindeer belonging to the same group are close to each other and mean group size is < 2) and evened out by following the same procedure on both sides of the transect line. If a reindeer individual or cluster was beyond the distance that the laser could measure with confidence (sometimes down to ~500 m), positions were marked on a topographic map (1:50 000) and the exact perpendicular distance was subsequently read from an electronic map (<www.toposvalbard.no>). Even in this relatively flat terrain, we consider based on qualitative inference that the mapping method is correct due to the fine map resolution (e.g. every little creek is shown) and the supporting use of a GPS. In order to reduce error in our estimation of mean cluster size, the observer counted the number of individuals in a cluster with binoculars. If a cluster that had not been observed initially became apparent while measuring the distance or cluster size (i.e. because of using binoculars), it was not included in the observation data. We only conducted DS surveys when conditions were adequate in terms of good visibility and little wind.

Data analysis

Total counts

To estimate reindeer abundance from TC data and its uncertainties we considered two types of errors related to the observers; 1) an animal could be counted twice with a probability p or 2) an animal could be undetected with a probability q. We expected the proportion of these two error types to be constant across years and similar in the two study sites, which share the same flat and open tundra landscape and therefore detectability of reindeer. Let X denote the total number of reindeer counted twice, Y the number of undetected animals, and N and n the estimated and true population size, respectively. Animal abundance from TCs can be expressed as $N = n + X - Y$. Given that p and q are small, N is approximately unbiased for the true population size n. We have several N (i.e. repeated TCs) of the same true abundance n at the different sites and years (Table 1). Note also that the number of individuals counted twice, never or once, i.e. X, Y and $n - X - Y$ respectively, is multinomially distributed with parameters $p, q, 1 - p - q$, if individuals are counted independently. From variance and covariance formulas for the multinomial distribution, a straightforward calculation then shows that the variance of a single count, $Var(N) = Var(n + X - Y)$, is proportional to the mean $E(N) = E(n + X - Y)$ with a scale parameter

$$\Phi = \frac{Var(N)}{E(N)} = \frac{p(1-p) + q(1-q) + 2pq}{1 + p - q} \qquad (1)$$

corresponding to the dispersion parameter of a quasi-Poisson likelihood model (McCullagh and Nelder 1989). Estimates, standard errors and profile likelihood 95%-confidence intervals for the true abundances n at each study site and year were obtained by fitting a generalized linear model from the quasi-Poisson family, with no intercept and with a four level fixed effect factor representing the two study sites and the two summers (i.e. 2009 and 2013). We obtained the coefficient of variation (CV) for n by dividing the standard error by its mean abundance estimate.

Distance sampling

Prior to estimating reindeer abundance from the DS line transect data, we divided the 11 line transects into 33 segments, i.e. three equal segments per transect (Sarsøyra: 15 segments 728–1544 m, Kaffiøyra: 18 segments 107–1047 m). This allowed us to fit density models that included covariates measured at the segment level (Royle et al. 2004, Miller et al. 2013). Transect lengths were relatively short compared with their half-widths due to the small scale of our study sites and the long detection distances of reindeer. Note that segment lengths could not be twice the half-transect width, because this would give only one to two segments per transect and reduce our ability to detect effects of habitat heterogeneity. We calculated the proportion of vegetated area within each segment area (segment length × truncation distance, ranging from 0.43 to 2.89 km^2) from a digital vegetation map (Johansen et al. 2012). This was the ratio of pixels (spatial resolution of 30 × 30 m) classified as vegetated (corresponding to classes 8 to 18 in Johansen et al. 2012) to the total number of pixels. We also right-truncated the DS data, as suggested by Buckland et al. (2001), by removing 5% of the reindeer clusters that were most distant from the line. The furthest observation after truncation was 953 m from the line and twice this distance defined the width of the surveyed area along the transect lines. Following Buckland et al. (2001, p. 109), we calculated along the segments of total length L, the encounter rate n/L, the encounter rate variance (n/L) (also corresponding to Fewster et al. 2009 'R3' estimate) and evaluated the homogeneity of clusters position using the ratio between the expected number of objects detected $E(n)$ and the sampling variance $var(n)$. A ratio close to 1 gives no evidence against a Poisson distribution. We used Pearson's correlation tests to investigate the correlation between the segment-based encounter rate or vegetation cover of adjacent segments on the same transect (22 total possibilities).

We estimated reindeer abundance by combining statistical tools available in R ver. 3.2.2 (<www.r-project.org>) and the packages *unmarked* ver. 0.10-2 (Fiske and Chandler 2011), *Distance* ver. 0.9.4 (Miller 2014) and *dsm* ver. 2.2.4 (Miller et al. 2013). Model selection was done in *unmarked* because it uses a one-stage model selection procedure (i.e. full likelihood approach), which is required for spatially confined study sites (Miller et al. 2013), as illustrated in earlier studies (Royle et al. 2004, Royle and Dorazio 2008, Johnson et al. 2010, Miller et al. 2013). In *unmarked*, the data have to be pooled into distance intervals. These were set to 1 m, simulating a continuous fit, because the cluster positions were precisely measured and we wanted to fit similar models in *Distance/dsm*. A hierarchical DS model implemented in the function 'distsamp' uses the multinomial-Poisson mixture (Royle et al. 2004, Fiske and Chandler 2011) to compute detection and density parameters simultaneously. The covariates Z_i of transect i were related to the detection parameter σ_i and mean density parameter λ_i with the log link function and α and β as their respective parameters estimates (Royle et al. 2004, Fiske and Chandler 2011, Sillett et al. 2012) as follows:

$$\log(\sigma_i) = \alpha_0 + \alpha_1 Z_i \tag{2}$$

$$\log(\lambda_i) = \beta_0 + \beta_1 Z_i \tag{3}$$

Different model combinations were analyzed using a half normal, hazard rate, exponential or uniform key for the detection function. No adjustment terms to the key functions could be implemented in *unmarked*. For each key detection function we included either the study site, the vegetation cover or none of these as covariates, while for the density estimation we included either the study site, the vegetation cover, both (i.e. additive effect) or no covariate. To avoid over-parameterization, no more than six parameters were allowed per model. We retained the best model ranked by Akaike information criteron (AIC, Burnham and Anderson 2002) from the *unmarked* model selection and implemented it in *Distance/dsm* using the same distribution, key functions and generalized linear models as presented in Eq. 2–3 (Marques et al. 2007, Miller et al. 2013). Only models with $\Delta AIC < 2.00$ were presented in Table 2. A Freeman–Tukey goodness-of-fit statistics with 500 bootstrap iterations (h^2, Brooks et al. 2000, Sillett et al. 2012) evaluated the model fit to the data. We verified whether group size was a potential covariate influencing detection at the observation level in *Distance*, since it was not possible in *unmarked*, using the top models from Table 2. A linear regression investigated whether group size increased with increasing vegetation cover (the vegetation cover around each DS cluster was extracted with a 200 m buffer; see details below).

We compared three different approaches to estimate animal abundances from the DS analyses. Firstly, we estimated cluster density using the top ranked model (termed 'estimate 1'). Secondly, we estimated density using model averaging, including all models with $\Delta AIC < 2.00$ ('estimate 2'). In both estimate 1 and 2, computed in *unmarked*, we used the function 'predict' (Fiske and Chandler 2011) to extract mean cluster density and its standard error for the proportion of vegetation found across the study sites. Then, we transformed estimated cluster densities to cluster abundances by multiplying by the respective area of each study site. Thirdly, we estimated cluster density using spatial density modeling methodology (Miller et al. 2013) in *dsm*. The top ranked model (Table 2) was used in the function *dsm* with segment length as an offset and the family set as quasi-Poisson with a logarithmic link function. We verified that the quasi-Poisson scale parameter was close to 1, indicating an absence of over-dispersion. The mean cluster abundance and standard error were extracted from the variance propagation function 'dsm.var.prop' ('estimate 3'). This standard error obtained from *dsm* do not account for the variance related to the detection function. Following La Morgia et al. (2014) we thus summed the coefficient of variation related to the detection function (*Distance*) with the coefficient of variation related to the spatial density modeling (*dsm*) using the delta method. From these calculations, we obtained the mean cluster standard error. Density from equation 3, using the function 'predict', was estimated at the pixel level (spatial resolution of 30 × 30 m) and afterward summed over the study site to obtain the site-specific cluster abundance estimate. Detection and density covariates (i.e. vegetation proportion) were thus required for each pixel. Because vegetation information from the vegetation map is binary (vegetated or not) at the cell level, we assigned each pixel a value calculated from a neighborhood consisting of a circular buffer zone (radius of 200 m, corresponding to an average of 63 pixels) around each mid-point of the pixel.

Estimated cluster abundances $\widehat{A}_i$ and their corresponding standard errors $\widehat{SE}_{A,i}$ from estimates 1, 2 and 3 were combined with mean expected clusters sizes $\overline{S}_i$ and their standard errors $\widehat{SE}_{S,i}$ for each site i, into estimates of the abundance of individuals, where $\widehat{N}_i = \widehat{A}_i . \overline{S}_i$. Assuming independence between $\widehat{A}_i$ and $\overline{S}_i$ and using an exact formula for the variance of products (Goodman 1960) rather than relying on the approximate delta method, the standard errors of abundance of individuals are

$$\widehat{SE}_{N,i} = \sqrt{\widehat{A}_i^{\,2} . \widehat{SE}_{S,i}^{\,2} + \overline{S}_i^{\,2} . \widehat{SE}_{A,i}^{\,2} + \widehat{SE}_{S,i}^{\,2} . \widehat{SE}_{A,i}^{\,2}} \tag{4}$$

Upper and lower 95% confidence intervals of individual abundance estimates were obtained using a normal approximation.

Table 2. Parameter estimates of the seven top ranked models ($\Delta AIC < 2.00$) for estimating Svalbard reindeer abundance using distance sampling analyses computed with the R package *unmarked*. These models used a continuous fit of the observed distances (1 m distance intervals), and the hazard rate (hz), half normal (hn) or exponential (exp) detection key function. Proportion of vegetation in transect line segments (veg) and/or study site (Sarsøyra or Kaffiøyra) were included as detection covariates (σ) and/or density covariates (λ). Estimated abundance = mean abundance estimate with 95% confidence intervals (corresponding to estimate 1 in Methods); CV = coefficient of variation.

Model					Sarsøyra		Kaffiøyra	
Rank	Key	σ	λ	ΔAIC	Estimated abundance	CV	Estimated abundance	CV
1	hz	–	veg	0.00	275 [186:364]	0.16	164 [101:227]	0.20
2	hn	site	veg + site	0.13	194 [132:256]	0.16	183 [112:253]	0.20
3	exp	veg	veg	1.70	300 [208:391]	0.16	172 [88:256]	0.25
4	hz	site	veg	1.77	273 [185:362]	0.17	165 [102:229]	0.20
5	hz	–	veg + site	1.89	268 [173:364]	0.18	168 [99:237]	0.21
6	hz	veg	veg	1.93	272 [180:363]	0.17	157 [74:239]	0.27
7	hn	site	veg	1.96	234 [176:292]	0.13	145 [98:193]	0.17

Total counts and distance sampling comparison

We calculated the difference between TC and DS reindeer abundance estimates with their 95% confidence intervals obtained using a normal approximation of mean $\widehat{N}_{TC} - \widehat{N}_{DS}$ and standard error $\sqrt{SE_{TC}^{2} + SE_{DS}^{2}}$. Thereafter for each site *i* in 2013, the probability that TC and DS estimates were significantly different from each other (in a two-sided test) used the absolute value of the normally distributed Z-statistic:

$$Z_i = \frac{\widehat{N}_{TC,i} - \widehat{N}_{DS,i}}{\sqrt{SE_{TC,i}^{2} + SE_{DS,i}^{2}}} \qquad (5)$$

We compared cluster density with vegetation cover intervals (every 10% from 0% to 100%) from both DS modeling and TC mapped cluster positions. In DS modeling we used the relationship from the top ranked model and predicted the cluster density using the function 'predict' from *unmarked* (corresponding to estimate 1). For each vegetation cover interval, we also summed the pixel-wise (30 × 30 m resolution) density estimated from spatial modeling (corresponding to estimate 3). For the TC, the vegetation cover around each cluster was extracted with a 200 m buffer and number of clusters were summed in intervals (every 10% from 0% to 100%).

Results

Total counts

The TC precision was high in both study sites and years (CV ranging between 0.02 and 0.06, Table 1). The high re-sighting rate of the VHF-marked female reindeer (100% in 2000) and the low rate of double counts (1.9%, i.e. one out of 53 reindeer) suggested a low bias of the TCs. Virtually all the VHF-collared female reindeer that were closely tracked stayed within their respective study site throughout the summer (97.5%, only 1 out of 42 changed study site; 19 in 1999 and 23 in 2000). This largely confirmed our assumption of closed populations. We expected the variance of the animal abundance to increase proportionally to the mean (Eq. 1) and estimated the dispersion parameter Φ to be 0.45 [0.10:0.92] (point estimate and 95% confidence interval derived via the approximate χ^2-distribution of $\frac{\hat{\Phi}(n-4)}{\Phi}$, Venables and Ripley 2002, p. 210). This under-dispersion relative to a Poisson variance is not surprising since the variability of the total counts originate from small probabilities of individuals being undetected or double counted.

Distance sampling

In total, we observed 143 reindeer clusters (88 in Sarsøyra and 55 in Kaffiøyra) during the DS surveys. There was a slight increase in the number of clusters detected between approximately 90 m and 170 m from the transect lines (Fig. 2). The mean cluster size was 1.68 ± 0.10 (mean ± SE) and 1.58 ± 0.11 in Sarsøyra and Kaffiøyra, respectively. The largest group had five animals and the correlation between group size and detected distances, if considered independent, was at the critical level to be statistically significant (cor = 1.16, t = 1.97, df = 141, p = 0.05). Nonetheless, we found no evidence in our data that cluster size influenced detection probabilities (ΔAIC = 4.17). Similarly, we found no evidence that vegetation cover influenced reindeer cluster size (linear regression: intercept = 1.47 ± 0.26, slope = 0.22 ± 0.32, p = 0.50). The encounter rate had a low segment-based variance, 4.62 ± 0.59 ($n/L \pm SE[n/L]$, Buckland et al. 2001, p. 109) and 3.68 ± 0.61 observations per km in Sarsøyra and Kaffiøyra, respectively. Adjacent segments on a transect were not found to be correlated in either their segment-based encounter rate (cor = –0.16, t = –0.72, df = 20, p = 0.48) or their vegetation proportion (cor = 0.20, t = 0.91, df = 20, p = 0.37). The low ratios between the expected number of objects detected and sampling variance (Sarsøyra = 1.42 and Kaffiøyra = 1.53) indicated no evidence against a homogenous Poisson distribution of reindeer clusters along the segments, i.e. they could occur at any position. Using a higher truncation percentage did not decrease this ratio. Accordingly, no over-dispersion was found in *dsm* (quasi-Poisson scale parameter of 1.04).

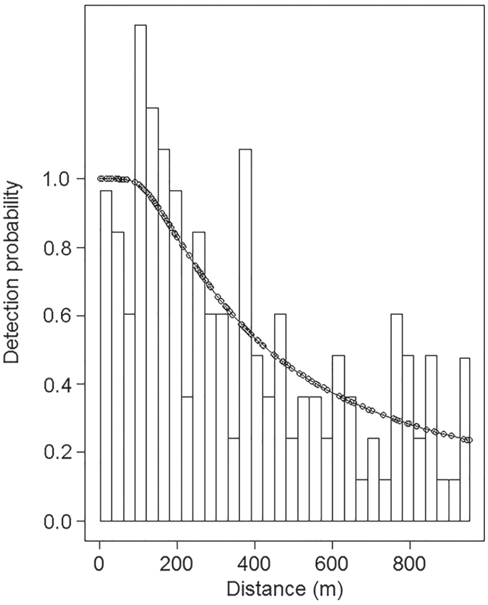

Figure 2. Detection probability function based on line transect distance sampling of Svalbard reindeer. The best model was fitted at a continuous scale for observed distances and included a hazard rate key detection function with no covariate. Observations of reindeer clusters are illustrated by dots along the curve. The rescaled histogram was plotted at 30 m distance intervals for ease of the visual illustration.

All models with ΔAIC < 2.00 included vegetation cover (proportion of vegetated area in each transect segment, ranging from 0.13 to 0.86) as a covariate positively influencing the cluster density function (Table 2). None of these models showed a significant lack of fit to the data (Freeman–Tukey goodness-of-fit statistics; $260.26 \pm 19.77 < h^2 < 263.87 \pm 22.26$ where $0.40 < p < 0.53$, the top-ranked model having the best fit). The top-ranked model used the hazard rate key detection function, with no covariate or factor influencing detection probability. As expected, transferring the best model from *unmarked* (with 1 m distance intervals) to *Distance* gave a similar detection probability (α_0 from equation 2 is 5.77 ± 0.27 in *unmarked* and 5.77 ± 0.36 in *Distance*) and density parameter estimate (β_1 from equation 2 is 2.02 ± 0.53 in *unmarked* and 2.02 ± 0.54 in *Distance*). The vegetation cover along the transect lines (69.6% in Sarsøyra and 54.1% in Kaffiøyra) was comparable to the total vegetation cover of the study sites (66.1% in Sarsøyra and 50.5% in Kaffiøyra). The precisions of the abundance estimates from all three DS estimates were ranging between CV = 0.16–0.26 (Table 3).

Total counts and distance sampling comparison

The mean reindeer abundance estimated from the TCs in both study sites were always within the DS 95% confidence intervals from the top ranked models ($\Delta\text{AIC} < 2.00$; Table 2). Accordingly, from the Z-statistics (Eq. 5, Table 3), none of the three DS abundance estimates differed significantly from the TC estimates in either of the sites. However, the precision of DS estimates was considerably lower than from the TC estimates, with the upper limit of the confidence interval close to twice the mean of TCs abundance estimates, Table 1, 3).

The importance of vegetation cover for spatial cluster density modeling was also supported by reindeer cluster positions from repeated TCs (Fig. 3). Nonetheless, based on the TC cluster positions this relationship appeared non-linear, with a sharp increase in reindeer abundance when more than about half of the ground was vegetated. Overall, the estimated density in the DS modeling tracked this apparent non-linearity well, yet slightly over- and underestimated reindeer abundance at low and high vegetation cover, respectively (Fig. 3).

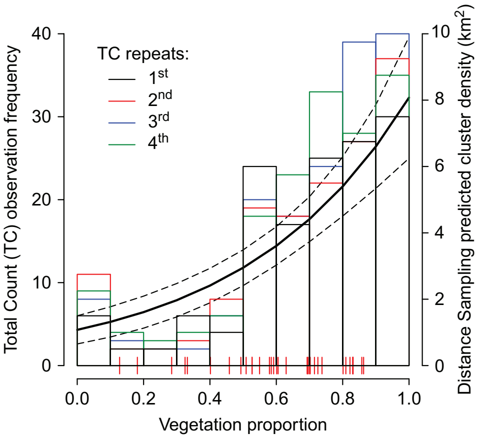

Figure 3. Histogram of the frequency of Svalbard reindeer clusters observed during total counts (left y-axis), pooled across study sites, plotted in relation to the proportion of vegetation covered area within a 200 m buffer zone around each reindeer cluster. Reindeer cluster observations were mapped during four repeated total counts (TC) in Sarsøyra and one total count in Kaffiøyra in 2013 (see Table 1). Estimated reindeer cluster density (right y-axis, solid curve) and associated standard error (dashed curves) in relation to vegetation cover, based on the selected model obtained from the R package *unmarked*. Red lines on the x-axis show the vegetation cover measured of each segment.

Table 3. Svalbard reindeer abundance in the two study sites (Sarsøyra and Kaffiøyra) estimated using distance sampling. The estimated reindeer abundances are shown according to the three estimation methods (see Methods for details). Estimate 1 = the estimated abundance using the top ranked model, and corresponding proportional cover of vegetation across the study site (*unmarked*). Estimate 2 = the estimated abundance using model averaging (models with $\Delta\text{AIC} < 2.00$) and corresponding to the proportion of vegetation across the study site (*unmarked*). Estimate 3 = the estimated abundance using the top ranked model and corresponding sum of densities projected for each pixel across the study site (30 × 30 m resolution, pixels have a vegetation proportion value, see Methods, *Distance/dsm*). CV = coefficient of variation, Z = the Z-statistic (see Methods), p = p-value from the Z-statistic. Difference = the difference between total counts and the respective distance sampling abundance estimates. Numbers in brackets are 95% confidence intervals.

Site		Estimate 1	Estimate 2	Estimate 3
Sarsøyra	abundance	275 [186:364]	253 [147:360]	313 [156:470]
		CV = 0.16	CV = 0.22	CV = 0.26
		Z = 1.19	Z = 0.59	Z = 1.15
		p = 0.24	p = 0.55	p = 0.25
	difference	54 [–35:143]	32 [–75:140]	92 [–65:250]
Kaffiøyra	abundance	164 [101:227]	167 [96:239]	201 [101:250]
		CV = 0.20	CV = 0.22	CV = 0.26
		Z = 0.61	Z = 0.63	Z = 1.10
		p = 0.54	p = 0.53	p = 0.27
	difference	20[–44:84]	23[–50:97]	57[–44:159]

Discussion

In the present study, we used total count (TC) and distance sampling (DS) line transect data from two isolated sub-populations of high-arctic Svalbard reindeer to compare methodologies of abundance estimation. We evaluated some of the potential sources of error and imprecision in both methodologies. We obtained unbiased and precise TC abundance estimates (Table 1) from the two reindeer sub-populations that inhabit a flat and open tundra landscape. These provided 'known' population sizes and were used as a reference for DS abundance estimates. We found no statistically significant differences between the DS and the TC abundance estimates, but DS estimates were considerably less precise (Table 3). The vegetation cover proved an important covariate for estimating reindeer density spatially (Fig. 3, 4).

Biased abundance estimates can result from various reasons, including violation of the major assumptions of the DS method, selection of statistical models for density estimation, or software limitations. In this study, the reindeer DS abundance estimates were not statistically different from the respective TC estimates. However, although not significant, our DS estimates tended to be consistently larger than TC estimates at both study sites. If this tendency is reflecting a true difference, the lack of a significant difference may be due to the large variance of DS estimates (Eq. 5).

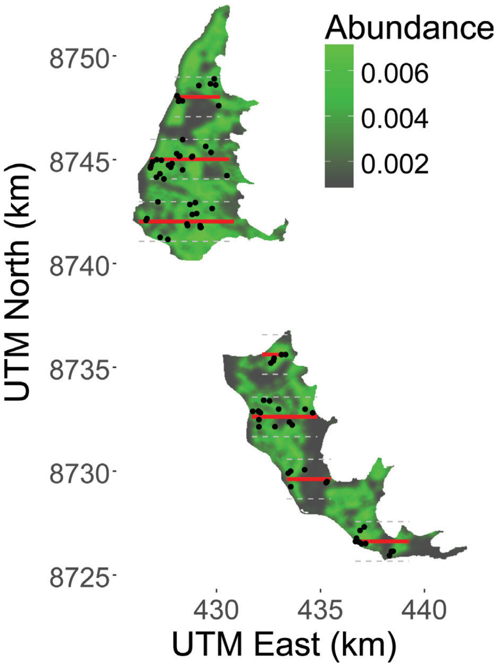

Figure 4. Map of the estimated reindeer abundance for each 30 × 30 m pixel (900 m^2, estimate 3; see Methods) in the two study sites, Sarsøyra (40 km^2, upper figure) and Kaffiøyra (35 km^2, lower figure), obtained from the R package *Distance/dsm*. Red horizontal lines show the distance sampling transect lines, the dotted lines show the 5% data truncation distance at 953 m and the black dots the positions of reindeer clusters from the first survey in both study sites.

Porteus et al. (2011) showed that attraction of sheep toward the observer inflated detected clusters around 100 m, resulting in underestimation of the detection probability and positively biased density estimation. Similarly, our histogram of detected distances close to the line indicated a hump between 90m and 170 m (Fig. 2), and the hump's effect on the hazard rate function could have led to an underestimated detection probability which further could overestimate reindeer abundance slightly (Fewster et al. 2008, Marques et al. 2010). Nonetheless, reindeer movement towards the line is not likely because of lack of Svalbard reindeer reaction towards human presence (Reimers et al. 2011, Hansen and Aanes 2015). We suggest this hump could have occurred by chance (see also a study on robin in Buckland et al. 2015, p. 71). Another explanation for the tendency of the DS estimates to be larger than the TCs could come from bias in the TCs themselves, but we consider this very unlikely, given the information from marked animals on false positives and negatives.

Other studies comparing TC and DS line transect performance have been conducted in ecosystems with more environmental complexity, for instance at sea (Williams and Thomas 2009 killer whales *Orcinus orca*), in forests (White et al. 1989 mule deer *Odocoileus hemionus*; Wegge and Storaas 2009 Nepal's ungulates) or in human disturbed landscapes with high animal density (> 100 animals km^{-2} in Porteus et al. 2011 for sheep and Glass et al. 2015 for kangaroo *Macropus giganteus*). The precision of our three DS abundance estimates was high (CV = 16–26%, Table 3) relative to the precision levels in other studies from the wild. However, the upper confidence interval of around 400 reindeer in Sarsøyra represents a density of ~10 reindeer km^{-2}, which is much higher than reported densities from more productive areas in Svalbard (~6 reindeer km^{-2} in Adventdalen, Tyler et al. 2008). A larger sample size (i.e. more transect lines and a larger number of observations) would likely increase model quality by reducing the confidence intervals and thus excluded such biologically unreasonable abundances (La Morgia et al. 2015).

Habitat structure and heterogeneity are also important potential sources of uncertainty (Pedersen et al. 2012, Sillett et al. 2012), yet the habitat structure was well captured overall by our DS study design, with only a negligible 3.5% difference in vegetation cover within the transects areas versus the total study site areas. Thereafter, a design-based method extrapolating the density from the transects areas to the whole study area would give comparable results to estimate 1 (predicting density to the vegetation cover of the total study site). While Miller et al. (2013) recommend a larger grid cell size to match the segment scale, our smaller grid cell size (i.e. 200 m circular buffer) captures changes in reindeer density in response to covariate values. Both estimated DS cluster density (from *unmarked*, using the segment scale) and the cluster number from TC (using the 200 m circular buffer scale) clearly responded to the changes in covariate values by a sharp increase at about half of the ground being vegetated (Fig. 3). The precision of the three different reindeer density estimates (i.e. using *unmarked* or *Distance*) was fairly similar, while estimating reindeer density at a small spatial scale (estimate 3, spatial resolution of 30 × 30 m in *Distance*) tended to give the largest and more imprecise abundance estimates (Table 3). One reason for this could be that although overall similar, the estimated vegetation cover effect on density deviated slightly from the actual relationship (Fig. 3) at low and high vegetation cover, as visualized by the animal positions from TC. Greater flexibility in the model building within a single analytical tool, could select a more precise model. A one-step modeling approach tool that enabled spatial density modeling (available in e.g. R package *DSpat*, Johnson et al. 2010, but no transect overlap is possible) with adjustment parameters for the detection key functions and covariates at the individual observation level (only available in *Distance*) would be ideal for small study areas.

Clearly, even with our relatively large sample sizes (recommended minimum of 60–80 observations, Buckland et al. 2001) and the associated DS uncertainty level, we may not be able to relate our DS abundance estimates to environmental drivers of annual population size fluctuations. By contrast, using TC time-series from these sub-populations, drivers like 'rain-on-snow' events and density dependence, have previously determined population growth rates (Kohler and Aanes 2004, Hansen et al. 2011). Hence, a mechanistic understanding of the system relating the state variables' responses to the environment requires a year to year unbiased and precise estimation of abundances (Yoccoz et al. 2001) or estimation of ecological indicators combining abundance indices, animal performance (i.e. body condition, reproductive and survival rate) and habitat quality (Morellet et al. 2007, Albon et al. 2016). In practice, mark–recapture is resource demanding, and TCs are not possible across large study areas, such as the much larger coastal plains found elsewhere in Svalbard, due to high demands for resources and logistics, as well as the challenges associated with false positives and negatives. In such cases, DS represents a promising alternative monitoring method to estimate animal abundance. With wider applications than analyses of annual population dynamics per se, DS may provide information on long-term population trends (if repeated annually) and may be used as a state evaluation tool across wider spatial scales (Buckland et al. 2004, Harrison et al. 2016). This could relate to major changes in animal spatial distribution and abundance declines after extreme climate events or overharvest like the local extinction and following re-colonization of Svalbard reindeer after protection in 1925 (Reimers 1983). Indeed, it is likely that a relatively low-cost DS monitoring program, repeated at regular intervals, would have detected the dramatic population crash (from 360 to 80 animals) on Brøgger Peninsula during the extremely icy winter of 1993–1994 (Aanes et al. 2000, Kohler and Aanes 2004), as well as the associated re-establishment of the Sarsøyra and the Kaffiøyra sub-populations. Nevertheless, a population abundance monitoring method without an investigation of the accuracy and estimation of detection probabilities is never reliable enough to draw strong inferences about the monitored system (Yoccoz et al. 2001).

Management implications

Accurate population size estimates improve our ability to detect the effects of environmental drivers or anthropogenic stressors on population dynamics in space and time (Yoccoz et al. 2001, Clark and Bjørnstad 2004, Knape et al. 2013). Because biased or imprecise estimates may lead to erroneous conclusions (Buckland et al. 2007), we encourage researchers and managers to apply the most appropriate statistical modeling tools to investigate the uncertainties and sources of error in their wildlife monitoring programs, and then adjust their management aims and decisions accordingly. TC is a resource demanding and logistically difficult field method for large study areas, especially when the detection probability is low due to environmental characteristics such as rugged terrain. The alternative DS methodology is widely used worldwide, often by non-experts. Nonetheless, a target sample size and precision of around 80 observations and a CV of 0.15 (Buckland et al. 2001, Porteus et al. 2011), may be insufficient to understand and predict dynamic processes related to e.g. climate change or harvest. Glass et al. (2015) stated that "considerably more than the recommended 60–80 observations (Buckland et al. 2001)" should be aimed for to estimate abundances. If the resources limit larger sample sizes and a higher precision, we advise the use of DS methodology for wide spatial scale population state assessments. For a mechanistic understanding of the system, DS should preferably be combined with other measures like highly precise local abundance estimates or animal performance (Morellet et al. 2007). When it comes to field work costs, the monitoring of our study area is approximately twice as expensive using TC versus DS methods, mainly due to the difference in number of people involved. This may be an important argument when choosing methods for long-term population monitoring at large spatial scales (La Morgia et al. 2015).

When choosing DS methodology, animal observation sample size and relevant habitat covariate information should always be maximized to obtain unbiased detection curves and accurate habitat structure effects (Miller et al. 2013, Buckland et al. 2015). Underestimation of detection probability and overestimation of animal density, even for a one-time state assessment, can have fundamental implications in management and conservation of wildlife populations (Thompson et al. 1998). To prevent this, we recommend the further development of easily accessible tools, preferably within a single R package. Such developments should simultaneously allow for: 1) a one-step modeling approach for relatively small study areas (i.e. the area covered is large relative to the entire study area); 2) modeling with data on a continuous scale; 3) adjustment parameters for the detection key functions; 4) detection and density covariates at the individual observation level; and 5) spatial density modeling tools that permit transect lines to overlap.

Acknowledgements – Thanks to the Sverdrup Research Station staff for logistical field help. We also thank B.-J. Bårdsen, S. T. Killengreen, S. Hamel, M. L. Bender, J. M. Milner and L. Little who provided comments on an early draft of the paper and V. Grøtan and I. Herfindal who gave useful advice in the analysis of the data.

Funding – This project was funded by the Research Council of Norway (POLARPROG project 216051, the Arctic Field Grant project 227456, NORKLIMA project 178561, SFF-III project 223257), the Norwegian Polar Institute and Centre for Biodiversity Dynamics at the Norwegian University of Science and Technology.

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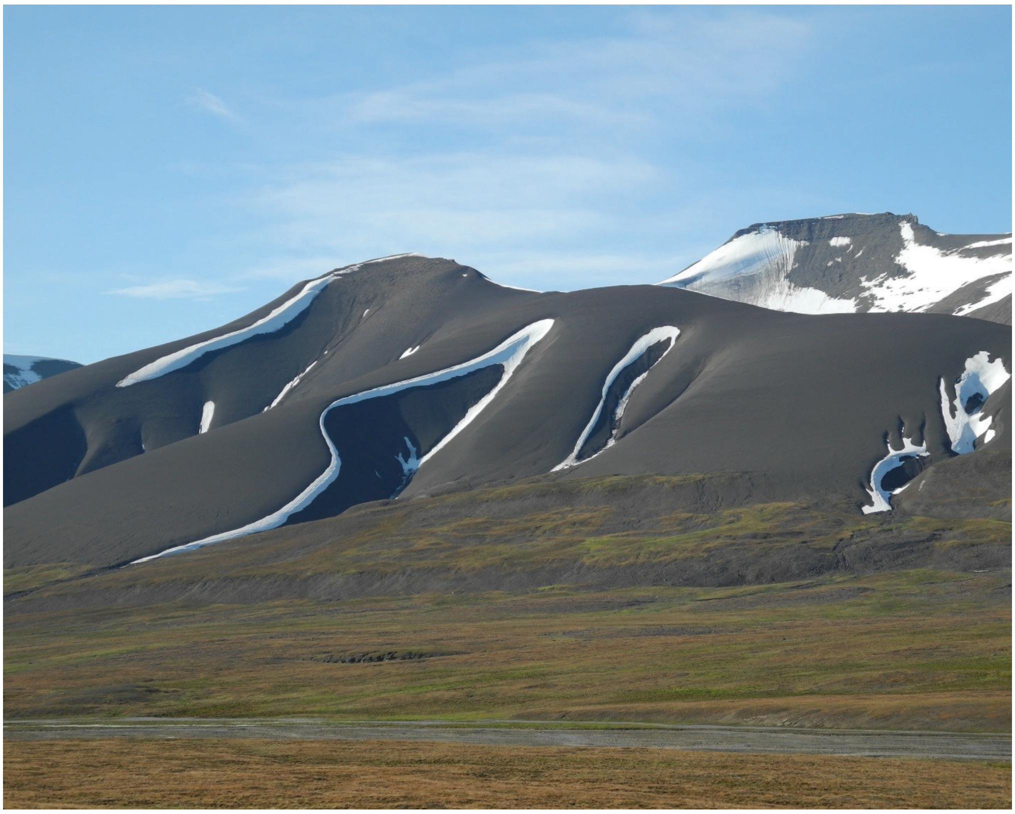
Paper II



Received: 24 March 2018 | Accepted: 25 June 2018
DOI: 10.1111/1365-2745.13036

RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

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

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Funding information
Norges Forskningsråd, Grant/Award Number: 223257, 244647, 246054 and 276080

Handling Editor: Tommaso Jucker

Abstract

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 reflect 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 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 abundant 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 differences in ring growth reflect between-year variation in above-ground biomass production. 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, including in remote places where annual field sampling is difficult to achieve.

KEYWORDS
dendrochronology, permanent plots, plant population and community dynamics, polar willow, *Salix polaris*, secondary growth, Svalbard, temperature, tundra ecosystem, vegetation production

1 | INTRODUCTION

Primary producers form the foundation of the Eltonian pyramid, fuelling higher trophic levels of the ecosystem (Elton, 1927; Field, 1998; Lindeman, 1942). 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, Przybylak, Ogilvie, & Isaksen, 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, Forbes, Zetterberg, & Kumpula, 2012)—with potential cascading effects on the population dynamics of animals as well as on carbon and nutrient cycling (Post et al., 2009; Stenseth et al., 2002; 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 (Babst et al., 2014; Dye et al., 2016; Klesse, Etzold, & Frank, 2016; Metsaranta & Lieffers, 2009). Such studies compare tree-ring readings to in situ measures of woody biomass in permanent forest plots, often sampled every 5–10 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 (Myers-Smith, Elmendorf, et al., 2015; Owczarek, Nawrot, Migała, Malik, & Korabiewski, 2014). These applications follow recent methodological developments which overcome the difficulties associated with high irregularity of ring growth in tundra shrubs (Myers-Smith, Hallinger, et al., 2015; Wilmking et al., 2012). 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 (Karlsen, Anderson, Van der Wal, & Hansen, 2018; Pettorelli et al., 2005; Vickers et al., 2016). Some studies using these tools have related e.g. Normalised Difference Vegetation Index (NDVI) to shrub expansion and growth traits (Babst, Esper, & Parlow, 2010; Blok et al., 2011; Forbes, Macias-Fauria, & Zetterberg, 2010; Macias-Fauria et al., 2012; Weijers, Pape, Löffler, & Myers-Smith, 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 (Milner, Varpe, Van der Wal, & Hansen, 2016; Ropars et al., 2017; Skarpe & Van der Wal, 2002). 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 et al., 2010; Speed, Austrheim, Hester, & Mysterud, 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, Grassein, Schurr, Vieilledent, & Violle, 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 (Berner et al., 2015; Bret-Harte, Shaver, & Chapin, 2002; Campioli et al., 2013; Magnin, Puntieri, & Villalba, 2014). They typically use retrospective measures of shoot primary growth (i.e. length and number of shoots per year) and relate it to the secondary growth, which can be measured as basal stem diameter, 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 interannual variability in arctic plant biomass production and a strong direct effect of

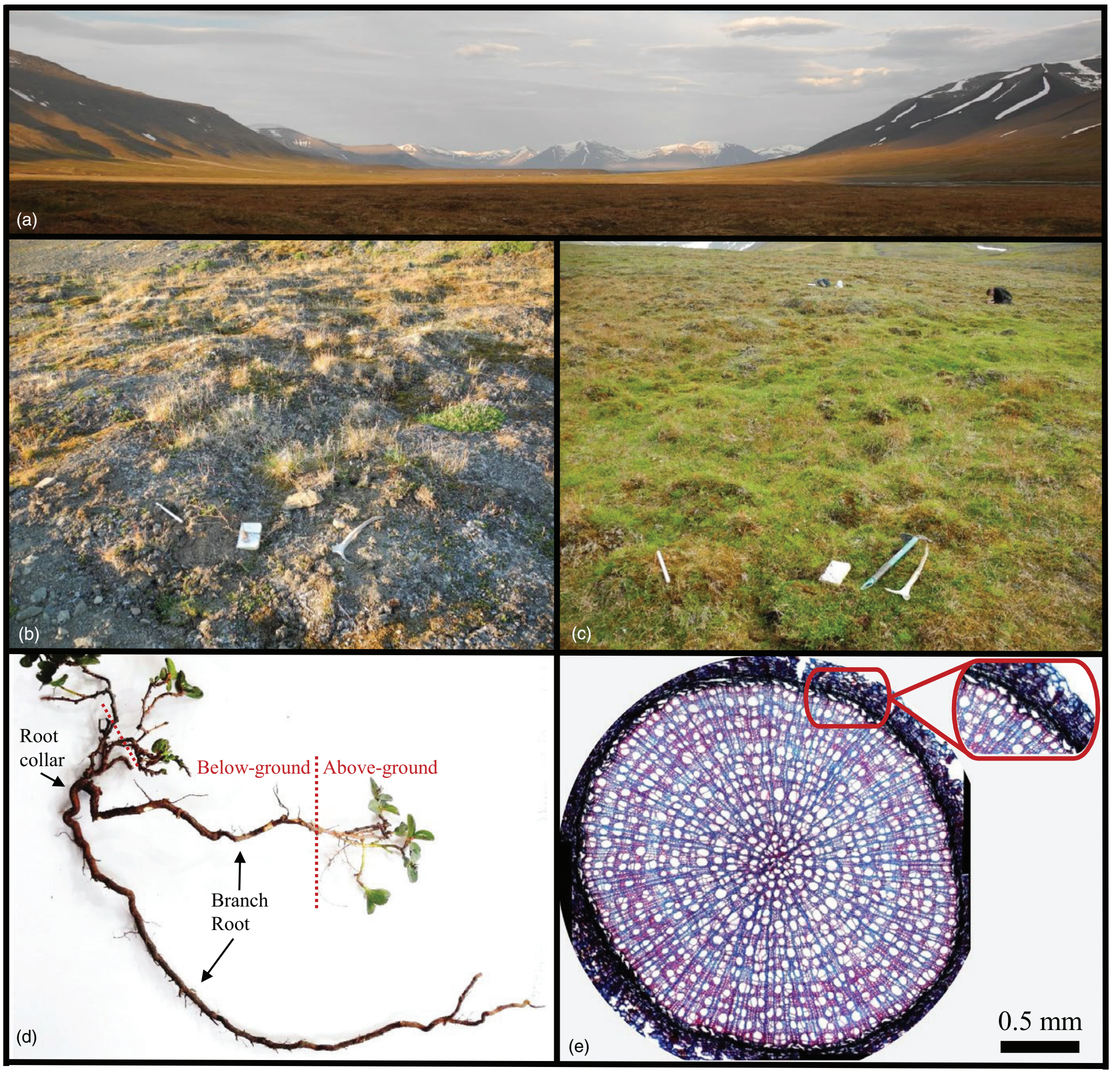

FIGURE 1 The study system. (a) The valley of Semmeldalen, central Spitsbergen, Svalbard, in early August 2015. (b) Ridge habitat. (c) Heath habitat. (d) An entire *Salix polaris* individual extracted from the ground, illustrating the substantial below-ground part composed of a main root, a root collar and nested branches in the ground. (e) The cross-sectional view of a *S. polaris* root (stained thin section of 20 μm thickness) with a radius of 1.125 mm. Note the outermost darker ring that represents mid-growing season of the year of sampling, 2015, which cells are not yet fully lignified

summer temperatures (Elmendorf et al., 2012; Gauthier et al., 2011; Karlsen et al., 2018; Van der Wal & Stien, 2014). The same pattern appears to characterise annual shrub ring growth (Myers-Smith, Elmendorf, et al., 2015; Weijers, Buchwal, Blok, Loffler, & Elberling, 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, Rachlewicz, Fonti, Cherubini, & Gärtner, 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.

2 | MATERIALS AND METHODS

2.1 | 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 (Figure 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 nonherding 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, Godfrey, Woodin, & Van der Wal, 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).

2.2 | Study species

Salix polaris has a circumpolar distribution (https://www.flora.dempstercountry.org/) and is the most widespread shrub species found across Svalbard, in habitats ranging from arctic meadow to polar desert (https://svalbardflora.no/, Nakatsubo, Fujiyoshi, Yoshitake, Koizumi, & Uchida, 2010; Rønning, 1996). Its abundance and high digestibility make it an important food resource for herbivores, especially reindeer (Bjørkvoll, Pedersen, Hytteborn, Jónsdóttir, & Langvatn, 2009; Van der Wal et al., 2000). 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 (Figure 1d). Overall, no more than 5%–6% of Svalbard's live vascular plant biomass is above the moss layer (Bardgett, Van der Wal, Jónsdóttir, Quirk, & Dutton, 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, Dormann & Skarpe, 2002; Rønning, 1996).

2.3 | Study design

2.3.1 | 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 *c.* 4.4 km^2 and did not exclude herbivory (see Van der Wal & 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 × 5 sites) by counting shoots of all species in small permanent quadrats (25 cm × 25 cm; 10 quadrats per site) in all 13 years (Supporting Information Figure 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 while not impacting plant performance therein. In the current study, we used three measures of above-ground biomass: (a) *S. polaris* biomass in the two focal habitats, separately and combined; (b) total community biomass, comprising all vascular plant species, in the two focal habitats combined; and (c) 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.

2.3.2 | 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 (Supporting Information Figure 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, Hallinger, et al., 2015, Supporting Information Figure S1d). We used a GLS-1 sledge microtome (Gärtner, Lucchinetti, & Schweingruber, 2014) to cut 5–6 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 Supporting Information Appendix S1.

2.3.3 | 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 (Supporting Information Figure 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, Rueden, Hiner, & Eliceiri, 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, Supporting Information Figure S2).

2.3.4 | 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, Hallinger, et al., 2015). We conducted three levels of cross-dating: (a) cross-dating between the four radial measurements within a single cross-section; (b) cross-dating between all five to six cross-sections of one shrub, to obtain a mean growth curve for an individual shrub; and (c) 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 Supporting Information Appendix S1 and Figure S2.

2.3.5 | 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 (Cook & Kairiukstis, 1990; Fritts, 1976; Helama, Lindholm, Timonen, & Eronen, 2004; Sullivan, Pattison, Brownlee, Cahoon, & Hollingsworth, 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 larger ring-widths at a young age (Supporting Information Figure 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 (Biondi & Qeadan, 2008; Cook & Kairiukstis, 1990). 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 (Supporting Information Figure S3b). Therefore, the final standardisation step consisted of detrending basal area increment series using the regional curve standardisation method (Briffa & Melvin, 2011) with a 20-year-window 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", Supporting Information Figure S3c). We additionally ran our analyses with other standardisation methods, which led to similar results (Supporting Information 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 (Figure 1e). Growth curves were also truncated to ensure a sufficient number of cross-sections for each year, resulting in a maximum number of chronologies over the period 1985–2014 (Supporting Information Appendix S1). 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, 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 Supporting Information Figure 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 shrubs ($r_{bar.wt}$), and the mean interseries 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, Cook & Kairiukstis, 1990; Wigley, Briffa, & Jones, 1984).

2.4 | Statistics

2.4.1 | 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 (Supporting Information Figure S4). To obtain normal distribution and constant variance in the model residuals, both measures were square-root transformed for analysis.

We ran linear mixed-effect models using the “lmer” function (R package “lme4”, Bates, Maechler, Bolker, & Walker, 2015). This modelling approach is recommended when analysing replicated data collected in a nested design (Cnaan, Laird, & Slasor, 1997; Grafen & Hails, 2002; Zuur, Ieno, Walker, Saveliev, & Smith, 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 (Supporting Information Figure S1); third, to give the correct weight to each observation when the sampling design is unbalanced (for instance, this applies to the 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 the assumption of measurement independence, resulting in too small *SE*s. Instead, using linear mixed-effects models, we included a random intercept structure (i.e. variation in means 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. Likewise, we added the interaction year × habitat to extract 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 1,000 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 1,000 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.

2.4.2 | 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 (https://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 ≥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 two and three-way interactions between the previous year’s ring growth, summer temperature and precipitation were included. To test for possible habitat effects, we proposed an interaction of habitat with the previous predictors presented (i.e. up to three-way interactions, see summary of all proposed predictors in Supporting Information 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 a hypothesis-based procedure using Pearson’s correlation (with the function “dcc” from the R package “treeclim”, Zang & Biondi,

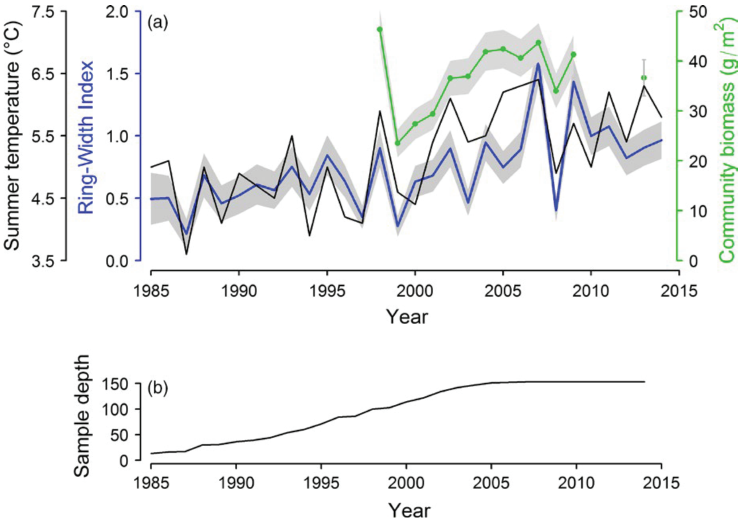

FIGURE 2 Time series of (a) the mean *Salix polaris* Ring-Width Index (blue line) for the Semmeldalen study location in central Spitsbergen, Svalbard, plotted together with the mean above-ground biomass of the total vascular plant community (green line) and mean summer temperature (June–July–August) (black line). The grey shades represent the *SE* 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

2015), to investigate for temperature and precipitation, which combination of summer months (June, July, August, June–July, July–August, June–July–August) best captured ring growth (Supporting Information Figure 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 with ring growth, and in the model selection (below) we therefore decided to use the same summer month combination as for temperature (Supporting Information Figure S5). For this period, the mean summer temperature was 5.2°C (min: 3.6°C in 1987, max: 6.4°C in 2007, Figure 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, 2016) was used for model ranking based on the parsimony principle of the corrected Akaike information criterion (AIC$_c$, 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.

3 | RESULTS

3.1 | Ring growth in time and space

Robust *S. polaris* ring growth curves were constructed for the period 1985–2014 in Semmeldalen, central Spitsbergen, Svalbard (Figure 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 (Figure 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 interannual 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 ($r_{\text{bar.wt}} = 0.65$), but rather high growth variability between shrubs ($r_{\text{bar.bt}} = 0.21$). Mean correlation between individual growth curves was relatively low ($r_{\text{bar.tot}} = 0.22$), but despite this the Expressed Population Signal for the period 1985–2014 was high (EPS = 0.90). Thus, the overall 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 ($t = 1.55$, $df = 55$, $p = 0.13$). 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 trend between the habitats, ring growth in heath and ridge co-fluctuated over time ($r = 0.42$ [0.04–0.69], $t = 2.29$, $df = 25$, $p < 0.05$, Supporting Information Figure S6), indicating shared drivers of annual growth.

3.2 | 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

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 *Salix polaris* ring growth are based on (raw) ring-widths (mm), while 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 1,000 bootstrap iterations) were calculated with linear models fitted to back-transformed mean-estimate time series

	Heath	Ridge	Both Heath and Ridge	All habitats
Salix polaris ring-width 1985–2014				
Mean estimates (mm)	0.040 [0.030–0.051]	0.049 [0.037–0.061]	0.045 [0.035–0.053]	–
Trend (RWI) per year	0.027 [0.018–0.037]	0.003 [−0.012 to 0.020][a]	0.021 [0.013–0.033][b]	–
Salix 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) per year	0.1 [−0.8 to 1.0]	0.6 [0.3–1.2]	0.4 [−0.3 to 1.1]	0.2 [−0.3 to 1.0]
All vascular plants biomass 1998–2013				
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]
Trend (g/m^2) per year	0.4 [−1.2 to 1.7]	0.9 [0.2–1.6]	0.7 [−0.4 to 1.7]	0.8 [−0.6 to 2.1]

[a] 1988–2014.

[b] Also an increasing trend when considering the same time scale as the biomass measurements 1998–2013.

in ridge habitat ($t = 3.58$, $df = 22$, $p < 0.01$, Supporting Information Figure S6). From 1998 to 2013, the overall tendency for a positive trend was nonsignificant; yet, biomass in ridge habitat increased over time (Table 1, Supporting Information Figure S6). Ridge and heath biomass co-fluctuated during the period 1998–2009 ($r = 0.61$ [0.05–0.88], $t = 2.41$, $df = 10$, $p < 0.05$), but not significantly when also including 2013 (no biomass monitoring took place in 2010–2012, Supporting Information Figure 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 ($t = -5.45$, $df = 24$, $p < 0.001$). 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).

3.3 | *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 (Figures 3c and 4). Both measures were significantly and positively related to summer temperature, suggesting this climate variable as the overall driver of *S. polaris* growth (Table 2, Figure 3a,b). When inspecting patterns by habitat, the strength of these relationships changed. 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, Figure 3h), while for ridge habitat this relation remained strong (Figure 3e). The opposite was the case for the relationship between ring growth and summer temperature, which weakened for ridge but remained strong for heath (Figure 4d,g). Thus, habitat-specific correlations between ring growth and biomass of *S. polaris* were weakened (Figure 4f,i).

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 (Figure 4). Even when removing *S. polaris* from the biomass of all habitats, the correlation remained strong ($r = 0.68$ [0.21–0.90]).

3.4 | 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 $\Delta AIC_c < 2$ (Supporting Information Table S3). Additionally, the summer temperature effect interacted with last year's ring growth (Table 2, Supporting Information Figure S7a). In warm summers, growth was less influenced by the previous year's 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

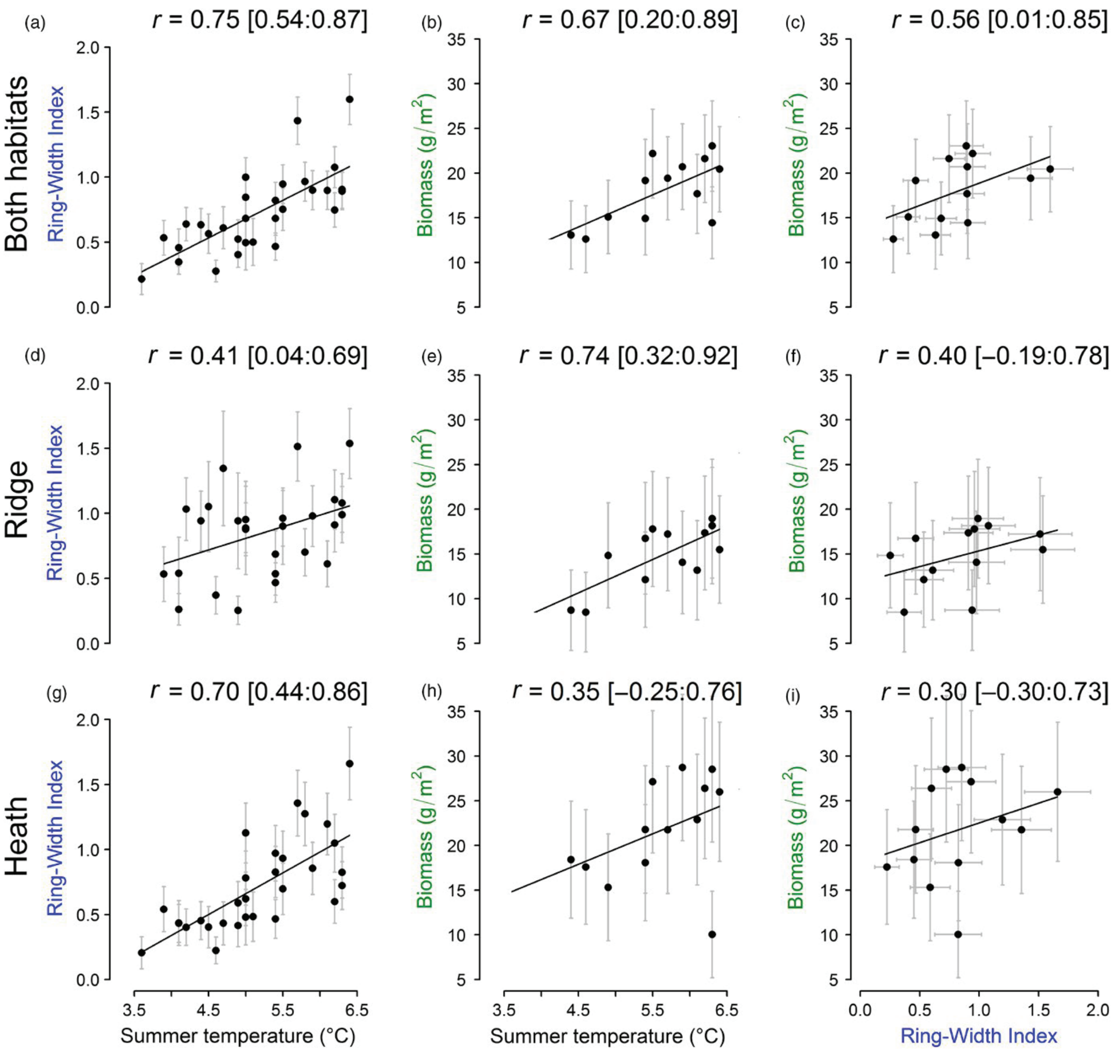

FIGURE 3 Pairwise relationships between Ring-Width Index of *Salix polaris*, above-ground *S. polaris* biomass and summer temperature (June–July–August) for (a–c) both habitats combined and for (d–f) Ridge and (g–j) Heath separately. Plotted mean values (circles) and associated *SE*s (whiskers) are estimates 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 [Colour figure can be viewed at wileyonlinelibrary.com]

suggested that the positive effect of previous year's ring growth was less pronounced in ridge than in heath habitat (Table 2, Supporting Information Figure S7b).

4 | 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 basis how well retrospective ring growth represents above-ground production of not only the focal shrub but also the vascular plant community as a whole (Figures 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,

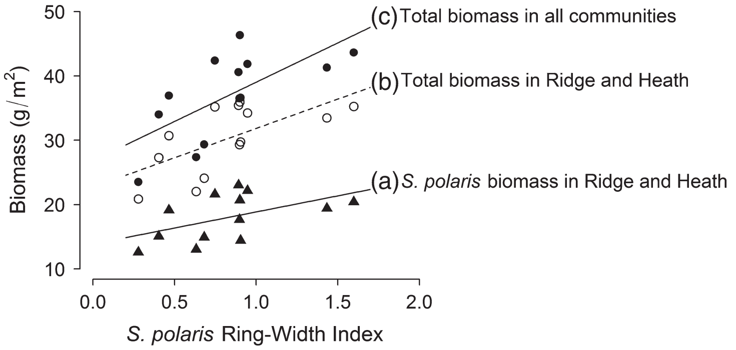

FIGURE 4 Relationships between *Salix polaris* Ring-Width Index (RWI) and above-ground plant biomass. (a) *Salix polaris* above-ground biomass versus *S. polaris* RWI in Ridge and Heath combined (triangles): *r* = 0.56 [0.01–0.85]. (b) Total vascular plant above-ground biomass versus *S. polaris* RWI in Ridge and Heath 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 (closed circles): *r* = 0.70 [0.25–0.90]. Plotted values are 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

TABLE 2 Parameter estimates β with their associated 95% confidence interval (from 1,000 bootstrap iterations) and test statistics (*t* and *p* values) of the top ranked model (using restricted maximum likelihood) from model selection, of *Salix polaris* Ring-Width Index (RWI) during the period 1985–2014. The response variable RWI (and the explanatory variable RWI_{t-1}, previous year's ring growth) is on the square-root scale

Parameter	β	*t*	*p*
Intercept (heath as reference)	−0.52 [−1.07 to 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 to 0.39]	1.26	0.23
RWI_{t-1}	0.67 [0.15–1.20]	2.59	<0.01
Habitat (Ridge) × RWI_{t-1}	−0.17 [−0.33 to −0.03]	−2.32	<0.05
Summer temperature × RWI_{t-1}	−0.08 [−0.18 to 0.01]	−1.82	0.07

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 spatio-temporal scales (Galván, Camarero, Gutiérrez, & Zuidema, 2014; Messier, McGill, & Lechowicz, 2010; 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 microhabitat 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 macrohabitat 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

TABLE 3 Variance partitioning across the different nested ecological factors (i.e. random effects) in a linear mixed-effects model where no fixed effects (other than the intercept) were included. All three response variables, *Salix 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

	Variance		
Ecological factor	***Salix polaris* RWI**	***Salix polaris* biomass**	**Community biomass**
Plant or plot	0.042 (30)	0.123 (94)	0.087 (272)
Site	0.016 (10)	0.152 (10)	0.050 (28)
Habitat	<0.001 (2)	<0.001 (2)	0.023 (6)
Year	0.031 (30)	0.011 (13)	0.018 (13)
Residuals	0.099 (673)	0.079 (1,159)	0.051 (2,158)

challenging (Buchwal, 2014; Wilmking et al., 2012). 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, Supporting Information Figure 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 ($r_{\mathrm{bar.tot}} = 0.22$) was lower than in other Svalbard species with more regular growth pattern such as *C. tetragona* ($r_{\mathrm{bar.tot}} = 0.32$, 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 ($r_{\mathrm{bar.bt}} = 0.21$) 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—to stand 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 (Ackerman et al., 2018; Buchwal et al., 2013; Elmendorf et al., 2012; Forbes et al., 2010; Myers-Smith, Elmendorf, et al., 2015; Van der Wal & Stien, 2014; Weijers et al., 2017, 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 (Muraoka et al., 2008; Van der Wal & Hessen, 2009; Wiegolaski, Bliss, Svoboda, & Doyle, 1981). Van der Wal and Stien (2014) pointed at the importance of cloud cover rather than just summer temperature in our study area, and suggested 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 year's 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). In high arctic plants, a substantial proportion of the biomass is situated below-ground (root-to-shoot ratio > 4; Iversen et al., 2015; Mokany, Raison & Prokushkin, 2006), as is the case for *S. polaris*. Indeed, even almost all of its woody stem material is buried into the ground (Figure 1). Woody tissues have much higher C to N ratios than for example leaves. We showed that wood deposits below-ground vary from year to year as a function of temperature, and so do the increases in carbon pool sizes they represent. A recent study by Berner, Jantz, Tape, and Goetz (2018) roughly estimated large-scale tundra below-ground biomass from above-ground measurements, whilst recommending that 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 Blume-Werry et al., 2018; Wang et al., 2016). Our work on below-ground secondary growth starts to fill this knowledge gap by providing a way to retrospectively assess annual green biomass production available to higher trophic levels, thereby fostering widely studied topics such as plant–herbivore interaction.

Given that *S. polaris* forms a major component of the diet of Svalbard reindeer (Bjørkvoll et al., 2009; Van der Wal et al., 2000), 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 per km^2 over an area of ca 150 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 (Supporting Information 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-level 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 and are 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 for wedging or missing rings, as well as sampling replication across the landscape, thereby accounting for the large habitat variation characterising high arctic landscapes.

ACKNOWLEDGEMENT

This project was supported by the Research Council of Norway through its Centres of Excellence funding scheme (project 223257), FRIPRO (project 276080), KLIMAFORSK (project 244647), and the Arctic Field Grant (project 246054), as well as the funding scheme MOBILITY PLUS (1072/MOB/2013/0). We profoundly thank A. Stien and V. Grøtan for valuable statistical advice; T.K. Kåsi and D.M. Alvsvåg for the help in the laboratory; Ø.H. Opedal, K.L. Matthews, L. Veylit and B. Peeters for fruitful discussions and comments on early drafts of the paper; and Jeffery. M. Welker for enabling a research stay at the University of Alaska, Anchorage.

AUTHORS' CONTRIBUTIONS

M.L.M., B.B.H. and R.vd.W. conceived the ideas and designed methodology; M.L.M., R.vd.W. and L.S. collected the data; M.L.M., L.S. and A.B. conducted the laboratory work; M.L.M. and B.B.H. analysed the data; M.L.M. wrote the manuscript, with the help of all coauthors.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: http://datadryad.org/resource/doi:10.5061/dryad.d7p3b40 (Le Moullec, Buchwal, Van der Wal, Sandal, & Hansen, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Le Moullec M, Buchwal A, van der Wal R, et al. Annual ring growth of a widespread high arctic shrub reflects past fluctuations in community-level plant biomass. *J Ecol*. 2018;00:1–16. https://doi.org/10.1111/1365-2745.13036

Supporting information for:

Annual ring growth of a widespread high arctic shrub reflects past fluctuations in community-level plant biomass (Le Moullec et al. 2018).

Appendix I Building the *Salix polaris* ring growth chronology

Laboratory analysis

After thin sectioning of the shrub specimens we stained each cross-section with a 2:1 solution of Astra Blue (1g/100 ml) and Safranin O Dye (1g/100 ml) in order to enhance the visibility of ring boundaries. Keeping the cross-section in place on a microscope slide with the tip of a de-sharpened pipette, we dehydrated dyed cross-sections by maintaining an energetic flow of ethanol (progressively 70 %, 96 % and 100 %, Schweingruber & Poschold 2005). The cross-sections were permanently fixed by applying non-synthetic Canada Balsam and a cover slip. Such prepared micro slides were dried in an oven at 60 °C for minimally 12 hours. After drying, slides were cleaned for image analyses. We captured images at 100x magnification using a Nikon DS-Ri1 camera attached to a Nikon Eclipse E800 light microscope configured with the NIS-Elements F 3.0 (NIKON) software. Single images were merged in AutoStitch demo version 2013 (Brown & Lowe 2007).

Cross-dating steps

Each shrub was subjected to a thorough cross-dating procedure. The following three levels of cross-dating were performed (see also Figure S2):

1) Cross-dating of radial measurements within a single cross-section. Positive pointer years, i.e. relatively wide and well developed continuous reference rings were colour-coded to ensure that each of the four radial measurements within a cross-section was aligned correctly (Kolishchuk

1990). To prevent introducing erroneous rings, partial missing rings (i.e. wedging rings) had to be clearly recognisable as such, and their anatomy was double-checked under the microscope. The four radial measurements were averaged to construct a mean growth curve for a single cross-section.

2) Cross-dating between all cross-sections of one shrub to obtain a mean growth curve for an individual shrub. Positive pointer years were visible throughout the whole shrub, making it possible to align single growth curves obtained for each cross-section. See Buchwal (2014) for an illustration of this procedure. Mean growth curves constructed for each cross-sections were plotted together in order to detect any consistent mismatch in alignments of pointer years (i.e. unidirectional mismatch since only missing rings can occur and no false rings should be introduced). Parallel to this, all digital images of analysed cross-sections were displayed to compare the number of rings between the pointer years. These steps combined allowed us to reconstruct a robust mean growth curve for each shrub.

3) Cross-dating between individual shrubs' mean growth curves within a site. Three shrubs had been collected within each sampling site (for a total of 10 sites), and all three shrubs' mean growth curves were plotted together for visual cross-dating. In case one shrub's growth curve showed an obvious one-year mismatch in alignment compared to that of another plant, a missing year was introduced in all cross-sectional mean growth curves of this shrub. Insertion of missing rings was always assured by re-checking the first and second steps of cross-dating. Nonetheless, some missing rings had, by definition, no signs of an anatomical evidence. Consecutive missing rings were rare, but occurred with a maximum of three missing rings. Through this third-step, we could obtain site-specific mean growth curves using linear mixed-effects models (see main text, Methods).

The study from Wrońska-Wałach *et al.* (2016) presents an additional fourth step of cross-dating, i.e. cross-dating between mean growth curves of different sites. We verified by visual comparison that this step was not necessary to obtain final chronologies since no consistent mismatch in alignment of sites' mean growth curves was observed. Avoiding this fourth cross-dating step enabled us to respect independency of mean growth curves between the sites.

Chronology truncation

To avoid chronology construction based on too few cross-sections (and specimen) at each sampling levels (i.e. site, habitat and overall location), we truncated the cross-dated time-series successively. First, a minimum of two cross-sections per site is needed for (within-site) cross-dating, corresponding to cross-dating between root collars (i.e. oldest plant part). From these truncated time-series, we then required a minimum of five cross-sections per habitat type. As a result, the heath habitat growth curve was represented for the study period 1985-2014 by 10-74 cross-sections and ridge habitat growth curve for 1988-2014 by 8-79 cross-sections (Fig. 3). Finally, the overall ring growth curve for Semmeldalen was restricted to at least 10 cross-sections, providing 10-153 cross-sections for the study period 1985-2014 (Fig. 2). Note that the year of collection (2015) was not included in the analysis because of possible incomplete ring growth.

Table S1. Comparison of different methods of ring-width standardisation, and their influence on the correlation coefficients (and [95 % confidence intervals]) for ring growth versus summer temperature and total above-ground community biomass of vascular plants (six habitats), respectively. The standardisation methods used were: the Basal Area Increment (BAI); Regional Curve Standardisation (RCS, 20 year windows cut-off, see Fig. S2); Spline (5 years window); and the C-method (Biondi & Qeadan 2008; Briffa & Melvin 2011). Detrending was performed in R version 3.3.2, using 'dplR' package (Bunn 2008). In the main text, we applied double detrending of raw ring-widths (i.e. first BAI and then RCS). Correlation coefficients were computed using time-series estimates from linear mixed-effects models on the square-root scale (see main text).

	Ring growth			
	BAI and RCS	BAI	BAI and spline	C-method
Community biomass	0.70 [0.25:0.90]	0.69 [0.23:0.90]	0.62 [0.10:0.87]	0.68 [0.21:0.90]
Summer temperature	0.75 [0.54:0.87]	0.77 [0.57:0.88]	0.50 [0.16:0.73]	0.68 [0.42:0.84]

Table S2. List of all predictors and their interactions proposed in the model selection step, using the function 'dredge' from the R package 'MuMIn' (Barton 2013). All combinations were tested and ranked based on the parsimony principle of the corrected Akaike Information Criteron (AICc), using a maximum likelihood approach. Interactions are shown by the sign (×).

Predictors	Definition
RWIt-1	Previous year's RWI
Hab	Habitat factor: Ridge or Heath
T°C	June-July-August mean temperature (°C)
Precip.	June-July-August precipitation sum (mm)
Snow	November-April snowfall amount (mm)
ROS	"Rain-On-Snow", November-April rain sum (mm) on the logarithmic scale.
Winter onset	Julian day of winter onset (see in main text)
Winter end	Julian day of winter end (see in main text)
T°C × Precip.	
RWIt-1 × T°C	
RWIt-1 × Precip.	
Hab × RWIt-1	
Hab × T°C	
Hab × Precip.	
Hab × Snow	
Hab × ROS	
Hab × Winter onset	
Hab × Winter end	
Hab × T°C × Precip.	
Hab × RWIt-1 × T°C	
Hab × RWIt-1 × Precip.	
Null model	Intercept only

Table S3. Summary table of the top ranked models (Δ AICc < 2) from the model selection, and associated parameter estimates using a maximum likelihood approach. Effects on *S. polaris* Ring-Width Index (RWI, the response variable) are presented on the square-root scale and cover the period 1985-2014. The variable names can be referred to in Table S2.

Rank	Intercept	RWI_{t-1}	Hab	T°C	Precip.	Snow	Hab × RWI_{t-1}	RWI_{t-1} × T°C	Hab × T°C	Hab × Snow	df	AICc	ΔAICc
1	-0.525	0.673	+	0.226			+	-0.084			10	425.65	0.00
2	-0.394	0.667	+	0.215	-1.47e-03		+	-0.083			11	426.07	0.42
3	-0.498	0.605		0.233				-0.085			8	426.70	1.06
4	-0.451	0.649	+	0.224		-7.97e-04	+	-0.080		+	12	426.82	1.18
5	-0.162	0.210	+	0.159			+				9	426.86	1.21
6	-0.368	0.599		0.222	-1.46e-03			-0.084			9	427.12	1.47
7	-0.035	0.210	+	0.149	-1.48e-03		+				10	427.18	1.54
8	-0.323	0.643	+	0.213	-1.47e-03	-7.51e-04	+	-0.079		+	13	427.24	1.60
9	-0.541	0.637	+	0.230			+	-0.078	+		11	427.28	1.64

Table S4. Summary table of the top ranked models (Δ AICc < 2) from the model selection including reindeer abundance and reindeer abundance interaction with habitat in addition to the list of proposed predictors from Table S2. Reindeer monitoring took place in 1994-2014 and expand over a larger area than Semmeldalen, also including Colsbay and part of Reindalen. Abundance estimates are derived from an integrated population model combining mark re-capture data and summer census on foot (see Lee et al. 2015). At the difference of Table S3, here the climate variable estimates cover a shorter period matching the reindeer census period. The reported parameter estimates are calculated using a maximum likelihood approach. Effects on *S. polaris* Ring-Width Index (RWI, the response variable) are presented on the square-root scale and cover the period 1994-2014. The variable names can be referred to in Table S2. Note that the interaction habitat × reindeer is not selected in the top ranked models, therefore not reported in the table.

Rank	Intercept	RWI_{t-1}	Hab	T°C	Precip.	**Reindeer**	ROS	Winter start	Winter end	Hab × RWI_{t-1}	RWI_{t-1} × T°C	Hab × T°C	Hab × Precip.	df	AICc	ΔAICc
1	0.090	0.178	+	0.137	-1.84e-03					+				10	393.99	0.00
2	-0.071	0.179	+	0.150						+				9	394.16	0.16
3	0.092	0.176	+	0.113	-2.11e-03	1.22e-04				+				11	395.50	1.50
4	0.113	0.177	+	0.136	-2.21e-03					+			+	11	395.53	1.54
5	0.018	0.173	+	0.146	-2.04e-03		0.018			+				11	395.65	1.65
6	0.614	0.178	+	0.140	-2.11e-03			-1.91e-03		+				11	395.71	1.72
7	-0.042	0.334	+	0.161	-1.84e-03					+	-0.028			11	395.80	1.80
8	0.049	0.176	+	0.145	-1.83e-03					+		+		11	395.82	1.83
9	0.361	0.176	+	0.127	-1.87e-03				-1.42e-03	+				11	395.85	1.86
10	-0.214	0.349	+	0.176						+	-0.030			10	395.90	1.91
11	-0.114	0.177	+	0.158						+		+		10	395.95	1.95

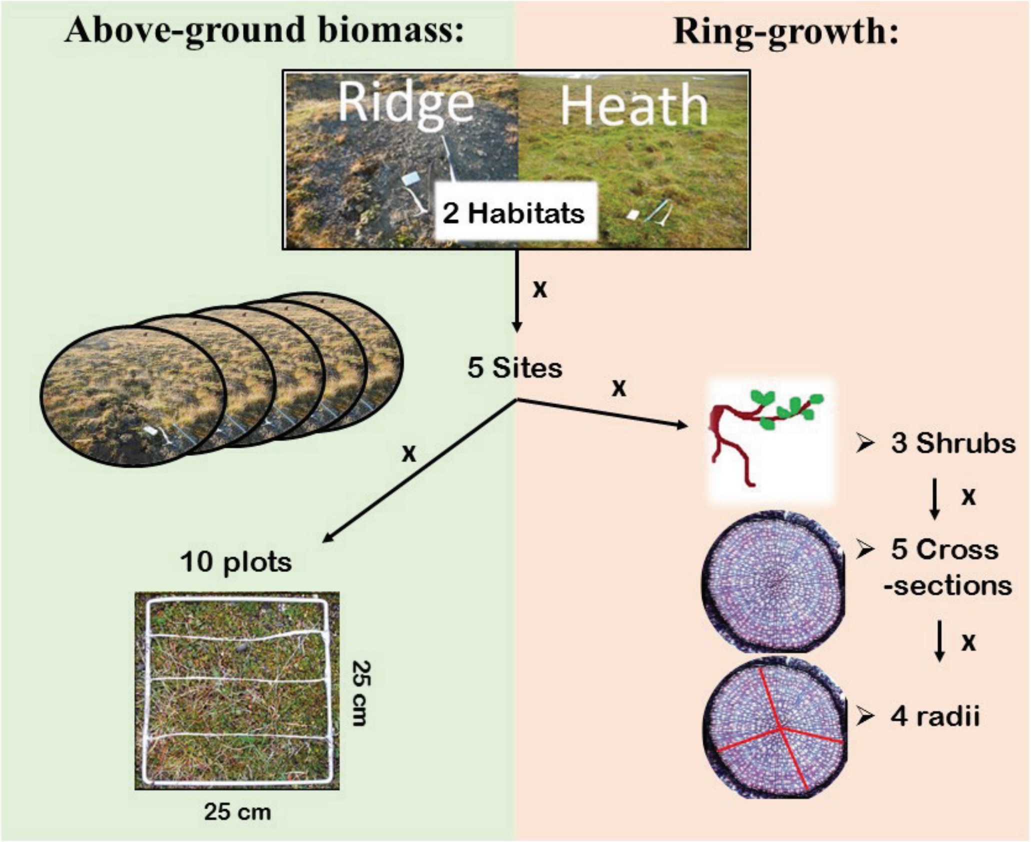

Figure S1. Graphical summary of the balanced sampling design followed for both the above-ground vascular plant biomass and the *S. polaris* specimens sampled for dendrochronology. Regarding the latter, three shrubs were sampled within each of five replicated sites, within each of two habitats = 30 individual shrubs. Note that the above-ground biomass was also sampled in four other habitats than ridge and heath.

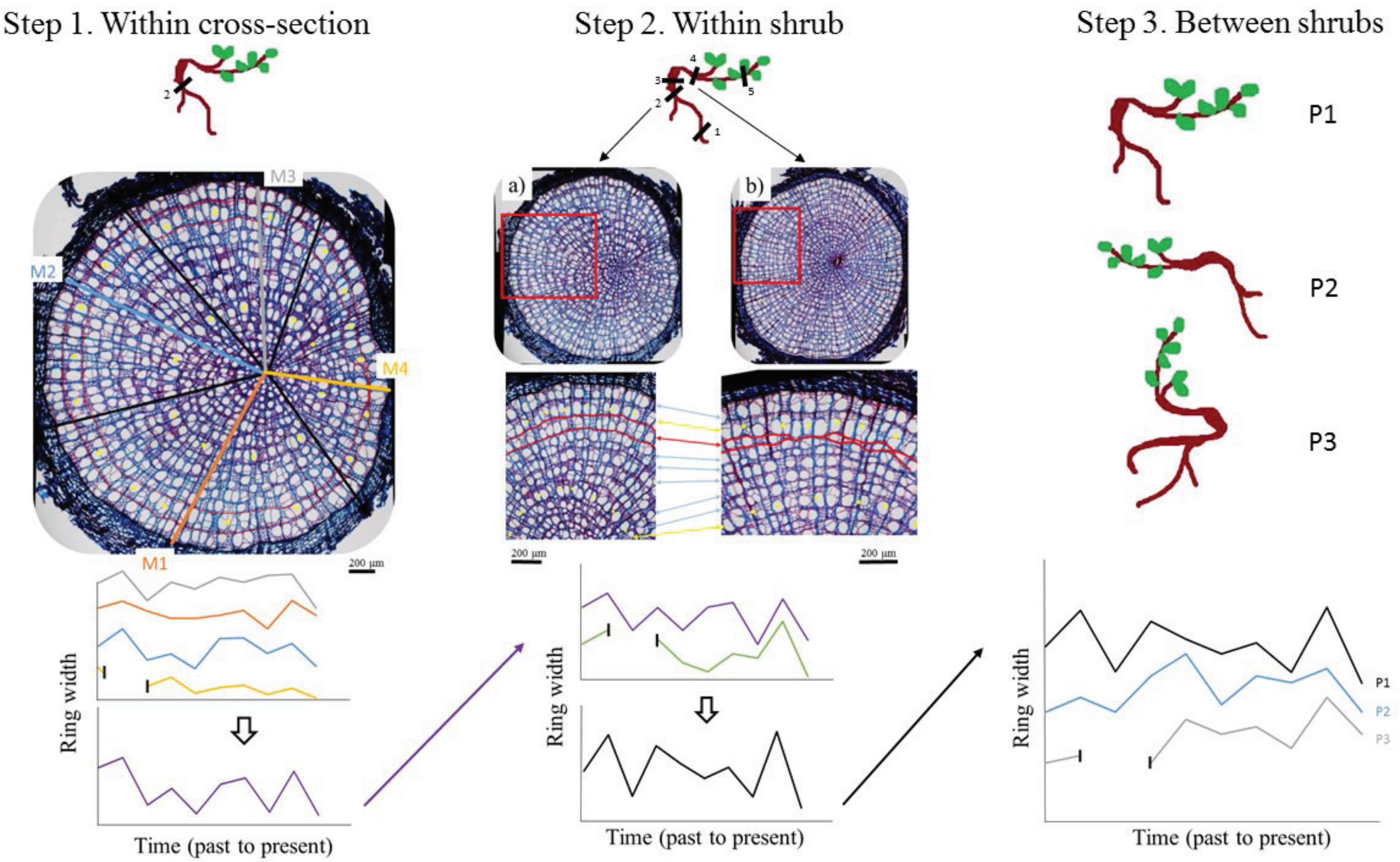
Step 1. Within cross-section
2
M1
M2
M3
M4
200 µm
Ring width
Time (past to present)
Step 2. Within shrub
1
2
3
4
5
a)
b)
200 µm
200 µm
Ring width
Time (past to present)
Step 3. Between shrubs
P1
P2
P3
Ring width
Time (past to present)
P1
P2
P3

Figure S2. Graphical presentation of the three cross-dating steps performed on *Salix polaris* from central Spitsbergen. Step 1 represents cross-dating of four radial measurements (M1 to M4, randomly drawn within each quarter [black lines]) of ring-widths growth within a single cross-section. Visual comparison of positive pointer years (yellow dots) ensured that each radial measurement was aligned correctly. If a ring was wedging (illustrated by the red coloured ring boundaries) a “gap” was introduced, as illustrated with the M4 yellow radial measurement curve (and pictures a and b). The four radial measurements were averaged using an arithmetic mean to construct a mean growth curve (purple curve, lower panel) for a single cross-section. Step 2 illustrates the cross-dating between cross-sections, on the example of two cross-sections (out of five), measured within one shrub: a root (picture a) and a branch (picture b) cross-sections. Positive pointer years (yellow dots) were visible throughout the whole shrub, making it possible to align cross-sections’ growth curves. For example, the ring represented with red boundaries can be wedging as in picture b, or can be entirely missing in another cross-section, as illustrated below in a line graph by the green curve where a “gap” was introduced to match alignments of pointer years from other cross-sections. We obtained a mean growth curve for an individual shrub (black curve, lower panel) by averaging all cross-sections’ mean growth curves. Step 3 represents cross-dating between three individual shrubs’ mean growth curves, each resulted via Step 1 and Step 2. All three shrubs’ mean growth curves were plotted together to verify if any shrub shows a mismatch in mean growth curves alignment compared to the other plants. In the example shown this was the case for the shrub P3 (grey curve) where a “gap” was introduced to obtain alignments of pointer years between the shrubs. Insertion of missing rings was always assured by re-checking Step 1 and Step 2. For visual illustration, all ring-widths growth curves are spread along the y-axis (without real units) and the time steps (x-axis) are annual.

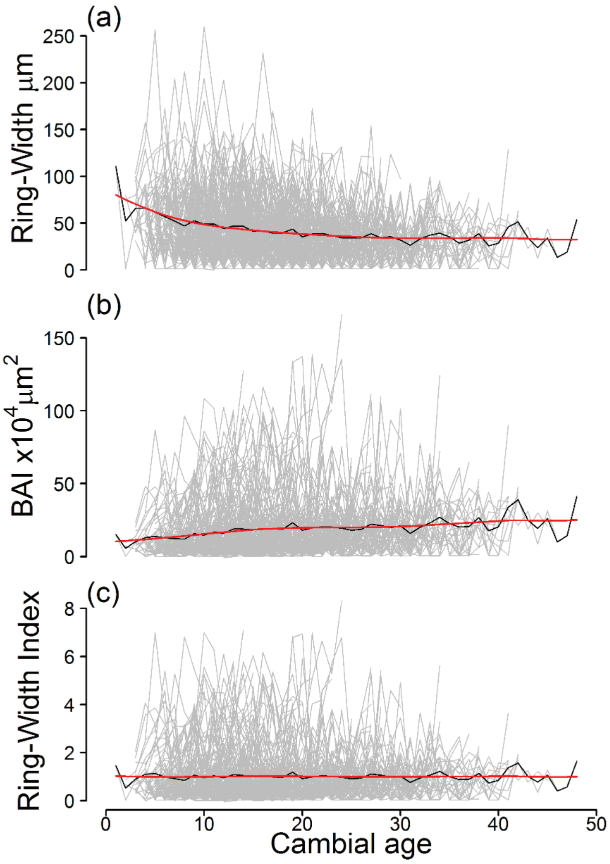

Figure S3. *Salix polaris* tree-ring chronology standardisation steps of the 153 cross-sections, and their relation to cambial age (i.e. biological age). (a) Display of how the raw ring-widths (μm) change with age, demonstrating higher growth at young age (i.e. juvenile effect). (b) Display of changes in the Basal Area Increments (BAI in μm^2, computed from raw ring-widths) with age, showing that the juvenile effect was removed when accounting for geometry, i.e. stem and root diameter becoming increasingly larger with age. However, a slight but constant increase of BAI with age remain visible. Therefore, we detrended BAI with a Regional Curve Standardisation. Accordingly, (c) any age effects were eliminated, resulting in a dimensionless Ring-Width Index measure centred around 1.

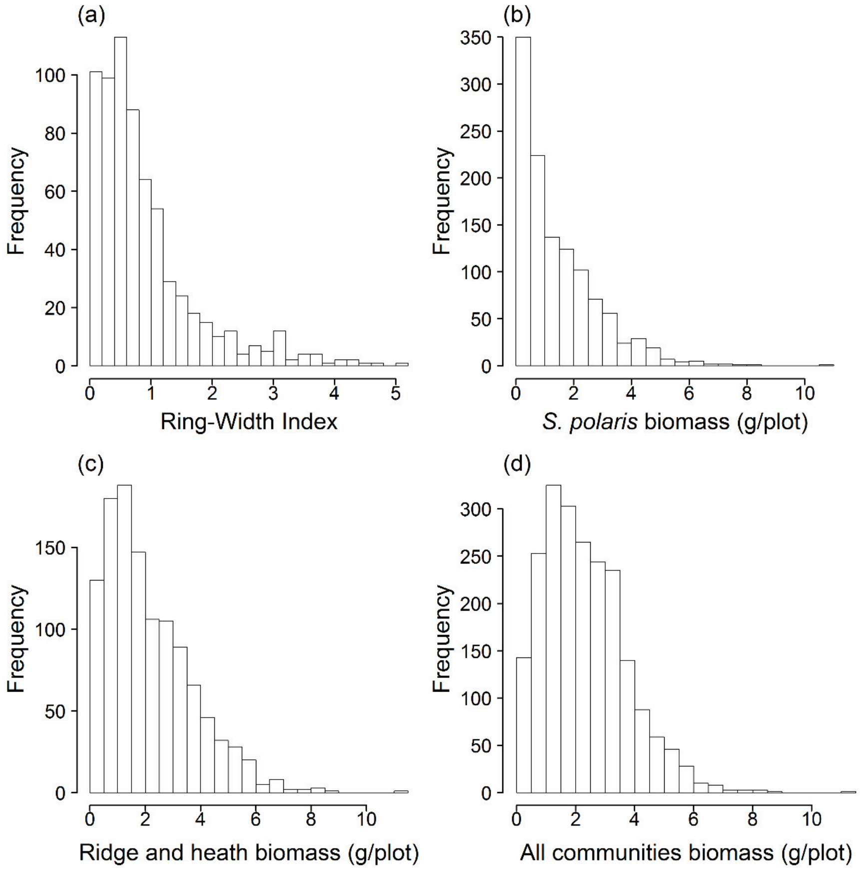

Figure S4. Frequency distribution of the lower hierarchical sampling level used in this study, i.e. individual shrub ring growth and plot biomass measures. (a) *S. polaris* annual mean Ring-Width Index per shrubs from 1985 to 2014. (b) *S. polaris* above-ground biomass frequency at the plot level (25 × 25 cm) from 1998-2009 and 2013. Similarly, (c) shows the above-ground biomass frequency of all vascular plants in ridge and heath habitat, while (d) combined all six habitats (i.e. total community-level vascular plant biomass). Prior to conduct the analysis, we applied a square-root transformation to the data.

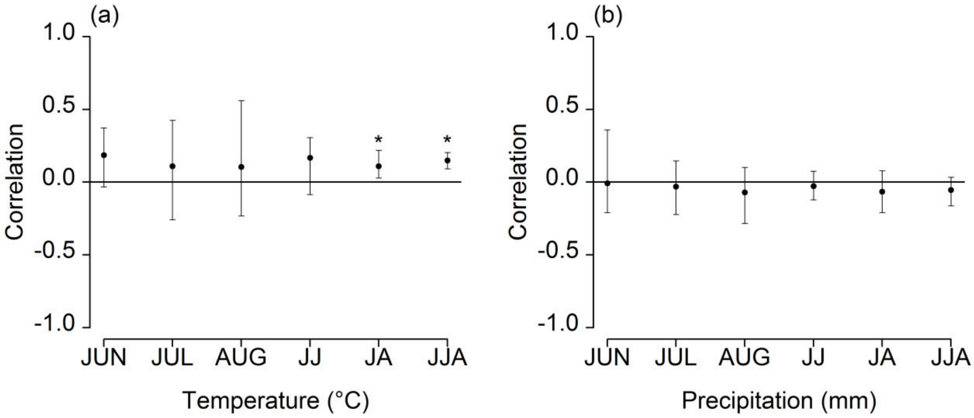

Figure S5. Pearson's correlation coefficients for the *S. polaris* Ring-Width Index chronology from Semmeldalen, central Spitsbergen and different temporal periods of two weather variables. Summer monthly temperature (a) and precipitation (b) and their different combinations (June, July, August, June-July, July-August, June-July-August) for the period 1985-2014. Weather data were acquired from Svalbard airport weather station (78°25 N, 15°46 E, 30 km distance from the study area) via http://eklima.met.no.

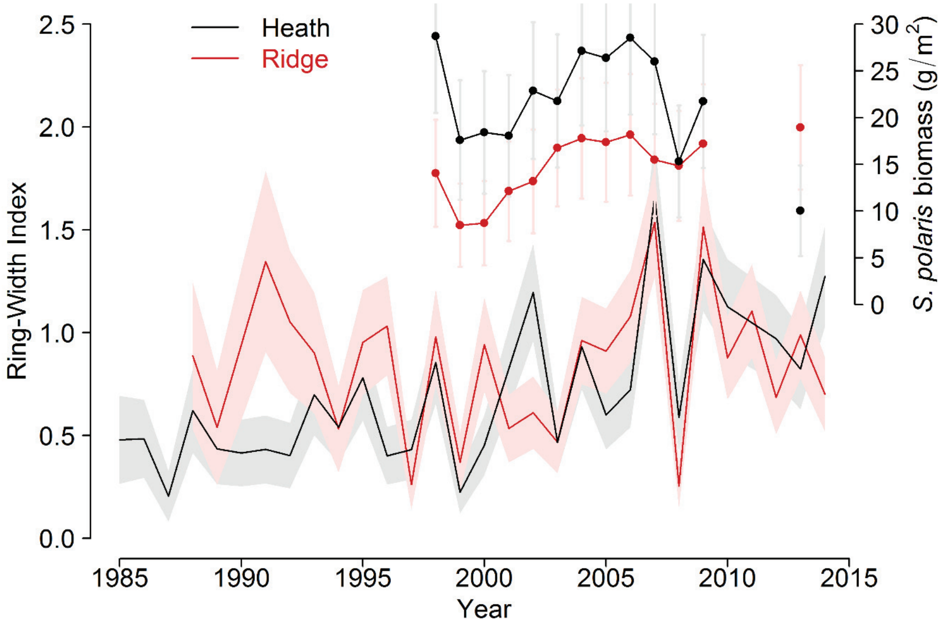

Figure S6. The Ring-Width Index and annual above-ground biomass of *S. polaris* estimated for ridge (red line/circles) and heath (black line/circles) habitats in Semmeldalen, central Spitsbergen. The estimates were obtained from linear mixed-effects models accounting for the nested structure of the data, back-transformed from the square-root scale (see Methods). Shades and bars are standard errors from these models, back-transformed with the Delta method.

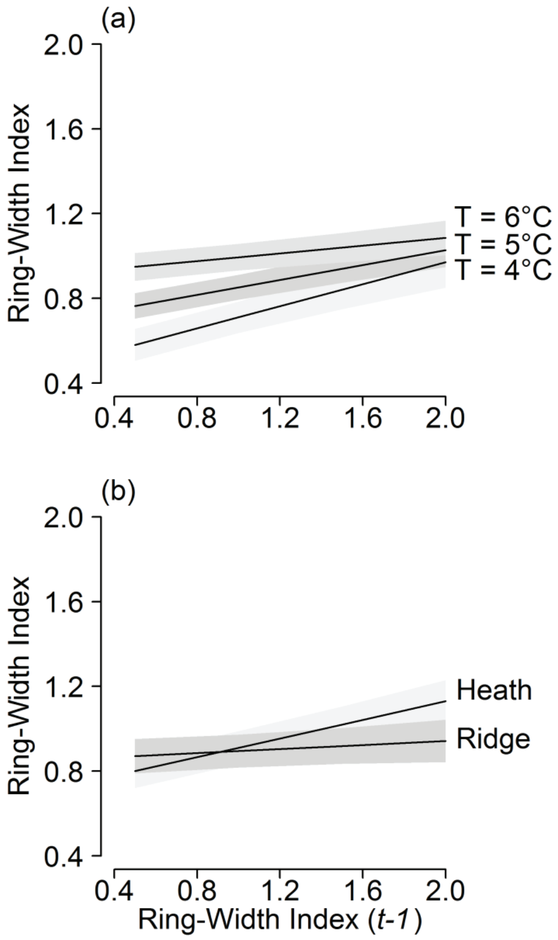

Figure S7. Interaction effects of (a) the previous year's growth [*t-1*] and summer temperature and (b) the previous year's growth [*t-1*] and habitat type on *S. polaris* Ring-Width Index, included in the top ranked model (Table 1 & Table S1). Ring growth is represented by standardised Ring-Width Indices (on the square-root scale) over the period 1985-2014 in heath and 1988-2014 in ridge habitat. Shades show standard error. Growth was less influenced by the previous years' growth in warm compared to cold summers, and the positive effect of growth the previous year was only present in the heath habitat.

Supporting information references

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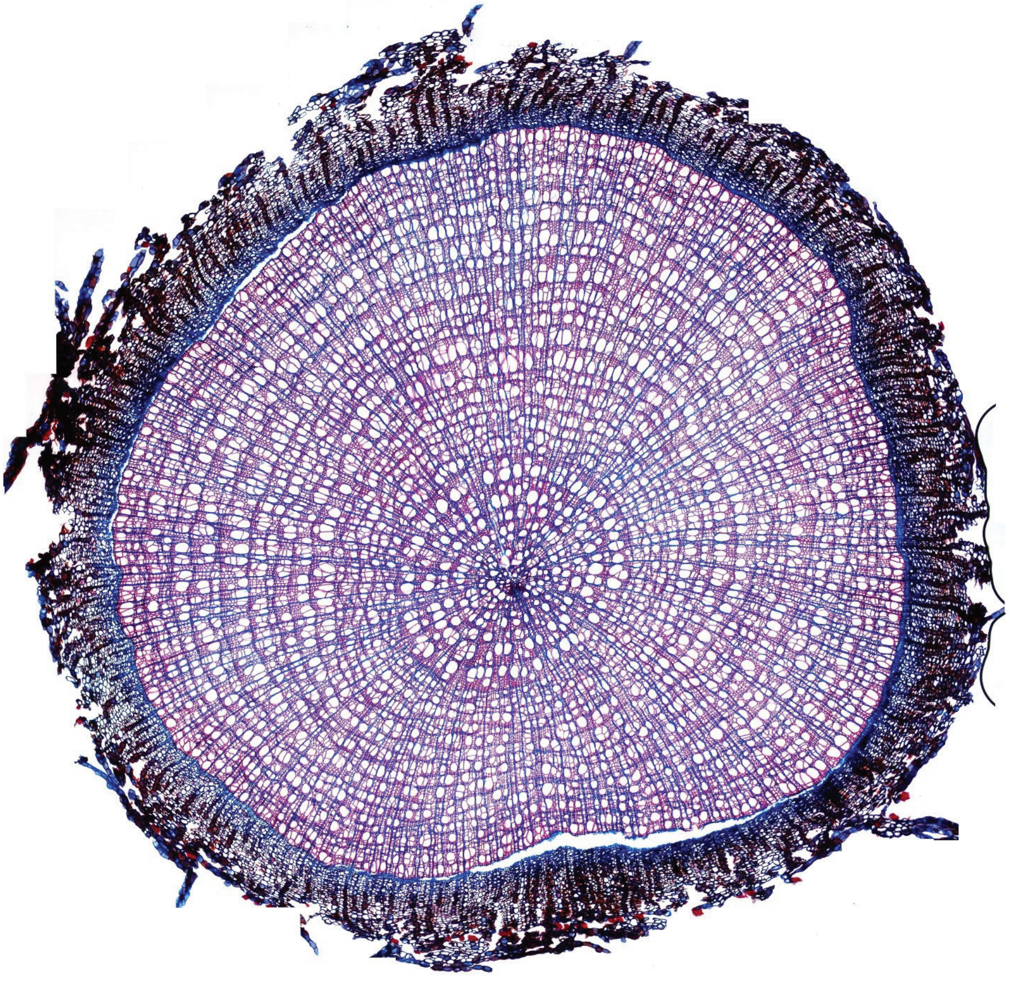
Paper III

Paper IV

Paper V



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Norwegian University of Science and Technology
Department of Biology

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1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
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1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
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1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
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1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

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1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
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1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
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1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
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2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
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2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
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2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*

2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations

2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography

			Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes

2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity

2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world:adaptions to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):*Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.

2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications

2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: Calanus, little auks (alle alle) and black-legged kittiwakes (Rissa tridactyla)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*

2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (***Giraffa camelopardalis tippelskirchi***) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for endusers.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (Lycaon pictus) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of Tanytarsus van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxixity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on Arabidopsis thaliana
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems

2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits