Improving ecological insights from dendroecological studies of Arctic shrub dynamics: research gaps and potential solutions

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Declarations

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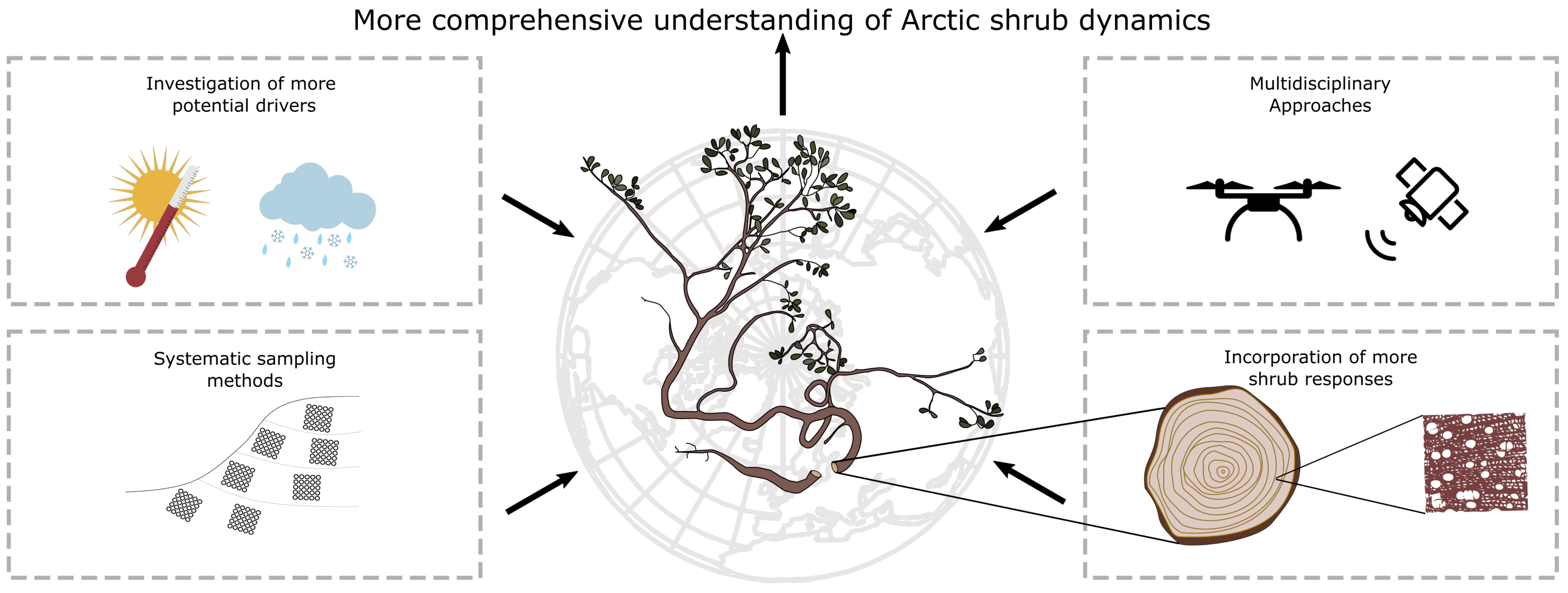
More comprehensive understanding of Arctic shrub dynamics
Investigation of more potential drivers
Multidisciplinary Approaches
Systematic sampling methods
Incorporation of more shrub responses

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Research Highlights

1. We provide a perspective on how to improve ecological insights using dendroecology
2. We highlight research gaps based on recent Arctic shrub dendroecological studies
3. More attention should be given to inter- and intra- specific demographic responses
4. More drivers and responses should be assessed at relevant spatial and temporal scales
5. An interdisciplinary approach is suggested to improve cross-scale ecological insights

ABSTRACT

Rapid climate change has been driving changes in Arctic vegetation in recent decades, with increased shrub dominance in many tundra ecosystems. Dendroecological observations of tundra shrubs can provide insight into current and past growth and recruitment patterns, both key components for understanding and predicting ongoing and future Arctic shrub dynamics. However, generalizing these dynamics is challenging as they are highly scale-dependent and vary among sites, species, and individuals. Here, we provide a perspective on how some of these challenges can be overcome. Based on a targeted literature search of dendroecological studies from 2005-2022, we highlight five research gaps that currently limit dendroecological studies from revealing cross-scale ecological insight into shrub dynamics across the Arctic biome. We further discuss the related research priorities, suggesting that future studies could consider: 1) increasing focus on intra- and interspecific variation, 2) including demographic responses other than radial growth, 3) incorporating drivers, in addition to warming, at different spatial and temporal scales, 4) implementing systematic and unbiased sampling approaches, and 5) investigating the cellular mechanisms behind the observed responses.

Focusing on these aspects in dendroecological studies could improve the value of the field for addressing cross-scale and plant community-framed ecological questions. We outline how this could be facilitated through the integration of community-based dendroecology and dendroanatomy with remote sensing approaches. Integrating new technologies and a more multidisciplinary approach in dendroecological research could provide key opportunities to close important knowledge gaps in our understanding of scale-dependencies, as well as intra- and inter-specific variation, in vegetation community dynamics across the Arctic tundra.

Keywords: demographic responses, shrub ring-width, spatial-temporal scales, earth observations, sampling approach, plant community-based dendroecological sampling

1. INTRODUCTION

Rising temperatures have been associated with increases in plant productivity across the Arctic over recent decades (Bjorkman et al., 2020; IPCC Working Group II, 2022). Shrubs, a dominant feature of Arctic tundra, have increased in height, biomass, cover, and abundance in many areas of the biome, a process referred to as “shrubification” (Martin et al., 2017; Myers-Smith et al., 2011; Tape et al., 2006). These shrub responses to warming have potentially wide-reaching impacts such as altering herbivory interactions (Le Moullec et al., 2020; Post et al., 2021; Skarin et al., 2020), albedo (Belke-Brea et al., 2020; Blok et al., 2011; Bonfils et al., 2012; Loranty et al., 2011), soil temperatures (Lawrence and Swenson, 2011), and land-atmosphere exchanges of carbon (CO_2 and CH_4) (Bonfils et al., 2012; Mekonnen et al., 2021). Thus, changes in shrub communities can contribute to large-scale climatic feedbacks (Pearson et al., 2013), although the net effect of the combined feedbacks remains uncertain (AMAP, 2021, 2017).

Despite many areas showing increases in shrub productivity, these changes are occurring heterogeneously throughout the landscape (Berner et al., 2020; Gamm et al., 2018; Guay et al., 2014), with evidence of substantial differences in local and regional scale trends (Bhatt et al., 2013; Gamm et al., 2018; Myers-Smith et al., 2015a; Phoenix and Bjerke, 2016; Post et al., 2021; Reichle et al., 2018). Currently, the mechanisms driving these different vegetation responses are not fully understood. In particular, we lack knowledge on how the responses of individuals scale to the responses of communities and vary across species' geographic ranges (Martin et al., 2017) (Fig. 1a). This contributes uncertainty to predictions of the magnitude and extent of ongoing local changes and their implications for climate feedbacks, as well as the structure and function of Arctic ecosystems (Kemppinen et al., 2021; Myers-Smith et al., 2011; Vowles and Björk, 2019). Therefore, to better understand and predict future global climate and ecosystem changes, it is necessary to understand the complex dynamics and interactions within and among Arctic shrubs and their responses to non-climatic and climatic factors from local to broad scales. This requires quantifying responses and their drivers across temporal and spatial scales, including where along the plant structure or life stage the driver acts, in which season it acts, and if the effect is immediate or gradual (Körner and Hiltbrunner, 2018). Advancements in technology and techniques across a spectrum of disciplines (e.g., remote sensing, dendroanatomy, dendrometers, and phenocams) now allow for investigations ranging from quantifying very fine cellular responses to broad scale patterns in both time and space (Anderson and Gaston, 2013; Dobbert et al., 2021a; Myers-Smith et al., 2020; Parmentier et al., 2021; Prendin et al., 2020).

Dendroecology is a branch of dendrochronology that examines annual and sub-annual growth patterns of woody plants in relation to ecological drivers (Fritts, 1976, 1971; Fritts and Swetnam, 1989; Schweingruber, 1996). Although long recognized for having dendroecological potential (Johnstone and Henry, 1997; Wilson, 1964; Woodcock and

Bradley, 1994), the widespread adoption of dendroecology to study dwarf shrubs growing above the tree line has been relatively recent. Notably, dendroecology, has been successfully applied to understand long-term temporal variation in shrub growth (Bär et al., 2008, 2006; Rayback and Henry, 2005; Schweingruber and Poschlod, 2005) and recruitment (Büntgen et al., 2015; Myers-Smith and Hik, 2018). Additionally, dendroanatomy has been successfully used to gain knowledge on structure–function responses of plants to climate and environmental variability (Fonti et al., 2010; Schweingruber et al., 2013). This discipline focuses on the quantitative assessment of wood anatomical traits (e.g., lumen dimensions and wall thickness of conducting cells, fibers, and several ray properties (von Arx et al., 2016)), and their link to the specific xylem functions (e.g., water and nutrient transport from the plant–soil interface to stems and leaves, mechanical support and storage (Myburg et al., 2013)), using a dendrochronological approach (Carrer et al., 2016; von Arx et al., 2016). Studies combining multiple approaches, e.g., ring-width measurements with time series of anatomical traits, have the potential to provide insight into current and past shrub dynamics and mechanistic responses (Prendin et al., 2020; Wilmking et al., 2018), and to inform predictions about future changes (Babst et al., 2018; McMahon et al., 2011). These techniques can provide information on an intra-annual to annual time scale. However, as these studies typically provide data from discrete geographic locations, the findings can be difficult to up-scale and generalize (Babst et al., 2018).

Geospatial analyses and remote sensing data on abiotic and biotic variables have become more accessible to ecologists in recent years due to improvements in sensor design and deployment, a push towards open access, cloud-computing, storage and software, and the availability of ready-to-use data products (Kwok, 2018). These emerging geospatial techniques and technologies could supplement and strengthen dendroecological studies to better link individual and plot-based observations with landscape scale patterns (Fig. 1a). For example, dendroanatomical (Prendin et al., 2020) and tree-ring (Babst et al., 2010) analyses can be combined with satellite-based remote sensing to reveal insights into impacts of insect outbreaks at scales not possible with *in-situ* observations alone. Such multi-proxy approaches have the potential to provide cross-scale ecological insight into how climate and environmental drivers affect plant growth and xylem structure at different temporal (i.e., seasonal, annual, intra-annual) and spatial (e.g., local, regional) scales (Fig. 1b), but they have not yet been widely adopted. Although possible with current technology, integrating these techniques requires new perspectives in dendroecological studies (Manzanedo and Pederson, 2019; Pearl et al., 2020) with increased attention on study design that allows for scaling responses from individuals to communities and ecosystems (Babst et al., 2018).

To evaluate the prevalence and potential for cross-scale perspectives in Arctic dendroecological research, we conducted a targeted literature review to highlight key gaps in contemporary Arctic dendroecological approaches that may limit cross-scale generalization. Building on these gaps, we outlined potential research priorities to improve cross-scale ecological insights of Arctic shrub dynamics. Specifically, we: (1) reviewed current methodologies and approaches; (2) highlighted research gaps and discussed the related priorities; and (3) outlined potential ways forward for integrating plant community perspectives and spatio-temporal approaches spanning from dendroanatomy to geospatial analyses and remote sensing. The highlighted research gaps and suggested ways forward are defined with respect to how dendroecological studies could contribute to the understanding of cross-scale Arctic plant community dynamics, and do not reflect any criticism of the individual studies included in the present review.

2. A TARGETED LITERATURE REVIEW

2.1 METHODS

We conducted a targeted literature review of studies using dendroecological methods and extracted spatial and temporal information on the investigated samples, responses, and drivers to obtain an overview of the research gaps that might limit cross-scale generalization of dendroecological research. We included studies published between January 1st 2005 and June 1st 2022. We searched the Scopus database for published articles including the following words in the title, abstract, or key words: 'Arctic or Oro-Arctic or tundra' and 'shrub or woody' and 'growth or recruitment or establishment or advancement or shrubline or anatomy or xylem or lumen or fiber or vessel or dendroecology or dendrochronology or ring'. Five-hundred and seventy articles were identified with this search (Appendix A).

2.1.1 Inclusion criteria

Of the 570 studies, 82 were included in our synthesis (Appendix B) based on the following geographic and methodological criteria: The study 1) has at least one site located in the Arctic, as defined by (Walker et al., 2005), or the 'Oro-Arctic' alpine tundra (Virtanen et al., 2016), including sites located within a 50 km buffer outside of these boundaries, to be consistent with previous literature (e.g. (Berner et al., 2020; Martin et al., 2017)); 2) quantifies shrub growth or age using annual growth-rings or stem increments, and/or 3) analyzes xylem anatomical traits. We organized the data both by study and by site (Appendix A). If a study included multiple sites, we considered the sites as unique if: a) they were within distinct geographic locations as defined by the authors, and b) when site-specific data was readily available. If multiple studies included the same site but with different analyses, the site was considered more than once. When articles included sites that were inside and outside of the Arctic, we only report on sites meeting our Arctic criteria.

We included studies that stated “shrubs” were sampled, regardless of how the authors define a shrub, but only if methods of dendrochronology adjusted for shrubs were used (i.e., not tree cores). The shrub species included range from prostrate (e.g., *Salix arctica* in high Arctic Canada and Greenland (Boulanger-Lapointe et al., 2014) to tall shrubs (e.g., >3m *Alnus viridis* in West Greenland (Wilmking et al., 2018)).

2.1.2 Extracted information

For each included study, we recorded: 1) geographic coordinates of the study location(s); 2) sampling strategy; 3) shrub part(s) sampled; 4) timespan of shrub growth and/or recruitment records; 5) responses tested; and 6) drivers tested. When not given, geographic coordinates were estimated based on the site description using Google Maps (maps.google.com).

We separated the sampling strategy into two main categories: 1) site selection (i.e., the strategy used to select the specific sampling site in the landscape), distinguishing whether the site selection was systematic or not; 2) shrub selection (i.e., the strategy used to select the specific individual shrubs to be sampled) distinguishing whether individuals were selected based on specific characteristics or using a systematic/unbiased approach. Here, we consider systematically placed plots those placed purposefully within a landscape, for example, to capture heterogeneity across an elevation gradient. We consider unbiased samples those selected in a systematic way (e.g., the closest individual to a transect), and not based on plant characteristics (e.g., the largest individual). We acknowledge that a systematic sampling design may also create biases, but, compared to the frequent dendroecological practice of targeted selection based on plant characteristics, these biases are more appropriate for upscaling. In this manuscript, we use the term “unbiased” to refer to this reduction in bias when comparing targeted selection and systematic sampling approaches.

For each study we extracted the maximum timespan of shrub growth and/or recruitment based on the length of the chronology for all species combined. When the study reported the age of the oldest shrub, we included that; otherwise, we included the time span of the final chronology. When not stated, we estimated the time span from the relevant figures provided in the manuscripts.

We identified responses measured using dendrochronological methods, grouping them as: 1) growth; 2) recruitment; 3) quantitative wood anatomy; 4) qualitative wood anatomy and 5) mortality. Growth was quantified either by 1) measuring radial ring-width increments; 2) measuring annual stem-increments (for example, measuring distances between wintermarksepta (dark bands of meristem tissue) (Rozema et al., 2009) of *Cassiope tetragona*) (Myers-Smith et al., 2015b); or 3) dividing the radius or diameter of the stem by the number of rings to obtain the average annual growth (e.g. (Schmidt et al., 2010)) Recruitment and mortality were included only if quantified using age estimates from dendroecological methods (i.e. quantifying representative age dynamics based on ring counts (e.g. (Büntgen et al., 2015)).

We extracted information on drivers of shrub dynamics that were explicitly tested in the studies. Tested drivers were grouped into nine categories: 1) air temperature, 2) precipitation, 3) large scale climate systems, 4) biotic factors, interactions, and disturbances, 5) geophysical factors (including soil moisture), processes, and disturbances, 6) growing season length and timing, 7) snow cover and depth, 8) ice dynamics, e.g., sea ice, glacial retreats or indirect influences of ice caps, and 9) other (including solar-related variables) (Table 1). While some of these are direct mechanistic drivers (e.g., temperature and precipitation), others are indirect and proxies for mechanistic drivers (e.g., ice dynamics and climate systems).

Below we report our findings based on the extracted information from the publications identified in our targeted literature search that meet our selection criteria. Since we did not perform a systematic and comprehensive review the specific percentages relate specifically to our criteria and may not be representative of the entire literature.

2.1.3 Illustrations and analyses

We used bar graphs to visualize the research gaps identified in our review. Additionally, we mapped the extracted study locations in relation to the bioclimate subzones from the Circumpolar Arctic Vegetation Map (CAVM) (Raynolds et al., 2019) with the addition of the Oro-Arctic (Virtanen et al., 2016) to visualize the spatial distribution of where drivers are tested (Martin et al., 2017). Hereafter, we refer to the combined area of the CAVM and the Oro-Arctic simply as "Arctic", "tundra", or "Arctic tundra". We also assessed how representative the study locations are with respect to the climate space of the tundra. For this analysis, we retrieved mean annual temperature and annual precipitation for all study locations, as well as 14,000 random locations across the Arctic tundra during the period from 1979-2013 using the CHELSA v1.2 bioclim dataset (Karger et al., 2017).

2.2 Highlighted Gaps, Research Priorities, and potential ways Forward

Based on our targeted literature review and the extracted information, we highlighted, what we see, as five key research gaps that limit cross-scale generalizations in the current Arctic dendroecological literature and discuss research priorities that address each gap. The key gaps and related research priorities are: 1) Knowledge of variation in shrub responses across and within species is limited. Including more species and individuals would enhance our understanding of inter- and intraspecific variation, 2) Shrub demographic responses to Arctic change are not yet fully understood. Including more life history responses (such as recruitment and mortality, and their relationship to growth) would provide a more comprehensive understanding, 3) Other potential drivers of shrub change aside from warming have not been adequately explored. Increased focus on multiple drivers, their spatial and temporal variation, and events could reveal insights into complex relationships, 4) Cross-site and -study comparisons are limited by varying sampling methods. Systematic and unbiased sampling of plant parts and individuals could reveal more cross-scale responses, and 5) Insight on the structural-functional relationships behind growth trends is limited. Incorporation of dendroanatomy could enhance this understanding.

2.2.1 Gap 1: Knowledge of variation in responses across and within species is limited. Including more species and individuals would enhance understanding of inter- and intraspecific variation.

Finding: Single species studies are the norm

Most studies assessed a dendroecological-derived response of just one species (67%), while 13% analyzed two species, 10% analyzed three to four species, and 11% analyzed over five species (Fig. 2a). While 26% (21) analyzed multiple species at the same site, only five studies used an unbiased sample from systematically placed plots. Twenty-seven studies (33%) analyzed the same species across multiple sites, though only five of these used systematic and unbiased sampling.

A total of 39 species from 12 genera were sampled across all studies. The three most studied species were *Betula nana* (in 19 studies), *Cassiope tetragona* (in 17 studies) and *Salix glauca* (in 15 studies). *Salix* was the most represented genus; eighteen different species were included, and 44 studies considered at least one *Salix* species.

In summary, the included literature represents the most widely distributed genera of Arctic shrubs. However, most studies focused on the same shrub taxa and investigated the response of just one species. Relatively few (6%) used an unbiased sample to compare responses of different species within the same sites or for the same species across multiple sites. This leaves a gap in our ecological understanding of the variation in responses among individuals of the same species across populations and species ranges, and of particular importance, in responses among species within local plant communities.

Research priority: Focus on inter- and intraspecific variation across sites

Overcoming this gap requires studying multiple species at individual sites, as well as studying the same species across multiple sites. Improved quantification of intra- and interspecific responses is important for several reasons: First, different species might respond to different drivers. For example, Weijers et al. (2018a), found that *Betula nana* growth in a Norwegian alpine site was best explained by summer precipitation, while the growth of three other species was best explained by summer temperature. Second, different species might respond differently, and with different rates, to the same drivers, e.g., deciduous species have been found to respond more rapidly to warming than evergreen ones (Demarco et al., 2014; Elmendorf et al., 2012; Gough et al., 2014). Similarly, individuals of the same species are expected to respond differently to the same driver across the geographic range, e.g., depending on local plant-plant interactions, micro-environmental conditions (Ackerman et al., 2017) or limiting resources (Post et al., 2021). Third, different species might have contrasting effects on ecosystems (Cahoon et al., 2012; Post et al., 2021). For example, it has been hypothesized that deciduous shrub expansion will have positive feedback on global warming, in contrast to overall negative feedback caused by evergreen shrub expansion, due in part to their lower stature and production of more recalcitrant litter (Vowles and Björk, 2019).

Steps forward: Analyzing more species and individuals, facilitated by data sharing

Future studies should represent as many individuals and species as feasible within and among sites. Although this intensive sampling approach is costly, data sharing can alleviate some of the additional work by providing site- and species-specific chronologies to assist chronology building and facilitating cross-species analyses. Myers-Smith et al. (2015a) provide an example of such a cross-species and cross-site approach by compiling and analyzing growth data from published and unpublished shrub chronologies of 25 species sampled across the Arctic-Alpine tundra. However, to use the full potential of shrub data, e.g., to study demographic responses other than growth (see Gap 2) and the underlying cellular responses (see Gap 5), unbiased sampling (see Gap 4, cf. (Klesse et al., 2018)) and detailed metadata across sites would be necessary (discussed further in section 3).

2.2.2 Gap 2: Shrub demographic responses to Arctic change are not completely understood. Including more life history responses (such as recruitment and mortality, and their relationship to growth) would provide a more comprehensive understanding.

Finding: Growth was the most common response investigated

In total, 89% of the studies analyzed growth, 27% recruitment, and 6% mortality. Only 18% included both growth and recruitment (Fig. 2b, 2c), one of which also included mortality. The shrubs in each study covered an average of 90 years (median: 84, range: 7-337; years: 1675-2018) (Fig. 3).

Ultimately, recruitment and mortality are understudied aspects of shrub dynamics, in terms of responses quantified using dendrochronological methods. Additionally, there is underutilized potential of applying these existing shrub ring time-series to gain retrospective insights into demographic parameters.

Research priority: Quantify growth, recruitment, and mortality

Recruitment is the driving mechanism behind shrub expansion at a landscape to global scale, as it is what drives new individuals to fill in gaps in the current range and to advance range limits, e.g., the northernmost shrubline (Büntgen et al., 2015; Myers-Smith et al., 2011). While studies of recruitment are especially important for understanding range expansion, increased insight on what drives mortality is important for understanding range contraction (Hampe and Petit, 2005; Lesica and Crone, 2017). Simultaneously investigating the drivers of growth, recruitment, and mortality is important for gaining a more comprehensive understanding of local plant community responses and mechanisms underlying species range dynamics (Normand et al., 2014).

Dendroecological methods have the unique ability to provide post-hoc time-series that enable the assessment of drivers of demographic responses across time, for example, linking previous growth and recruitment pulses to climate (Büntgen et al., 2018, 2015). Further investigation of the drivers of growth and recruitment in long time-series is important for several reasons. First, what drives growth and recruitment is not always the same. For example, *Salix* spp. growth in Yukon, Canada was best explained by variation in summer temperatures while recruitment pulses were best explained by variation in winter temperatures (Myers-Smith and Hik, 2018). Second, drivers of recruitment vary among sites and species. For example, while winter temperature drives variation in recruitment in the Yukon (Myers-Smith and Hik, 2018), increasing summer temperatures have been found to drive recruitment in eastern Greenland (Büntgen et al., 2015).

Steps forward: Adjust sampling strategies to obtain demographic data from shrub chronologies

Obtaining data on age dynamics requires a different sampling approach than traditionally used for growth data. To establish retrospective demographic time series, it is necessary to sample a large and unbiased subset of the population to get an accurate estimate of the age structure. This also requires sampling of the oldest part of the shrub to obtain the maximum age estimation for each individual. Additionally, shrub mortality across life stages could be quantified, by, e.g., long-term monitoring of individuals in permanent plots (such as with a long-lived herb in (Edelfeldt et al., 2019)) or systematically collecting dead shrubs and dating their year of death by using dendroecology or radio-carbon dating of their outermost ring (cf. (Pizano et al., 2014). High-resolution landscape photomosaics, captured from overlooks with phenocams or drones can also provide valuable baselines for identifying periods before/after recruitment/mortality pulses. Taken in sequence over many years at long-term monitoring sites, these data can provide landscape-scale insights into such processes.

2.2.3 Gap 3: Other potential drivers of shrub change aside from warming have not been adequately explored. Increased focus on multiple drivers, their spatial and temporal variation, and events could reveal insights into complex relationships.

Finding: Summer warming was the most common driver investigated

Most studies focused on climate as the main driving factor, with 76% and 53% of the studies investigating summer temperature and precipitation, respectively (Fig. 2e, Table 1). In total, we identified 39 different drivers, but most of these have been included in only 1 study each (mean: 7.8, median: 2, range: 1-62) (Table 1). Relating to the limited temporal availability for the different groups of drivers (Appendix C), time-series were only used for a subset of the drivers (e.g., climate, sea ice) while many drivers were assessed by average site characteristics. Furthermore, most studies focus on responses to mean conditions and trends with only 21% considering extreme abiotic or biotic events (Fig. 2h).

The focus on few climatic drivers leaves a gap in our ecological understanding of how the climate sensitivity of shrubs is influenced by other factors including micro-environmental conditions, plant-plant and trophic interactions, and mostly overlooks the effects of extreme events, such as icing or the loss of snow cover in winter (Phoenix and Bjerke, 2016).

Research priority: Investigate a variety of potential drivers

Closing this gap requires more studies to focus on the interaction between shrub responses and variation in abiotic and biotic drivers across time and space, including both trends and events. Consideration of time-series of non-climatic drivers is important for several reasons. First, although climate has long been known to affect shrub growth, considerable variation between sites has been observed (Myers-Smith et al., 2015a). With a decoupling observed between tree growth and climate in recent decades (Martin et al., 2017; Wilmking et al., 2020), it is clear there are other driving and limiting factors to be considered, e.g., soil moisture has been identified as a key limiting factor for shrub growth and driver of variation among Arctic sites (Ackerman et al., 2017; Myers-Smith et al., 2015a).

Second, the climatic data frequently used is often not ecologically meaningful in terms of spatial and temporal relevance to the actual conditions impacting shrub growth (Körner and Hiltbrunner, 2018). For instance, the growing conditions experienced by low-lying shrubs, where much of the growth occurs near the soil surface, likely differs from the annual mean temperatures recorded 2m above ground kilometers away from the sampled shrub. In addition, the same conditions may have very different consequences on seedlings in early spring compared to dormant stems in the winter. Thus, recording of the actual growing conditions at the relevant scale for shrub growth as well as the relevant timing in relation to phenology and life stage is essential to gain a holistic understanding of the drivers behind shrub growth.

Third, responses of Arctic shrubs to abiotic and biotic disturbances are understudied even though both have been identified as important co-drivers for tundra vegetation growth and expansion (Myers-Smith et al., 2011). For example, wildfires may have greater effect on alder recruitment than temperature in Canada (Lantz et al., 2010); defoliation events due to insect outbreaks influence the climate sensitivity of *Salix glauca* and *Alnus viridis* growth in western Greenland (Prendin et al., 2020; Wilmking et al., 2018); and the presence of large herbivores alters shrub response to warming in western Greenland (Post et al., 2021; Post and Pedersen, 2008).

Steps forward: Utilize in-situ and remote sensing-derived data

Although growth time series can span many decades, we typically lack such temporal data for potential ecological covariates (e.g., temperature, precipitation, length of growing season, etc.) (Fig. 3, Appendix C). This is due to either the lack of long-time meteorological station data or local environmental variation (e.g., soil moisture) only being measured at the time of sampling. Remote sensing may be used to overcome this gap in some cases (further discussed in Section 3).

Various sources of remote sensing data can be used to measure or estimate most, but not all, of the drivers identified in our review at least to some degree (Table 1). Contemporary satellite-derived measures (e.g., such as indices of soil moisture or topography variables based on satellite-derived digital elevation models) can provide information at grain sizes suitable for cross-site and increasingly also intra-site studies. These measures, including gridded datasets, provide opportunities to incorporate the potential covariates and scales of inquiry needed to better identify and evaluate ecological drivers. For example, they can provide information about spatial and temporal patterns of disturbance events or maps of historical influences on contemporary ecological processes (Babst et al., 2010; Prendin et al., 2020).

While gridded datasets and weather stations can provide valuable information on trends within sites and relative differences among sites, the conditions experienced by low-lying shrubs can be drastically different than those quantified using such methods. Therefore, to truly understand the mechanisms behind shrub responses, quantification of the growing conditions at the relevant spatial and temporal scales for the shrub is necessary (Körner and Hiltbrunner, 2018). Many downscaling approaches are emerging in the literature (e.g. Microclima (Maclean et al., 2018)) but they remain unvalidated and little used in published empirical dendroecological studies to date. Recording *in-situ* microsite growing conditions is now more feasible and affordable through recent sensor developments, e.g., measuring synchronous soil moisture, as well as soil, surface, and air temperature using specialized loggers (e.g., Tomst TMS-4 (Wild et al., 2019)), and can reveal patterns not discernable with the more common macro-site data (Lembrechts et al., 2020).

2.2.4 Gap 4: Cross-site and -study comparisons are limited by varying sampling methods. Systematic and unbiased sampling of plant parts and individuals could reveal more cross-scale responses

Finding: Sampling methods varied between studies and sites

Sampling efforts vary across climatic (Fig. 4a) and geographic (Fig. 4b) space for all drivers and responses. Less than half (43%) of the included studies systematically selected sampling sites and even fewer (33%) sampled shrub individuals using an unbiased approach (Fig. 2f). When considering site and shrub selection combined, 23% of studies sampled shrubs using unbiased criteria in systematically chosen sites, and 2% selectively sampled shrubs in nonsystematically chosen sites (Fig. 2f). The majority of studies (82%) analyzed either root collars or stems, while only 12% included below ground parts (Fig. 2g). Most studies (44%) analyzed one shrub part, while fewer analyzed two or three shrub parts (26% and 11%) (Fig. 2g).

While sites were distributed across the Arctic, responses and drivers were not all assessed evenly across regions and bioclimatic zones (Fig. 4), thus potentially biasing our understanding of ongoing changes across the Arctic (Metcalfe et al., 2018). Additionally, differences among sampling techniques (shrub and site selection and shrub part sampled) make it challenging to compare data and draw generalizable conclusions from different studies.

Research priority: Implement sampling approaches that allow for comparison of shrub responses across individuals and sites

Closing this gap requires sampling that captures the variation across the tundra biome, both in shrub responses and in environmental conditions. Unbiased sampling is important in relation to several research topics. First, while it is common in dendroecological studies to sample the largest individuals in the attempt to maximize chronology length, this approach does not give insight into the range of responses in a population. Trees selected to maximize climate signal have been found to overestimate climate sensitivity (Klesse et al., 2018), which can potentially skew our understanding of ongoing and future responses to climate change. In generally harsh environments such as the Arctic, we might further expect the tallest/oldest individuals to grow and survive at favorable and protected microsites. To our knowledge such biases have not yet been directly tested for Arctic shrubs.

Second, different shrub parts are sampled across different sites and studies (Fig. 2g) (Ropars et al., 2017). This non-uniform sampling is problematic when attempting to generalize findings and compare datasets because shrub climate sensitivity is non-uniform within individuals (Ropars et al., 2017; Shetti et al., 2018) thus hindering accurate cross- individual and site comparisons. While serial sectioning of above and below parts is well established and recommended to aid with cross-dating (Bär et al., 2006; Buchwal et al., 2013; Kolishchuk, 1990; Myers-Smith et al., 2015b; Wilmking et al., 2012), it is less common to use these sections to compare growth sensitivities along the length of the stem and roots to assess intra-individual variation. Notably, below ground relationships remain understudied, despite most of Arctic plant biomass occurring below ground (Iversen et al., 2015; Mokany et al., 2006) and being especially important for soil dynamics and carbon storage.

Steps forward: Representative sampling of sites and individuals

Representative sampling of sites and individuals can be reached through standardized protocols, data sharing, and the use of remote sensing derived stratifications as the basis for dendroecological sampling designs. This will ultimately facilitate the selection of comparable sections, individuals and sampling sites that cover the ecological variation of interest for the specific study questions (discussed further in Section 3).

2.2.5 Gap 5: Insight on the structural-functional relationships behind growth trends is limited. Incorporation of dendroanatomy could enhance this understanding

Finding: Few studies assessed functional mechanisms behind growth trends

In the included studies, 10% (8) of the studies assessed xylem anatomy, with seven assessing quantitative (i.e., cell lumen area, cell grouping and cell wall thickness) and one assessing qualitative (reaction wood and scars) anatomical features (Fig. 2b). Out of these eight studies, one assessed three responses (growth, recruitment, and qualitative wood anatomy); five assessed growth and quantitative wood anatomy; and two focused solely on quantitative wood anatomy (Fig. 2c). In summary, few studies combine assessment of xylem traits together with ring widths, leaving a gap in our understanding in the mechanisms behind the variation of intra- and inter- individual responses to ecological drivers.

Research priority: Investigate cellular mechanisms behind growth responses

Closing this gap requires analyses of shrub responses at a cellular level to fully understand growth trends. Xylem functional traits (e.g., the ones related to hydraulic transport and mechanical support) have been shown to provide valuable information on functional and structural adaptation (Fonti et al., 2010). First, while ring widths quantify annual growth, anatomical traits reveal insights of plant functioning on an intra-annual scale (von Arx et al., 2016) (further discussed in Section 3.2). Second, anatomical traits may reveal shrub responses to growing conditions that are not detectable with just annual ring widths. For example, Buras et al. (2017) found that cell wall thickness, but not ring width, in *Juniperus communis ssp. nana* in Kobbefjord (southwest Greenland) was significantly correlated with Greenland Ice Sheet melt. It is possible that no significant relationship was found with ring widths due to a higher sensitivity of radial growth to episodically occurring moth outbreaks (Buras et al., 2017). Third, anatomical features can impact the climate-growth relationship. For example, Nielsen et al. (2017) found that *Betula nana* in western Greenland optimized growth by increasing its hydraulic conductivity. These examples demonstrate how dendroanatomy can be incorporated into dendroecological studies to lead to a better understanding of shrub responses and the mechanisms behind them.

Steps forward: Adjust dendroecological protocols to incorporate anatomical analyses

Although still uncommon, recent studies have shown the potential for quantifying xylem anatomical traits in dendroecological shrub studies. The inclusion of such analyses can give a more comprehensive picture of changes that occur within shrubs and can allow for estimations of future changes in the community, for example, why some species or individuals thrive more than others at a given site (Huang et al., 2021). Notably, linking anatomical features and their relative position within growth rings to variables of interest can provide further mechanistic understanding behind the cellular responses at a higher (intra-annual) temporal resolution (Fonti et al., 2010; Lenz et al., 2013). Incorporating such microscopic features into dendroecological studies requires careful sample preparation (Gärtner et al., 2015) and techniques (von Arx et al., 2016) that can be included in protocols that have already been implemented for the small size of shrub rings (Schweingruber et al., 2013). In addition to dendroanatomy, the field is further moving towards fine-scale analyses with advancements in technology and techniques, for example, using high-precision dendrometers to capture variations in shrub stems at unprecedented resolutions (Dobbert et al., 2021b, 2021c).

3. SYNTHESIS: CROSS-SCALE INTEGRATION FROM CELLS TO SATELLITES TO IMPROVE OUR UNDERSTANDING OF ARCTIC SHRUB COMMUNITY DYNAMICS

Our targeted review summarizes the methodologies used in recent Arctic dendroecological studies. Despite the numerous recent advances in the field, we found that in our selected literature: a) most studies focused on how the growth of a limited number of species is affected by trends in specific climatic drivers, mostly summer temperature and precipitation (Gaps 1-3), b) sampling is not uniform across geographic or climatic gradients (Gap 4), and c) only few studies investigate several plant parts and the mechanisms behind the observed shrub responses (Gap 4, 5). More generally, this reflects a field that is producing diverse and informative research, but few studies that are specifically designed to produce cross-scale insights. To address this, we propose that research priorities should more often encompass the quantification of additional responses (e.g., growth, recruitment, and mortality), and their cellular mechanistic underpinnings, of a range of plant parts, individuals and species sampled unbiasedly within and across sites. Doing so will require comprehensive sampling; cellular analyses; and data on trends and events of multiple drivers derived from *in-situ* and satellite-based measurements. This would ultimately allow for linking fine-scale individual shrub responses to large-scale trends and events occurring across the tundra landscapes and biome. However, conducting such multidisciplinary studies is challenging and requires a synergetic approach.

One possible approach to upscale *in-situ* information to larger scales is to combine emerging approaches in dendroanatomical and remote sensing analyses with a plant community-based perspective on dendroecological sampling. By presenting this approach we hope to inspire more dendro and Arctic ecologists to adopt spatially unbiased, systematic, and cross-scale sampling methodologies, which we think are needed to further our ecological understanding of shrub dynamics across the rapidly changing Arctic.

In the following subsections we briefly outline the three main components of the proposed synergetic approach: dendroanatomical analyses (section 3.1); remote sensing and geospatial analyses (section 3.2), and community-based dendroecological (CBDE) sampling (section 3.3) (Fig. 5). We then conclude with a synthesis of the approach (section 3.4) and provide examples of ecological questions that such an approach can address (section 3.5).

3.1. Dendroanatomy as a key to understand the cellular mechanistic underpinnings behind growth responses at inter-annual level

Dendroanatomical analyses, based on quantitative wood anatomy, will provide novel and high-resolution information from dated woody plant annual rings (Fig. 5f) (Fonti et al., 2010) and insight in the cellular mechanistic underpinnings behind inter-annual growth responses (Gap 5). Adjustments in the xylem structure remain permanently fixed and chronologically archived in the annual growth-rings (Fonti et al., 2010). Thus, they provide an explicit time record of structural and functional responses, linking biological processes and plant functioning (Fonti and Jansen, 2012). The analysis of xylem structure, therefore, allows to reconstruct growth dynamics under different climatic and environmental conditions over decades and even centuries (von Arx et al., 2016).

While growing, plants continuously adjust their structure to achieve an optimal balance of carbon costs for the competing biomechanical and hydraulic requirements that sustain transpiration and thus carbon assimilation (Prendin et al., 2018a). The axial organization of cells follows a pattern common to all vascular plants (Anfodillo et al., 2013; Olson et al., 2014). Conduits progressively increase in diameter from the apex towards the stem base, which minimizes the adverse effect of height growth on pathway length resistance (Carrer et al., 2014). This pattern is also reflected radially with the conduits increasing in dimension from the pith outwards (Carrer et al., 2014), but largely stable during ontogeny (Prendin et al., 2018b). To disentangle how climatic and environmental factors are influencing the structural plant development it is fundamental to use an appropriate standardization procedure to remove the hydraulic-path length effect (Lechthaler et al., 2019) on the different anatomical traits (Prendin et al., 2018b).

The recent advancements in methods and standard protocols (Gärtner and Schweingruber, 2013; von Arx et al., 2016), automated image-analysis systems (von Arx et al., 2013; von Arx and Carrer, 2014; von Arx and Dietz, 2005) and processing using artificial intelligence (Resente et al., 2021) allow to significantly increase the number of measured anatomical features, while also reducing the time required for the analysis. Nevertheless, the establishment of the new quantitative wood anatomy network (Q-NET) reflects the need of a growing community to share knowledge and experience, but also to advance methodologies (Resente et al., 2021) and to profit from interdisciplinary collaborations to tackle broader ecological questions at multiple temporal and spatial scales (von Arx et al., 2021).

3.2 Incorporating remote sensing and geospatial analyses to promote cross-scale understanding

Remote sensing and geospatial analyses are essential tools for linking site-based drivers and responses to ecological patterns that span across spatiotemporal scales that are infeasible to study with *in-situ* measurements. There are a variety of available remote sensing products and approaches, spanning from direct measures of spectral or structural properties of a landscape to more derived products. In the approach proposed here, remote sensing contributes to bridge Gap 3 (lack of drivers studied) and 4 (lack of multi-site analyses) by allowing for: 1) the selection of representative sampling of shrub individuals, within study sites, based on landscape stratification; and 2) the collection of additional data on vegetation responses and potential drivers at relevant scales to assess shrub responses to a wide range of variables. These two aspects are discussed in further detail below.

The landscape of an Arctic study site might include large environmental variation at different scales due to topography and small-scale heterogeneity (Fig. 5a,b). A useful method for the selection of representative study sites is to stratify the landscape to select locations that represent the variation of the relevant co-variates based on the ecological questions and drivers of interest. Methodologies that classify and stratify vegetation as well as environmental parameters such as climate and soil moisture are well established at global, regional (Lara et al., 2018; Raynolds et al., 2019), and local scales (Bartsch et al., 2020; Boelman et al., 2016). As an example, landscapes can be stratified based on elevation (e.g., using satellite-derived digital elevation models), proxies for plant available water (e.g., using normalized difference water index) and vegetation productivity (e.g., using normalised difference vegetation index, NDVI) (Fig. 5a,c).

Additionally, remote sensing can be used to collect data on a range of potential drivers as well as on vegetation changes. Satellite-derived indices have provided evidence of widespread Arctic vegetation change, for example, increasing NDVI values show a greening of the Arctic tundra in many regions (Berner et al., 2020). Drones (Assmann et al., 2020; Cunliffe et al., 2020; Fraser et al., 2016; Siewert and Olofsson, 2020), phenocams (Richardson et al., 2018), and repeat photography (Myers-Smith et al., 2019a; Tape et al., 2006) can be utilized to capture fine-scale patterns and dynamics of Arctic tundra communities to bridge scale gaps between site- and satellite-based data. For example, drone flights over a sampling area can obtain high-resolution (centimeter-scale) visual, multispectral and thermal imagery, and detailed digital elevation models using drone-based light detection and ranging (LiDAR) or structure from motion (SfM) photogrametry. Challenges and opportunities using satellite imagery and its interpretation in the Arctic (Beamish et al., 2020; Berner et al., 2020; Myers-Smith et al., 2020) along with the challenges and opportunities for combining dendroecological studies of trees with remote sensing (Babst et al., 2018) have been recently discussed in more detail. These studies also highlight the importance of ensuring the limitations and intricacies of remote sensing measures are accounted for in the analyses and interpretation of the acquired data, particularly with reference to scale and proxies. In addition, there is a need for continued updating of dendrochronologies (Babst et al., 2017; Larson et al., 2013) as they can quickly lag behind the recent rapid environmental changes and most current remote sensing datasets (Fig. 3).

3.3 A plant community-based perspective for dendroecological studies

Community-based dendroecological (CBDE) sampling can be used to increase understanding of shrub growth, expansion, and demographics (Gap 2) and how the responses of shrub individuals, species, and communities relate to micro-environmental conditions, plant-plant interactions, and larger scale climatic factors (Gap 1, Gap 3). Yet, it has not been widely implemented (but see, for example, (Büntgen et al., 2015)). This CBDE approach focuses on collecting a subset of shrubs that is representative of the study site (Gap 4). This implies, however, sampling a larger number of individuals at both plot- and site-level than what is typical in dendro-based protocols. Using systematic unbiased sampling strategies of a large number of individuals (Fig. 5b,d) will allow for assessing within-population variation and age dynamics, thus allowing for the study of retrospective growth and establishment patterns (Fig. 5f). Compared to a sampling strategy that focuses on the largest individuals, unbiased sampling might result in a shorter chronology with more variation in climate-growth patterns. It will, however, be better suited for answering ecological questions on shrub communities (e.g., see section 3.5). To assess demographic responses, it is essential to get the best estimate possible of shrub ages by extracting complete shrubs to collect the root collar. Furthermore, sampling of the whole individuals allows for assessment of growth responses of different shrub parts (Ropars et al., 2017; Shetti et al., 2018) and quantification of biomass (Berner et al., 2015). In addition, we suggest collecting a range of *in-situ* data both on the sampled individuals and the surrounding growing conditions. Depending on research questions, such data could include information on functional traits, e.g., plant height and specific leaf area (Fig. 5e), the exact location of the sampled individual, vegetation cover, soil condition, and micro topography.

3.4 Synthesis of synergetic approach

In summary, the core of our proposed synergetic approach is to collect a representative sample of shrubs from across and within environmental gradients by stratifying the landscape using remote sensing tools and geospatial analyses. This will allow for cross-scale investigations and demographic assessments of shrub communities and individuals (i.e., contributing to bridging Gap 1 and 4). While excavating entire shrubs and collecting both above and below ground parts allows for the collection of the oldest part of the shrub (the root collar) which is necessary for age estimation, this also provides the opportunity to assess intra- individual variation in responses to various drivers obtained from remote sensing and *in-situ* data (Gap 2-4). Combined with detailed analyses of cellular responses and functional traits (e.g., stem, root, leaf), this would allow for multidisciplinary studies linking different responses and ecosystem functions across time and space (Gap 5).

Our approach is not without limitations, mainly due to the inherent difficulties when working with tiny and irregular growth rings of Arctic shrubs and the costly workload involved with collecting and analyzing large numbers of individuals from remote locations. However, making data comparable across sites and studies could help alleviate some of the practical and logistical constraints of data collection by facilitating further collaboration and data sharing (e.g. through open access repositories). Additionally, the approach can and should be adjusted to better suit particular research questions, needs, and constraints. For example, if long and clear time-series are required, typical in dendroclimatic studies, CBDE sampling can be supplemented by additionally collecting the largest individuals at a site - as long as such selectively sampled individuals are clearly marked and are not taken into account in demographic assessments requiring representative sampling.

To facilitate synergetic integration of dendroanatomy, remote sensing, and CBDE-sampling across sites, there is a need for standardized analytical methods and detailed metadata. This is especially important since shrub-rings and anatomical features are not uniform within individuals. Standardized sampling, sample preparation, and analyses will help with disentangling environmental effects from axial trends of xylem anatomical traits (Anfodillo et al., 2013; Carrer et al., 2014; Lechthaler et al., 2019; Olson and Rosell, 2013) and shrub-rings. The goal of this being to make data comparable between sampled individuals, sites (Lechthaler et al., 2019), and growth forms (e.g., climbing, prostrate etc.). Extensive metadata with information on how the plant was selected (Klesse et al., 2018), where on the plant the wood was sampled, and distance of the sample to the shoot apex (Fig. 5e) (Lechthaler et al., 2019; Olson et al., 2021) should be included in all studies. Recording coordinates of the location of each collected individual will facilitate the integration of satellite derived environmental data. Finally, recommended methods of microsection preparation and measurements of shrub rings (Myers-Smith et al., 2015b) should be followed, giving attention to prepare high quality microsections which will allow quantification of anatomical features such as lumen area, cell-wall thickness, and the number and distribution of the main cell types (von Arx et al., 2016).

We hope the approach presented here can be adopted in future studies to further our ecological understanding of shrub dynamics across the rapidly changing Arctic. The wealth of data that can be attainable with such synergic approaches will allow addressing a larger variety of questions and will foster collaboration both within the field of dendroecology and between dendroecology and other scientific fields.

3.5 Examples of key ecological questions that could be addressed

The synergetic approach can be used to answer a wide range of interdisciplinary questions and can be adjusted to fit different needs, here we highlight three examples:

Example 1: Linking ring widths with biomass

With the collection of whole shrubs, ring widths can be linked with biomass-allometry functions and plant traits. Knowledge on species-specific allometric relationships (Berner et al., 2015) and tools to more easily include allometry in dendroecological studies (Kašpar et al., 2019) can be incorporated to study biomass-allometry patterns across a range of species and site characteristics. This area of research is gaining attention because of its important role in carbon storage and how it provides the possibility for ring width data to contribute to vegetation-climate and carbon models.

Example 2: Linking microscopic responses to remotely-sensed patterns

With the incorporation of data from a micro (e.g., cells, rings) to a macro scale (e.g., satellites), local field-based biotic and abiotic measurements can be linked with remotely sensed information (e.g., satellite derived indices) across time and space. For example, it could be used to assess the links between NDVI and ring widths (Macias-Fauria et al., 2012; Ropars et al., 2015; Weijers et al., 2018b), as well as xylem anatomical traits (Prendin et al., 2020). Systematically sampling across the landscape, quantifying shrub growth and anatomical traits, and using near surface remote sensing devices (e.g., drones, phenocams) can be used to help build the bridges between microscopic responses, field-based observations, and patterns observed by satellites that will allow us to gain a more complete picture of Arctic shrub dynamics.

Example 3: Linking above and below ground traits

The collection of information on a wide range of plant traits from a variety of systematically selected individuals, e.g., wood (density, anatomy), leaf (specific leaf area, leaf phosphorus concentration, leaf dry matter content), below ground (root growth), and structural characteristics (maximum height) (Iturrate-Garcia et al., 2020; Kunstler et al., 2016), enables insight into links between different traits among individuals, species, and locations. As an example, collecting data on full shrubs can facilitate more below-ground trait research, which is particularly important, but still understudied in tundra ecosystems (Bjorkman et al., 2018; Iversen et al., 2015; Myers-Smith et al., 2019b) where most biomass allocation is below ground (Iversen et al., 2015; Mokany et al., 2006). This multidisciplinary approach can provide a more comprehensive understanding of the impacts of vegetation change and ecosystem processes (Díaz et al., 2007, 2004).

4. OUTLOOK

Dendroecology provides a unique opportunity to study current and past shrub dynamics in the drastically changing Arctic. Here we propose a synergetic approach that combines a comprehensive and community-based sampling design; quantitative wood anatomical analyses that can reveal underlying functional mechanisms; and satellite-based and *in-situ* data describing trends and events of multiple drivers. Such a multidisciplinary and cross-scale community-based perspective in dendroecological studies could improve insight in relation to understanding: (i) the cellular mechanistic underpinnings of inter- and intraspecific variation in shrub growth (e.g., adjustments in xylem functional traits); (ii) the links between demographic responses (e.g., growth, recruitment, mortality) and drivers (e.g., abiotic and biotic trends and events), within and among shrubs communities; (iii) links and allocation between above and below ground plant responses; and (iv) how plant responses translate into ecosystem functions. These insights, achieved through the implementation of standardized protocols, data sharing, dendroanatomical analyses, and remote sensing, can ultimately be used to improve quantification of the magnitude and extent of current shrub community responses.

Development of efficient management and conservation strategies requires information at local to landscape/regional scales. As there is remaining uncertainty regarding how Arctic vegetation is changing and will continue to change on local scales in the current period of rapid warming, this improved understanding is necessary for predicting the impacts on Arctic biodiversity and ecosystems across time and space. These comprehensive predictions can ultimately better inform the development of local and regionally relevant climate change conservation and mitigation strategies.

APPENDIX A: LITERATURE REVIEW DATA

APPENDIX B: ARTICLES INCLUDED IN REVIEW

APPENDIX C: EXAMPLES OF GRIDDED GLOBAL DATASETS

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Table 1: Drivers and driver categories identified in the literature search, potential remote sensing sources that could be used to quantify the drivers, and example datasets or studies that include such drivers. Left column: Overview of drivers we identified in the 82 publications included in our review of recent Arctic dendroecological studies. We placed each driver in one of nine categories (the categories are written in bold). Numbers inside parentheses represent how many studies included the driver or category at least once. Middle column: Remote sensing sources available as direct measures or proxies for the driver variables. Right column: Selected datasets or studies related to the driver and remote sensing source. The sources and examples list are not exhaustive, but a relevant selection based on our knowledge at the time of writing.

Driver (number of studies)	Remote Sensing Source	Example Dataset or Study
Air temperature (62)		
Summer Temperature (62)	Gridded climate reanalysis datasets including satellite data	ERA5 reanalysis of climate variables at 0.1° resolution CHELSA downscaled ERA5 data at 33 arcsec resolution (Karger et al., 2017) Also, see (Sun et al., 2018) for a recent review on gridded precipitation datasets.
Winter Temperature (42)		
Frost day frequency (2)		
Precipitation (45)		
Summer Precipitation (43)		
Winter Precipitation (37)		
Wet Day Frequency (2)		
Rain on Snow Events [b] (4)	Microwave remote sensing	(Forbes et al., 2016) (Grenfell and Putkonen, 2008)
Geophysical factors, processes, and disturbances (39)		
Habitat characteristics (18)	Multispectral Satellite imagery Airborne Laser Scanning	Global vegetation mapping (Raynolds et al., 2019) Fine-scale habitat mapping with airborne laser scanning (Boelman et al., 2016)
Soil nutrients (5)	-	-
Soil moisture (4)	Microwave remote sensing Optical imagery	Accurate models at coarse grain sizes (e.g. Copernicus Soil Moisture Product) Proxies at medium grain sizes: (Bartsch et al., 2020)
Standardized Precipitation-Evapotranspiration Index (SPEI) (5)	-	-
Ground temperature (2)	Infrared reflectance from multispectral imagery	Landsat (https://www.usgs.gov/core-science-systems/nli/landsat/landsat-collection-2-surface-temperature) or Copernicus Imagery (https://land.copernicus.eu/global/products/lst)
Soil temperature (1)	Models based on satellite data	ESA GlobPermafrost (Obu et al., 2018)
Potential Evapotranspiration PET) (2)	Infrared reflectance from multispectral imagery	(Nedbal et al., 2020)
Road [a] (1)	-	-
Slope (1)	DEMs derived from satellite and airborne remote sensing, including laser scanning, stereographic imagery and radar data	Panarctic datasets like the Arctic DEM (Porter et al., 2018) National / Regional datasets like GIMP (Howat et al., 2014)
Solar radiation index (2)		

Thaw depth [a] (1)	-	-
Thaw ponds/ slumps [b] (2)	Fine grain optical imagery	IKONOS (Belshe et al., 2013) or Worldview imagery.
Tsunami [b] / Storm surge [b] (2)	-	-
Dew point (1)	-	-
Humidity (1)	-	-
Sea ice and ice caps (8)		
Sea ice (5)	Microwave (coarse grain) Optical imagery (fine grain)	NSIDC CDR Sea-ice concentration (https://nsidc.org/data/g02202) (Cooley et al., 2020)
Glacial retreat (1)	Various sources	See special issue in Remote Sensing (https://www.mdpi.com/journal/remotesensing/special_issues/remotesensing_glaciers)
Greenland Ice Sheet (1)	Passive microwave and various other sources	NSIDC Greenland Ice Sheet Melt (Abdalati, 2007)
Years since glaciation (1)	-	-
Biotic factors, interactions, and disturbances (20)		
Biotic site characteristics (14)	-	-
Caribou & Sheep herbivory [a b] (4)	-	-
Insect outbreak [b] (3)	Multispectral imagery	(Prendin et al., 2020)
Fire (2)	Multispectral imagery	MODIS Fire Product (https://modis.gsfc.nasa.gov/data/dataprod/mod14.php)
Climate system (6)		
Arctic Oscillation (5)	Gridded climate reanalysis datasets including satellite data	ERA5 reanalysis at 0.1° resolution
North Atlantic Oscillation (3)		
Greenland Blocking Index (1)		
Scandinavian Pattern (1)		
Growing season (6)		
Growing season length and timing (6)	Multispectral imagery	MODIS and AVHRR imagery (Zeng et al., 2011)
Snow cover and depth (9)		
Snow cover / Snow depth [a] (9)	Microwave remote sensing Multispectral imagery	NSIDC CDR Snow Cover (Brodzik and Armstrong, 2013)(Robinson et al., 2012)
Other (4)		
Cloud cover (2)	Optical imagery	MODIS imagery (Seddon et al., 2016)
Sunlight duration (1)	DEMs derived from satellite and airborne remote sensing, including laser scanning, stereographic imagery and radar data	Global datasets like the Arctic DEM National / Regional datasets

[a] *variables we believe could be theoretically measured using remote sensing data, but further developments of the methods are likely required.* [b] variables we identify as events with the remainder being trends.

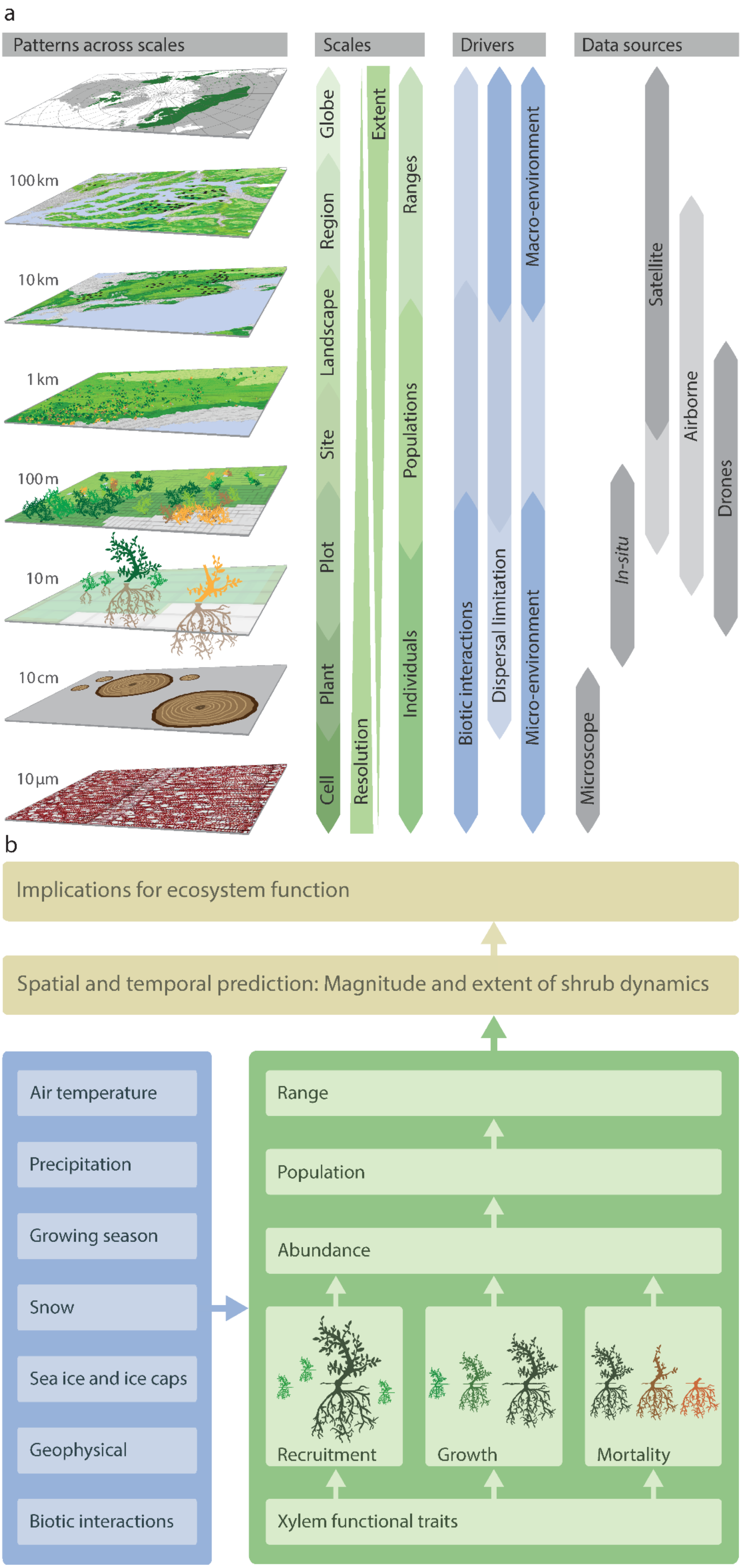
a
Patterns across scales
Scales
Drivers
Data sources
100 km
10 km
1 km
100 m
10 m
10 cm
10 µm
Globe
Region
Landscape
Site
Plot
Plant
Cell
Extent
Resolution
Ranges
Populations
Individuals
Macro-environment
Biotic interactions
Dispersal limitation
Micro-environment
Satellite
Airborne
Drones
In-situ
Microscope
b
Implications for ecosystem function
Spatial and temporal prediction: Magnitude and extent of shrub dynamics
Air temperature
Precipitation
Growing season
Snow
Sea ice and ice caps
Geophysical
Biotic interactions
Range
Population
Abundance
Recruitment
Growth
Mortality
Xylem functional traits

Figure 1: Linking shrub dynamics and their drivers across spatial and temporal scales. **(a)** Effects of environmental drivers are initiated at the level of individuals through their cellular and demographic responses (e.g., recruitment, growth, mortality). They propagate across populations to determine plant community and species range dynamics (green arrows). Key drivers (blue arrows) of local to macro-scale shrub dynamics (i.e., biotic interactions, dispersal limitation, and macro- to micro-environmental conditions) are expected to vary in importance across scales (different shadings). Combining cellular analyses; *in-situ* measurements; and satellite, airborne, and drone-based remote sensing contributes to linking these dynamics and drivers across spatial and temporal scales (grey arrows). **(b)** Interlinking information on multiple drivers (blue) and multiple responses (green) from local- to macroecological scales provides the basis for understanding why shrub responses differ across individuals, communities and species geographic ranges. Such understanding can allow for better spatial and temporal predictions of the magnitude and extent of the ongoing shrub dynamics, ultimately increasing our ability to estimate the implications for ecosystem functioning (yellow).

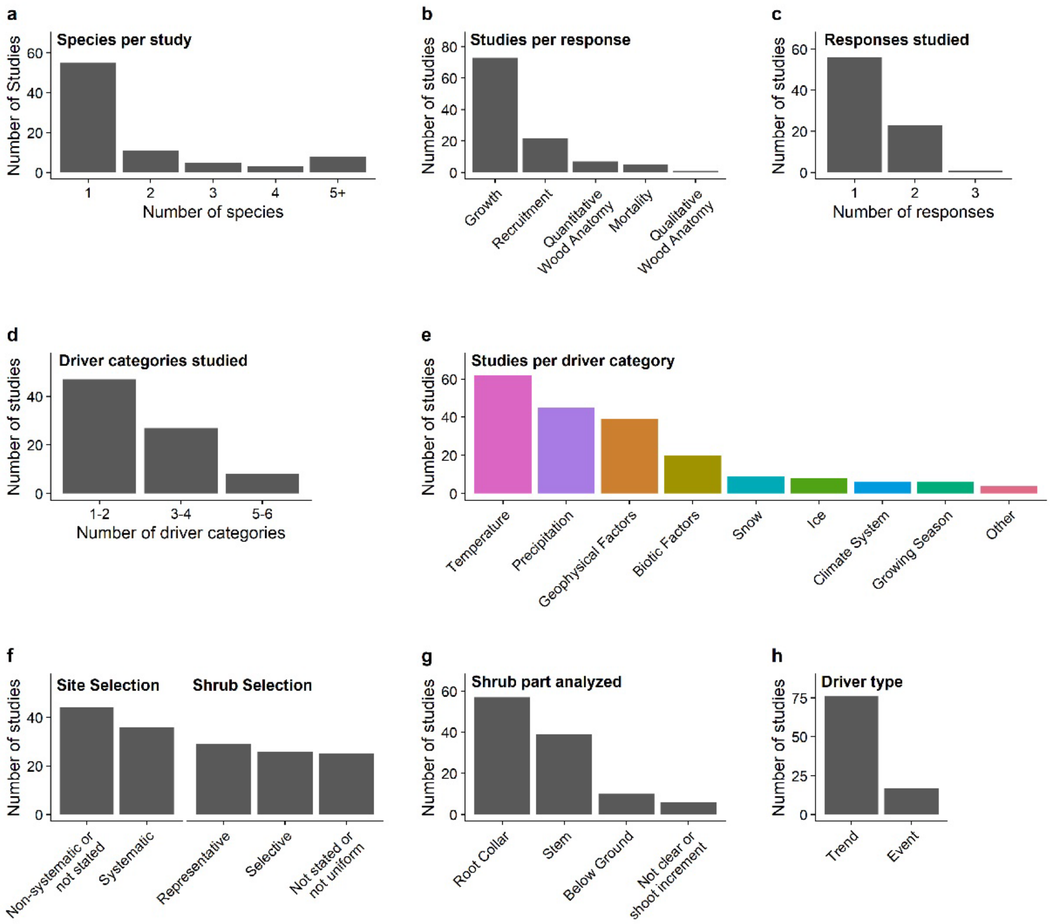

Figure 2: Overview of the main drivers, responses and methods used based on 82 Arctic dendrochronological studies from 2005-2022, showing: (a) the number of species, (b) the response type, (c) the number of responses, (d) the number of driver categories, (e) the driver categories, (f) the site and shrub selection method, (g) the shrub part analyzed and (h) the inclusion of drivers categorized as events or trends.

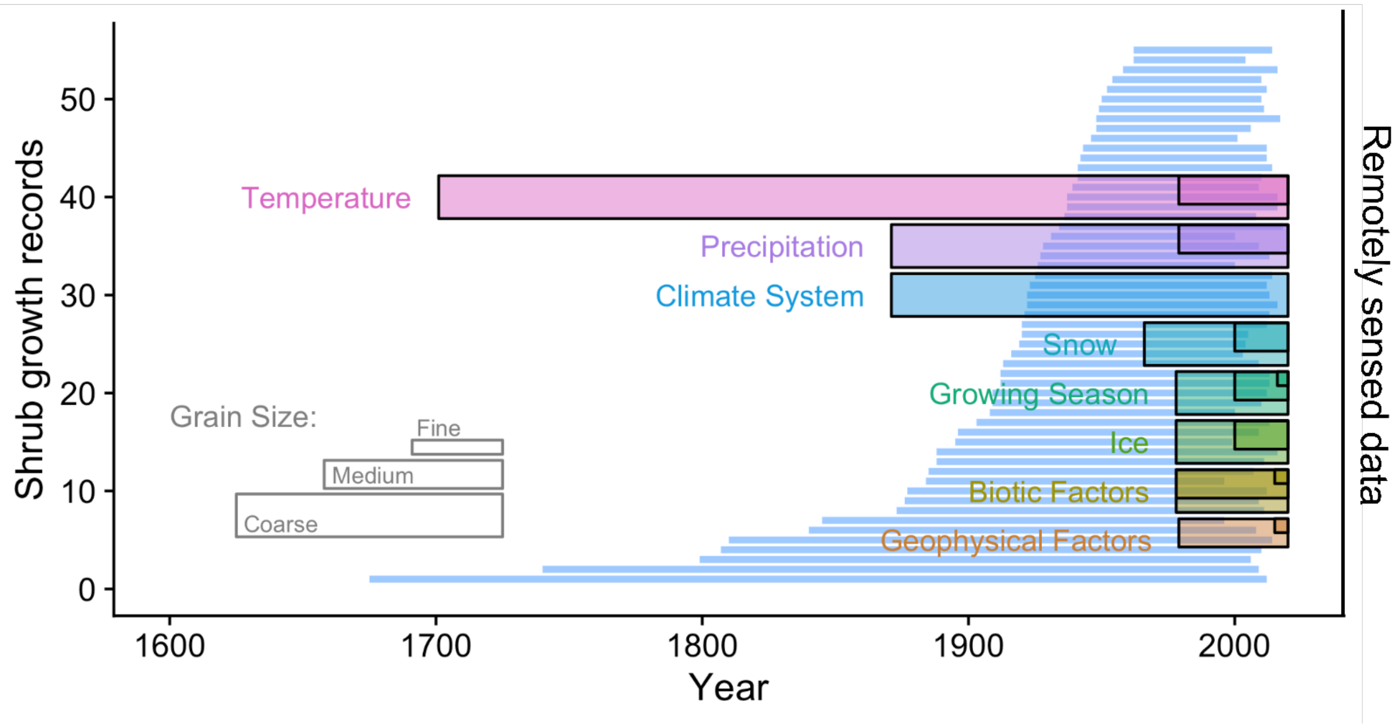

Figure 3: Extent of dendrochronological growth records and remotely sensed drivers. Left y-axis: Maximum extent of dendrochronological growth records from the reviewed studies (range: 1675-2018). We present the longest period covered by shrub growth in each study site, for all species combined. Right y-axis: The temporal availability of fully or partially remote sensing-based spatial datasets with global coverage that could provide direct or indirect measures for some of the drivers in the major categories identified in our review (see Table 1). The width of the bars indicates the grain size available: coarse (> 1 km), (10 m – 1 km) and fine (≤ 10 m). Table S1 provides a more detailed description of the remotely sensed data included.

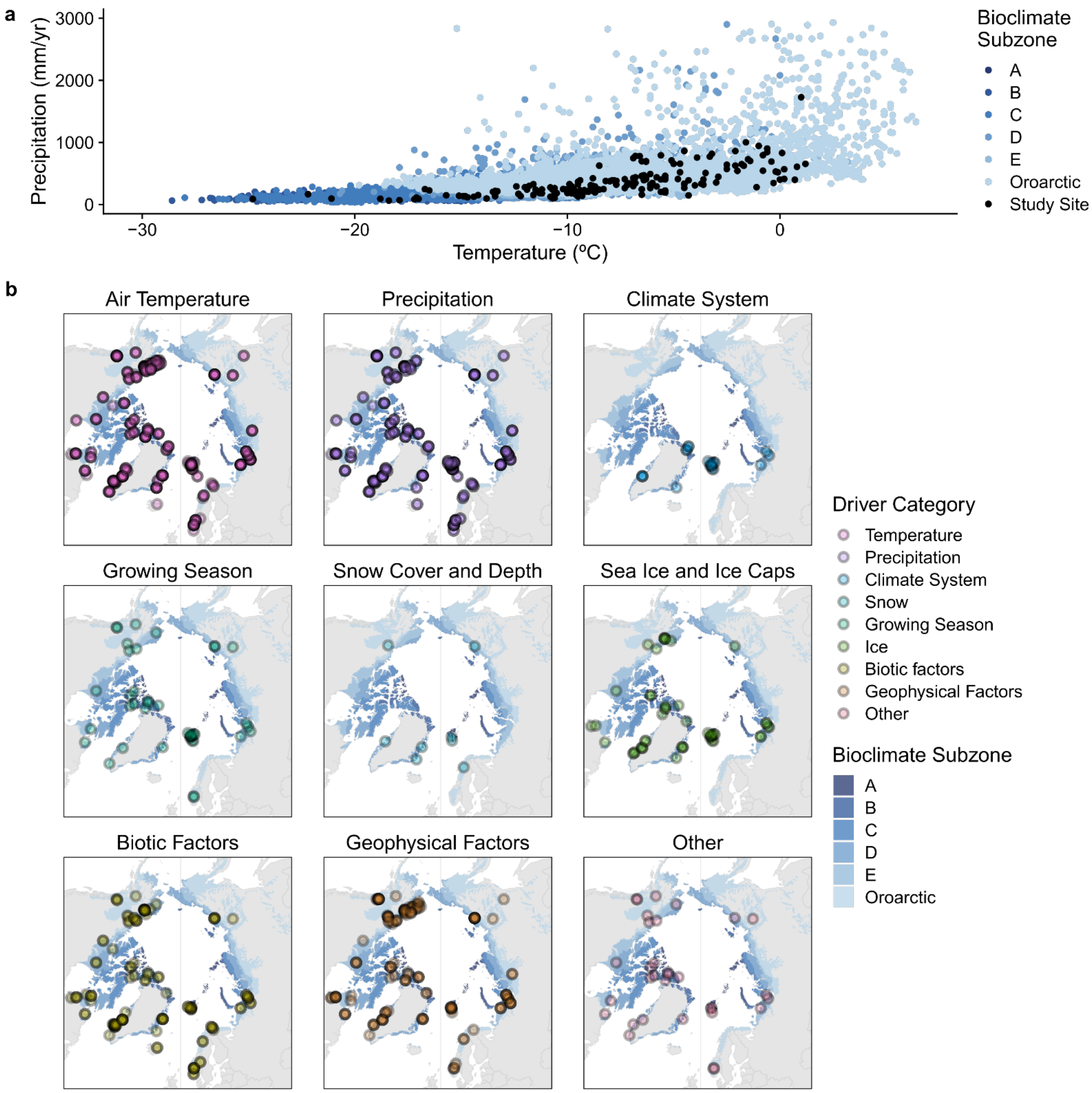

Figure 4: Location of study sites in the 82 reviewed studies in bioclimatic and geographic space. (a) The mean annual temperature and sum of annual precipitation at the study sites from 1979-2013, extracted from the CHELSA dataset v1.2.1 (Karger et al., 2017), plotted on top of 14k random locations across six Arctic bioclimate subzones to illustrate the climate space of the Arctic tundra. (b) Spatial distribution of study site locations by major driver category in the context of the tundra subzones.

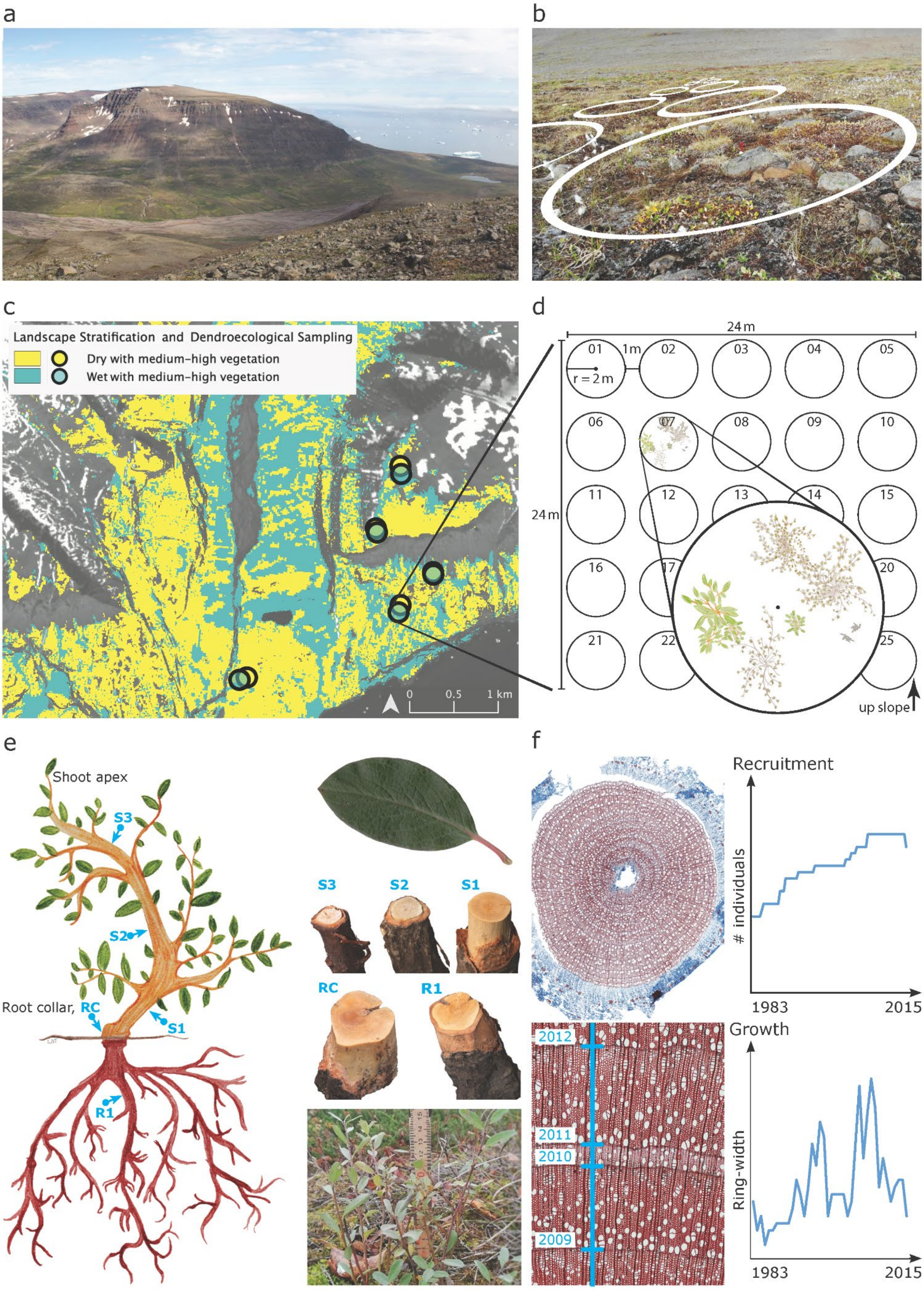
a
b
c
Landscape Stratification and Dendroecological Sampling
Dry with medium–high vegetation
Wet with medium–high vegetation
0 0.5 1 km
d
24 m
01 1m 02 03 04 05
r = 2 m
06 07 08 09 10
11 12 13 14 15
16 17 20
21 22 25
24 m
up slope
e
Shoot apex
S3
S2
Root collar, RC
S1
R1
S3 S2 S1
RC R1
f
Recruitment
individuals
1983 2015
Growth
2012
2011
2010
2009
Ring-width
1983 2015

Figure 5: Illustration of the main components of our synergetic approach for cross-scale understanding of Arctic shrub community dynamics: (c) remote sensing-based environmental stratification; (b, d, e) community-based dendroecological (CBDE) sampling, and (f) dendroanatomy. Arctic environments can be heterogeneous at both (a) landscape and (b) local scales, as exemplified with this mountainous site located on Qeqertarsuaq (Disko Island), in western Greenland (69°16 N 53°27 W). (c)The landscape was stratified based on information from remotely-sensed data sources, i.e., a moisture proxy and vegetation greenness, and was the basis for selection of sampling plots (b,c). At each plot, a systematic sampling design was applied (d) by setting up a grid of 25 circles. In each circle, the shrub closest to the center point (d) was excavated, as completely as possible, and abiotic and biotic information was recorded (e). To aid with cross-dating and to facilitate within-individual analyses, sections of wood samples were taken along the main stem (S1, S2, S3) and root (R1), including the oldest part of the plant (the root collar (RC)), with the distance between each sample and the shoot apex recorded. Additional data and samples were collected per shrub, e.g., leaves for genetic and functional trait analyses (plant height, specific leaf area). The wood samples allow for detailed inference of growth and recruitment of the collected plants (f). In addition, anatomically detected growth anomalies (e.g., year 2010 (f)) can help to understand extreme events (here defoliation caused by an insect outbreak, e.g., Prendin et al 2020).

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