Potential of shrubs in the evolving field of Arctic and Alpine Dendro-Ecology

Methods in shrub dendro-ecology: Understanding the processes influencing shrub growth in the Arctic and Alpine ecosystems.

I n a u g u r a l d i s s e r t a t i o n

zur

Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften (Dr. rer. nat.)

der

Mathematisch-Naturwissenschaftlichen Fakultät

der

Ernst-Moritz-Arndt-Universität Greifswald

vorgelegt von

Rohan Shetti

geboren am 31.08.1987

in Pune, India

Greifswald, im Mai 2018

Dedicated to my parents, wife, teachers, friends and gurus who at every step made me aware of the ever-changing nature of life. It was this basic thought that seeded my interest in Natural Sciences.

A blade of grass or a mighty tall tree,

It is a perfect design as it is supposed to be.

Don't judge life by the size you see,

No flower looks complete without a buzzing bee.

The fabric of life is woven by all,

So treat no tree as big, or no shrub as small.

- Rohan Shetti

Table of Contents

Abstract

Dendrochronology, the science of tree-rings is a tool which has been widely used for many years for understanding changes in the environment, as trees react to environmental changes over time. In the contemporary situation, where climate warming in the Arctic is unequivocal and its effects on the Alpine and tundra ecosystems are seen pronouncedly in the past decade, the role of dendro-studies and the use of trees and shrubs alike as proxies of change has become critical. Studies clearly indicate that warming in the Arctic and Alpine tundra has resulted in increased vegetation in recent years. Shrubs, in these sensitive ecosystems, have proven to be highly instrumental as they likely benefit from this warming and hence are good indicators and auditees of this change. Therefore, in this study, we investigate the potential of shrubs in the evolving field of dendro-ecology/climatology.

Studies from classical dendrochronology used annual rings from trees. Further, because of shrub sensitivity to contemporary change, shrub-based dendrochronological research has increased at a notable scale in the last decade and will likely continue. This is because shrubs grow even beyond the tree line and promise environmental records from areas where tree growth is very limited or absent. However, a common limitation noted by most shrub studies is the very hard cross-dating due to asynchronous growth patterns. This limitation poses a major hurdle in shrub-based dendrochronological studies, as it renders weak detection of common signals in growth patterns in population stands. This common signal is traced by using a 'site-chronology'.

In this dissertation, I studied shrub growth through various resolutions, starting from understanding radial growth within individuals along the length of the stem, to comparison of radial growth responses among male and female shrubs, to comparing growth responses among trees and shrubs to investigation of biome-wide functional trait responses to current warming. Apart from Chapter 4 and Chapter 6, I largely used *Juniperus communis sp.* for investigations as it is the most widely distributed woody dioecious species often used in dendro-ecological investigations in the Northern Hemisphere.

Primarily, we investigated radial growth patterns within shrubs to better understand growth within individuals by comparing different stem-disks from different stem heights within

individuals. We found significant differences in radial growth from different stem-disks with respect to stem heights from same individuals. Furthermore, we found that these differences depending on the choice of the stem-disk affect the resulting site-chronology and hence climate-sensitivity to a substantial extent and that the choice of a stem-disk is a crucial precursor which affects climate-growth relationships.

Secondly, we investigated if gender difference – often reported causing differential radial growth in dioecious trees – is an influential factor for heterogeneous growth. We found that at least in case of *Juniperus communis.* L and *Juniperus communis* ssp *nana.* WILLD there is no substantial gender biased difference in radial growth which might affect the site-chronology. We did find moderate differences between sexes in an overall analysis and attribute this to reproductive effort in females.

In our study to test the potential of shrubs for reconstruction, we used a test case of *Alnus viridis* ssp *crispa*. We found a strong correlation between ring-width indices and summer temperature. Initially, the model failed the stability tests when we tested the stability of this relation using a response function model. However, using wood-anatomical analysis we discovered that this was because of abnormal cell-wall formation resulting in very thin rings in the year 2004. Pointer year analysis revealed that the thin rings were caused because of a moth larval outbreak and when corrected for these rings the model passed all stability tests.

Furthermore, to see if trees and shrubs growing in same biomes react to environmental changes similarly, a network analysis with sites ranging from the Mediterranean biome to the Ural Mountains in Russia was carried out. We found that shrubs react better to the current climate warming and have a decoupled divergent temperature response as compared to coexisting trees. This outcome reiterated the importance of shrub studies in relation to contemporary climate change. Even though trees and shrubs are woody forms producing annual rings, they have very different growth patterns and need different methods for analysis and data treatment.

Finally, in a domain-wide network analysis from plant-community vegetation survey, we investigated functional relationships between plant traits (leaf area, plant height, leaf nitrogen content, specific leaf area (SLA), and leaf dry matter content (LDMC)) and abiotic factors viz.

temperature and soil moisture. We found a strong relation between summer temperature and community height, SLA and LDMC on a spatial scale. Contrarily, the temporal-analysis revealed SLA and LDMC lagged and did not respond to temperature over the last decade. We realized that there are complex interactions between intra-specific and inter-specific plant traits which differ spatially and temporally impacting Arctic ecosystems in terms of carbon turn over, surface albedo, water balance and heat-energy fluxes. We found that ecosystem functions in the Arctic are closely linked with plant height and will be indicative of warming in the short term future becoming key factors in modelling ecosystem projections.

Author's contribution to scientific research papers

Chapter 1: General Introduction

I worked on this chapter completely by myself.

Chapter 2: Climate sensitivity is affected by growth differentiation along the length of *Juniperus communis* L. shrub stems in the Ural Mountains

The main idea for this chapter was seeded by Allan Buras and I. I measured and cross-dated most of the ring-width from scanned images and wrote major sections of the manuscript. Martin Wilmking and Allan Buras helped me extensively with editing and proofing the manuscript. Allan Buras and Marko Smiljanic helped with my queries and guided me while developing my R-script for the analysis.

Chapter 3: Does sex matter? Gender specificity and its influence on site-chronologies in the common dioecious shrub *Juniperus sp.*

The main idea for this study was conceived by Martin Wilmking. I did all of the ring-width measurements and cross-dating for Juniper samples from Ural sites and cross-dated data from Kirkenes and developed the analysis. Principle component gradient analysis (PCGA) was developed by Allan Buras and Cluster analysis was developed by Marko Smiljanic. I developed the rest of the analysis for differentiation of site-chronologies, cumulative growth analysis, and climate-sensitivity analysis and wrote the manuscript. All co-authors also gave valuable input by proofing the manuscript.

Chapter 4: Influence of larval outbreaks on the climate reconstruction potential of an Arctic shrub.

The main idea for this study was by Martin Wilmking, Allan Buras and Ernst van der Maaten. I helped with the scanning of stem-disk images and proofing the manuscript.

Chapter 5: Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent

This study was a network analysis developed by Ellena Pellizzari. I contributed to this study with datasets from the Ural Mountains and helped with comments and suggestions while proofing and editing the manuscript.

Chapter 6: Changes in plant functional traits in a changing tundra biome.

The main concept of this study was developed by Isla Mayers and Anne Bjorkmann. I contributed to the research by providing plant traits data from all the Ural sites. I gave suggestions and inputs while proofing the manuscript.

Chapter 7: Synthesis and Discussion

I worked on this chapter by myself.

I confirm the Authors contribution statements:

Supervisor: Prof. Martin Wilmking, (Ph.D.)   **Student:** Rohan Shetti

Chapter 1: General Introduction

Chapter 1: General Introduction

Shrub Sensitivity to Climate Change in the Arctic-Alpine Tundra

Climate change and its effects on the Arctic ecosystems is one of the most concerning topics that has been on the forefront of research in the present times. It is only just, as the Arctic and Alpine Tundra ecosystems are most markedly affected by it as compared to other eco-regions of the world (IPCC: Anisimov et al., 2007; Myers-Smith et al., 2015a). Being highly sensitive, the Arctic and subarctic environments are also studied intensively using different environmental proxies like patterns in ice-cores (Haflidason et al., 1995), paleo-ecology with peat-cores (Rozema. et al., 2006) and dendrochronology (Schweingruber, 1988; Sturm et al., 2001; Speer, 2010; Myers-Smith et al., 2011) using annual radial growth in vegetation. Vegetation response to climate is one of the major indicators of warming which is seen through effects like treeline shifts (Greenwood and Jump, 2014) and increasing shrub covers above the treelines across the circumpolar Arctic (Tape et al., 2012).

Classical dendrochronology uses ring-width from trees to reconstruct a variety of environmental parameters ranging from climatic parameters like temperature (McKay and Kaufman, 2014), precipitation/drought (Scharnweber et al., 2011) to geo-hydrological processes like changes in water levels (Scharnweber et al., 2013), landslides (Malik and Wistuba, 2012), sea surface temperatures (D'Arrigo et al., 1993) and fire occurrences (Holz et al., 2012). However, in the last decade there has been a noticeable increase in shrub based dendro-ecological and dendro-climatological studies as 1) shrubs seem to be sensitive to the current warming and likely benefit from it (Sturm et al., 2001; Blok et al., 2011; Elmendorf et al., 2012a; Myers-Smith et al., 2015a) and 2) can provide information from eco-regions where trees are sparse or completely absent.

In the past decade, shrub based dendro-ecological/climatological studies have shown promising potential of shrub rings to be good proxies in the reconstruction of past climate records like temperature (Rayback and Henry, 2006; Liang and Eckstein, 2009; Weijers et al., 2010) and humidity (Liang et al., 2012). Furthermore, processes like permafrost degradation (Osterkamp, 2007; Blok et al., 2010), glacial melting (Buras et al., 2012; Buras et al., 2017), reduction in summer albedo, (Juszak et al., 2014), advances in treeline and shrubline, which are very crucial in understanding the Arctic environment have been brought to light by shrubs based dendro-

ecological/climatological investigations. Therefore, it is only likely that the use of shrubs in dendro-ecology and dendro-climatology will gain more importance in the coming years.

Differing Dendrochronological Methods from Trees to Shrubs:

In tree-based dendrochronology, it is a standard procedure to take two cores at breast height. A ring-width series is then developed from cross-dating and averaging measurements from these cores per individual. A site-chronology developed from all individuals in a population stand is then developed (Cook and Kairikustis, 1992), which is further used as per the aims of a study for example: reconstruction models (Lehejček, 2015), testing for climate-growth relationships, or radial / apical growth response to environmental parameters. These site-chronologies from ring-width series from trees are checked for growth synchronicity using various statistical parameters like Gleichläufigkeit, inter-series correlation and expressed population signal. Individual ring-width series which show heterogeneous growth patterns, as compared to other members of the population stand, are commonly omitted from analysis presuming that they might be responding to other environmental parameters and hence not exhibiting the common signal shown by other individuals. Therefore to obtain what a population stand might be responding to (common signal), synchronicity in growth is crucial (Schweingruber, 1988; Cook and Kairikustis, 1992; Speer, 2010). Many studies using ring-width series from shrubs report highly asynchronous or heterogeneous growth and subsequent difficult cross-dating (Woodcock and Bradley, 1994; Bär et al., 2007; Hantemirov et al., 2011; Pellizzari et al., 2014). This is because even though being woody growth forms, shrubs have a different growth architecture than trees (Körner, 2012b). Shrubs growing in harsh conditions often grow gnarled, twisted and have irregular radial and apical growth. Therefore treating these irregularities is highly imperative and assessing and developing new methods for shrub-based dendrochronological studies is essential (Schweingruber and Poschold, 2005; Körner, 2012a).

Evolving methods in shrub-based dendrochronology and knowledge gaps:

A common procedure used in shrub sampling is to harvest the longest stem of the shrub and to use to the lowermost stem-disk for analytical purposes. The roots of this procedure go back to

methods described for serial sectioning by Kolishchuk (1990). This logically makes sense as the lowermost stem-disk has the most number of rings and is the oldest above-ground part of a shrub individual. However, a study by Wilmking et al. (2012) showed that under extremely stressful conditions woody plants can reduce cambial activity to a minimum and could cease wood formation all the way to the bottom of the stem. This could lead to missing outer rings or in some cases locally missing rings- causing missing rings in lowermost stem disks. Further, Buras and Wilmking (2014) showed that eccentric growth – which is commonly pronounced at lowermost stem-disks – could result in low inter-series correlations between radial measurements from within a stem-disk section. Therefore, minimum of four radial measurements were advised for best radial growth representation. The latest comprehensive review of methods in shrub dendrochronology presented by Myers-Smith et al. (2015b) also identifies serial sectioning as a promising method and recommends the use of root-collars for analytical purposes as presumably, it has the most number of rings. A recent study by Ropars et al. (2017) showed that different stem-disks along the length of the stem of a shrub individual can have differing climate sensitivities. This clearly showed that differentiation in radial growth along the length of the stem can affect climate-growth relationships and that selection of stem-disk is a crucial aspect. All the above mentioned literature has contributed to understanding various aspects like causes of missing rings, need for more number of radial measurements for adequate growth representation, serial sectioning to understand growth intricately to identify very narrow rings, leading to the question - 'how and where to measure shrubs when aiming for climate-growth relationships ?'

Another important aspect that can potentially affect ring-width formation is resource allocation which is known to differ in tree species exhibiting sexual dimorphism (Cavigelli et al., 1986; Gauquelin et al., 2002). Similarly, in shrubs, sexual dimorphism and its associated effects have been studied with various aspects like flowering times, spatial segregation (Barradas and Otilia, 1999; Boulanger-Lapointe et al., 2016) and differential sex ratios (Ortiz et al., 2002) with respect to site preferences. However, what do these differences mean to radial growth in shrubs? Could this be a point to be considered while sampling? These questions were not clearly addressed in the available literature. Therefore overall, it is evident from the recently evolving methods in

shrub-based dendrochronology that there are knowledge gaps, especially pertaining to sampling procedures with respect to 1) stem-disk selection i.e. which stem-disk to choose, 2) sample selection as in how a gender bias in a chosen sample set can influence ring-width series and 3) treatment of radial measurements for developing optimal response functions.

Research Questions:

Even though many studies with ring-widths from shrubs show promising results there exists a fair ambiguity about how to treat heterogeneous growth. This is reported by many studies in terms of cross-dating difficulties, low inter-series correlations among individuals from a population stand and low EPS (expressed population signal) values (Woodcock and Bradley, 1994; Bär et al., 2007; Wilmking et al., 2012; Pellizzari et al., 2014). Consideration of sexual dimorphism and its effects on site-chronology is barely even addressed in the present state of literature. This thesis closely looks at the following key questions using case studies of two widely distributed shrub species viz. *Juniperus communis* sp. and *Alnus viridis* ssp *crispa*.

1) How heterogeneous growth along the length of the stem influences climate-growth relationships/sensitivity?

2) Do sexual differences impact ring-width formation and should these be considered while selecting samples?

3) Reconstruction potential of shrubs using a synergetic approach of ring-width measurement and wood-anatomy.

4) Are there differences in climatic responses between shrubs and trees, and if so, how should they be interpreted and contextualized in different biomes?

5) How response of shrub functional traits can be used as a proxy to trace contemporary warming in the Arctic and Alpine Tundra.

This dissertation compositely looks at the mentioned aspects with the aim of bridging the prevalent knowledge gaps pertaining to methods and applications of shrubs based dendro-ecological/climatological studies. This investigation aims at critically looking at the potential of shrubs as proxies to monitor contemporary change in the Arctic and Alpine environments, yet to

point out the requirement to revise and devise new methods for understanding shrub growth and its response to the environment.

Sampling Sites and Methods:

The main dataset I worked with is from the Ural Mountains in Russia. I personally collected samples from the Northern Ural Mountains. To study vegetation dynamics at and above the treeline, we sampled across an altitud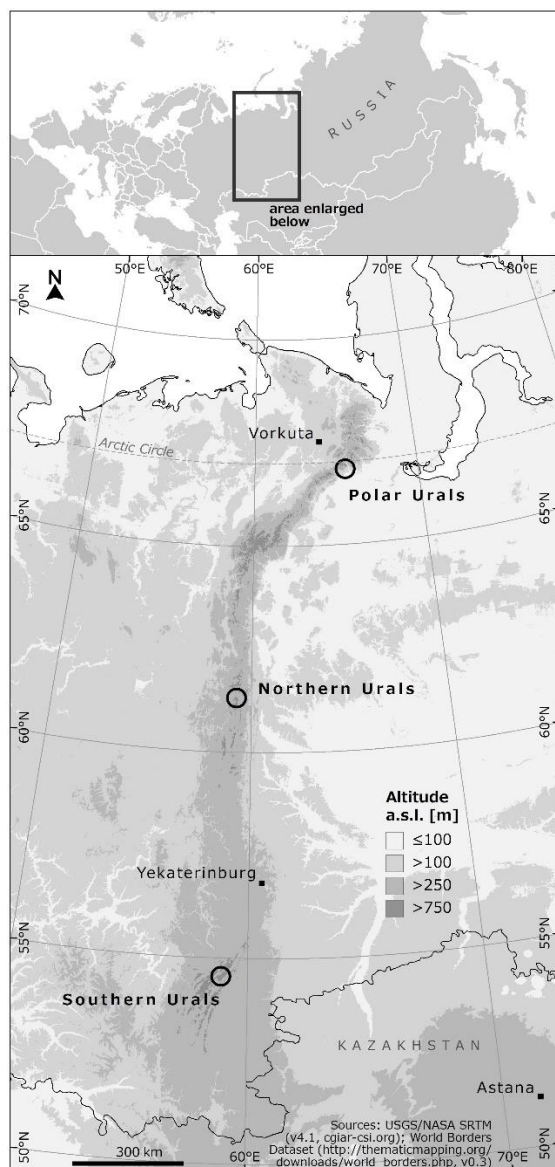inal and latitudinal gradient across the Ural Mountains in Russia. At every site, we sampled at three elevational levels from the treeline to the shrubline. We collected *Juniperus communis.* L samples from all sites. A detailed summary of sites is available in the supplementary material of **Chapter 2: Supplement Table S1**. We chose to work with Juniper species as it one of the most widely distributed species in the Arctic and Sub-arctic regions and is extensively used in dendro-ecological and dendro-climatological studies (Hantemirov et al., 2011; Adams, 2014; Pellizzari et al., 2014).

Figure 1

Juniper samples from Kirkenes site were collected formerly by Martin Hallinger which were used in gender analysis in **Chapter 3.** The site details are available in **Chapter 3; Figure 1, Table 1.** The Juniper ring-width dataset from Polar Urals and Northern Urals was also used in a network analysis (**Chapter 5**) to study the responses of trees and shrubs through a network of sites starting from the Polar Urals through the Alps to the Mediterranean region; a detailed site description of which is

Figure 1 showing sampling sites in the Ural Mountains

available in **Chapter 5; Figure 1, Table 1.** In **Chapter 4** where we discuss the reconstruction potential of shrub *Alnus viridis* ssp *crispa,* all the sampling was done by Martin Wilmking and Allan Buras close to Kobbefjord in Greenland, the site details for which are available in **Chapter 4; Figure 1, Table 1.** Finally in **Chapter 6**, plant functional trait data was pooled from 117 locations in the Arctic. This is a circumpolar network analysis of plant functional traits data which included parameters like crown-area, shrub height, specific leaf area, leaf nitrogen content and leaf dry matter content. The site details and descriptions are available in **Chapter 6; Figure 1**.

In the following section I briefly elucidate the research questions and methods for individual chapters followed by a discussion and synthesis which comprehensively discusses the findings and limitations of each investigation.

Chapter 2: Climate sensitivity is affected by growth differentiation along the length of *Juniperus communis* L. shrub stems in the Ural Mountains (Dendrochronologia 2018).

In this chapter, we studied the effect of asynchronous growth along the length of the stem of Juniper shrubs from the Ural Mountains and its effects on site-chronologies. While comparing radial measurements from different stem-disks (from different stem heights) from within a shrub individual we found significant differences. We inferred that these differences could affect the site-chronologies which would be subsequently derived from them and hence investigated how site-chronologies from different stem heights influences climate-growth relationships. This investigation brought in a novel perspective that the normal procedure of selecting the lower most stem-disks or single stem-disk for analytical purposes needs to be revised and that different sections of the stem can show different climate sensitivity. In a previous investigation, Buras and Wilmking, (2014) have shown that multiple radial measurements are essential for a fair representation of radial growth when growth is highly eccentric. Our study furthermore brings to light that even measurements from single stem-disks do not completely capture the environmental signal that a shrub individual might be responding to.

Chapter 3: Does sex matter? Gender specificity and its influence on site-chronologies in the

common dioecious shrub *Juniperus sp.* (Dendrochronologia 2018).

Sexual dimorphism and associated differences in radial and apical growth in trees is a feature well documented in the literature (Cavigelli et al., 1986; Obeso et al., 1998; Lushuang Gao et al., 2010). In this study we investigated if sexual differentiation in shrubs affects radial growth - and if so - how does this impact the resulting site-chronologies which are commonly used for determining climate-growth relationships to reconstruct past climates. We used Juniperus communis (*Juniperus communis* L. with ssp *nana* WILLD.) as a test case. We did this using a series of analyses of gender-separated subgroups, which included Cluster Analysis, Principle Component Gradient Analysis (PCGA), Comparison of Cumulative Annual Increments, Climate-Sensitivity Analysis and comparison of gender-separated chronologies with site-specific site-chronologies. Only in an overall comparison of gender-separated chronologies to site-chronologies did we find a moderately significant difference between male and female shrubs. We saw that the female chronologies induced more noise to the site-chronology. However, we could not explain if this is a genotypic attribute of Juniper shrubs or a resultant of heterogeneous growth due to the strong influence of micro-site conditions impacting the growth architecture.

Chapter 4: Influence of larval outbreaks on the climate reconstruction potential of an Arctic

shrub (Dendrochronologia 2018).

In this investigation, we studied the reconstruction potential of a commonly occurring Arctic shrub *Alnus viridis* ssp. *crispa* in Greenland. Shrubs can be good proxies for reconstructions for remote high latitude regions. However, as shrub growth can be ununiformed with reasons which can vary from herbivory to harsh micro-site conditions, there is a very high probability of obscuration of climate signal - which is a common attribute that is reconstructed. Here we developed site-chronologies using ring-width data and cell-wall thickness. Climate-sensitivity analysis revealed strong positive correlations with summer temperature for the entire period with the exception of the present decade. Initially, the temperature reconstruction failed stability tests but wood anatomical analysis revealed the presence of unusual cell structures in very

narrow rings of the year 2004, which corresponded to an insect outbreak at the sampling site. When corrected for the recovery period, the reconstruction passed all stability tests. This confirmed that the abnormal cell structure affecting the ring-widths were not a resultant of climate but were because of a larval outbreak in the region. We inferred that the combined use of ring-width series and wood anatomy can be a promising method for climate reconstructions.

Chapter 5: Diverging shrub and tree growth from Polar to the Mediterranean biomes across
European continent (Global Change Biology 2017).

Study of climate-growth relationships is one of the central aspects of dendroclimatology. In this chapter we compare growth responses of shrubs with trees, ranging in a wide range of eco-regions spanning from the Polar Urals in the Subarctic through the Italian Alps to the Spanish Iberian systems in the Mediterranean regions. We hypothesized that as shrubs and trees are co-habitants in most ecological niches they would respond similarly to the contemporary warming. We assumed that shrubs being dwarf woody forms they might be more coupled to local surface temperatures and could be less affected by 'overall-warming' seen post-1950s as compared to trees. Contrarily, we found that across all the eco-regions, shrubs and trees show diverging responses to contemporary warming. We found that Juniper shrubs did better in terms of growth than trees in Mediterranean region as compared to Polar, and Alpine regions. Overall, we inferred that even being co-habiting plant lifeforms, climate warming affects shrubs and trees differently.

Chapter 6:   Changes in plant functional traits in changing Tundra biome (in revision - Nature
2018).

In this study we investigated how plant traits are linked with temperature and soil moisture across the tundra biome. Secondly, we investigated the relative influence of intra-specific trait variability (ITV) versus community level trait variation. Finally, we tried to analyse if temperature-trait relationships are explained by among-site differences by species abundance or by species turnover.   We studied relationships between plant traits and soil moisture and temperature.

Specific plant traits included attributes like plant height, leaf area, specific leaf area (SLA), leaf nitrogen content (LN), leaf dry matter content (LDMC), community woodiness and evergreenness. The data for this study was collected from vegetation surveys from 117 sites in the Arctic and Alpine tundra. We inferred notable spatial connection between summer temperature and community plant growth, SLA, LDMC and community height. Similarly, we found that soil moisture substantially influenced SLA and LDMC indicating functional relationships between water availability and future plant trait change. This study shows how specific plant traits react to contemporary warming whereas others lag behind suggesting a complex relationship between plant growth and resource availability. We inferred that study of these trade-offs could improve projections of ecosystem modelling in the Arctic.
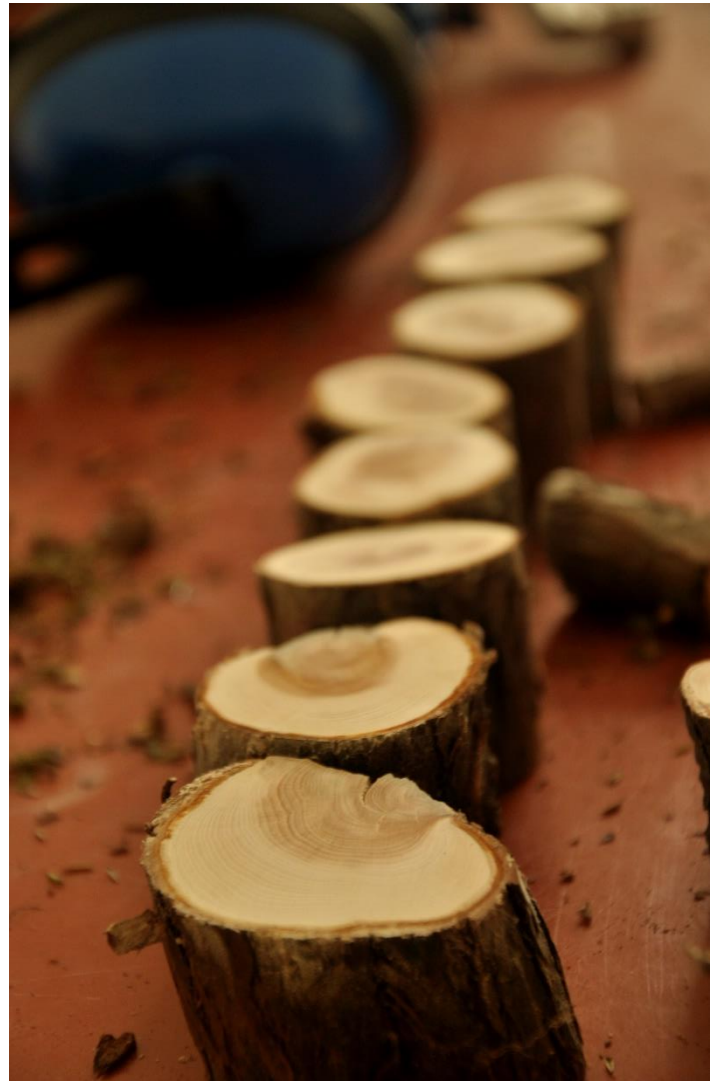
Chapter 2

Climate sensitivity is affected by growth differentiation along the length of *Juniperus communis* L. shrub stems in the Ural Mountains (**Dendrochronologia 49 (2018): 29-35**)
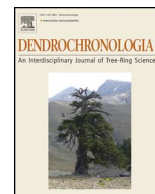
Climate sensitivity is affected by growth differentiation along the length of *Juniperus communis* L. shrub stems in the Ural Mountains

Rohan Shetti[a,*], Allan Buras[b], Marko Smiljanic[a], Martin Wilmking[a]

[a] *Institute of Botany and Landscape Ecology, Ernst-Moritz-Arndt University Greifswald, Soldmannstrasse 15, D-17487 Greifswald, Germany*
[b] *Professorship of Ecoclimatology, TU München, Hans-Carl-von-Carlowitz Platz 2, D-85354 Freising, Germany*

ABSTRACT

Arctic and alpine shrubs are valuable for future dendro-ecological and dendro-climatological studies in regions where trees are sparse or absent. A commonly accepted procedure of sampling shrub stem disks is at the root collar. However many shrub studies report low inter-series correlations in radial measurements as compared to trees. Many studies also report cross-dating difficulties with radial measurements from shrubs within a stand and commonly attribute this to differential growth along the length of the stem. So does one stem disk entirely represent the environmental parameters the shrub might be reacting to? Does change in sampling location of the stem disk affect the subsequent ring-width chronologies and climate sensitivity? To tackle these questions, we investigated *Juniperus communis* L. – a species wide spread in the circumpolar arctic – across a latitudinal gradient in the Ural Mountains. Based on traditional radial ring-width measurements we assessed growth synchronicity along the length of shrub stems. We also compared ring width chronologies representing different stem heights with respect to their relationships with temperature and the standardized precipitation evapotranspiration index (SPEI). Growth patterns often varied significantly among stems disks of the same shrubs, resulting in dissimilar climate-growth relationships of stem disk chronologies. For correlations with temperature, stem disks at 20 cm distance from the root collar captured the best signal. For correlations with SPEI data we could not find any specific stem disk chronology with highest sensitivity. At least in our dataset, no "perfect sampling height" with high climate sensitivity exists and our results thus highlight that a single stem disk from a shrub may not completely represent the shrub's growth response to climate parameters.

1. Introduction

Alpine and arctic shrub sensitivity to contemporary climate change around the circumpolar arctic is well established (Sturm et al., 2001; Danby and Hik, 2007; Forbes et al., 2010; Hallinger et al., 2010; Hallinger and Wilmking, 2011; Myers-Smith et al., 2011, 2015a). Due to this sensitivity, many recent dendrochronological studies use growth-ring parameters from shrubs for reconstructions of environmental conditions in Arctic and alpine Tundra (Lehejček, 2015) ranging from temperature (Meinardus et al., 2011; Weijers et al., 2013), humidity (Liang and Eckstein, 2009; Liang et al., 2012), and sea surface temperatures (Beil et al., 2015) to understanding ecological processes like permafrost degradation (Blok et al., 2010; Blok et al., 2011), glacial retreat (Buras et al., 2012; Buras et al., 2017) and effects of reducing summer albedo and treeline advances and greening at high latitudes (Raynolds et al., 2006; Tape et al., 2006; Ropars and Boudreau, 2012; Tape et al., 2012; Juszak et al., 2014). This multi-faceted utility of shrubs makes them pivotal for future studies of climate change and vegetation dynamics in the arctic tundra.

Albeit the high utility of shrubs, many shrub studies report substantial difficulties in measuring and cross-dating shrubs (Hantemirov et al., 2011; Pellizzari et al., 2017), commonly attributed to narrow, wedging and missing rings (Wilmking et al., 2012). One important factor hampering cross-dating might be eccentric growth within stem disks (Buras and Wilmking, 2014), and a recent study by Ropars et al. (2017) concluded that selection of stem disks while analysing shrubs for climate sensitivity is crucial and sensitivity from different measurements along the length of the stem can differ significantly. In their study Ropars et al. (2017) discuss various factors like differential resource allocation within individuals which might be due to micro-site drivers which dampen a more general macro-climate signal and exhibit responses based on more local drivers. Their study inferred that sections from the root collar demonstrated best climate sensitivity. A prior study by Sadras and Denison (2009) reported that resource allocation can vary along different parts of the stem in case it benefits the overall fitness of the plant. Logically, this poses an important question: Is a

single shrub stem disk representative enough to be considered for tracing an individual's sensitivity to environmental parameters?

Until now the common shrub-dendrochronological approach selects the lower most stem disk (closest to the root collar), because it presumably has the largest number of rings, and measures multiple radial measurements (two to four radii per disk) depending on stem architecture (erect, prostrate, eccentric growth) (Gazol and Camarero, 2012; Pellizzari et al., 2014; Beil et al., 2015; Myers-Smith et al., 2015b; Pellizzari et al., 2017). Furthermore the review by Myers-Smith et al. (2015b) suggests serial sectioning and investigating radial measurements from serial sections from multiple stem disks for best growth representation. However, in the context of the findings by Buras and Wilmking (2014) and Ropars et al. (2017), it is imperative to test whether the commonly used single lowermost stem disks does indeed capture most of the climate signal or not.

In our study we investigated:

1. How does synchronous/or asynchronous radial growth along the length of the stem impacts ring-width chronologies.
2. Do ring-width measurements from a single stem disk adequately capture the climate signal that a shrub individual might be responding to by using ring-width data from *Juniperus communis* L.

We chose *Juniperus communis* L. as it is a one of the most widely distributed shrub species in the circumpolar arctic with clearly discernible rings and has been commonly used for many dendro-ecological studies (Hantemirov et al., 2011; Liang et al., 2012; Pellizzari et al., 2014; Buras et al., 2017). In accordance with the established sampling protocol, we hypothesized that the climatic signal in ring-width data is consistent along the length of the stem.

2. Materials and methods

2.1. Sampling design

Our study was carried out along a latitudinal gradient in the Ural Mountains. We sampled three sites, from north to south: Polar Urals (PU), Northern Urals (NU) and Southern Ural Mountains (SU). At all three locations south facing slopes were sampled for *Juniperus communis* L. shrubs at three elevations from treeline to shrubline (Fig. 1, Supplement Table S1). At each elevation, three (20 m × 20 m) quadrats were set up using measuring tapes and all *Juniperus communis* L. shrubs within each respective quadrat were destructively harvested for one stem per individual. GPS locations of each quadrat were recorded, and the location of each sampled individual was recorded in an x–y coordinate format with respect to the borders of that plot. For each specimen, we sampled the longest stem, following the recommended sampling procedure, i.e. serial sectioning (Kolishchuk, 1990; Myers-Smith et al., 2015b). In total, we collected stems from 191 individual shrubs.

2.2. Sample treatment and measuring

From each specimen, we considered the lowermost three stem disks for further analyses, i.e. at 0 cm, 10 cm, and 20 cm distance to the root-collar. These 573 stem disks were polished on a belt-sander using sandpapers with increasingly finer grit from P-60 to P-400. This process ensured complete polishing making single rings visible. The stem disks were then scanned on an EPSON-V700 high resolution scanner at 4800 dpi and measured for annual ring widths using Coo-Recorder software (Version 8.1, Cybis AS, Sweden). Every stem disk was measured for four (Buras and Wilmking, 2014) and in some cases where the growth was too eccentric for three radii.
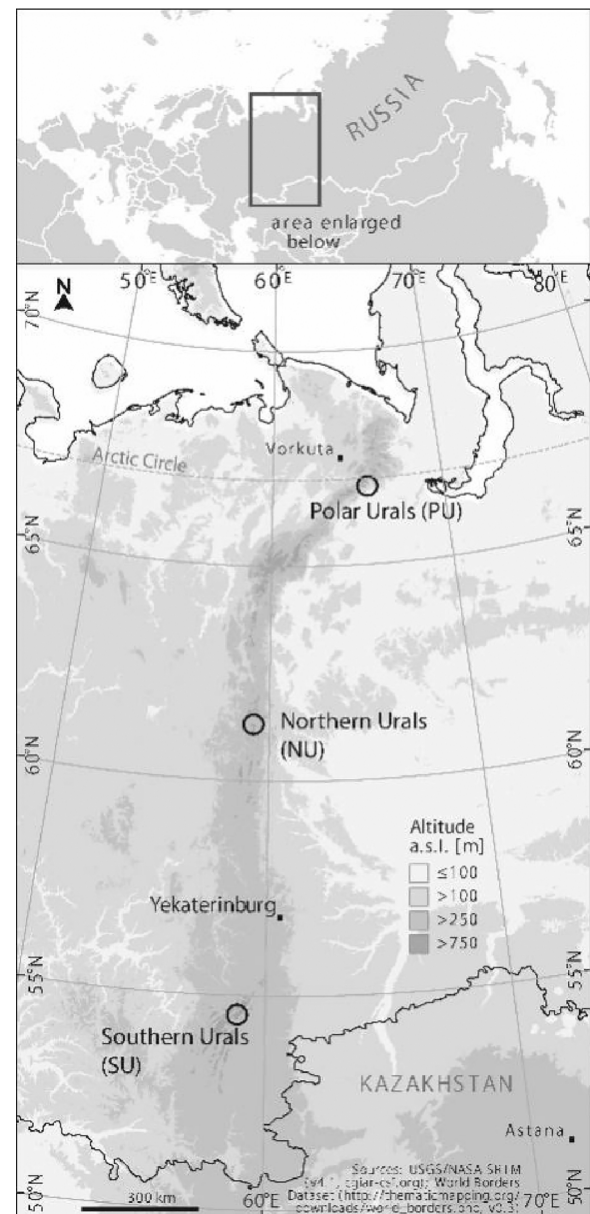

Fig. 1. We sampled 191 individual *Juniperus communis* L. shrubs at three sites along a latitudinal gradient in the Ural Mountains.

2.3. Cross-dating

We cross-dated all the ring-width measurements in CDendro (Version 8.1, Cybis AS, Sweden (Larsson and Larsson, 2013)). First, radial measurements from within stem disks were cross-dated with each other to account for wedging rings and missing outer rings. Then they were averaged to form a stem disk chronology. The resulting stem disk chronologies were cross-dated among stem disks from the same shrub using inter-series correlation and Gleichläufigkeit. Basal stem disks of all shrubs within an elevational level were then cross-dated with each other. Finally all the individuals (comprising multiple individual stem disks) within an elevational plot were cross-dated. It was often difficult to cross-date basal stem disks since shrubs from most of the plots had very differential growth patterns. The final dating was agreed upon by visual inspection as stated in Schweingruber, (1988). From the 191 sampled shrubs, we were able to cross-date 99 individuals. However, to base our correlation analyses on a meaningful period length and lower the effects of juvenile growth on climate correlations, we further excluded another 22 individuals being younger than 30 years, thus
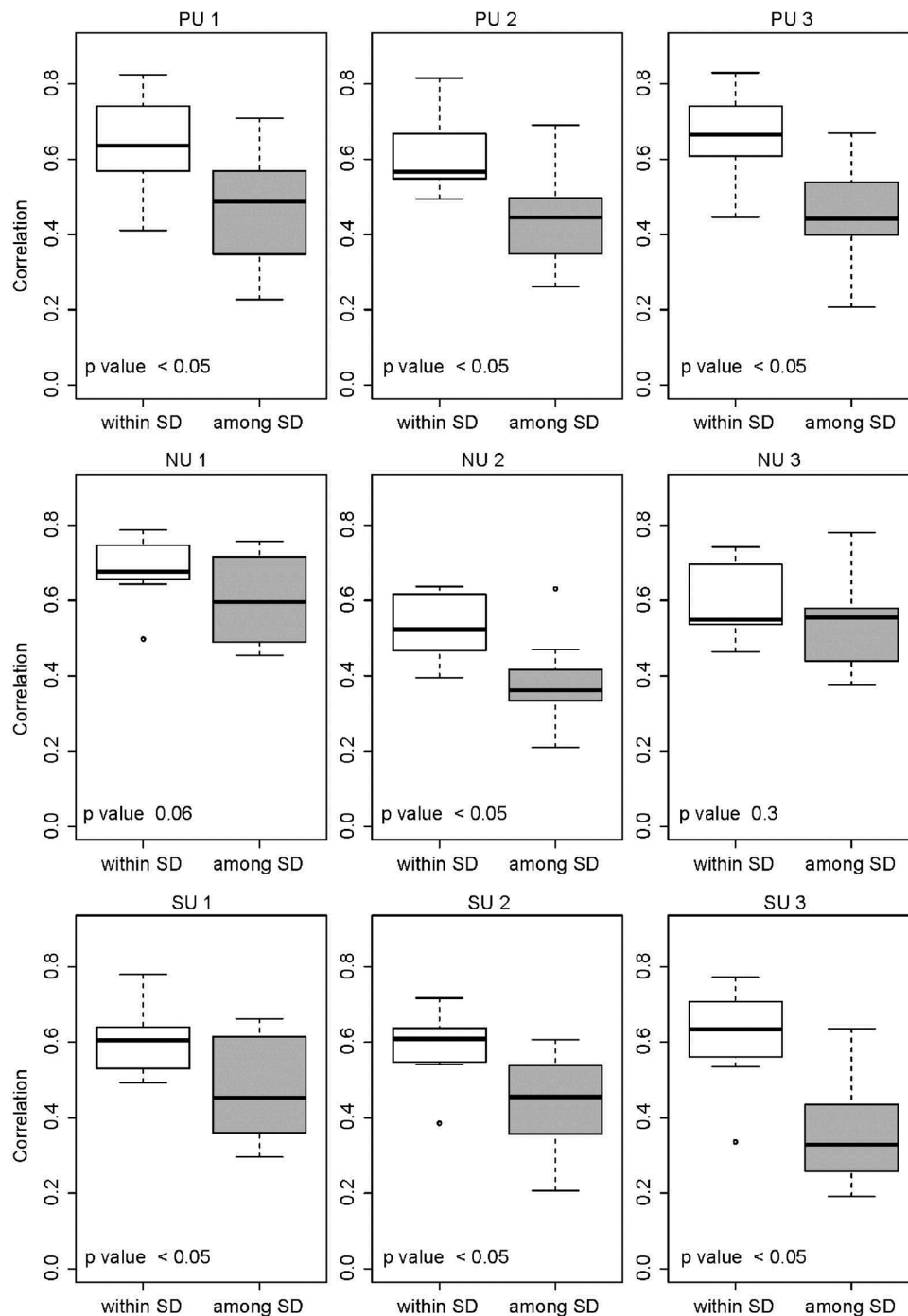
Fig. 2. Comparison of radial ring-width measurements at all elevational plots at each site. At all sites the elevational plots range from the shrubline to treeline marked with abbreviations (Polar Ural: PU1, PU2, PU3. Northern Ural: NU1, NU2, NU3. Southern Ural: SU1, SU2, SU3). Within stem disk (SD) (white boxplot) correlations of several radii are higher at every site and plot (often significantly so) than among stem disk (SD) (grey boxplot) correlations.

leaving us with 77 individuals for analyses (Table S2).

2.4. Statistical analysis

Our aims were 1) to evaluate potential growth variability along the length of the stem and 2) to see whether and – if so – how growth patterns from different stem heights affect climate signals of stem-height specific site-chronologies.

To compare growth variability along the length of the stem we correlated radial measurements from within stem disks (intra stem disk) and then among stem disks (inter stem disk) from all individuals. At each plot we tested for significance of difference among the intra stem

disk and inter stem disk correlation scores using Wilcoxon rank-sum test. Similarly, to compare synchronicity in radial measurements we performed Gleichläufigkeit analysis between intra-stem disk and inter-stem disk radial measurements (Supplement Fig. S1).

2.5. Mean sensitivity analysis

To evaluate the difference in the high frequency amplitude of ring-width data which is commonly used as a measure for responder's sensitivity we performed a mean sensitivity analysis of individual stem height specific chronologies from each singular shrubs. This was done using "sens2" function from dplR package (Bunn, 2008) in R

programming language (R Core Team, 2013). The base equation used for testing mean sensitivity is as per the second equation stated in Biondi and Queadan (2008).

2.6. Development of chronologies

To determine how radial measurements from different stem heights responded to climate signals we developed four chronologies for each plot. We chose three stem disks from every individual viz. the ones at 0 cm, 10 cm and 20 cm. We only chose three stem disks for analytical purposes as in many individuals stem sections above 20 cm were less than thirty years of age. All individuals from a plot which cross-dated well and had three lower stem disks above 30 years of age were included in the analysis.

Corresponding to the stem height we averaged all radial measurements from respective stem disks from shrub samples in a plot. For each of the three stem heights, i.e. at 0 cm, 10 cm and 20 cm chronologies SD0, SD10 and SD20 were generated. We then created a master chronology (MC) by averaging all stem disk measurements from the plot. A minimum common overlap time of thirty years was chosen. The details of the time intervals are available in Supplement Table S2. All the chronologies were developed using raw ring-width data. We also tested our analysis using horizontal mean detrended series and found very similar results to the raw chronologies. This might be because of the short time interval of thirty years and generally little low frequency trend in growth patterns.

2.7. Climate correlation analysis

We correlated the three stem disk chronologies (SD0, SD10, SD20) and master chronology (MC) generated from raw ring-width data from all the plots with temperature and standardized precipitation evapotranspiration index (SPEI). We used the time interval starting from May of the previous year to September of the current year as these are most relevant for radial growth. At all Ural sites temperatures post September are mostly around 0° or subzero. We chose only monthly temperature and SPEI (standardized precipitation-evapotranspiration index) data for correlation analysis. We tested correlations with gridded as well as climate station data (similar results) but here we report correlations only with monthly temperature station data (Russian Federation Meteorological Station Data). We used the CRUTEM gridded data set (KNMI Climate Explorer) for SPEI as we could not compute SPEI from station data since there were gaps in precipitation records. All the analysis was done in R (R Core Team, 2013) version 3.2.0 under dplR package (Bunn, 2008).

3. Results

3.1. Intra stem disk and inter stem disk correlation analysis

Comparing radial measurements from within a stem disk and between stem disks of a shrub individual we found that generally at all sites intra stem disk correlations were higher (r-bar ranging: 0.5–0.6) than inter stem disk correlations (r-bar ranging 0.3–0.5) (Fig. 2). At all sites except Northern Ural, (Fig. 2 NU1, NU3) the difference between the intra stem disk and inter stem disk correlation was significant ($p < 0.05$). Similarly, within stem disk Gleichläufigkeit was significantly higher ($p < 0.05$) than between stem disk Gleichläufigkeit at all sites (Supplement Fig. S1).

3.2. Mean sensitivity analysis

We compared mean sensitivity of individual radial measurements from the three chosen stem disks from individuals in a plot and found that there was generally no significant difference in them. We found that across all sites and all stem disks the mean sensitivity ranged from

0.3 to 0.4 consistently. Only on site SU2 a weak differentiation with low mean sensitivity (0.29) was seen with the radial measurements, however the differentiation was statistically insignificant ($p > 0.1$) (Supplement Fig. S2).

3.3. Comparing temperature-growth relationships between different stem heights

Across all three elevations of all sites we found differing responses of stem disk chronologies from different stem heights with temperature data. Generally, at all sites the strongest responses to temperatures were seen for the months of June, July and August (for previous and current years). This is the growing season and therefore we could expect best radial growth response for this period. Across all sites, the chronology with the strongest correlation with temperature data was SD20, followed by SD10 and SD0 chronologies. Generally, during the growing season significant positive correlations existed in sixteen cases (site – month combinations) across all sites for the SD10 chronology, in eighteen cases for the SD20 and MC chronologies and only in eight cases for the SD0 chronology. Other significant correlations existed but were not as strong or as frequent as the growing season temperature. Consistently throughout all sites the master chronology showed marginally lower correlations with temperature data compared to SD0, SD10 and SD20 chronologies In all reported cases correlations were significant with $p < 0.05$ (Fig. 3).
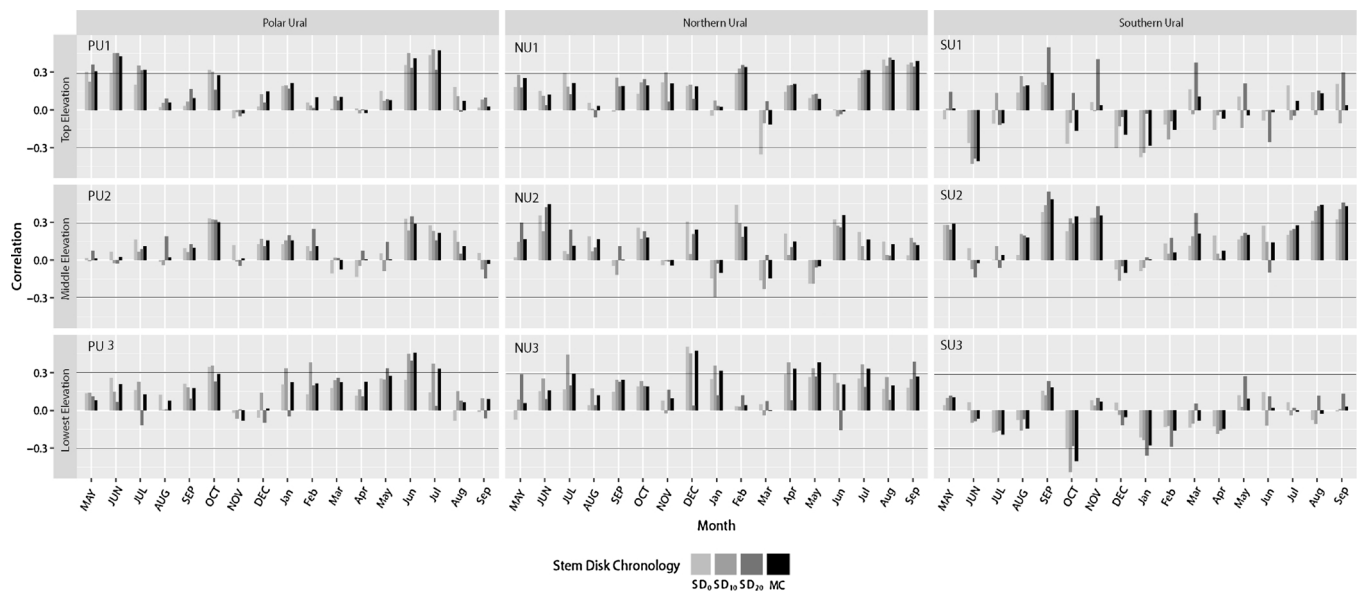
3.4. Comparison of chronologies from different stem heights with monthly standardized precipitation evapotranspiration index (SPEI) data

Highly varied responses of different stem disk chronologies existed across all sites. At the Polar Ural sites, SD20 had the highest number of significant correlations with SPEI (7 cases), followed by SD10 (6 cases) and SD0 chronologies (5 cases). At the Northern Ural sites, SD10 had the highest number of significant correlations with SPEI (11 cases), followed by SD20 (9 cases) and SD0 chronologies (4 cases). At the Southern Ural sites, SD0 had the highest number of significant correlations with SPEI (11 cases), followed by SD20 (9 cases) and SD10 chronologies (6 cases).The response of master chronology (MC) to SPEI data was generally weaker than that of individual stem disk chronologies (Fig. 4). Overall, contrasting to the response to temperature data, the correlations of individual height chronologies with SPEI was not consistent and highly variable. In all reported cases correlations were significant with $p < 0.05$.–

4. Discussion

One of the major hurdles commonly reported in shrub studies is the difficult cross-dating, possibly because of missing and wedging rings, eccentric or asynchronous growth patterns in a population stand (Hantemirov et al., 2011; Wilmking et al., 2012; Pellizzari et al., 2014). Heterogeneous growth within (intra stem disks and between different parts of the stem) and in between individuals in a population stand can potentially be due to strong influence of microsite conditions like the nature of substrate, slope inclination, wind direction, snow cover etc. and intrinsic factors like branching near the root collar, formation of multiple piths, or partial rotting (Schweingruber and Poschold, 2005; Sadras and Denison, 2009). Our study is no exception, with only 52% of successfully cross-dated individuals. This low value might also be species specific, as juniper shrubs grow twisted, gnarled and often prostrate.

These difficulties are also reflected in the frequently reported low inter-series correlation and Gleichläufigkeit values for shrubs (e.g. Buras and Wilmking, 2014; Myers-Smith et al., 2015a,b). Low r-bar and Gleichläufigkeit values indicate remarkable differences between the single measurements. Based on the measurement of eight radii per a stem disk and climate correlation analyses, Buras and Wilmking (2014)
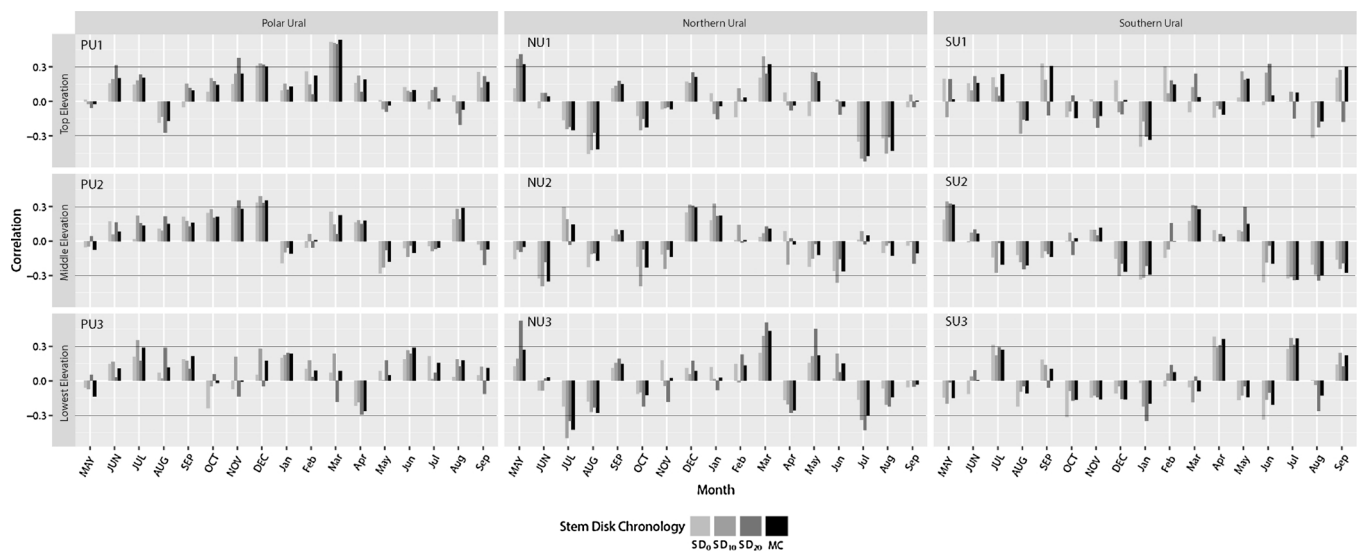
Fig. 3. comparison of correlation of three stem disk (SD) chronologies with temperature data. SD0, SD10 and SD20 represent stem disk chronologies from respective stem heights 0 cm, 10 cm and 20 cm from all shrubs from a plot. MC is master chronologies which comprises of measurement from all three stem disks from all shrubs in a plot. At all sites the elevational plots range from the shrubline (1), followed by intermediate altitude (2), to treeline (3) marked with abbreviations (Polar Ural: PU1, PU2, PU3. Northern Ural: NU1, NU2, NU3. Southern Ural: SU1, SU2, SU3).

could show that different stem sectors expressed different climate signals.

Our results clearly indicated significant reduction in inter-series correlations for between stem disks when compared to intra stem disk correlations (Fig. 2, Supplement Fig. S1). This could be attributed to two factors: i) improper cross-dating or ii) asynchronous heterogeneous radial growth. To eradicate the cross-dating errors we chose individuals which had a common overlap of radial growth in time (of 30 years). We confirmed that all individuals and their three stem disks had the same overlap period. Therefore, we could minimise the dating errors as radial measurements were double checked, once for a relative dating of stem disks from the same individual and then with other individuals from the same plot. Therefore, we attribute our findings to heterogeneous radial growth along the length of the stem within individuals. With these findings the logical subsequent questions are then "*where to measure*

stem disks for capturing optimal responder climate signals with respect to radial growth?" and "*how does this asynchronous growth affect any climate signal present in ring-width chronologies?*". We therefore analysed mean sensitivity (Supplement Fig. S2) to see which stem disk measurements are relatively more sensitive and consistently across all sites found no significant differentiation in mean sensitivity confirming that amplitude of differences in ring-width measurements are not a contributing factor to asynchronous growth trends.

Then we correlated monthly data of temperature and standardized precipitation evapotranspiration index (SPEI) with individual stem disk chronologies from three stem heights and found very heterogeneous results at most of the sites (Figs. 3 and 4). Varying combinations of stem disk chronologies or individual stem disk chronologies (example: SD0 and SD10 chronologies, or just SD10 chronology and so on) had significant correlations with temperature and SPEI data. In very few cases

Fig. 4. comparison of correlation of three stem disk (SD) chronologies with standardized precipitation evapotranspiration index (SPEI) data. SD0, SD10 and SD20 represent stem disk chronologies from respective stem heights 0 cm, 10 cm and 20 cm from all shrubs from a plot. MC is master chronologies which comprises of measurement from all three stem disks from all shrubs in a plot. At all sites the elevational plots range from the shrubline (1), followed by intermediate altitude (2), to treeline (3) marked with abbreviations (Polar Ural: PU1, PU2, PU3. Northern Ural: NU1, NU2, NU3. Southern Ural: SU1, SU2, SU3).

did we see an agreement in correlations of all three stem disk chronologies with SPEI and temperature data, suggesting different parts of a stem (with respect to varying stem heights) might contain differing micro-signals. This could mean that asynchronous growth along the length of the stem likely affects ring-width data and subsequently any climate signal which might be prevalent. These results are indicative that, when aiming at the identification of climate signals, investigators may have to consider analysing different stem parts, as growth in different parts may have differing signal strengths (Sadras and Denison, 2009; Buras and Wilmking, 2014). Partially our results are in agreement with the recent findings by Ropars et al. (2017) who inferred that root collars and stem sections have a varying sensitivity to climate signal. Another inference from their study was that root collars (analogous to SD0 chronologies in our study) best captured the climate signal, however in our study we found on most sites (Fig. 3) except sites PU2, NU1, NU2 and NU3, SD10 and SD20 chronologies were better correlated to temperature data than SD0 chronology. In case of correlation with temperatures at all sites we found that SD20 chronologies in most cases correlated well with different months in the vegetation period, but that SD10 showed the highest correlation scores. Hypothetically, stem sections higher than SD20 could also show differing correlations with climate data (better/worse) but we could not test this as sections higher than 20 cm did not reach the thirty years threshold. Therefore, from our findings we might infer that asynchronous growth along the length of the stem likely influences ring-width series data and subsequently any signal therein. Whether this is a feature specific to *Juniperus communis* L. or a general shrub growth feature remains to be studied in the future. Another factor influencing our results might be the strong influence of micro-site conditions as we sampled at and above the treeline which have extreme weather conditions such as heavy snow during winter, melt water runoff during summer and all year around influence of wind (Moiseev et al., 2010; Grigor'ev et al., 2013).

Marginally lower correlations were seen of master-chronology (MC) with climate records as compared to stem height specific chronologies. This could be a result of mean averaging. When measurements from different stem heights are averaged together it might add noise (mixed micro-signals) to the resultant chronology as at different stem heights the signal strength might differ depending on the positioning and architecture of different stem parts. Therefore, the resultant chronology which could have more noise might deteriorate the quality of climate growth relationships and subsequently could be misleading. Hence averaging multiple stem heights might not be advisable for creating chronologies if aiming at establishing climate-growth relationships. This result is surprising, since chronology building normally is considered as an effective means to lower the influence of individual noise.

Overall from our study we infer that different stem disks frequently captured slightly differing climate signals. However, we fail to clearly determine which stem disk as a standard procedure can be chosen for sampling shrubs for studying climate growth relationships. However, for *Juniperus communis* L. at Ural sites, SD20 chronologies (i.e. stem disks at 20 cm from root collar) best captured the temperature signal in most instances and could be considered while investigating climate growth relationships.

5. Conclusion

From our investigation we found significantly differential radial growth along the length of the stem of individual shrubs. We saw that this differential growth did influence climate growth relationships as we found very heterogeneous results with varying height specific chronologies correlating to different temperature and SPEI records of different months.

The main inferences of our study were as follows,

1. Asynchronous growth patterns along the length of the stem

considerably affect the resulting site-chronologies.
2. Ring-width measurements from just one stem disk might not wholly capture a shrub individual's response to climate, as different stem disks express varying strengths of climate-growth relationships. This might be because of noise induced by locally dominant intrinsic and extrinsic growth drivers.
3. Another finding from our study is that climate correlations (temperature and SPEI) do not necessarily improve or deteriorate according to stem heights. We found that at some sites stem disk chronologies from higher up the stem better correlated with temperature and SPEI and the same was true vice versa.
4. Averaging radial measurements over several stem disks per shrub did not increase but rather decreased the strength of climate signals.

Therefore, for future investigations we recommend considering investigation of multiple stem disks from individuals and look more closely at micro signals which might be prevalent and influential in annual ring formation in shrubs. A next step could be to monitor shrub growth with micro-site data like soil temperature with respect to changing soil depth, snow depth and snow cover measurements around the stem. This might help to improve our understanding of how radial and apical growth is impacted by micro and macro environmental drivers.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.dendro.2018.02.006.

References

Beil, I., Buras, A., Hallinger, M., Smiljanic, M., Wilmking, M., 2015. Shrubs tracing sea surface temperature–Calluna vulgaris on the Faroe Islands. Int. J. Biometeorol. 59, 1567–1575.

Biondi, F., Queadan, F., 2008. Inequality in paleorecords. Ecology 89, 1056–1067.

Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C., Berendse, F., 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Global Change Biol. 16, 1296–1305.

Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M.M.P.D., Sauren, P., Berendse, F., 2011. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences 8, 1169–1179.

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

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

Buras, A., Hallinger, M., Wilmking, M., 2012. Can shrubs help to reconstruct historical glacier retreats? Environ. Res. Lett. 7, 044031.

Buras, A., Lehejček, J., Michalová, Z., Morrissey, R.C., Svoboda, M., Wilmking, M., 2017. Shrubs shed light on 20th century Greenland Ice Sheet melting. Boreas 667–677.

Danby, R.K., Hik, D.S., 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. J. Ecol. 95, 352–363.

Forbes, B.C., Fauria, M.M., Zetterberg, P., 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. Global Change Biol. 16, 1542–1554.

Gazol, A., Camarero, J.J., 2012. Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. Plant Ecol. 213, 1687–1698.

Grigor'ev, A.A., Moiseev, P.A., Nagimov, Z.Y., 2013. Dynamics of the timberline in high mountain areas of the nether-polar Urals under the influence of current climate change. Russ. J. Ecol. 44, 312–323.

Hallinger, M., Wilmking, M., 2011. No change without a cause- why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia. New Phytol. 89, 902–908.

Hallinger, M., Manthey, M., Wilmking, M., 2010. Establishing a missing link: warm

summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. New Phytol. 186, 890–899.

Hantemirov, R., Shiyatov, S., Gorlanova, L., 2011. Dendroclimatic study of Siberian juniper. Dendrochronologia 29, 119–122.

Juszak, I., Erb, A., Maximov, T.C., Schaepman-Sturb, G., 2014. Arctic shrub effects on NDVI, summer albedo and soil shading. Remote Sens. Environ. 153, 78–79.

Kolishchuk, V.G., 1990. Dendroclimatological study of prostrate woody plants. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Applications in the Environmental Sciences. Kluwer Dordrecht, Boston, London, pp. 51–55.

Larsson, L.-Å., Larsson, P.O., 2013. CooRecorder. Cybis Elektronik & Data AB, 8.1 ed. .

Lehejček, J., 2015. Dwarf tundra shrubs growth as a proxy for late Holocene climate change. Czech Polar Rep. 5, 185–199.

Liang, E., Eckstein, D., 2009. Dendrochronological potential of the alpine shrub Rhododendron nivale on the south-eastern Tibetan Plateau. Ann. Bot. 104, 665–670.

Liang, E., Lu, X., Ren, P., Li, X., Zhu, L., Eckstein, D., 2012. Annual increments of juniper dwarf shrubs above the tree line on the central Tibetan Plateau: a useful climatic proxy. Ann. Bot. 109, 721–728.

Meinardus, C., Weinert, B., Löffler, J., Lundberg, A., Bräuning, A., 2011. The potential of dwarf shrub betula nanaL. as a climate indicator above the tree line in the southern norwegian Scandes. TRACE-Tree-Rings Archeol. Climatol. Ecol. 9, 181–186.

Moiseev, P.A., Bartysh, A.A., Nagimov, Z.Y., 2010. Climate changes and tree stand dynamics at the upper limit of their growth in the North Ural mountains. Russ. J. Ecol. 41, 486–497.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ. Res. Lett. 6, 045509.

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., Speed, J.D.M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N.M., Baittinger, C., Trant, A.J., Hermanutz, L., Collier, L.S., Dawes, M.A., Lantz, T.C., Weijers, S., Jørgensen, R.H., Buchwal, A., Buras, A., Naito, A.T., Ravolainen, V., Schaepman-Strub, G., Wheeler, J.A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015a. Climate sensitivity of shrub growth across the tundra biome. Nat. Clim. Change 5, 887–891.

Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S.A., Weijers, S., Trant, A.J., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Dawes, M.A., Wheeler, J.A., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B.C., Lévesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilmking, M., 2015b. Methods for measuring arctic and alpine shrub growth: a review. Earth Sci. Rev. 140, 1–13.

Pellizzari, E., Pividori, M., Carrer, M., 2014. Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps. Environ. Res. Lett. 9, 104021.

Pellizzari, E., Camarero, J.J., Gazol, A., Granda, E., Shetti, R., Wilmking, M., Moiseev, P., Pividori, M., Carrer, M., 2017. Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. Global Change Biol. 23, 3169–3180.

R Core Team, 2013. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raynolds, M.K., Walker, D.A., Maier, H.A., 2006. NDVI patterns and phytomass distribution in the circumpolar Arctic. Remote Sens. Environ. 102, 271–281.

Ropars, P., Boudreau, S., 2012. Shrub expansion at the forest–tundra ecotone: spatial heterogeneity linked to local topography. Environ. Res. Lett. 7, 015501.

Ropars, P., Angers-Blondin, S., Gagnon, M., Myers-Smith, I.H., Lévesque, E., Boudreau, S., 2017. Different parts: different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. Global Change Biol. 23, 3281–3291.

Sadras, V.O., Denison, R.F., 2009. Do plant parts compete for resources? An evolutionary viewpoint. New Phytol. 183, 565–574.

Schweingruber, F.H., 1988. Tree Rings: Basics and Applications of Dendrochronology Springer, Dordrecht, Netherlands.

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

Sturm, M., Racine, C., Tape, K.D., Cronin, T.W., Caldwell, R.L., Marshall, J., 2001. Increasing shrub abundance in the Arctic.pdf. Nature 411.

Tape, K.D., Sturm, M., Racine, C.H., 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biol. 12, 686–702.

Tape, K.D., Hallinger, M., Welker, J.M., Ruess, R.W., 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. Ecosystems 15, 711–724.

Weijers, S., Wagner-Cremer, F., Sass-Klaassen, U., Broekman, R., Rozema, J., 2013. Reconstructing High Arctic growing season intensity from shoot length growth of a dwarf shrub. Holocene 23, 721–731.

Wilmking, M., Hallinger, M., Van Bogaert, R., Kyncl, T., Babst, F., Hahne, W., Juday, G.P., de Luis, M., Novak, K., Völlm, C., 2012. Continuously missing outer rings in woody plants at their distributional margins. Dendrochronologia 30, 213–222.

Web/Dataset references

[dataset] Salekhard Climate Station Data 2016. Russian Federation Meteorological Station Data Access date 02.02.2016 available at < http://meteo.ru/data > .

[dataset] Taganay Climate Station Data 2016. Russian Federation Meteorological Station Data Access date 02.02.2016 available at < http://meteo.ru/data > .

[dataset] Cherdin Climate Station Data 2016. Russian Federation Meteorological Station Data Access date 02.02.2016 available at < http://meteo.ru/data > .

[dataset] Climate Explorer. Koninklijk Nederlands Meteorologisch Instituut Access date 10.05.2017 available at < https://climexp.knmi.nl/start.cgi?id=someone@somewhere > .

Supplements
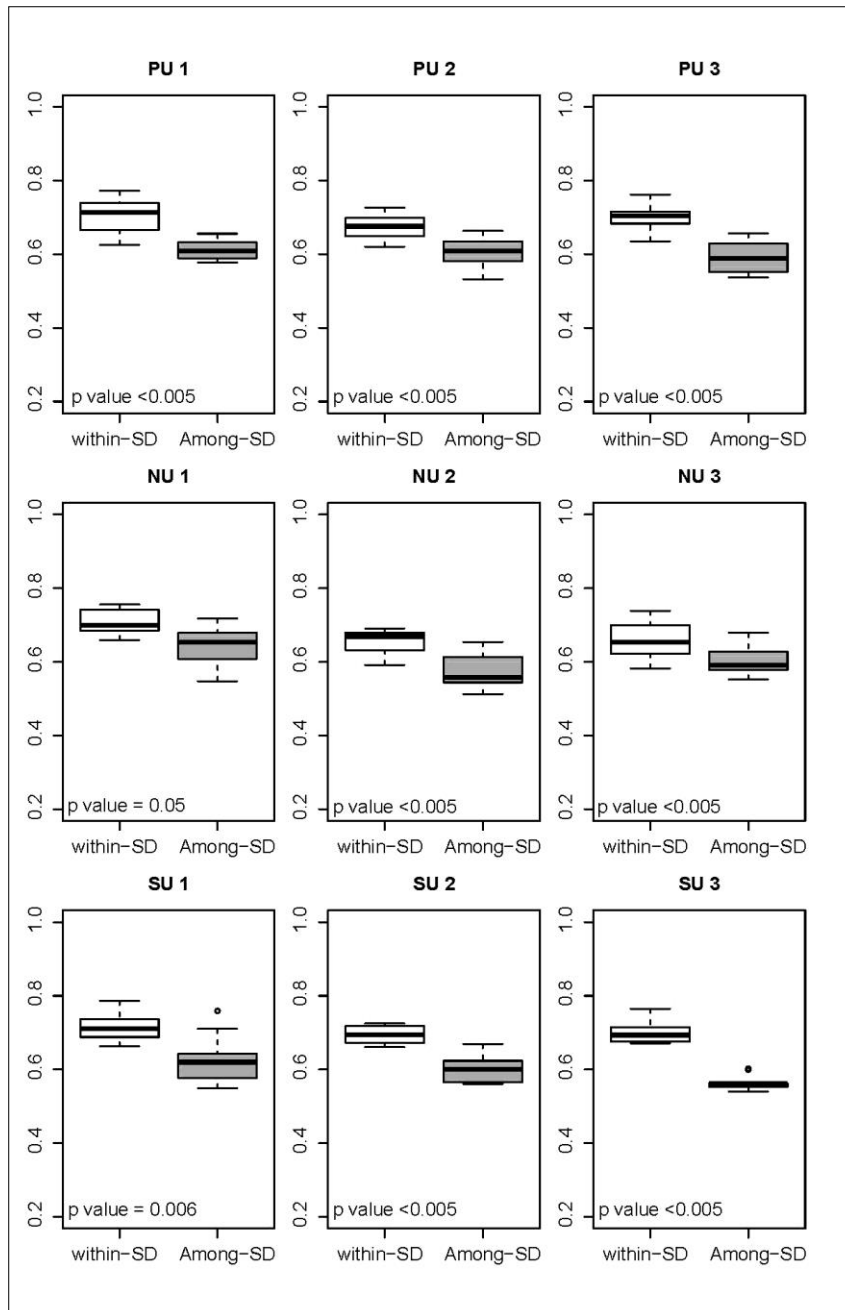
Figure: S1

Figure S1 Showing comparison of Gleichläufigkeit of within SD (stem disk) radial ring-width measurements (white boxplot) to among SD (grey boxplot) radial measurements wherein in all cases the within-SD Gleichläufigkeit is significantly higher than among-SD gleichlaeufigkeit. At all sites the elevational plots range from the shrubline to treeline marked with abbreviations (Polar Ural: PU1, PU2, PU3. Northern Ural: NU1, NU2, NU3. Southern Ural: SU1, SU2, SU3)

Figure S2

Mean sensitivity analysis

Figure S2 Shows comparison of mean sensitivity of radial measurements from individual stem disk (SD) chronologies (SD0,SD10 and SD20). At all sites the elevational plots range from the shrubline to treeline marked with abbreviations (Polar Ural: PU1, PU2, PU3. Northern Ural: NU1, NU2, NU3. Southern Ural: SU1, SU2, SU3)

Supplements: Table S1

Temperature and precipitation climate station data sourced from Russian Federation Meteorological data website (RIHMI-WDC, 2017)

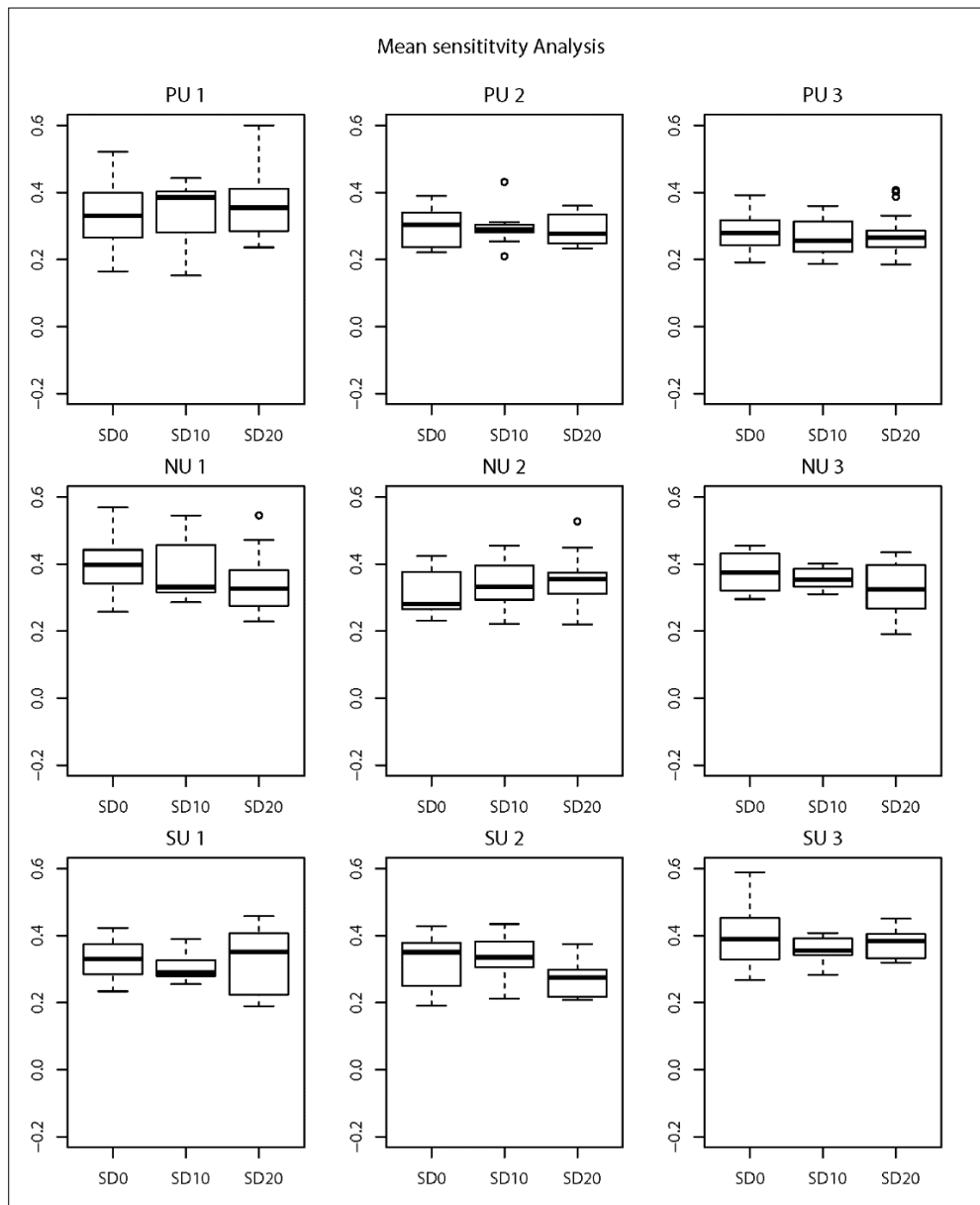| Polar Urals [PU]	Latitude	Longitude	Elevation [m]	Exposition	Dominant/Co-dominant vegetation	*Mean summer temperature [°C]	**Mean Winter Temperature [°C]	Mean annual precipitation [mm]	Climate Station	Distance to sampling site [km]
PU 1	N66°49 12.9"	E65°33 28.9"	303	South	*Juniperus communis* L./ *Betula nana,* *Vaccinium uliginosum*	7.56	-16.12	370	Salekhard	50
PU 2	N66°48 37.5"	E65°35 19.2"	202	South						
PU 3	N66°48 62.8"	E65°35.313"	169	South						
Northern Urals [NU]										
NU 1	N61°19 07.7"	E59°14 00.4"	890	South	*Juniperus communis* L. / *Betula nana,* *Vaccinium uliginosum*	12.35	-8.4	632	Cherdyn	90
NU 2	N61°18 13.6"	E59°13 07.8"	790	South						
NU 3	N61°17 49.7"	E59°13 38.7"	777	South						
Southern Urals [SU]										
SU 1	N54°33 10.7"	E58°53 20.4"	1391	South west	*Juniperus communis.*L / *Betula tortuosa,* *Salix glauca,* *Picea sp.*	8.92	-9.28	318	Taganay	88
SU 2	N54°33 19.4"	E58°52 46.9"	1359	South west						
SU 3	N54°33 50.3"	E58°52 13.3"	1307	South west						

*mean summer temperature are the annual averages for the months May to September. ** mean winter temperature are the annual averages for the months October to April.

Table S2: Measurement details: Ring-width series descriptive statistics over a 30 years overlap.

Site	No of individuals	SD0	SD10	SD20	EPS	$\acute{r}$	GLK within SD	GLK among SD	GLK inter series	Years overlap
PU 1	7	25	28	28	0.73	0.17	0.64	0.52	0.54	1978-2007
PU 2	9	32	39	38	0.84	0.35	0.61	0.55	0.61	1978-2007
PU 3	13	32	36	34	0.54	0.17	0.61	0.51	0.52	1978-2007
NU 1	9	36	36	36	0.61	0.15	0.66	0.56	0.58	1982-2011
NU 2	10	29	30	31	0.35	0.04	0.58	0.51	0.51	1978-2007
NU 3	7	28	23	26	0.60	0.16	0.59	0.51	0.51	1978-2007
SU 1	7	25	32	40	0.59	0.13	0.61	0.56	0.56	1978-2007
SU 2	6	24	23	24	0.70	0.20	0.74	0.59	0.61	1978-2007
SU 3	9	33	39	35	0.87	0.40	0.56	0.52	0.57	1978-2007

$\acute{r}$: Mean inter series correlation. Calculated for SD0 chronology (Basal Stem Disks)

EPS: Expressed Population Signal calculated for SD0 chronology.

SD0, SD10, SD20: amount of radial measurements which were used in calculating EPS, $\acute{r}$,

Gleichläufigkeit and all other analysis throughout this investigation

Gleichläufigkeit (GLK) within stem disk: Mean Gleichläufigkeit among radial measurements

within stem disks

Gleichläufigkeit (GLK) among stem disk: Mean Gleichläufigkeit among radial measurements

among stem disks within an individual

Gleichläufigkeit (GLK) inter-series: Mean Gleichläufigkeit among individual shrubs within a plot.
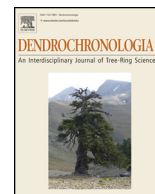
Chapter 3

Does sex matter? Gender specificity and its influence on site-chronologies in the common dioecious shrub *Juniperus communis* **(Dendrochronologia 49 (2018) 118-126)**

Does sex matter? Gender-specificity and its influence on site-chronologies in the common dioecious shrub *Juniperus communis*

Rohan Shetti[a,*], Allan Buras[b], Marko Smiljanic[a], Martin Hallinger[c], Andrey A. Grigoriev[d], Martin Wilmking[a]

[a] *Institute of Botany and Landscape Ecology, Ernst-Moritz-Arndt University Greifswald, Soldmannstrasse 15, D-17487 Greifswald, Germany*
[b] *Forest Ecology and Forest Management, Wageningen University and Research, Droevendaalsestag 3a, 6708 PB Wageningen, Netherlands*
[c] *Swedish University of Agricultural Sciences Uppsala, Biology Department, 750 07 Uppsala, Sweden*
[d] *Institute of Plant and Animal Ecology, 8 Marta St. 202, Yekaterinburg 620144, Russia*

ABSTRACT

In recent years an increasing number of studies have shown shrubs to be reliable proxies of environmental conditions in regions where Trees − due to harsh climate conditions − are absent. Although many shrubs are monoecious, some are dioecious, which poses certain questions related to gender-specific growth as observed for trees in previous studies. Here, we address the questions whether dioecious shrubs, similar to trees, show growth differences between male and female plants, and − if so − whether this difference needs to be considered in terms of sample selection. We chose *Juniperus communis*. L., the most widely distributed woody plant, and a common and well-studied dioecious shrub species in the northern hemisphere, especially in the Boreal, Subarctic tundra and Alpine regions. Our samples were collected from four sites − three from the Ural Mountains and one site from Kirkenes in Norway. To see if there were differences in radial growth between sexes we performed four different analyses. First, we used multivariate explorative statistics to see if there were gender biased sub-populations and generally found no differences. Secondly, to compare growth over the lifetime of shrubs we computed cumulative annual increments of basal area which revealed no gender-specific growth patterns. Thirdly, to test if differences in radial growth between male and female shrubs affect the resulting site-chronology, we compared individual shrub chronologies with the site-chronology and found a significant differentiation between normalized correlations of gender-specific chronologies to the site-chronology. This significant difference was restricted to an overall comparison, but not evident at individual site-level. Lastly, we compared correlations of gender-specific chronologies and a mean site-chronology with monthly climate records to find only very few meaningful differences in their responses. In summary, we could not detect any clear gender-specific growth pattern in *Juniperus communis* but observed a trend towards more non-climatic signals in female junipers which may affect the resulting site-chronology.

1. Introduction

The last decade has seen a remarkably increased number of arctic and alpine shrub studies. Many studies suggest shrub growth is highly sensitive to current climate warming (Sturm et al., 2001; Forbes et al., 2010; Myers-Smith et al., 2015a). Future warming will probably benefit shrub growth and reproduction in the circumpolar Arctic with consequences for carbon and nutrient cycling, surface albedo, permafrost degradation, and species distribution and competition (Cornelissen et al., 2007; Hudson and Henry, 2009; Myers-Smith et al., 2011; Elmendorf et al., 2012; Tape et al., 2012; Juszak et al., 2014). Shrubs form annual growth rings like trees and many recent studies

have shown that these annual rings in shrubs are sensitive to changes in the environment, especially climate variability, for example Danby and Hik (2007); Hallinger et al. (2010); Blok et al. (2011); Hallinger and Wilmking (2011). Consequently, ring-width data from shrubs can be useful for ecological reconstructions (Lehejček, 2015) like temperature (Liang and Eckstein, 2009; Weijers et al., 2010; Meinardus et al., 2011; Weijers et al., 2012; Weijers et al., 2013), humidity (Liang et al., 2012), glacier melting (Buras et al., 2012; Buras et al., 2017), permafrost degradation (Blok et al., 2010), sea surface temperatures (Beil et al., 2015) and fire history in a landscape (Oddi and Ghermandi, 2015). Therefore, increased use of shrubs in future dendrochronological research is very likely.

Fig. 1. Map showing sampling locations.

mean for radial growth, which is often a key factor considered in dendrochronological studies. Therefore to investigate if sex-biased differences impact radial growth and the resulting site-chronologies − commonly used for environmental and climate reconstructions − we hypothesized that radial growth patterns between male and female shrubs differ.

To test our hypothesis, we investigated the radial growth in *Juniperus communis* L. (with subspecies *nana* WILLD) across a network of sites at the transition from boreal to alpine and subarctic environments with a special focus on whether gender-specific growth rates and responses exist, and − if so − how these may bias the overall site-chronology.

Many studies using dioecious tree or shrub species did not consider sex-specific differences (Zalatan and Gajewski, 2006; Liang and Eckstein, 2009; Hantemirov et al., 2011; Gazol and Camarero, 2012; Liang et al., 2012; Pellizzari et al., 2014). Especially in light of the growing amount of shrub studies it becomes imperative to understand if gender-specific differences are substantial and if they influence radial growth and should be considered during sampling and analysis.

2. Materials and methods

For our study, we collected *Juniperus communis* L. (including ssp *nana* WILLD) samples from four sites across the Eurasian Arctic and Subarctic: Three sites along the Ural Mountains, Russia, and one site in northern Norway at Kirkenes (Fig. 1, Table 1).

2.1. Sampling design

At the Russian sites, the samples were collected along an elevational gradient starting from the treeline to the shrubline, in Norway samples were collected at or beyond treeline. For every individual, we harvested the longest stem and adhered to the procedures as prescribed by Kolishchuk (1990) and Myers-Smith et al. (2015a). The samples were checked for presence of berries, cones and flowers at the time of harvesting to determine their gender and labelled accordingly. In total we collected 221 samples over four sites, but were only able to successfully cross-date 71 samples which were then used for our analysis. A detailed summary of samples and corresponding measurements is available in Table 2.

2.1.1. Sample treatment and measuring

We harvested the longest stem of the individuals and took stem disk sections at every 10 cm along the length of the stem beginning from the root collar at 0 cm (closest to the root and soil surface) up to the apical shoot (Kolishchuk, 1990; Wilmking et al., 2012). The stems ranged from minimum of 40 cm to maximum 130 cm. Depending on the length of the stem we took a minimum of four to a maximum of eleven stem disks per shrub. In the lab, we polished all sampled stem disks on a belt sander using sand papers with increasingly fine grit from P-60 to P-400 and then scanned them on an EPSON-V700 scanner at 4800 dpi. We measured ring width using POS (position files) in CooRecorder software (Version 8.1, Cybis AS, Sweden) and cross-dated the series in CDendro software (Version 8.1, Cybis AS, Sweden) (Larsson and Larsson, 2013). Following the recommendation by Buras and Wilmking (2014) we aimed at four radial measurements for every stem disk but in some

Table 1
Sampling Location.

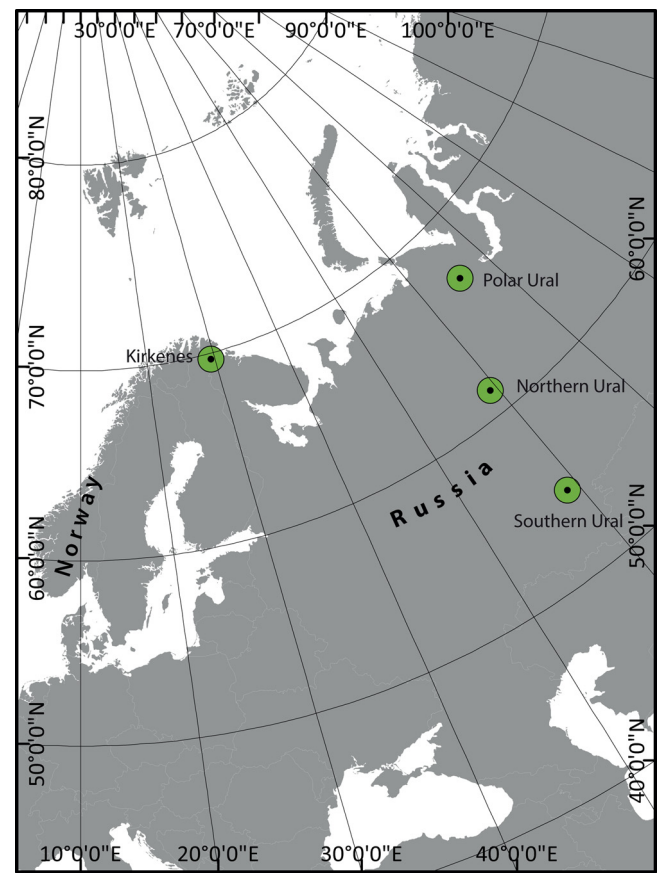| Site	Latitude	Longitude	Elevation a.s.l [m]	Exposition	Species	Climate Data
Polar Ural	N66°48′ 37.5″	E65°35′ 19.2″	202	S	*Juniperus communis.* L.	Salekhard Climate Station
Northern Ural	N61°18′ 13.6″	E59°13′ 07.8″	790	S		Cherdyn Climate Station
Southern Ural	N54°33′ 19.4″	E58°52′ 46.9″	1359	S		Taganay Climate Station
Kirkenes	N69°41′ 8.41″	E29°23′ 04.54″	63	S	*Juniperus communis* ssp *nana.* WILLD	CRUTEM Gridded Data

However, some abundant shrub species like willows or junipers exhibit sexual dimorphism (Verdu et al., 2004; Sakai et al., 2006). Tree-based studies have shown gender-specific growth patterns in species exhibiting sexual dimorphism (Rozas et al., 2009). These differences are commonly associated with reproductive effort in female plants (Boulanger-Lapointe et al., 2016) which causes higher resource investment into reproductive organs and therefore lower resource availability for radial or apical growth (Lloyd and Webb, 1977; Meagher and Antonovics, 1982; Banuelos and Obeso, 2004). Other sex specific differences such as difference in time of maturity for production of flowers (Godley, 1976), spatial segregation (Freeman et al., 1976; Marion and Houle, 1996; Barradas and Otilia, 1999), rate of mortality and resistance to diseases and pests (Ward, 2007), age dependent sensitivity to climate (Rozas et al., 2009), and difference in sex ratios between population stands to ecologically differing micro-sites (Freeman et al., 1976; Gauquelin et al., 2002) have also been reported. Prior studies with *Salix arctica* have shown that males and females have notable differences in water uptake and stomatal conductance leading to differences in water use efficiency (Dawson and Bliss, 1989). These differences resulted in an overall difference in apical growth and plant biomass, which is hypothesized to cause a sex bias in ecological niche selection (Dawson and Bliss, 1989; Boulanger-Lapointe et al., 2016).

However, there is still a knowledge gap on what do these differences

Table 2

Chronology statistics.

Site Name	total (n) harvested	(n) cross-dated	♂(n)	♀(n)	♂ rbar	♀ rbar	♂ GLK	♀GLK	Missing-rings[%]
Polar Ural	50	20	11	9	0.49	0.37	0.58	0.59	0.14
Northern Ural	111	25	11	14	0.36	0.13	0.59	0.57	0.00
Southern Ural	30	18	11	7	0.18	0.16	0.56	0.60	0.25
Kirkenes	30	8	5	3	0.37	0.26	0.66	0.60	0.00

Table 2 shows details about harvested samples and chronology statistics of radial measurements; n: number of samples; ♂ rbar : mean inter-series correlation calculated for individual male shrub ring-width chronologies; ♀ rbar : mean inter-series correlation calculated for individual female shrub ring-width chronologies; ♂ GLK : mean Gleichläufigkeit of male shrub chronologies; ♀ GLK : mean Gleichläufigkeit of female shrub chronologies.

cases it was only possible to measure three radii because of asymmetric and lobed growth forms.

2.1.2. Cross-dating

In a first step we cross-dated all the radial measurements of a specific stem disk with each other to account for possibly wedging or missing rings. Secondly, by averaging all radial measurements from within a stem disk we prepared an average chronology for every stem disk in an individual and then cross-dated it with other stem disks from that individual. This was done to get a relative date of the stem disk and identify possibly missing outer rings and wedging rings in lower stem disks, which are common in many woody species at their distributional limit (Wilmking et al., 2012). We found it hard to cross-date individual samples because of asynchronous growth patterns − evident from ring-width chronologies- among different individuals in a sampling plot at a site. These differences might be due to strong influences of micro-site conditions like wind, snow cover and substrate conditions causing differential growth in basal stem disks (Sonesson and Callaghan, 1991; le Roux and Luoto, 2014; Ropars et al., 2017). Generally, the cross-dated basal stem disk (section at 0 cm) was used for subsequent analyses. In some cases, sections from 10 cm or 20 cm were used for analytical purposes if the lower-most stem disk had multiple piths, or structural damage due to burial and/or rot. We then cross-dated the lower-most stem disks from every individual in a stand with one another and then we used the cross-dated measurements to generate site- and gender-specific chronologies for every site. Cross-dating was done in CDendro software (Larsson and Larsson, 2013) (Version 8.1, Cybis, AS, Sweden) using inter-series correlation, blockwise correlation (compares time segments of chronologies using Correlation and Gleichläufigkeit) and Gleichlaeufigkeit (Eckstein and Bauch, 1969). We agreed upon the final dating with visual inspection as prescribed by Schweingruber (1988).

2.1.3. Detrending

We used two different types of detrending 1) To normalise the ring-width series we used horizontal mean detrended ring-width indices for cluster analysis, and the principle component gradient analysis (PCGA) (Buras et al., 2016). For climate sensitivity analysis we detrended the raw ring-width data with a 30 years spline to remove any low frequency trends and developed prewhitened chronologies. Similarly, we detrended climate data with a 30 years spline as well. This was done in R software (version 3.0.2) (R Core Team, 2013) extended for the dplR (Bunn, 2008) package version 1.6.5 (Bunn et al., 2015). 2) Basal area increment chronologies were developed from raw ring-width data and used for cumulative incremental growth analysis.

2.2. Statistical analysis

Our analysis consisted of four key steps which are described in detail in the following sections: 1) We investigated if there are sex-biased differences in radial growth by using a cluster analysis and principle component gradient analysis (PCGA, Buras et al., 2016). 2) Then we

compared cumulative annual increments of basal area to see if growth differs over age between sexes. 3) We correlated and compared individual shrub chronologies of both sexes with the site-chronology to see if the difference between gender-specific chronologies was statistically significant and − if so − how this might affect the resulting site-chronology. Since the sample sizes per site were rather low and to gain a general overview, we aggregated normalized correlations of all individual gender separated chronologies at each site with their respective site-chronologies and compared the correlation scores. 4) Finally to compare the response of gender-specific chronologies to climate we correlated gender-specific chronologies and a mean site-chronology from every site with monthly temperature and precipitation records. All analyses were computed using 'R' (version 3.0.2) (R Core Team, 2013).

2.2.1. Cluster analysis

To test if there were any differences in radial growth between males and females we conducted a cluster analysis of ring-width indices (horizontal mean detrended series) using all individuals per site. This was done by using Euclidian distances and hierarchical agglomerative clustering. The results were plotted as cluster dendrogram for each site.

2.2.2. Principle Component Gradient Analysis

We used Principle Component Gradient Analysis (PCGA), an approach developed for detecting gradients in time-series populations (Buras et al., 2016). PCGA makes use of the individual loadings from an ordinary PCA (Principal Component Analysis) to place single time-series within a statistical gradient. That is, in PCGA time-series are related to each other by their loadings, and − if the first two principal components explain a fair amount of the overall variance − this directly reflects the inter-series correlations of those series. Thus, time-series with rather similar loadings will be more similar to each other than time-series with dissimilar loadings, and the variation of loadings may resemble an actual gradient inherent to the data (Buras et al., 2016). For our analyses, PCGA was used to investigate whether male and female shrub-ring series are clearly differentiated from each other.

2.2.3. Annual increments

Prior studies with juniper shrubs have reported differential growth over their lifetime as a response to physiological and ecological stress. This difference is commonly linked with reproductive effort of female plants which results in reduced apical shoot growth in females (Ward, 2007) and delayed flowering (Gauquelin et al., 2002; Rozas et al., 2009). Therefore, we aligned all the BAI (basal area increment) measurements for every individual per site by cambial age and computed an incremental function for every year's growth to be added to the original value and plotted it as a curve.

2.2.4. Correlation with site-chronology

To study the influence of individual ring-width series on the "site-chronology" a common parameter used in reconstructions and response functions, we generated a site-chronology per site which included all

the individual ring-width series from that respective site. Then we individually correlated males and females from the respective site with this site-chronology, after first removing them from the averaged chronology. We used horizontal mean detrended ring-width series for this analysis. The scores were stored as vectorised values and were then plotted as box plots. To see if there was a difference in the correlation scores of males and females with the site-chronology we administered a Wilcoxon rank-sum test on the gender-differentiated sub group correlations at every site.

To gain an overall perspective of influence of individual gender-specific radial measurements on site-chronologies, we normalised the correlation scores of gender-separated ring-width indices with the respective site-chronologies. That is, since correlation strengths varied among sites, each site-specific correlation had to be normalized by the site-specific correlation mean prior to the analyses. Then we pooled the normalized correlations scores from all sites by gender and compared them using Wilcoxon rank-sum test.

2.2.5. Climate sensitivity analysis

To study the relationships of gender-specific chronologies and the site-chronology to climate data, we correlated monthly temperature and precipitation records with ring-width measurements. For every site we generated three chronologies, one for males, one for females, and a mean site-chronology. For climate records, we used station data for all Ural sites (Russian Federation Meteorological Station Data) and

CRUTEM gridded data (KMNI Climate Explorer) for Kirkenes as there were substantial gaps in the station data there.

3. Results

### 3.1. Differences in radial growth

Neither the cluster analysis (Fig. 2) nor the PCGA (Fig. 3) did show any gender biased clustering in any of the sites. In all the plots of the cluster analysis, the secondary tiers were relatively longer than the primary tiers (longer line heights indicating greater Euclidian distances). In none of the cases did the primary tier cluster show a gender-biased differentiation. The apparent gender biased cluster in the Polar Ural site, however, is characterized by the height of the top cluster (indicating only little difference between them). This height length being lesser than the height length of potential gender based cluster indicated that there is no substantial difference between the two subsets and demonstrated potential preference of the algorithm towards being one large cluster (Fig. 2).

3.2. Comparison of BAI cumulative increments

In the comparison of BAI (basal area increment) chronologies arranged by cambial age, we observed no sex defined separations in annual increments at any site. There were no consistent differences seen in
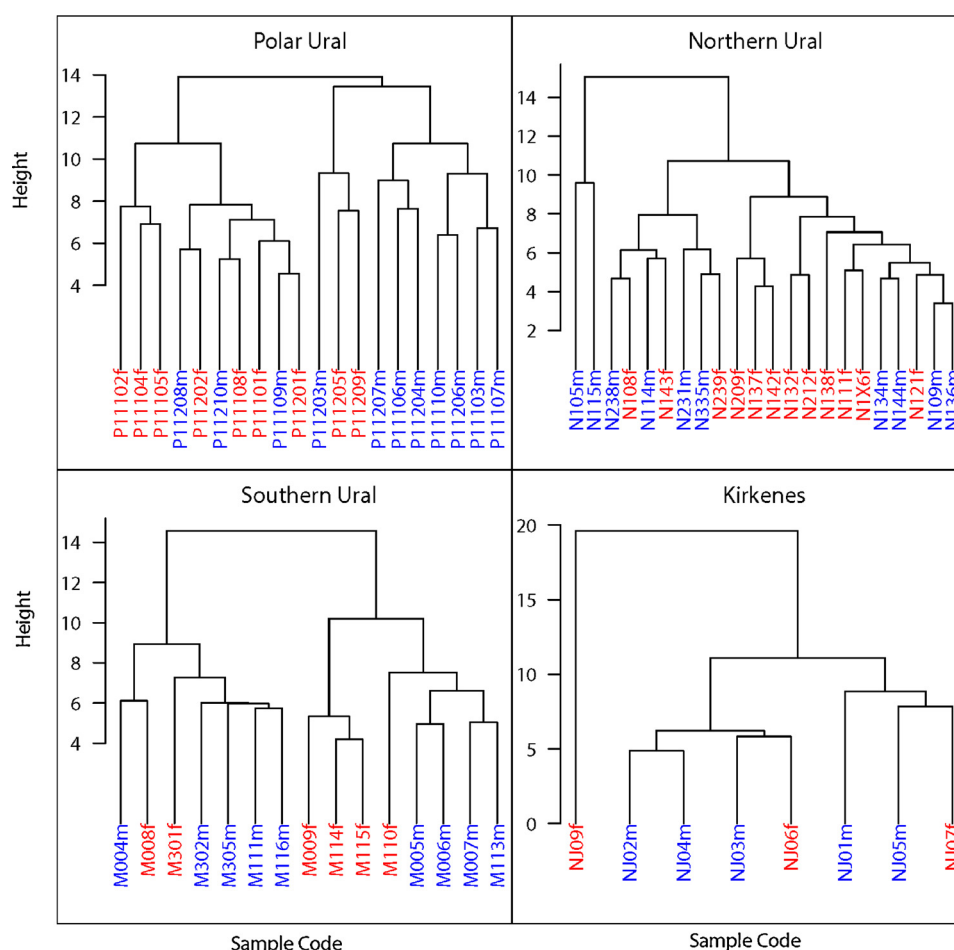
Fig. 2. Dendrogram plots from the cluster analysis for all sites. Sample codes marked in red are female samples and codes marked in blue are males. No clear clustering at any site is apparent. In all cases secondary tiers of clustering have lager Euclidian distances than primary tiers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

37
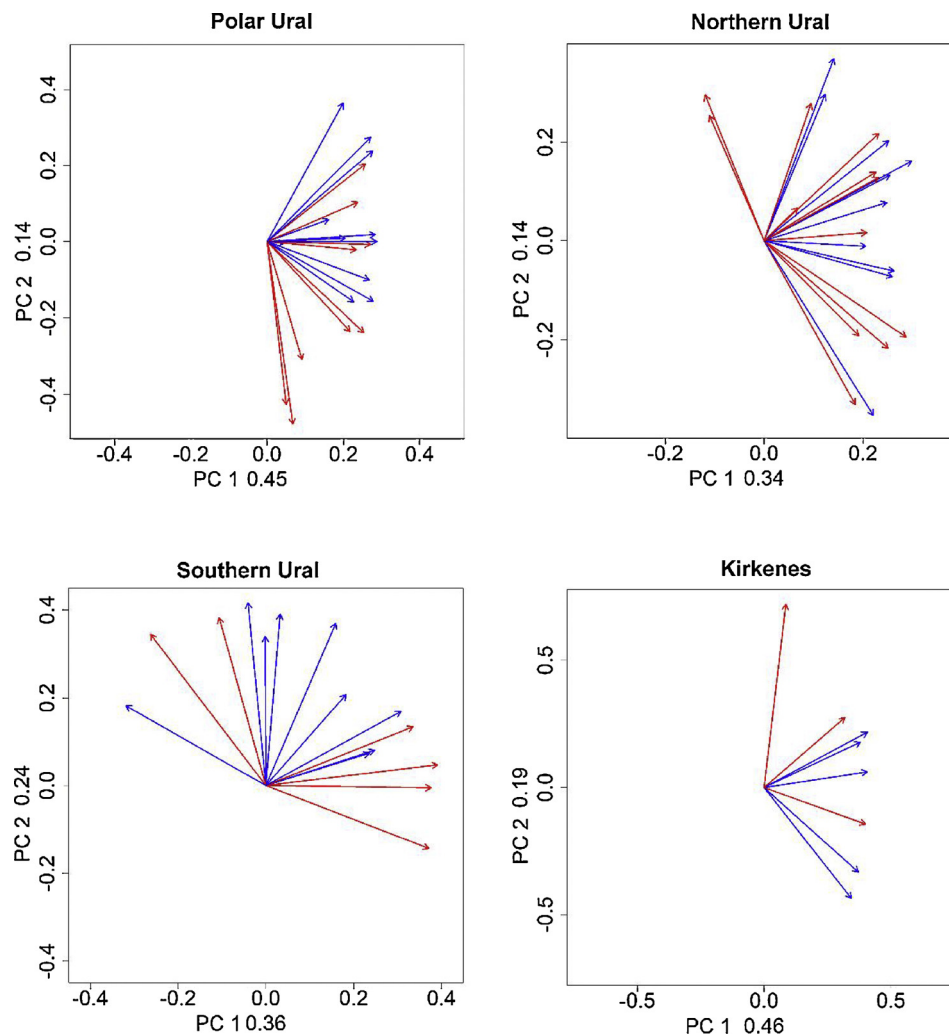
Fig. 3. Biplots showing results of principle component gradient analysis (PCGA). Blue arrows represent male and red arrows represent female shrubs. No clear differentiation between male and female shrub growth records is apparent. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

growth patterns at growth onset nor with the increasing age of individuals. Both sexes showed similar growth patterns over increasing age at all the sites (Fig. 4).

3.3. Comparison of individual series with site-chronology

Comparing influence of individual ring-width series on site-chronology indicated lower correlations for female shrubs (Fig. 5). Although all underlying tests were insignificant, Northern Ural (NU) site showed an almost significant difference (p = .05). This general tendency was confirmed by the analysis including all sites, since it revealed significantly lower correlation scores for female junipers (Fig. 6; p = .01). Altogether, we noticed a considerable amount of variation within sites with series having weak and in some cases (Fig. 5: Northern Ural) negative correlations with their site-chronology. Low rbar (mean interseries correlation) values confirmed heterogeneous growth within sites and individual gender series and supported the general impression that the population signal was weaker for female shrubs since they overall expressed lower rbar values as compared to male shrubs (Table 2).

3.4. Sex-specific climate sensitivity

In our analyses of climate-growth relationships, we found that all chronologies from Ural sites correlated positively with temperature.

Contrarily, at the Kirkenes site all chronologies showed negative and relatively (as compared to Ural sites) weaker correlations with temperature. On most of the sites there was a moderate difference in correlations with temperature of gender-specific chronologies as compared to each other and with the site-chronology (Supplement; Fig. S1). At Kirkenes there is a significant differentiation evident in response to previous year July and current year February and March temperatures wherein females show a pronounced negative correlation as compared to male chronology and the site-chronology.

Comparing responses of males, females and site-chronology with precipitation data we found that across all sites the correlations were very weak (−0.3 to 0.3) and barely significant. Only at Northern Ural and Kirkenes sites could we see moderately significant correlations. At Northern Ural site, females better correlated with current year May and June records as compared to males. At Kirkenes females seem to strongly negatively correlate to precipitation records for current year February as compared to males. (Supplement; Fig. S2).

4. Discussion

Our study looked at data from radial measurements (i.e. ring-width indices and BAI) and compared measurements from both sexes using multivariate and time series analysis. Furthermore, we studied responses of gender-specific chronologies with climate records to
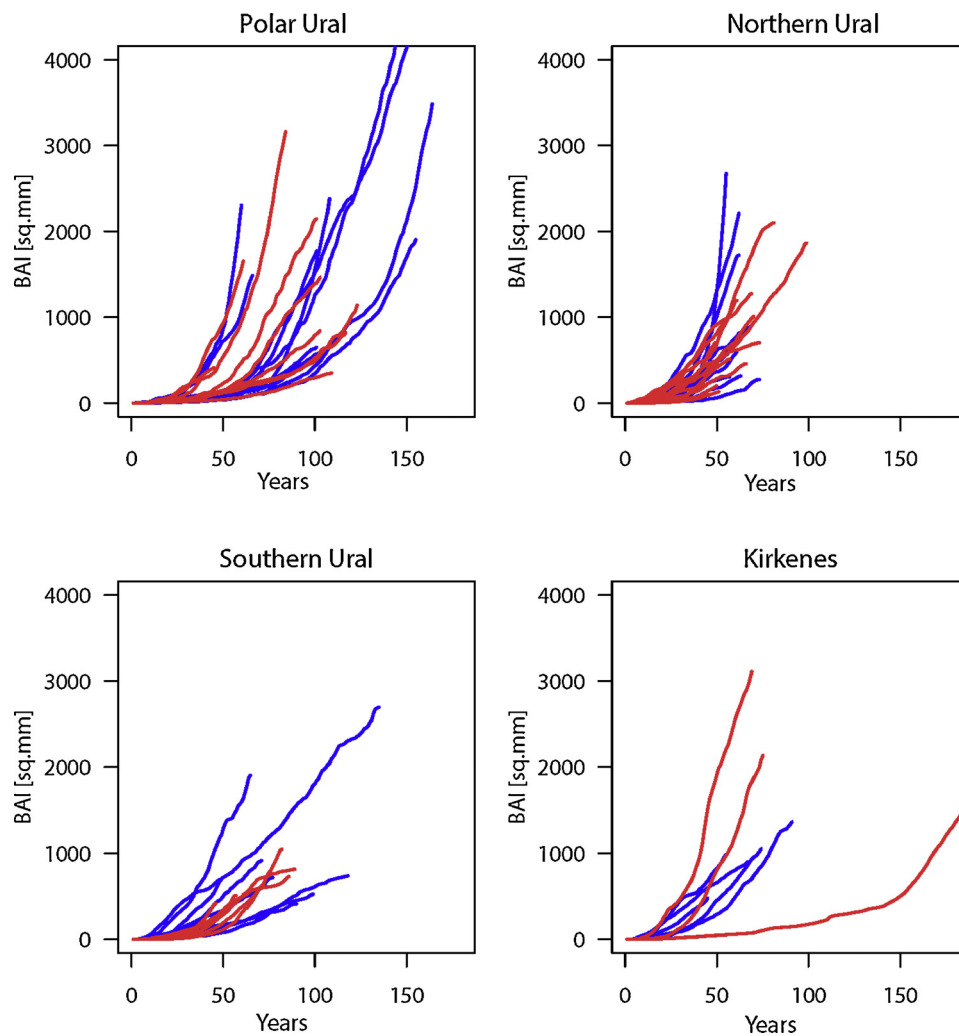
Fig. 4. Cumulative annual increment of cambial age aligned basal area. Blue lines represent male and red lines represent female shrubs. No clear differentiation between male and female shrub growth over time is apparent. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

understand if a sex bias in sampling affects climate-growth relationships.

4.1. Sex-specific indifferences and differences in ring-widths

In the initial part of our investigation, we used multivariate explorative statistics viz. Cluster Analysis and Principle Component Gradient Analysis (PCGA) and found no gender biased sub-groups in either of the cases. A major advantage of using Cluster Analysis and PCGA is that we could compare ring-width chronologies from individuals from a stand and quantify differences in them. However, a possible reason for not detecting any gender biased subgroups might be that ring-width formation between separate genders does not differ consistently over time. Therefore, event or time specific responses – which could potentially differ- are not reflected in these analyses as entire chronologies are compared as singular units of time-series. This means that entire ring-width chronologies are compared and individual time segments which could have differential growth are not represented in these analyses. A limitation of cluster analysis is that it can be interpreted subjectively as Euclidian distances show relative distances among tiers. Even in PCGA results across all the sites, there were no clearly separated gender biased subgroups (Fig. 3), confirming the results of the cluster analysis. These two results basically indicate, that there seems to be no gender-specific growth signal. Thus, it seems likely

that both sexes react to a common environmental driver.

To see if 'reproductive effort' in females, which is reported to be more resource intensive towards maturity of the individual, becomes a differentiating factor with increasing age (Ortiz et al., 2002; Banuelos, 2004), we compared incremental growth from both sexes, but did not find any gender-specific absolute growth rates (Fig. 4). In prior studies with the tree *Juniperus thurifera* (Gauquelin et al., 2002) and shrub *Juniperus communis* subsp. *alpina* (Ortiz et al., 2002) gender-related difference in radial growth and apical shoot in response to climate have been observed. However, our analysis demonstrated no consistent differentiation in secondary growth which could be attributed to gender-specificity.

A pivotal aspect of most dendrochronological studies is the site-chronology, as it represents the overall growth signal of a population. Heterogeneous growth within populations can be due to various intrinsic and extrinsic factors (Schweingruber and Poschold, 2005). In the context of gender-related differences, intrinsic factors could be the differing allocation of photo-assimilates between the different sexes (Boulanger-Lapointe et al., 2016). More specifically, female junipers from time to time invest a remarkable amount of resources in reproduction, since it can take up to three seasons in harsh environments such as the Arctic and alpine for female cones ("berries") to ripen (Singh, 1978; Ortiz et al., 2002). It therefore seems possible that secondary growth rates in these periods differ from males and/or other

39

Fig. 5. Comparison of correlation scores of individual gender-specific shrub growth records with the respective site-chronology. Blue colour represents male and red colour represents female shrubs respectively. No significant differentiation between male and female shrubs and the composite site-chronology is apparent. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
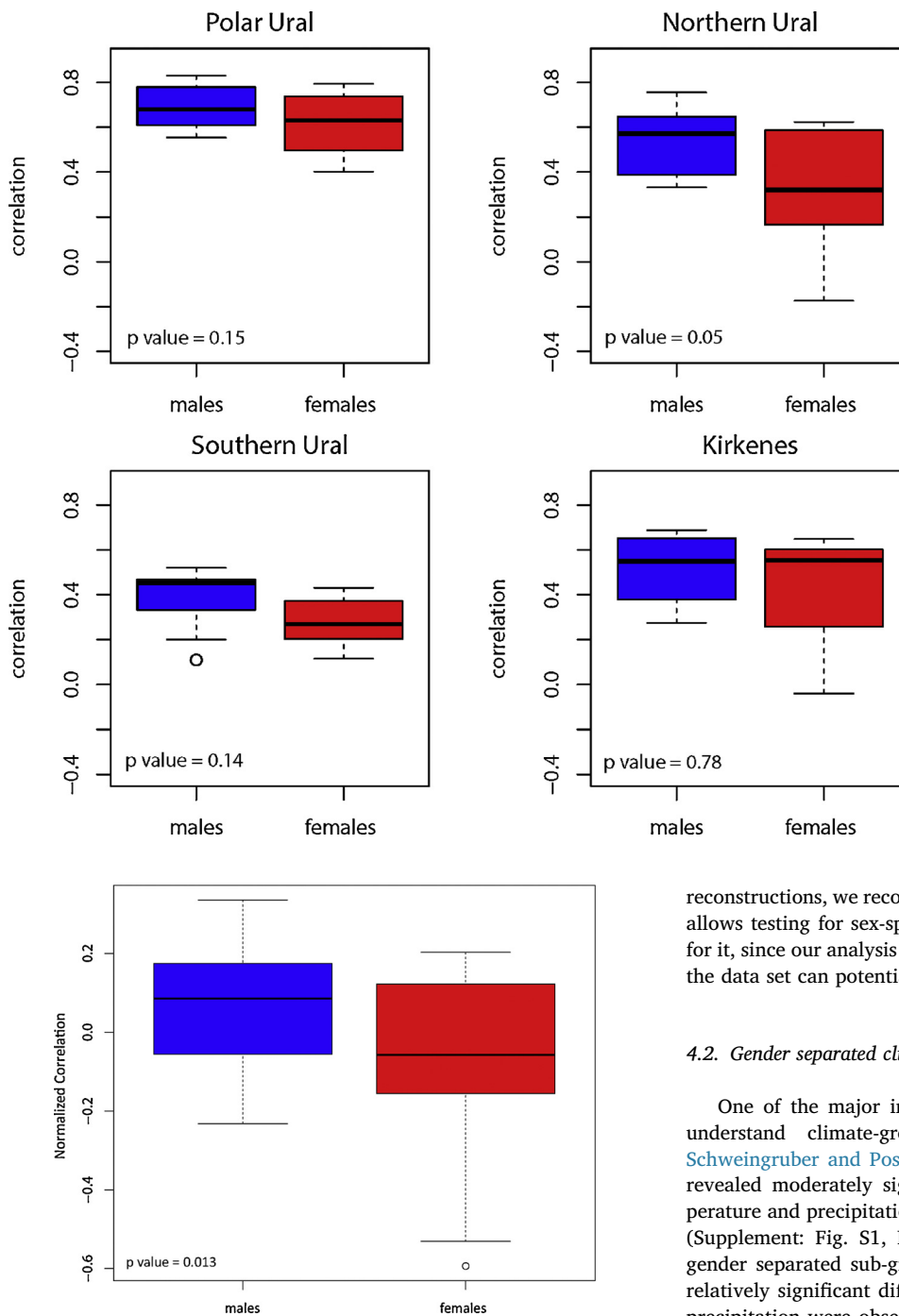

Fig. 6. shows an overall comparison of normalized correlations of gender-separated chronologies compared to the site-chronology across all sampling sites.

females which in that period invest less resources in reproduction. Our analyses appeared to confirm this assumption. That is, we observed a general tendency towards lower site-chronology correlations of female junipers which were significant if analysed across all sites (Figs. 5 and 6). This impression was supported by generally lower rbar values for the female junipers (Table 2). Although we were unable to identify the specific reasons, our results indicate that when building a master chronology, female junipers may contribute more noise (i.e. non-climate driven growth variations) to the population signal when compared to male junipers.

However, one man's noise is another man's signal and therefore, to avoid possible gender-specific biases of dendroclimatological

reconstructions, we recommend a balanced sampling of both sexes. This allows testing for sex-specific differences and, if necessary, correcting for it, since our analysis seems to suggest that a potential female bias in the data set can potentially add noise.

4.2. Gender separated climate sensitivity

One of the major implications of dendrochronological data is to understand climate-growth relationships (Schweingruber, 1988; Schweingruber and Poschold, 2005; Forbes et al., 2010). Our results revealed moderately significant differences in correlation with temperature and precipitation records among gender separated sub-groups (Supplement: Fig. S1, Fig. S2). Overall no contrasting responses of gender separated sub-groups were observed. However in some cases relatively significant differences in correlations with temperature and precipitation were observed e.g. Northern Ural and Kirkenes. A probable reason for this statistically just significant differentiation might be that differences in radial growth patterns among males and females do not differ consistently over time. Therefore differential responses to specific events like harsh winters or drought or growth release due to some extreme events which could have gender-specific responses − as many times coping mechanisms differ between genders − could not be traced in our analysis. Another factor is individual growth reactions which is commonly observed in shrubs and is reflected by low inter-series correlation (Table 2 and e.g. Buras and Wilmking, 2014). Differential radial and axial growth might be the result of intrinsic factors like branching, formation of multiple piths or extrinsic factors like irregular substrates, soil or snow burial, rotting and might be independent of sex (Sadras and Denison, 2009; Myers-Smith et al., 2015b).

Furthermore, at the Ural sites the climate stations were at a considerable distance (about 100 km) from the sampling sites. The

sampling was done in mountainous regions and micro-climate might differ notably from station data. Even so with gridded data, in case of Kirkenes site micro-site conditions can differ significantly. This also might result in weak climate sensitivity as evident from our analysis.

4.3. Sexual dimorphism in trees and shrubs

Many studies with sexually dimorphic tree species suggest differences in radial growth, allocation of resources, flowering and also with sex ratios within populations (Cavigelli et al., 1986; Obeso et al., 1998; Gao et al., 2010). Contrarily, a study by Robinson et al. (2014) on *Populus tremula* showed no differentiation in male and female trees with respect to growth, flowering or resource allocation. Therefore it seems as if sex-based differentiation can vary among different species. With respect to Juniper shrubs in our investigation, we could not find consistent and statistically significant differences in males and females with respect to radial growth. An overall analysis (Fig. 6) did show more differential growth within females which could potentially be a result of reproductive effort. An aspect that could be a differentiating factor between gender expression in trees and shrubs could be that as shrubs grow prostrate and/or are smaller in size, they are highly influenced by micro-site conditions. Trees, on the other hand, have more uniform growth along the length of the one stem which facilitates detection of differentiation in the radial growth of gender-separated subgroups. From our investigation, it remains unclear if the observed marginal differentiation in sexes is a genotypic trait particular to Junipers or is a result of asymmetric growth due to influence of local site conditions influencing the stem architecture and cloaking gender-specific differences − if any.

4.4. Challenges and limitations

We have to stress, that our site-specific analyses were based on relatively few samples. With only eight cross-dated series, sample size was particularly low in Kirkenes. The low sample sizes possibly caused the insignificance of statistical tests. This is directly reflected in the decreasing p-values with increasing sample size (compare p-values in Fig. 5 with sample sizes in Table 2). And indeed, when combining our correlation analysis over all sites, the general trend over lower site-chronology correlations for female shrubs turned significant. Therefore, we perceive our analyses as representative despite the partly low sample sizes.

Another possible cause of error is the determination of sexes in the field. While it was straightforward to identify the "berries" and thus classify an individual as a female plant, the male cones were a lot smaller and some plants did not have any reproductive organs visible. These individuals we excluded from the analyses. While some cases of monoecious *Juniperus communis* plants exist at least in mid-latitudes (personal observation: Martin Wilmking), we did not find any in the sampling sites and thus a bias due to incorrectly classified plants is very unlikely in our analysis. Taken together, we are confident that our analyses reflect the real situation at our field sites, but further studies from additional sites and addressing different species are desirable to gain a better understanding of gender-specific growth variations in boreal, subarctic and alpine shrubs.

5. Conclusion

Sexual dimorphism and associated differences in growth in dioecious plants is well established in the ecological literature. Our study investigated possible gender-related differences in radial growth of *Juniperus communis*. L. Although we neither found gender-specific growth patterns nor growth rates, our correlation analyses indicated, that females provide more noise to the population signal, possibly caused by temporarily varying reproductive efforts. The observed effects were moderately significant and subsequently influenced response

to precipitation and temperature data. Therefore, this may play a role in terms of dendroclimatiological and dendro-ecological reconstructions if based on chronologies dominated by female shrubs, since the reproductive efforts may introduce non-climatic short-term growth variations. To test whether this observation is specific for juniper or may also hold true for other dioecious shrubs, corresponding investigations are needed to better understand differences in growth processes and their effects on radial and apical growth across the broad spectrum of boreal and alpine shrubs.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.dendro.2018.03.006.

References

Banuelos, M.J., Obeso, J.R., 2004. Resource allocation in the dioecious shrub Rhamnus alpinus: the hidden costs of reproduction. Evol. Ecol. Res. 6, 397–413.

Banuelos, J.-M., 2004. Resource allocation in the dioecious shrub Rhamnus alpins, the hidden costs of reproduction. Evol. Ecol. Res. 6, 1–17.

Barradas, M.C.D., Otilia, C., 1999. Sexual dimorphism, sex ratio and spatial distribution in male and female shrubs in dioecious species Pistacia lentiscus Folia. Geobotanica 34, 163–174.

Beil, I., Buras, A., Hallinger, M., Smiljanic, M., Wilmking, M., 2015. Shrubs tracing sea surface temperature–calluna vulgaris on the Faroe Islands. Int. J. Biometeorol. 59, 1567–1575.

Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C., Berendse, F., 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Global Change Biol. 16, 1296–1305.

Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M.M.P.D., Sauren, P., Berendse, F., 2011. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences 8, 1169–1179.

Boulanger-Lapointe, N., Lévesque, E., Baittinger, C., Schmidt, N.M., 2016. Local variability in growth and reproduction of Salix arctica in the High Arctic. Polar Res. 35, 24126.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2015. Dendrochronology Program Library in R. R Package Version 1.6.2.

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

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

Buras, A., Hallinger, M., Wilmking, M., 2012. Can shrubs help to reconstruct historical glacier retreats? Environ. Res. Lett. 7, 044031.

Buras, A., van der Maaten-Theunissen, M., van der Maaten, E., Ahlgrimm, S., Hermann, P., Simard, S., Heinrich, I., Helle, G., Unterseher, M., Schnittler, M., Eusemann, P., Wilmking, M., 2016. Tuning the voices of a choir: detecting ecological gradients in time-series populations. PLoS One 11.

Buras, A., Lehejček, J., Michalová, Z., Morrissey, R.C., Svoboda, M., Wilmking, M., 2017. Shrubs shed light on 20th century Greenland ice sheet melting. Boreas 667–677.

Cavigelli, M., Paulos, M., Lacey, E.P., 1986. Sexual dimorphism in a temperate dioecious tree ilex montana. Am. Midland Nat. 115, 397–406.

Cornelissen, J.H., van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S., Alatalo, J., Chapin, F.S., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A.E., Hik, D.S., Hofgaard, A., Jonsdottir, I.S., Karlsson, S., Klein, J.A., Laundre, J., Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V.G., Quested, H.M., Sandvik, S.M., Schmidt, I.K., Shaver, G.R., Solheim, B., Soudzilovskaia, N.A., Stenstrom, A., Tolvanen, A., Totland, O., Wada, N., Welker, J.M., Zhao, X., M.O.L. Team, 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecol. Lett. 10, 619–627.

Danby, R.K., Hik, D.S., 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. J. Ecol. 95, 352–363.

Dawson, T.E., Bliss, L.C., 1989. Patterns of water use and the tissue water relations in the dioecious shrub, Salix arctica: the physiological basis for habitat partitioning between the sexes. Oecologia 79, 332–343.

Eckstein, D., Bauch, J., 1969. Beitrag zur rationalisierung eines dendrochronologischen verfahrens und zur analyse seiner aussagesicherheit. Forstwissenschaftliches Centralblatt 88, 230–250.

Elmendorf, S.C., Henry, G.H., Hollister, R.D., Bjork, R.G., Bjorkman, A.D., Callaghan, T.V., Collier, L.S., Cooper, E.J., Cornelissen, J.H., Day, T.A., Fosaa, A.M., Gould, W.A.,

Gretarsdottir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jonsdottir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver, G.R., Stenstrom, A., Tolvanen, A., Totland, O., Troxler, T., Wahren, C.H., Webber, P.J., Welker, J.M., Wookey, P.A., 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol. Lett. 15, 164–175.

Forbes, B.C., Fauria, M., Zetterberg, P., 2010. Russian Arctic warming and 'greening' are closelz tracked by tundra shrub willows. Global Change Biol. 16, 1542–1554.

Freeman, D.C., Klikoff, L.G., Harper, K.T., 1976. Differential resource utilization by the sexes of dioecious plants. Science 193, 597–599.

Gao, Lushuang, Zhang, Chunyu, Zhao, Xiuhai, Gadow, K.V., 2010. Gender-related climate response of radial growth in dioecious Fraxinus manshurica trees. Tree-Ring Res. 66, 105–112.

Gauquelin, T., Bertaudière-Montès, A., Badri, W., Montès, N., 2002. Sex ratio and sexual dimorphism in mountain dioecious thuriferous juniper (Juniperus thurifera L., Cupressaceae). Bot. J. Linn. Soc. 138, 237–244.

Gazol, A., Camarero, J.J., 2012. Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. Plant Ecol. 213, 1687–1698.

Godley, E.J., 1976. Sex ratio in Clamatis gentianoides. N.Z. J. Bot. 14, 299–306.

Hallinger, M., Wilmking, M., 2011. No change without a cause- why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia. New Phytol. 89, 902–908.

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

Hantemirov, R., Shiyatov, S., Gorlanova, L., 2011. Dendroclimatic study of Siberian juniper. Dendrochronologia 29, 119–122.

Hudson, J., Henry, G.H., 2009. Increased plant biomass in a High Arctic heath communityfrom 1981 to 2008. Ecology 90, 2657–26663.

Juszak, I., Erb, A., Maximov, T.C., Schaepman-Sturb, G., 2014. Arctic shrub effects on NDVI, summer albedo and soil shading. Remote Sens. Environ. 153, 78–79.

Kolishchuk, V.G., 1990. Dendroclimatological study of prostrate woody plants. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Applications in the Environmental Sciences. Kluwer Dordrecht, Boston london (pp. 51–55).

Larsson, L.-Å., Larsson, P.O., 2013. CDendro, 8.1 ed. Cybis Elektronik & Data AB.

le Roux, P.C., Luoto, M., 2014. Earth surface processes drive the richness, composition and occurrence of plant species in an arctic–alpine environment. J. Veg. Sci. 25, 45–54.

Lehejček, J., 2015. Dwarf tundra shrubs growth as a proxy for late Holocene climate change. Czech Polar Rep. 5, 185–199.

Liang, E., Eckstein, D., 2009. Dendrochronological potential of the alpine shrub Rhododendron nivale on the south-eastern Tibetan Plateau. Ann. Bot. 104, 665–670.

Liang, E., Lu, X., Ren, P., Li, X., Zhu, L., Eckstein, D., 2012. Annual increments of juniper dwarf shrubs above the tree line on the central Tibetan Plateau: a useful climatic proxy. Ann. Bot. 109, 721–728.

Lloyd, D.G., Webb, C.J., 1977. Secondary sex characters in plants. Bot. Rev. 43, 177–216.

Marion, C., Houle, G., 1996. No differential consequences of reproduction according to sex in Juniperus communis var. depressa (Cupressaceae). Am. J. Bot. 83, 480–488.

Meagher, T.R., Antonovics, J., 1982. The population biology of chamaelirium luteum, a dioecious member of the lily family: life history studies. Ecology 63, 1690–1700.

Meinardus, C., Weinert, B., Löffler, J., Lundberg, A., Bräuning, A., 2011. The potential of dwarf shrub betula nana L. as a climate indicator above the tree line in the southern Norwegian Scandes. TRACE-Tree-Rings Archeol. Climatol. Ecol. 9, 181–186.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ. Res. Lett. 6, 045509.

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., Speed, J.D.M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N.M., Baittinger, C., Trant, A.J., Hermanutz, L., Collier, L.S., Dawes, M.A., Lantz, T.C., Weijers, S., Jørgensen, R.H., Buchwal, A., Buras, A., Naito, A.T., Ravolainen, V., Schaepman-Strub, G., Wheeler, J.A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015a. Climate sensitivity of shrub growth across the tundra biome. Nat. Clim. Change 5, 887–891.

Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S.A., Weijers, S., Trant, A.J., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Dawes, M.A., Wheeler, J.A., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B.C., Lévesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilmking, M., 2015b. Methods for measuring arctic and alpine shrub growth: a review. Earth Sci. Rev. 140, 1–13.

Obeso, J.R., Alvarez-Santullano, M., Retuerto, R., 1998. Sex ratios, size distributions, and sexual dimorphism in the dioecious tree ilex aquifolium (Aquifoliaceae). Am. J. Bot. 85, 1602.

Oddi, J.F., Ghermandi, L., 2015. Dendroecological potential of shrubs for reconstructing fire history at landscape scale in mediterranean type climate grasslands. Dendrochronologia 33, 16–24.

Ortiz, P.L., Arista, M., Talavera, S., 2002. Sex ratio and reproductive effort in the dioecious Juniperus communis subsp. alpina (Suter) Čelak. (Cupressaceae) along an altitudnal gradient. Ann. Bot. 89, 205–211.

Pellizzari, E., Pividori, M., Carrer, M., 2014. Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps. Environ. Res. Lett. 9, 104021.

R Core Team, 2013. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, K.M., Delhomme, N., Mähler, N., Schiffthaler, B., Önskog, J., Albrectsen, B.R., Ingvarsson, P.K., Hvidsten, T.R., Jansson Street, S.N.R., 2014. Populus tremula (Eurpean Aspen) shows no evidence of sexual dimorphism. BMC Plant Biol. 14, 1–14.

Ropars, P., Angers-Blondin, S., Gagnon, M., Myers-Smith, I.H., Lévesque, E., Boudreau, S., 2017. Different parts: different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. Global Change Biol. 23, 3281–3291.

Rozas, V., DeSoto, L., Olano, J.M., 2009. Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree Juniperus thurifera. New Phytol. 182, 687–697.

Sadras, V.O., Denison, R.F., 2009. Do plant parts compete for resources? An evolutionary viewpoint. New Phytol. 183, 565–574.

Sakai, A., Sasa, A., Sakai, S., 2006. Do sexual dimorphisms in reproductive allocation and new shoot biomass increase with an increase of altitude? A case study of the Shrub Willow Salix reinii (Salicacea). Am. J. Bot. 93, 988–992.

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

Schweingruber, F.H., 1988. Tree Rings: Basics and Applications of Dendrochronology. Springer Dordrecht, Netherlands.

Singh, H., 1978. Embryology of Gymnosperms. Gebrüder Borntraeger, Berlin.

Sonesson, M., Callaghan, T.V., 1991. Strategies of survival in plants of the Fennoscandian tundra. Arctic 44, 95–105.

Sturm, M., Racine, C., Tape, K., 2001. Increasing shrub abundance in the Arctic. Nature 411, 546.

Tape, K.D., Hallinger, M., Welker, J.M., Ruess, R.W., 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. Ecosystems 15, 711–724.

Verdu, M., Villar-Salvador, P., Gracia-Fayos, P., 2004. Gender effects on the post-facsilitation performance of two dioecious Juniperus species. Funct. Ecol. 18, 87–93.

Ward, L.K., 2007. Lifetime sexual dimorphism in Juniperus communis var communis. Plant Species Biol. 22, 11–21.

Weijers, S., Broekman, R., Rozema, J., 2010. Dendrochronology in the High Arctic: july air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub Cassiope tetragona. Quat. Sci. Rev. 29, 3831–3842.

Weijers, S., Greve Alsos, I., Bronken Eidesen, P., Broekman, R., Loonen, M.J., Rozema, J., 2012. No divergence in Cassiope tetragona: persistence of growth response along a latitudinal temperature gradient and under multi-year experimental warming. Ann. Bot. 110, 653–665.

Weijers, S., Wagner-Cremer, F., Sass-Klaassen, U., Broekman, R., Rozema, J., 2013. Reconstructing High Arctic growing season intensity from shoot length growth of a dwarf shrub. The Holocene 23, 721–731.

Wilmking, M., Hallinger, M., Van Bogaert, R., Kyncl, T., Babst, F., Hahne, W., Juday, G.P., de Luis, M., Novak, K., Völlm, C., 2012. Continuously missing outer rings in woody plants at their distributional margins. Dendrochronologia 30, 213–222.

Zalatan, R., Gajewski, K., 2006. Dendrochronological potential of Salix alaxensis from the Kuujjua River Area, Western Canadian Arctic. Tree-Ring Res. 62, 75–82.

Web/Dataset References

[dataset] Salekhard Climate Station Data 2016. Russian Federation Meteorological Station Data
Access date 02.08.2017 available at < http://meteo.ru/data >

[dataset] Taganay Climate Station Data 2016. Russian Federation Meteorological Station Data
Access date 02.08.2017 available at < http://meteo.ru/data >

[dataset] Cherdyn Climate Station Data 2016. Russian Federation Meteorological Station Data
Access date 02.08.2017 available at < http://meteo.ru/data >

[dataset] Climate Explorer. Koninklijk Nederlands Meteorologisch Instituut
Access date 02.08.2017 available at < https://climexp.knmi.nl/start.cgi?id=someone@somewhere >

Supplement

Figure S1

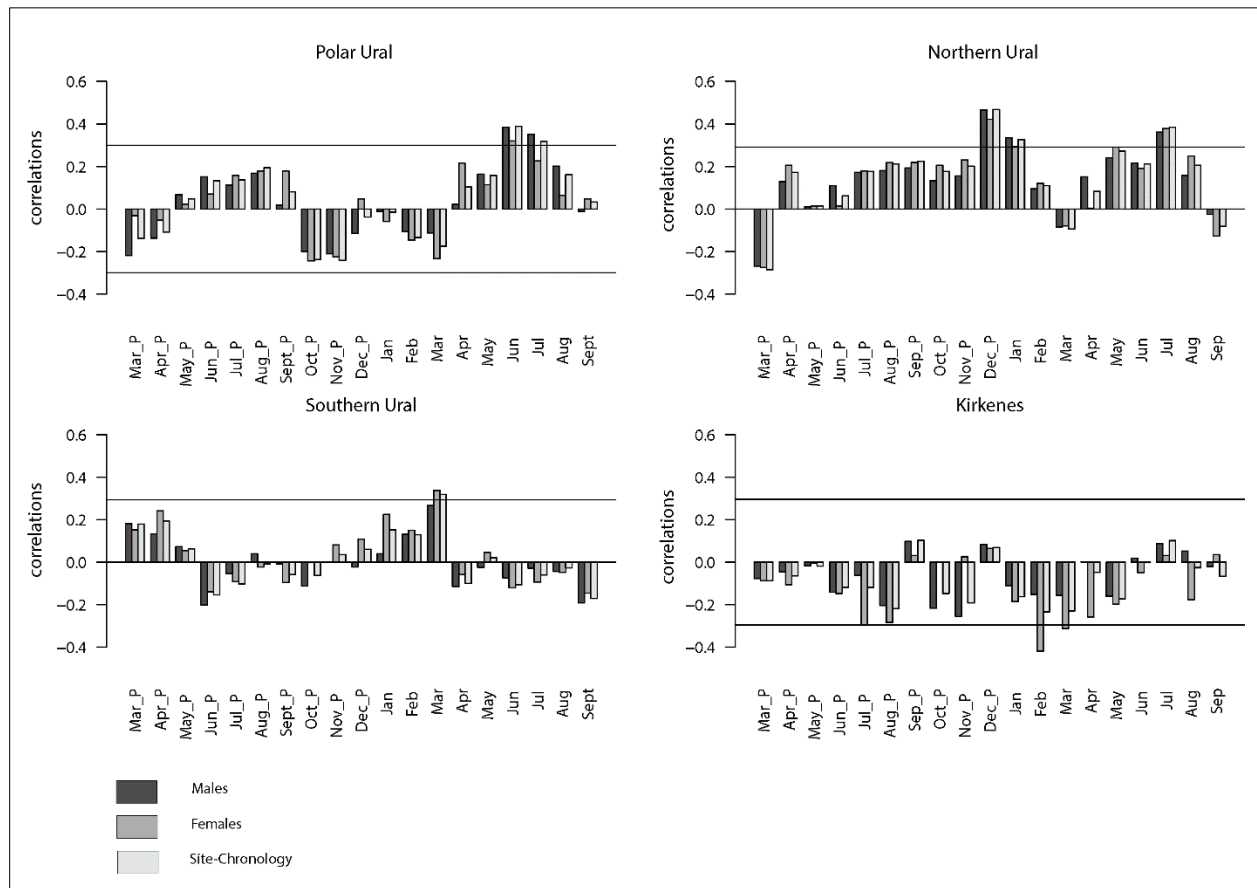Figure S1 showing comparison of correlations of male, female and site-chronology with monthly temperature records.
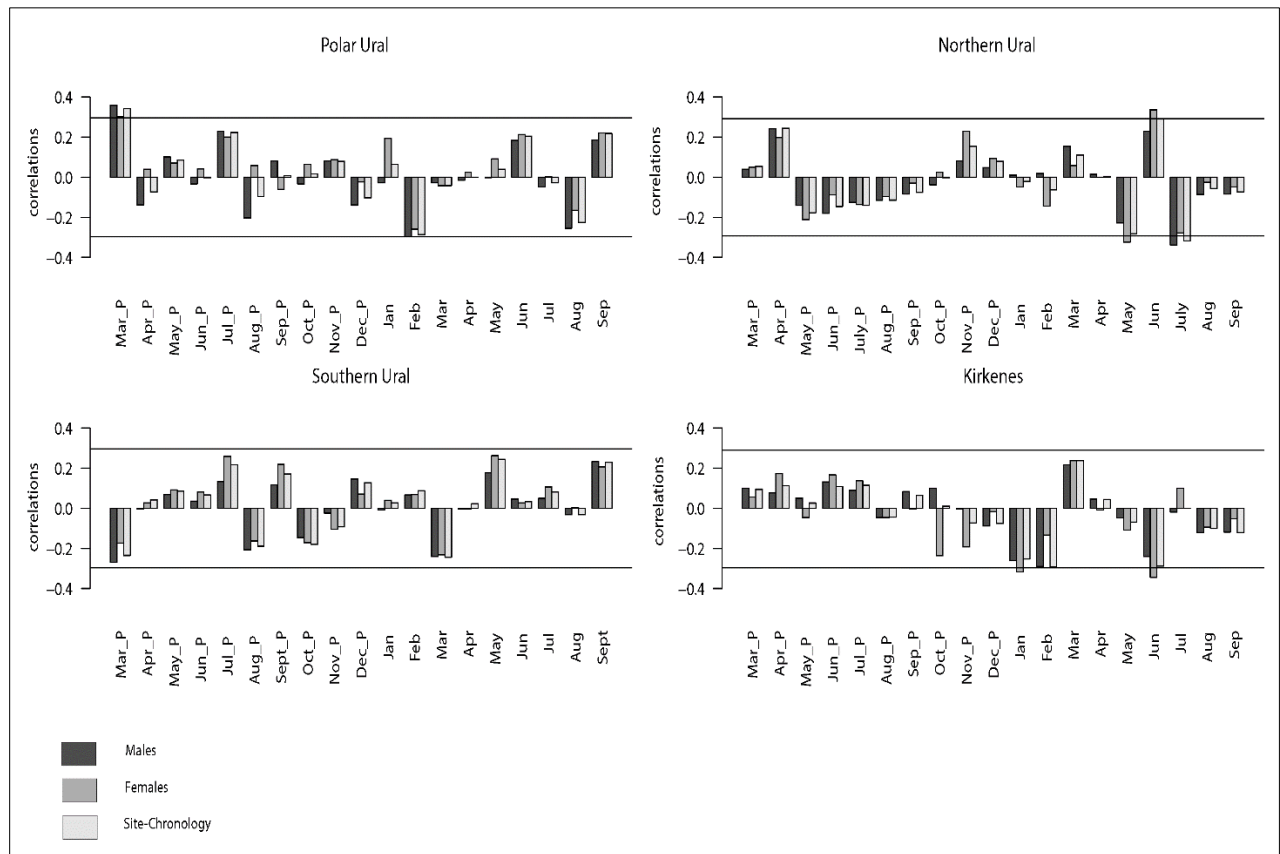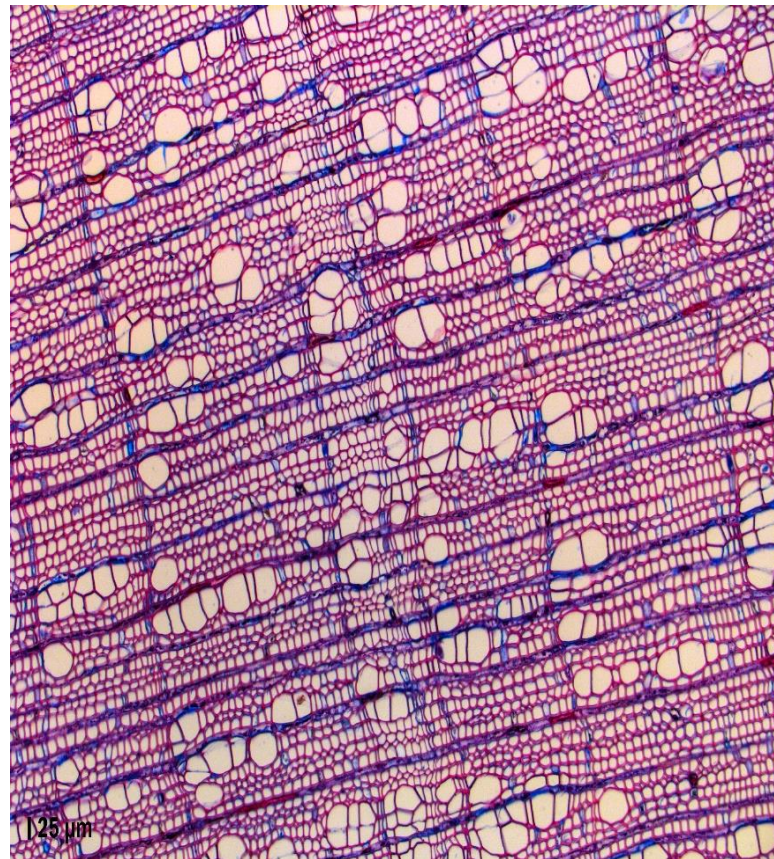
Supplement

Figure S2

Figure S2 showing comparison of correlations of male, female and site-chronology with monthly precipitation records.
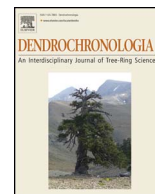
2004

25 µm

Chapter 4

Influence of larval outbreaks on the climate reconstruction potential of an Arctic shrub
(Dendrochronologia (2018) 49: 36-43)

Influence of larval outbreaks on the climate reconstruction potential of an Arctic shrub

Martin Wilmking[a,*], Allan Buras[a,1], Jiří Lehejček[b], Jelena Lange[a], Rohan Shetti[a], Ernst van der Maaten[a,2]

[a] *Institute of Botany and Landscape Ecology, University Greifswald, Soldmannstr. 15, 17487 Greifswald, Germany*
[b] *Department of Environmental Security, Faculty of Logistics and Crisis Management, Tomas Bata University in Zlín, nám. T.G. Masaryka 5555, 760 01 Zlín, Czech Republic*

ARTICLE INFO

ABSTRACT

Arctic shrubs have a strong potential for climate and environmental reconstructions in the chronically under-studied regions of the high northern latitudes. The climate dynamics of these regions are important to understand because of large-scale feedbacks to the global climate system. However, little is known about other factors influencing shrub ring growth, possibly obscuring their climate signal. For example, as of yet we are not able to differentiate between herbivory or climatically induced growth depressions. Here, we use one of the most common Arctic shrubs, *Alnus viridis* as a test case to address this question. We sampled *Alnus* in Kobbefjord, Greenland, measured shrub-ring width and cell wall thickness and built site chronologies of each parameter. We analysed climate-growth relationships, tested their stability over time and employed a pointer-year analysis to detect growth depressions. We employed bootstrapped transfer function stability tests (BTFS) to assess the suitability of our shrub chronologies for climate reconstruction. Correlations with climate data showed strong significantly positive and stable correlations between summer temperature and ring-width with the exception of the recent decade. A climate reconstruction model failed stability tests, when the complete period of record was used for calibration and verification. Wood anatomy analysis uncovered the occurrence of unusual cell structure (very thin cell walls) in the exceptionally narrow ring of 2004, a recorded insect outbreak year in other parts of Greenland. When excluding the affected ring and a recovery period, the reconstruction model passed all tests, suggesting that the unusual 2004 ring was not climate driven, but rather the result of an insect attack. When combining anatomical analysis with traditional ring-width measurements, we move a step further in potentially distinguishing small rings caused by insect attacks from small rings formed in climatically challenging years. While this study does not provide unambiguous evidence, it does provide potential useful methodological combinations to enable more robust climate reconstructions in areas where climatic records are extremely sparse.

1. Introduction

Temperatures in the Arctic are rising faster than any other region worldwide, because of several feedback mechanisms related to temperature gradients, sea-ice cover, water vapor and albedo (Chapin et al., 2005; Pithan and Mauritsen, 2014; Serreze and Barry, 2011). A spatially explicit, longer-term perspective of that temperature rise is difficult to assess however, because climate stations are sparsely spread and not many stations have been operating for longer than a few decades (Cowtan and Way, 2014). Spatially explicit past and projected variability of climate change in the Arctic is mainly a result of modeling exercises (e.g. see CRU data set) and surrounded by relatively high error estimates (Hodson et al., 2013).

Arctic shrubs can help fill this gap, because they can be found in large parts of the Arctic, can live to considerable ages and form annual growth rings, like trees. Since temperatures are usually limiting growth at these high latitudes, the link between Arctic shrub growth and climate is often strong (Bär et al., 2008; Beil et al., 2015; Blok et al., 2011; Buchwal et al., 2013; Forbes et al., 2010; Gamm et al., 2017; Hallinger et al., 2010; Hallinger and Wilmking, 2011; Hollesen et al., 2015;

Jørgensen et al., 2015; Myers-Smith et al., 2015a; Rozema et al., 2009; Weijers et al., 2017; Young et al., 2016), generally qualifying shrubs for climate and environmental reconstructions (Buras et al., 2012, 2017a; Rayback and Henry, 2006; Rayback et al., 2012; Weijers et al., 2010, 2013). While shrub ring width variability over time has been linked to temperature variability (Havstrom et al., 1995), wood anatomical studies (e.g. using cell wall thickness or vessel lumen area) have recently provided additional insights into the relationship between shrub growth and climate drivers or other environmental parameters such as glacier melt (Buras et al., 2017a; Lehejček et al., 2017; Nielsen et al., 2017), opening up new avenues to interpret the shrub ring record.

Shrub growth can be influenced by a combination of climate and environmental factors, and disentangling these different factors is often challenging, since they might act at different time scales, for different time periods or only episodically. One widespread example of an environmental factor affecting shrub growth with varying periodicity or only episodically in the Arctic is herbivory. Herbivory in Arctic shrubs can be the result of animal species ranging from large vertebrates such as moose (Tape et al., 2016), caribou, reindeer or muskox (Post and Pedersen, 2008; Vowles et al., 2017) to snowshoe hares (Ewacha et al., 2014), and birds such as ptarmigan (Tape et al., 2010) (for a review see Christie et al., 2015), or invertebrates (Barrio et al., 2017; Kozlov and Zvereva, 2017; Young et al., 2016 and references therein). In the case of insects, larval stages e.g. from *Epirrita autumnata, Operophtera brumata* or *Eurois occulta* can episodically defoliate large areas of subarctic and arctic vegetation, which has been documented for Fennoscandia and Greenland (Dahl et al., 2017; Tenow et al., 2007; Young et al., 2016). Generally, herbivory in the Arctic leads to the (partial) loss of foliage, a reduced photosynthetic apparatus, and subsequent lower growth resources, which might result in lower net ecosystem productivity (Lund et al., 2017) and lower radial growth of stems. When then using shrub stem growth as proxy of past climate variability, the subsequent logical question becomes: How to differentiate between narrow rings caused by climate and those caused by herbivory?

This study has therefore two main aims:

1) To investigate the climate signal and climate reconstruction potential in a widespread Arctic shrub, using *Alnus viridis* ssp. *crispa* (mountain alder) as an example.
2) To explore the potential of wood anatomy to disentangle climatic influences on mountain alder shrub growth from herbivory induced growth depressions.

2. Methods

2.1. Sample species

Alnus viridis has a near circumpolar northern distribution and can be found in large parts of the Subarctic and Low Arctic. It is generally a mid to large size shrub growing along small water courses or in moist habitats. It can defend its twigs and buds with the toxins pinosylvin and pinosyl, making it less palatable at least to snowshoe hares (Bryant et al., 1987). *Alnus viridis* has the ability to grow rapidly, while at the same time investing in effective antibrowsing defenses, likely a consequence of its capacity to fix nitrogen (Hendrickson et al., 1991 in Christie et al., 2015). The species can be subdivided in several subspecies which are ecologically very similar. In Northeastern North America and Greenland, our sample region, the subspecies is *Alnus viridis* ssp. *crispa* (hereafter alder). Its distribution in Greenland is concentrated on the south-western coastal areas to approximately 68°N (Fig. 1).

2.2. Field site

Our field site was in Kobbefjord, Greenland, close to the Kobbefjord Research Station (64.136578°N, 51.380204°E). The vegetation in the
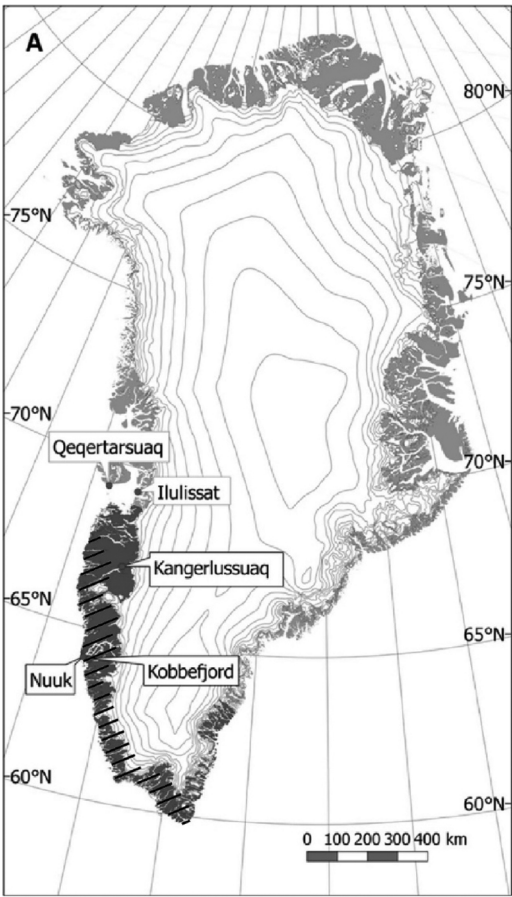
Fig. 1. Map of Greenland modified after Lund et al. (2017) with distribution of *Alnus viridis* ssp. *crispa* (hatched) and the moth *Eurois occulta* (in dark grey).

research area was generally low arctic tundra with several shrub species such as *Salix glauca, Betula nana, Juniperus communis* and, as the largest shrub, alder. Alder in the area reached canopy heights of up to 3 m in thickets and could be found mainly on the south facing slopes.

2.3. Sampling

We employed a nested sampling design which combined intensive and extensive sampling strategies for alder shrubs (Table 1). First, we intensively sampled alder in August of 2012 in a relatively restricted area in an elevational belt between 200 and 240 m above sea level (m.a.s.l.) on a slope with south to southwest exposure. From each individual shrub, we selected the thickest and/or highest stem and cut it as low as possible, often at the root collar. We selected three to five stem sections along the length of that stem, according to the serial sectioning technique (Kolishchuk, 1990; Myers-Smith et al., 2015b; Wilmking et al., 2012). All sampled shrubs were dominant (except one, which was co-dominant) and all had erect stem forms and full foliage. Stem length varied between 135 and 350 cm. Second, we extensively sampled alder in 2013 at different elevations and at several locations on

Table 1
Metadata for shrub sampling and analysis.

	intensive sampling	extensive sampling	total
n shrubs	20	22	42
n stem sections	62	22	84
n radii measured	156	22	178
n shrubs crossdated	20	18	38
n shrubs used	19	18	37

the southfacing slope of Kobbefjord. From these shrubs we only harvested the lowest stem section possible, mainly the root collar.

2.4. Sample preparation and ring width measurement

In the lab, all stem sections were polished with progressively finer sandpaper (up to 400 or 800 grit if necessary) and ring width was measured to 0.01 mm either using a LinTab 5/TSAPWin system or scanned images and CooRecorder (v. 7.7, Cybis Elektronik & Data AB, Sweden) or WinCell. Each stem section (three per shrub) from the intensive sampling effort was measured along 2–3 radii to detect locally missing rings, avoiding tension wood sections, resulting in 156 measured radii from 20 shrubs. Samples from the extensive effort were measured along one radius.

2.5. Crossdating and chronology building

In a first step, we used only the shrub samples from the intensive sampling effort (n = 20) due to the availability of serially sectioned stem-discs which allows for better identification of possibly missing outer rings (Wilmking et al., 2012). Using CDendro (Cybis AS, Sweden), we crossdated all radii of a specific stem section and build an average for that stem section. Then we crossdated between different stem sections of an individual shrub and built individual shrub growth ring chronologies. Missing rings, wedging rings or "completely missing outer rings" (Wilmking et al., 2012) were common, especially at lower stem sections. Next, we crossdated between individual shrubs from the intensive sampling effort and built an average chronology from that relatively restricted sampling area. Using that chronology we then finally crossdated the basal stem sections of the extensive sampling effort (n = 22).

2.6. Analysis

To detect potential bias due to effects of different detrending methods, shrub-ring series were detrended using 1) traditional straight line fits, 2) negative exponential functions and 3) a 30 year cubic smoothing spline with a frequency cut-off of 50%, which will remove a large part of the low frequency variability. Subsequently, we built average ring-width chronologies (aka master chronologies) using a robust mean (function 'chron' in the 'dplR' package) (Bunn, 2008). The chronologies were characterized by the constant addition of younger shrubs and we considered the chronologies reliable from 1948 onwards when a minimum of ten shrubs contributed data. We will here present the results of the cubic smoothing spline only, the other detrending methods lead to similar results.

To analyze temperature-growth relationships we used gridded CRU TS v4.01 (Harris et al., 2014) temperature data for the closest grid-cell from 1958 onwards. The restriction to the period 1958 onwards was based on Hanna et al. (2005) who considered this period reliable concerning reanalyzed climate data. We also considered monthly precipitation sums extracted for the closest grid cell from GPCC v7 (Schneider et al., 2016), but since we only found a few weak and generally instable relationships with growth, we present here only results derived from temperature correlations. Climate-growth relationships were investigated using Spearman's rank correlation accounting for the partly non-normal distribution of data and considering the period from March in the year prior to ring formation until September in the year of ring formation. To obtain an impression of the spatial representation of climate-growth relationships, which is of particular interest when considering the reconstruction of Greenland Ice Sheet melt (Buras et al., 2017a,b), we also computed monthly correlations with the CRU TS v4.01 gridded temperature data over the same period covering the area between 50 and 90°N and 10 and 80°E.

The stability of climate-growth relationships and resulting transfer functions was assessed using the bootstrapped transfer function stability test (BTFS) (Buras et al., 2017b). In BTFS, transfer function parameters (model significance, intercept, slope, and explained variance) of a calibration and a verification period are bootstrapped over 1000 iterations and the stability of the parameters over these two periods is tested based on empirical cumulative distribution functions of bootstrapped parameter estimates (for details see Buras et al., 2017b). That is, BTFS p-values below 0.05 will indicate instable transfer functions and consequently instable climate-growth relationships. Stability assessments were undertaken on the basis of the complete period considered (1958–2012) and compared to assessments based on a period which excluded the years 2004 through 2007 since they appeared to be affected by an exceptionally strong moth outbreak.

2.7. Pointer year analysis

To detect growth depressions (negative pointer years) in the shrub-ring width record, we used the package pointRes (van der Maaten-Theunissen et al., 2015, and references therein). We used the raw ring width as input for the pointer year analysis and employed the methods after Cropper, Neuwirth, and the relative growth change method (RGCM). A pointer year was defined as a year in which 75 or more percent of the individual shrub growth records showed an event year. Pointer year analyses can be affected by multiple strong growth deviations in close temporal proximity, since they are calculated by using average values of the respective growth parameter over a moving normalization window. We therefore experimented with different window sizes for the normalization moving window in the Cropper and Neuwirth methods by using 5, 7, 9, 11, and 13 years. We used RGCM in pointRes to quantify negative growth deviation, where the pointer year growth reduction is compared to the average growth of the prior years. For pointer year detection we used the same periods as for the pointer year analysis after Cropper and Neuwirth, for the quantification of growth reduction the previous 4 years (Schweingruber et al., 1990).

2.8. Wood anatomy

The results of the pointer year analysis were used to select specific shrubs (n = 10) for a wood anatomical analysis. This analysis was meant to address aim 2 and we therefore selected shrubs, which clearly showed a growth depression for ring width in the common pointer year 2004 and were old enough to also have recorded possible previous insect attacks and the coldest summer on record, 1972. A sliding lab-microtome/Leica rotary microtome (RM 2245) was used to obtain 15–20 μm thick and about 1 cm wide thin-sections of the longest axis of shrub disc samples. Thin-sections were made perpendicular to the tracheids' growth and after applying corn starch/water solution (Schneider and Gärtner, 2013), so that we preserved the cellular structure for the subsequent wood anatomy analysis. Sodium hypochlorite was then used as a bleaching agent for some of the samples, prior to cleaning the thin-sections with water, and double staining for at least 5 min in a 1:1 solution of Safranin and Astrablue (Schweingruber et al., 2013). Finally, the thin-sections were washed again from redundant stain. Increasing ethanol concentrations were used (70, 90, and 98%, respectively) to dehydrate the samples. Finally, the samples were preserved by Canada balsam/Euparal, embedded under a cover glass (Schweingruber et al., 2008) and dried for at least 12 h at 60 °C. Images of thin-sections (933 μm wide) were taken using a digital camera (Canon EOS 650D/Leica DFC450C) connected to a microscope (Olympus BX41/Leica DM2500) under ×100 magnification. WinCell 2013 software (Regent Instruments WinRHIZO 2013) was used to measure cell wall thickness (CWT). CWT was measured for each annual ring using areal measurements. The exclusion measurements filters were set in order to measure cells correctly as follows: all lumens < 20 μm^2, > 9000 μm^2, > 3 length/width ratio as well as all object with identified "cell walls" > 4.5 μm were ruled out. We also set a conservative threshold for classification of vessels at 560 μm^2. All

remaining cell wall values were first averaged per individual cell (right and left wall) and then all cell values were averaged per individual shrub ring. We repeated the climate-growth and pointer year analysis described above with time series of cell wall thickness.

Finally, we also computed a linear regression between raw CWT and RW values to explore for specific relationships of these two parameters, also in years with herbivory impact, which may allow for distinguishing such years from those with climatically adverse conditions. In this context, we z-transformed the regression residuals as well as RW and CWT to express their normalized deviation from their overall mean.

3. Results

3.1. Crossdating and chronology building

We sampled 42 shrubs in total and measured 178 radii from 84 stem sections for ring-width. Missing or wedging rings occurred throughout our sample, but were successfully detected and crossdated with other samples from the same individual or with the alder chronology from the intensive sampling effort, resulting in 38 crossdated shrubs. Seven individuals had completely missing outer rings (varying in number between 1 and 3) at the lowest sampled stem section. One shrub was established after 1991 and was excluded from subsequent analyses.

3.2. Chronology statistics

The resulting shrub-ring width (RW) chronologies covered the time period from 1923 to 2012 and were characterized by the constant addition of younger shrubs over time (Fig. 2). A maximum sample size of 37 existed from 1986 to 2010. The CWT chronologies covered the same time period from 1923 to 2012, with more than 5 shrubs contributing from 1950 onwards. A constant sample size of 10 existed from 1977 to 2006, 9 shrubs contributed data until 2011. The raw RW chronology had an EPS of 0.87, mean GLK of 0.71 and rbar of 0.258, the raw CWT chronology had an EPS of 0.76, mean GLK of 0.59 and rbar of 0.316.

3.3. Pointer year analysis

The year 2004 was detected as a negative pointer year for RW in 12 of the 15 possible combinations of pointer year analysis method and normalization window. When detected by the Neuwirth method it was classified as "negative strong" or "negative extreme". No other year was detected as ubiquitously (1955 and 1970 were detected 5 times out of

Fig. 3. Example of alnus wood anatomy in the year of the coldest summer, 1972 (left), and the pointer year 2004 (right). The very narrow ring in 2004 has visibly thinner CWT than the preceding and following years, most likely the result of an insect attack.

15). RW in 2004 was 66.2% smaller than expected (mean of the previous four years), the strongest deviation in all of the analysis period.

For CWT, 2004 was detected as a negative pointer year in 15 out of 15 possible combinations of pointer year analysis method and normalization window, and classified as "negative extreme" by the Neuwirth method with one exception. The next frequent pointer year for CWT was 1972 (detected in 14 out of 15 possible combinations), and, if detected by the Neuwirth method, always classified as "negative extreme". No other year was detected in more than 5 out of 15 possible combinations. CWT in 2004 was 31.7% smaller than expected, the strongest deviation in all of the analysis period. CWT in 1972 was on average 17.5% smaller than expected (Fig. 3).

3.4. Ring-width versus cell wall thickness

There was a clear general positive relationship between ring-width and cell wall thickness ($r^2 = 0.39$, $p < 0.001$; Fig. 4). While there were no years in the RW record with ring-width values below -2 standard deviations, CWT expressed -3.3 standard deviations in 2004, and -1.95 in the exceptionally cold summer of 1972. Regression residuals expressed the lowest value in 2004 (z-score = -2.72) and very high values in 1964 (z-score = $+2.14$).
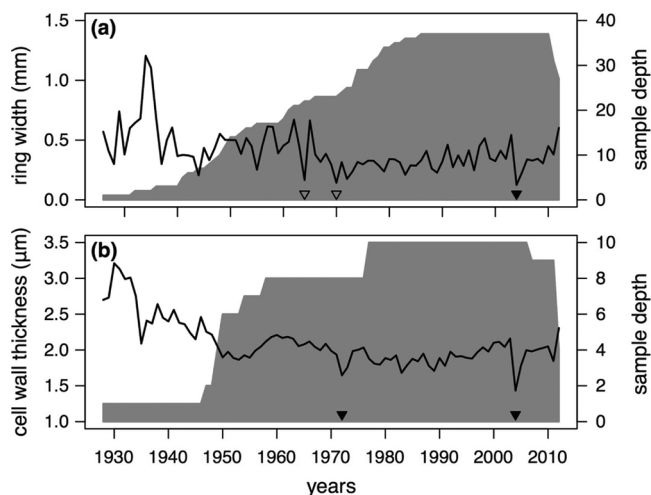

Fig. 2. Chronologies of raw RW (a) and CWT (b) with sample depth in grey. Downward triangles indicate pointer years, filled in more than 10, empty in 5–9 possible combinations (15) between pointer year detection method and normalization window. Only the year 2004 is consistent across RW and CWT.
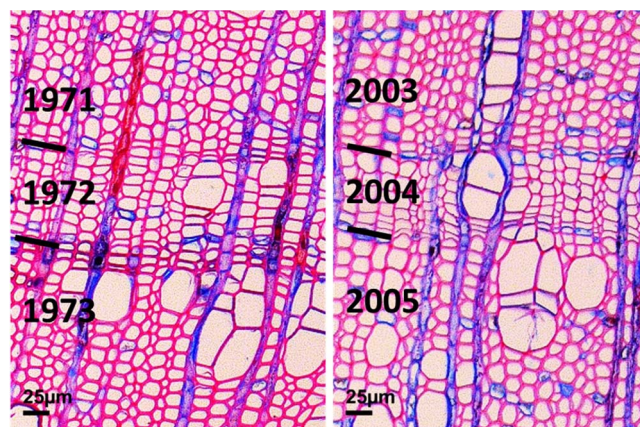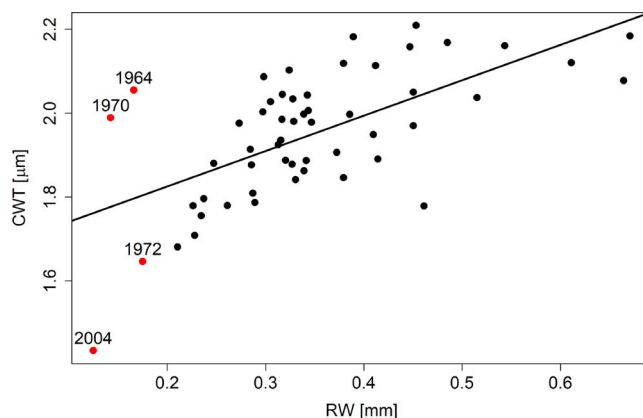

Fig. 4. RW and CWT show a clear positive relationship ($r^2 = 0.39$, $p < 0.001$). However, some years show distinct deviations from this general relationship, notably the years 1964 and 1970 with thin rings and thick cell walls and the year 2004 with narrow rings and thin cell walls. Red dots indicate years with RW smaller than 0.2 mm. 2004 stands out as the year with the smallest ring and the thinnest cell walls and the absolutely highest regression z-score. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
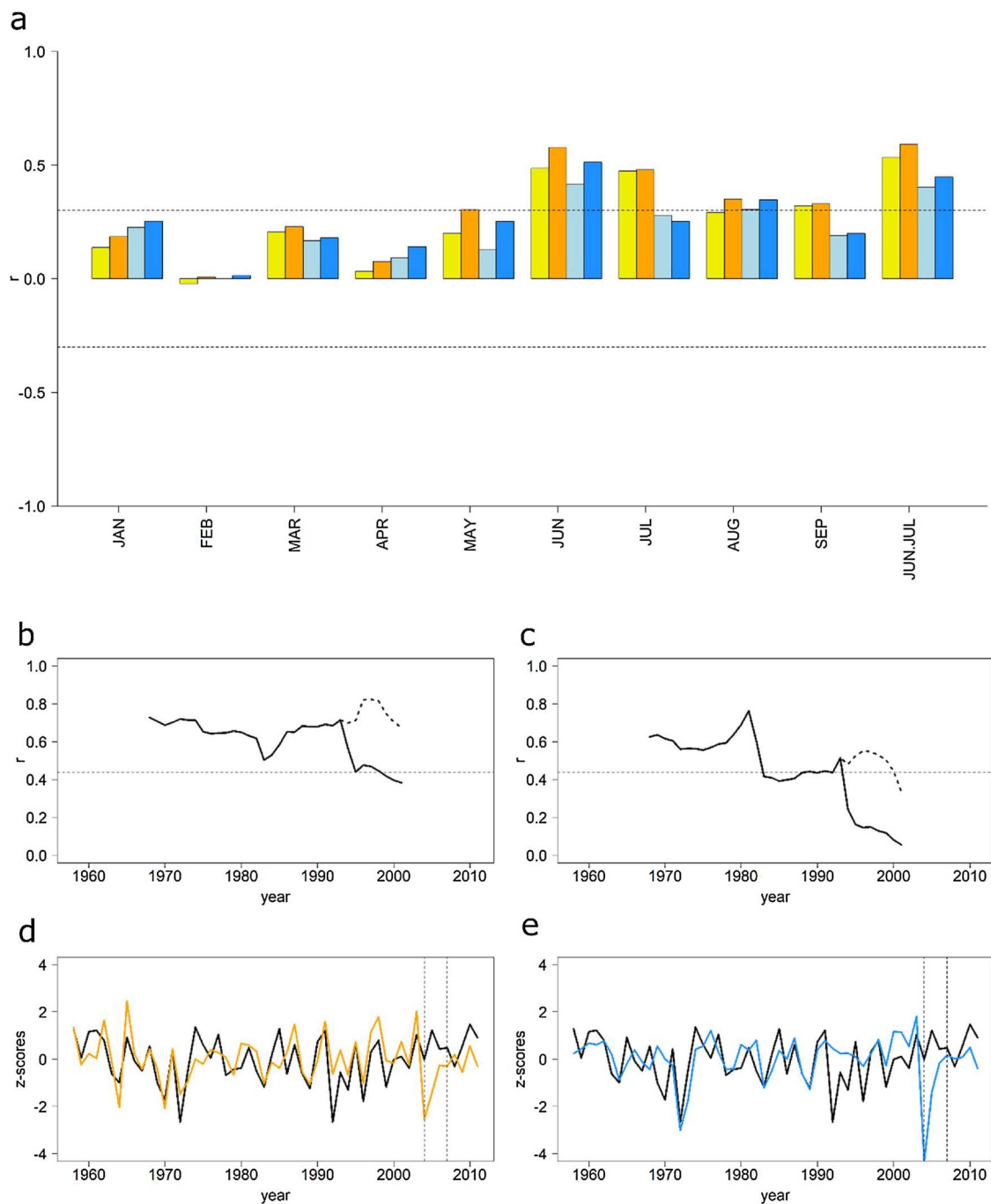
Fig. 5. Temperature growth correlations (r) between RW (yellow) and CWT (light blue) for the period 1958–2011, dashed lines indicate significance at the 0.05 level (a). Excluding the insect affected years 2004–2007 leads to increased correlations in RW (orange) and CWT (dark blue). Since correlations with previous year temperatures were all insignificant, we here only present correlations representative of the year of growth. Running correlations (solid lines) between RW (b), CWT (c) and June-July temperature show decreasing sensitivity to temperature in both proxies, after exclusion of 2004–2007 (dotted line) significantly positive and stable correlations over time exist at least for RW (b). Moving window lengths was 21 years. Z-transformed time series of RW (d) and CWT (e) clearly show a strong offset from summer temperature (solid black line) in both proxies in the period 2004–2007 (vertical dashed lines).

3.5. Climate-growth relationships

Alder radial growth showed strong, significant positive correlations with summer temperatures (mainly June and July) of the year of growth (Fig. 5a). Strength of correlation was generally stable in the early record, but less so in recent periods (Fig. 5b). Correlation scores increased when the period 2004–2007 (strongest pointer year and recovery period) was eliminated from the correlation calculation and the strength of the correlation with summer temperatures remained stable over the whole record (Fig. 5b). Correlations scores with CWT generally mirror those of RWI, but are less strong and not stable over time (Fig. 5c). We only found a weak negative and instable correlation with march precipitation. The spatial signature of the strongest correlation between the alder ring width record and climate (June temperature, year of growth) was centered on south-western/south-central Greenland, but significant correlations were recorded in an area around Baffin Bay including the eastern parts of Nunavut, Canada to the southwestern part of Iceland (Fig. 6).
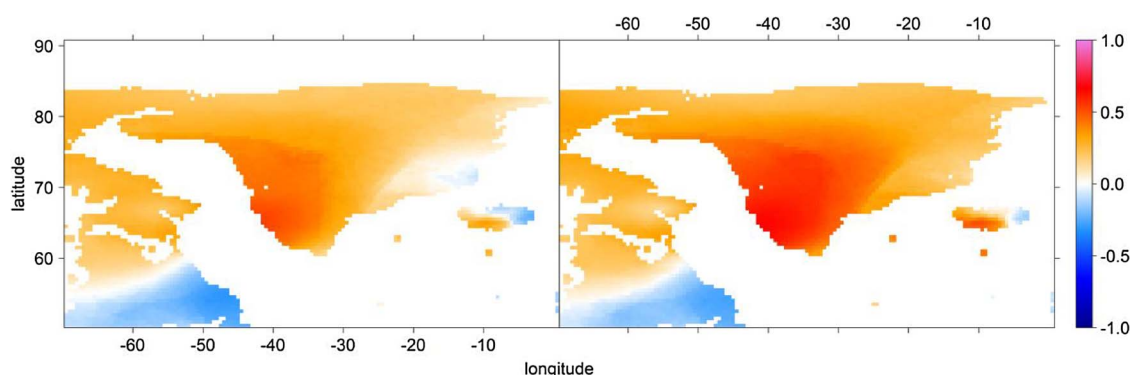
Fig. 6. Spatial correlations between June temperature and RWI for the complete period (left) and excluding the insect affected years 2004–2007 (right).

3.6. Reconstruction potential

BTFS indicated instable ring-width based transfer functions for June, July, and mean June-July temperature if the whole period (1958–2011) was considered for the regression (slope p ≈ 0.01, explained variance p ≈ 0.001). However, when excluding the period 2004–2007 from the record, transfer functions turned stable (all p-values > 0.1) and the proxy time series captured temperature variation quite well (Fig. 5d and e). This was also reflected in a differing amount of explained variance (r^2) between the models with 0.19 vs. 0.32, 0.28 vs. 0.34, and 0.30 vs. 0.43 for June, July, and June-July, respectively. In comparison, the reconstruction based on the full period on average predicted 0.1 °C higher summer temperatures and the overall difference between the two reconstructions was highly significant (paired Wilcoxon rank-sum test p < 0.001). A similar impact was observed for CWT. That is, when excluding the period 2004–2007 from the record, instable transfer functions (here intercept and r^2 were instable) turned stable (again all p-values > 0.1).

4. Discussion

Alnus viridis is one of the main shrub species of the northern low Arctic, but has been only recently tested for its response to climate (Jørgensen et al., 2015; Tape et al., 2012). Ecologically, it seems to be one of the Arctic shrub species rapidly spreading due to favorable climate conditions (Rinas et al., 2017; Tape et al., 2006), possibly because of its ability to translate additional warmth in summer into additional growth. Also in our study, a clear positive and significant relationship between radial growth of alnus shrubs and summer temperatures existed and adds to the growing body of evidence of a direct temperature link (Bär et al., 2008; Beil et al., 2015; Blok et al., 2011; Buchwal et al., 2013; Forbes et al., 2010; Gamm et al., 2017; Hallinger et al., 2010; Hallinger and Wilmking, 2011; Hollesen et al., 2015; Jørgensen et al., 2015; Myers-Smith et al., 2015a; Rozema et al., 2009; Weijers et al., 2017; Young et al., 2016) or a moisture mediated temperature link (Ackerman et al., 2017; Myers-Smith et al., 2015a) with shrub growth in the Arctic. However, at least in Greenland, varying and partially negative responses of radial growth of willows and birch to summer temperatures have recently been reported, possibly due to drought induced stomatal closure or repeated insect attacks (Gamm et al., 2017). Alnus, on the other hand, might be well suited for climate reconstruction tests, since its relationship with summer temperature is strong, significantly positive and stable, once the influence of insect attacks is removed from the record.

Climate reconstructions rely on a significant and time-stable relationship between a climatic driver and a proxy. This relationship is always affected by noise of varying origin and the challenge is to separate noise from signal. In case of Arctic shrubs, herbivory is an important co-driver ("noise") of growth variation (Myers-Smith et al., 2011; Post and Pedersen, 2008) at least in broad-leaved shrubs and can occur constantly or episodically (Barrio et al., 2017; Kozlov and Zvereva, 2017). When the occurrence of herbivory is episodically, it is extremely difficult to isolate herbivory events in time, but undetected events can negatively influence the quality and reliability of the resulting climate reconstructions (Humbert and Kneeshaw, 2011). Here we tested, whether insect related growth disturbance in alder from Greenland can be detected and possibly corrected for by the combined analysis of pointer years and wood anatomy.

While pointer year detection varied to some extent by proxy and detection method, there was one year which stood out in terms of detection and growth deviation, both in RW, in CWT and regarding the residuals of a regression of CWT against RW, the year 2004. Ring width was 2/3 smaller and cell wall thickness about 1/3 smaller than expected. For CWT, 2004 was the only year with more than two standard deviations below the overall mean CWT and the residuals of the CWT prediction from RW had highest values. The summer climate (JJ) of 2004 however, was slightly above average and thus not an obvious factor to explain the observed growth depression. For comparison, the coldest summer on record, 1972, also resulted in smaller rings and thinner cell walls, but the reduction in RW was only 32%, about half of the reduction on the year 2004, and 1972 was not a pointer year for RW. For CWT, the reduction of about 17.5% (z-score −1.95) in 1972 did result in a pointer year, but was also just a little more than half of the record reduction in 2004 (−32%, z-score −3.3). Other climate factors, such as drought, were also not apparent in the year 2004, but a late frost event cannot be ruled out, although was highly unlikely given the monthly mean temperatures. The 2004 growth depression was thus clearly outstanding, both in terms of RW and CWT and most likely not a result of climatic drivers.

In our opinion, the reduction in radial growth and cell wall thickness of alnus in 2004 in Kobbefjord, Greenland, was the result of an insect outbreak, most likely of *Eurois occulta*. In other parts of western Greenland, close to Kangerlussuaq Fjord, a two-year caterpillar outbreak of *Eurois* was recorded in 2004/2005 (Pedersen and Post, 2008; Post and Pedersen, 2008; Young et al., 2016). Peaking in 2005, it led to a massive reduction of above-ground biomass, especially in leaf biomass (more than 80% in birch and willow). In 2011, a one-year *Erois occulta* outbreak was recorded at our field site Kobbefjord, basically "switching off" the tundra ecosystem carbon sink that summer (Lund et al., 2017). Kobbefjord is well within the reported range of *Eurois occulta* (Fig. 1) and in this light it is likely that an outbreak occurred also in 2004 in Kobbefjord, reducing the photosynthetic apparatus of alder shrubs leading to strongly reduced growth resources, and narrower rings and thinner cell walls of alder.

However, alder is generally browsed far less than willows or birch shrubs, since it invests resources in anti-browsing defense (Bryant et al., 1987; Christie et al., 2015), and we were actually surprised to see such a clear growth depression signal in a species with antibrowsing defense even in a reported insect outbreak year. However, the related *Alnus incana* is classified as a secondary host plant for *Eurois occulta* and the

antibrowsing defenses of alder might be more targeted towards vertebrates (Christie et al., 2015) and not effective for invertebrates. Also, heavy insect outbreak years are characterized by extreme food shortage for herbivores (insects and others alike) and it is possible that browsing pressure on non-preferred browsing plants increases in such years (Karlsen et al., 2013; Lund et al., 2017). It seems thus likely, that despite the antibrowsing defenses of alder, it was browsed heavily in 2004, most likely by *Eurois occulta*.

If we assume an insect outbreak as the most likely cause of the extreme negative growth variation in alder in 2004, it is within reason to exclude this period from a calibration trial for a climate reconstruction. In our case, the result was ideal in terms of climate reconstruction: After the exclusion of the period 2004–2007, the relationships between climate driver and shrub growth became stable in time, the climate reconstruction models passed all tests, and the explained variance of the models increased.

Three issues, however, should be mentioned. First, why did the recorded *Eurois occulta* outbreak in 2011 in our research area did not lead to pointer years and growth reductions in alder? Several points come together here. I) Our chronologies had a smaller sample size in 2011. II) Concerning the pointer year analysis it is a technical question of not having enough years after the attack to calculate pointer years. III) The relative growth change method however, was possible and resulted in about average growth in that year. A closer look at individual growth records showed that apparently only a few shrubs in our chronologies were affected by the outbreak in 2011 (recording event years), pointing to less severity as one possible explanatory factor for the differences between 2004 and 2011. Primary palatable species, such as willows and dwarf birch were affected, non-host plants such as alder and less palatable species such as *Empetrum nigrum* not (Lund et al., 2017). Possibly the outbreak in 2011 did either not reach the dimensions of 2004 and caterpillars fed mainly on their primary palatable species, and not on alder shrubs, or the outbreak was more localized spatially. Even though we cannot confirm that alder was affected in 2011, the apparent inability of our records to capture the 2011 outbreak points to the need for more detailed studies and analyses.

Second, if we think about using alder or other shrubs for climate reconstructions, it is likely that the signature of the insect outbreak we found in our samples (strongly reduced ring width and cell wall thickness) could potentially also result from very severe summer conditions. In both cases, i.e. the insect attack and a very cold summer, the production of growth resources is severely limited, either by the loss of canopy and photosynthetic tissue or by very low temperatures physiologically affecting photosynthesis and wood production. In our record (covering only about 55 years), the effect of the coldest summer (1972) was only about half of that of the insect attack and recovery was within the next year, but the well-known "years without summer" following major volcanic eruptions, e.g. 1783 or 1815, might show growth reductions similar to the one described here (but see D'Arrigo et al., 2011). However, as indicated by our analyses, the relationship between CWT and RW may serve as an additional marker of herbivory, since we observed exceptionally low residuals of a corresponding regression. To test this hypothesis, further research is needed, ideally including material which was affected severely and more frequently.

Third, it is possible that when using alder to reconstruct climate beyond instrumental records, one may encounter previous insect attacks. These would, like severe summer conditions, lead to reduced ring width and thinner cell walls. The ability to disentangle climate from insect driven growth depressions might hinge on the impact of each of these events. While we could show in our case study that insect driven growth depressions lead to narrower rings and thinner cell walls than climate driven growth depressions and moreover exceptionally low residuals of CWT predictions by RW, this remains to be tested for extreme summer temperature deviations as discussed above.

5. Conclusions

Using a combination of shrub-ring width and wood anatomy analysis on alder shrubs in Greenland, we could show that insect driven growth depressions seem to be more severe than cold summers and heavily affect the positive relationship between CWT and RW. When excluding the years with insect driven growth depressions, climate reconstruction models passed calibration-verification tests. Our approach of combining traditional shrub-ring width analysis with wood anatomy seems, at least in this example, a promising avenue to potentially disentangle growth depressions due to climate from growth depressions due to insect attacks. However, more severe climatic conditions or less severe insect outbreaks might lead to similar signature in the wood, which could not be tested in our samples. If this approach can be applied to other species or disturbance intensities remains to be seen and tested, but we are hopeful that our approach can serve as an example for such an endeavor.

Data accessibility

All shrub ring width and cell anatomical data will be made available on the International Tree Ring Data Bank (ITRDB) administered and managed by NCEI's Paleoclimatology Team and the World Data Center for Paleoclimatology.

Author contributions

Acknowledgements

References

Ackerman, D., Griffin, D., Hobbie, S.E., Finlay, J.C., 2017. Arctic shrub growth trajectories differ across soil moisture levels. Glob. Change Biol. 23, 4294–4302.

Bär, A., Pape, R., Bräuning, A., Löffler, J., 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. J. Biogeogr. 35, 625–636.

Barrio, I.C., Lindén, E., Te Beest, M., Olofsson, J., Rocha, A., Soininen, E.M., Alatalo, J.M., Andersson, T., Asmus, A., Boike, J., Bråthen, K.A., Bryant, J.P., Buchwal, A., Bueno, C.G., Christie, K.S., Denisova, Y.V., Egelkraut, D., Ehrich, D., Fishback, L., Forbes, B.C., Gartzia, M., Grogan, P., Hallinger, M., Heijmans, M.M.P.D., Hik, D.S., Hofgaard, A., Holmgren, M., Høye, T.T., Huebner, D.C., Jónsdóttir, I.S., Kaarlejärvi, E., Kumpula, T., Lange, C.Y.M.J.G., Lange, J., Lévesque, E., Limpens, J., Macias-Fauria, M., Myers-Smith, I., van Nieukerken, E.J., Normand, S., Post, E.S., Schmidt, N.M., Sitters, J., Skoracka, A., Sokolov, A., Sokolova, N., Speed, J.D.M., Street, L.E., Sundqvist, M.K., Suominen, O., Tananaev, N., Tremblay, J.-P., Urbanowicz, C., Uvarov, S.A., Watts, D., Wilmking, M., Wookey, P.A., Zimmermann, H.H., Zverev, V., Kozlov, M.V., 2017. Background invertebrate herbivory on dwarf birch (Betula glandulosa-nana complex) increases with temperature and precipitation across the tundra biome. Polar Biol. 11, 2265–2278.

Beil, I., Buras, A., Hallinger, M., Smiljanić, M., Wilmking, M., 2015. Shrubs tracing sea surface temperature—Calluna vulgaris on the Faroe Islands. Int. J. Biometeorol. 59, 1567–1575.

Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M.M.P.D., Sauren, P., Berendse, F., 2011. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences 8, 1169–1179.

Bryant, J.P., Chapin, F.S., Reichardt, P.B., Clausen, T.P., 1987. Response of winter chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. Oecologia 72, 510–514.

Buchwal, A., Rachlewicz, G., Fonti, P., Cherubini, P., Gärtner, H., 2013. Temperature

modulates intra-plant growth of Salix polaris from a high Arctic site (Svalbard). Polar Biol. 36, 1305–1318.

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

Buras, A., Hallinger, M., Wilmking, M., 2012. Can shrubs help to reconstruct historical glacier retreats? Environ. Res. Lett. 7, 044031.

Buras, A., Lehejček, J., Michalová, Z., Morrissey, R.C., Svoboda, M., Wilmking, M., 2017a. Shrubs shed light on 20th century Greenland Ice Sheet melting. Boreas 46, 667–677.

Buras, A., Zang, C., Menzel, A., 2017b. Testing the stability of transfer functions. Dendrochronologia 42, 56–62.

Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.-L., Tape, K.D., Thompson, C.D.C., Walker, D.A., Welker, J.M., 2005. Role of land-surface changes in Arctic summer warming. Science 310, 657–660.

Christie, K.S., Bryant, J.P., Gough, L., Ravolainen, V.T., Ruess, R.W., Tape, K.D., 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis. BioScience 65, 1123–1133.

Cowtan, K., Way, R.G., 2014. Coverage bias in the HadCRUT4 temperature series and its impact on recent temperature trends. Q. J. R. Meteorol. Soc. 140, 1935–1944.

D'Arrigo, R., Seager, R., Smerdon, J.E., LeGrande, A.N., Cook, E.R., 2011. The anomalous winter of 1783-1784: was the Laki eruption or an analog of the 2009-2010 winter to blame? Geophys. Res. Lett. 38, L05706.

Dahl, M.B., Priemé, A., Brejnrod, A., Brusvang, P., Lund, M., Nymand, J., Kramshøj, M., Ro-Poulsen, H., Haugwitz, M.S., 2017. Warming, shading and a moth outbreak re-duce tundra carbon sink strength dramatically by changing plant cover and soil microbial activity. Sci. Rep. 7, 16035.

Ewacha, M.V.A., Roth, J.D., Brook, R.K., 2014. Vegetation structure and composition determine snowshoe hare (Lepus americanus) activity at arctic tree line. Can. J. Zool. 92, 789–794.

Forbes, B.C., Fauria, M.M., Zetterberg, P., 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. Glob. Change Biol. 16, 1542–1554.

Gamm, C.M., Sullivan, P.F., Buchwal, A., Dial, R.J., Young, A.B., Watts, D.A., Cahoon, S.M.P., Welker, J.M., Post, E., 2017. Declining growth of deciduous shrubs in the warming climate of continental western Greenland. J. Ecol. 00, 1–15.

Hallinger, M., Wilmking, M., 2011. No change without a cause – why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia. New Phytol. 189, 902–908.

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

Hanna, E., Huybrechts, P., Janssens, I., Cappelen, J., Steffen, K., Stephens, A., 2005. Runoff and mass balance of the Greenland ice sheet: 1958–2003. J. Geophys. Res.: Atmos. 110, D13108.

Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2014. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. Int. J. Climatol. 34, 623–642.

Havstrom, M., Callaghan, T., Jonasson, S., Svoboda, J., 1995. Little ice age temperature estimated by growth and flowering differences between subfossil and extant shoots of Cassiope tetragona, an Arctic Heather. Funct. Ecol. 9 (4), 650–654.

Hodson, D.L.R., Keeley, S.P.E., West, A., Ridley, J., Hawkins, E., Hewitt, H.T., 2013. Identifying uncertainties in Arctic climate change projections. Clim. Dyn. 40, 2849–2865.

Hollesen, J., Buchwal, A., Rachlewicz, G., Hansen, B.U., Hansen, M.O., Stecher, O., Elberling, B., 2015. Winter warming as an important co-driver for Betula nana growth in western Greenland during the past century. Glob. Change Biol. 21, 2410–2423.

Humbert, L., Kneeshaw, D., 2011. Identifying insect outbreaks: a comparison of a blind-source separation method with host vs non-host analyses. For.: Int. J. For. Res. 84, 453–462.

Jørgensen, R.H., Hallinger, M., Ahlgrimm, S., Friemel, J., Kollmann, J., Meilby, H., 2015. Growth response to climatic change over 120 years for Alnus viridis and Salix glauca in West Greenland. J. Veg. Sci. 26, 155–165.

Karlsen, S.R., Jepsen, J.U., Odland, A., Ims, R.A., Elvebakk, A., 2013. Outbreaks by ca-nopy-feeding geometrid moth cause state-dependent shifts in understorey plant communities. Oecologia 173, 859–870.

Kolishchuk, V.G., 1990. Dendroclimatological study of prostrate woody plants. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology: Applications in the Environmental Sciences. Kluwer Academic Publishers, Dordrecht, pp. 51–55.

Kozlov, M.V., Zvereva, E.L., 2017. Background Insect Herbivory: Impacts, Patterns and Methodology. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 1–43.

Lehejček, J., Buras, A., Svoboda, M., Wilmking, M., 2017. Wood anatomy of Juniperus communis: a promising proxy for palaeoclimate reconstructions in the Arctic. Polar Biol. 40, 977–988.

Lund, M., Raundrup, K., Westergaard-Nielsen, A., López-Blanco, E., Nymand, J., Aastrup, P., 2017. Larval outbreaks in West Greenland: instant and subsequent effects on tundra ecosystem productivity and CO2 exchange. Ambio 46, 26–38.

Myers-Smith, I.H., Bruce, C.F., Martin, W., Martin, H., Trevor, L., Daan, B., Ken, D.T., Marc, M.-F., Ute, S.-K., Esther, L., Stéphane, B., Pascale, R., Luise, H., Andrew, T., Laura Siegwart, C., Stef, W., Jelte, R., Shelly, A.R., Niels Martin, S., Gabriela, S.-S., Sonja, W., Christian, R., Cécile, B.M., Susanna, V., Scott, G., Laia, A.-H., Sarah, E., Virve, R., Jeffrey, W., Paul, G., Howard, E.E., David, S.H., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ. Res. Lett. 6, 045509.

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., Speed, J.D.M., Boulanger-

Lapointe, N., Rixen, C., Levesque, E., Schmidt, N.M., Baittinger, C., Trant, A.J., Hermanutz, L., Collier, L.S., Dawes, M.A., Lantz, T.C., Weijers, S., Jorgensen, R.H., Buchwal, A., Buras, A., Naito, A.T., Ravolainen, V., Schaepman-Strub, G., Wheeler, J.A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015a. Climate sensitivity of shrub growth across the tundra biome. Nat. Clim. Change 5, 887–891.

Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S.A., Weijers, S., Trant, A.J., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Dawes, M.A., Wheeler, J.A., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B.C., Lévesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilmking, M., 2015b. Methods for measuring arctic and alpine shrub growth: a review. Earth Sci. Rev. 140, 1–13.

Nielsen, S.S., Arx, G.v., Damgaard, C.F., Abermann, J., Buchwal, A., Büntgen, U., Treier, U.A., Barfod, A.S., Normand, S., 2017. Xylem anatomical trait variability provides insight on the climate-growth relationship of Betula nana in Western Greenland. Arct. Antarct. Alp. Res. 49, 359–371.

Pedersen, C., Post, E., 2008. Interactions between herbivory and warming in aboveground biomass production of arctic vegetation. BMC Ecol. 8, 17.

Pithan, F., Mauritsen, T., 2014. Arctic amplification dominated by temperature feedbacks in contemporary climate models. Nat. Geosci. 7, 181–184.

Post, E., Pedersen, C., 2008. Opposing plant community responses to warming with and without herbivores. Proc. Natl. Acad. Sci. 105, 12353–12358.

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

Rayback, S.A., Henry, G.H.R., Lini, A., 2012. Multiproxy reconstructions of climate for three sites in the Canadian High Arctic using Cassiope tetragona. Clim. Change 114, 593–619.

Rinas, C.L., Dial, R.J., Sullivan, P.F., Smeltz, T.S., Tobin, S.C., Loso, M., Geck, J.E., 2017. Thermal segregation drives patterns of alder and willow expansion in a montane ecosystem subject to climate warming. J. Ecol. 105, 935–946.

Rozema, J., Weijers, S., Broekman, R.O.B., Blokker, P., Buizer, B., Werleman, C., El Yaqine, H., Hoogedoorn, H., Fuertes, M.M., Cooper, E., 2009. Annual growth of Cassiope tetragona as a proxy for Arctic climate: developing correlative and experi-mental transfer functions to reconstruct past summer temperature on a millennial time scale. Glob. Change Biol. 15, 1703–1715.

Schneider, L., Gärtner, H., 2013. The advantage of using a starch based non-Newtonian fluid to prepare micro sections. Dendrochronologia 31, 175–178.

Schneider, U., Becker, A., Finger, P., Meyer-Christoffer, A., Rudolf, B., Ziese, M., 2016. GPCC Full Data Reanalysis Version 7.0: Monthly Land-Surface Precipitation from Rain Gauges Built on GTS Based and Historic Data. Research Data Archive at the National Center for Atmospheric Research. Computational and Information Systems Laboratory, Boulder, CO.

Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., Bräker, O.U., 1990. Identification, presentation and interpretation of event years and pointer years in den-drochronology. Dendrochronologia 8, 9–38.

Schweingruber, F.H., Börner, A., Schulze, E.-D., 2008. Atlas of Woody Plant Stems – Evolution, Structure, and Environmental Modifications. Springer.

Schweingruber, F.H., Hellmann, L., Tegel, W., Braun, S., Nievergelt, D., Büntgen, U., 2013. Evaluating the wood anatomical and dendroecological potential of arctic dwarf shrub communities. IAWA J. 34, 485–497.

Serreze, M.C., Barry, R.G., 2011. Processes and impacts of Arctic amplification: a research synthesis. Glob. Planet. Change 77, 85–96.

Tape, K.E.N., Sturm, M., Racine, C., 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Glob. Change Biol. 12, 686–702.

Tape, K.D., Lord, R., Marshall, H.-P., Ruess, R.W., 2010. Snow-mediated ptarmigan browsing and shrub expansion in Arctic Alaska. Ecoscience 17, 186–193.

Tape, K.D., Hallinger, M., Welker, J.M., Ruess, R.W., 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. Ecosystems 15, 711–724.

Tape, K.D., Gustine, D.D., Reuss, R.W., Adams, L.G., Clark, J.A., 2016. Range expansion of moose in arctic Alaska linked to warming and increased shrub habitat. PLoS One 11, e0152636.

Tenow, O., Nilssen, A.C., Bylund, H., Hogstad, O., 2007. Waves and synchrony in Epirrita autumnata – Operophtera brumata outbreaks. I Lagged synchrony: regionally, locally and among species. J. Anim. Ecol. 76, 258–268.

van der Maaten-Theunissen, M., van der Maaten, E., Bouriaud, O., 2015. pointRes: an R package to analyze pointer years and components of resilience. Dendrochronologia 35, 34–38.

Vowles, T., Gunnarsson, B., Molau, U., Hickler, T., Klemedtsson, L., Björk, R.G., 2017. Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range. J. Ecol. 105, 1547–1561.

Weijers, S., Broekman, R., Rozema, J., 2010. Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub Cassiope tetragona. Quat. Sci. Rev. 29, 3831–3842.

Weijers, S., Wagner-Cremer, F., Sass-Klaassen, U., Broekman, R., Rozema, J., 2013. Reconstructing High Arctic growing season intensity from shoot length growth of a dwarf shrub. Holocene 23, 721–731.

Weijers, S., Buchwal, A., Blok, D., Löffler, J., Elberling, B., 2017. High Arctic summer warming tracked by increased Cassiope tetragona growth in the world's northernmost polar desert. Glob. Change Biol. 23, 5006–5020.

Wilmking, M., Hallinger, M., Van Bogaert, R., Kyncl, T., Babst, F., Hahne, W., Juday, G.P., de Luis, M., Novak, K., Völlm, C., 2012. Continuously missing outer rings in woody plants at their distributional margins. Dendrochronologia 30, 213–222.

Young, A.B., Watts, D.A., Taylor, A.H., Post, E., 2016. Species and site differences in-fluence climate-shrub growth responses in West Greenland. Dendrochronologia 37, 69–78.

55

Chapter 5

Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the
European continent **(Global Change Biology (2017) 23: 3169-3180)**

Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent

ELENA PELLIZZARI[1], JESUS JULIO CAMARERO[2], ANTONIO GAZOL[2], ELENA GRANDA[2], ROHAN SHETTI[3], MARTIN WILMKING[3], PAVEL MOISEEV[4], MARIO PIVIDORI[1] and MARCO CARRER[1]

[1]*Deaparment of TeSAF, Università Degli Studi di Padova, Legnaro I-35020, Italy,* [2]*Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza 50059, Spain,* [3]*Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald 17487, Germany,* [4]*Institute of Plant and Animal Ecology UD RAS, Yekaterinburg 620144, Russia*

Abstract

Climate warming is expected to enhance productivity and growth of woody plants, particularly in temperature-limited environments at the northernmost or uppermost limits of their distribution. However, this warming is spatially uneven and temporally variable, and the rise in temperatures differently affects biomes and growth forms. Here, applying a dendroecological approach with generalized additive mixed models, we analysed how the growth of shrubby junipers and coexisting trees (larch and pine species) responds to rising temperatures along a 5000-km latitudinal range including sites from the Polar, Alpine to the Mediterranean biomes. We hypothesize that, being more coupled to ground microclimate, junipers will be less influenced by atmospheric conditions and will less respond to the post-1950 climate warming than coexisting standing trees. Unexpectedly, shrub and tree growth forms revealed divergent growth trends in all the three biomes, with juniper performing better than trees at Mediterranean than at Polar and Alpine sites. The post-1980s decline of tree growth in Mediterranean sites might be induced by drought stress amplified by climate warming and did not affect junipers. We conclude that different but coexisting long-living growth forms can respond differently to the same climate factor and that, even in temperature-limited area, other drivers like the duration of snow cover might locally play a fundamental role on woody plants growth across Europe.

Keywords: climate warming, dendroecology, junipers, latitudinal transect, thermal uncoupling, tree growth

Received 10 October 2016; revised version received 7 November 2016 and accepted 10 November 2016

Introduction

Climate warming is unequivocal, and since the 1950s, the rapid rise of air temperatures due to increasing atmospheric CO_2 concentrations is unprecedented over millennia in many regions (IPCC, 2014). This is the case of Europe, where the average land temperature of the 2004–2013 period is 1.3 °C above the pre-industrial level, which makes it the warmest decade on record (Rohde *et al.*, 2013). Interestingly, this warming is seasonally heterogeneous and spatially variable with highest rates observed in peripheral European regions such as E. Spain (40°N) and NW. Russia (65°N) (Vautard *et al.*, 2014). Furthermore, European temperatures are projected to continue increasing by 2.4–4.1 °C during the 21st century, that is more than global averages (Kjellström *et al.*, 2011). Here, we explore whether different seasonal warming trends observed across European biomes (Polar, Alpine and Mediterranean biomes) translate into different growth patterns in

Correspondence: Jesus Julio Camarero, tel. +34 976 716031, fax +34 976 716019, e-mail: jjcamarero@ipe.csic.es

prostrate vs. arborescent conifer growth forms. We discuss how the shrub vs. tree dichotomy determines growth reactions to climate warming and could influence future changes in productivity of woody European biomes.

Rapid climate warming is expected to impact woody plants in the Polar biome more intensely and rapidly than elsewhere leading to enhanced growth in the species' northernmost limits of distribution, and promoting tree shifts and shrub encroachment northwards as has been already observed in boreal forests and the arctic tundra (Suarez *et al.*, 1999; Sturm *et al.*, 2001; Danby & Hik, 2007; MacDonald *et al.*, 2008; Harsch *et al.*, 2009; Hallinger *et al.*, 2010; Myers-Smith *et al.*, 2011, 2015). Such treeline shifts and shrub encroachment phenomena are the result of warming-enhanced productivity success of these woody communities (Esper *et al.*, 2010; Forbes *et al.*, 2010; Hallinger & Wilmking, 2011), albeit warming-related drought stress has also been detected at some boreal forests (Barber *et al.*, 2000; Trahan & Schubert, 2016).

In the Alpine biome, where trees and shrubs reach their uppermost distribution limits, growth of woody

plants is mainly constrained by decreasing temperatures upwards (Körner, 2012a), and for this reason, enhanced tree and shrub growth by climate warming is expected at high elevations in these mountain regions (Büntgen *et al.*, 2008a; Salzer *et al.*, 2009; Lu *et al.*, 2016). However, such environments illustrate at small spatial scales a fundamental dichotomy between arborescent (tree) and prostrate (shrub) growth forms and their expected responses to climate warming. Due to the erect growth and tall stature of trees, meristems are well coupled with free atmospheric conditions which enforce convective air exchange (Wilson *et al.*, 1987; Grace *et al.*, 1989). For this reason, trees are usually more sensitive to thermal air limitations than shrubs (Körner, 2012a). Contrastingly, in low-stature and prostrate shrubs, meristems are more coupled to ground microclimate conditions, which are usually warmer with respect to free atmospheric conditions due to the reduction of heat exchange (Körner, 2012b). This more favourable microclimate allows shrub growth to be partially decoupled from atmospheric thermal states which explains their existence above the treeline (Körner, 2012b). In addition, during winter shrub, meristems are often covered and protected by snow, limiting the risk of freezing and mechanical damages as compared to tree buds (Bokhorst *et al.*, 2009; Rixen *et al.*, 2010). However, the insulating benefits of snow pack to shrub meristems may also be detrimental whether the snow pack is so thick or dense to induce a delayed snow melting and a shortening of the growing season (Pellizzari *et al.*, 2014).

Lastly, in the Mediterranean biome, shrub and tree growth is mainly constrained by seasonal drought (Gazol & Camarero, 2012), even at high-elevation sites (Garcia-Cervigón Morales *et al.*, 2012). Therefore, warmer conditions could amplify drought stress in this biome, and the aridification trend already observed in southern Europe (Vicente-Serrano *et al.*, 2014) may lead to slower growth of woody plants if precipitation is assumed not to change (Matías & Jump, 2015). Moreover, warmer growing season conditions have already induced moisture limitation and reduced juniper growth in temperate mountains such as the Tibetan Plateau (Liang *et al.*, 2012), so warming-related drought constrains should be fully considered not just for the Mediterranean but also for similar dry biomes.

We aim to quantify the radial growth responses to rising temperatures of junipers and co-occurring trees (larch and pine species) across a NE-SW European transect including sites located in Polar, Alpine and Mediterranean biomes. By assuming the decoupling between air temperature and shrubs growth, we hypothesize that erect trees will be more sensitive to recent climate warming than shrubby junipers,

particularly in the case of the most cold-limited sites (Polar and Alpine biomes). We also expect to detect drought-related growth limitations in Mediterranean sites, chiefly affecting trees because they are more responsive to drought amplification by climate warming (Williams *et al.*, 2013).

Materials and methods

Study species and sample collection

Common juniper (*Juniperus communis* L.) is a shrubby gymnosperm considered to be the most widespread conifer over the Northern Hemisphere (Farjon, 2005). We selected 10 sites located in three contrasted biomes on the European continent going from the Russian Polar Urals to eastern Spain. In these biomes, Polar (Polar Urals), Alpine (Italian Alps) and Mediterranean (Spanish Iberian System, Apennines in S. Italy), the species grows at the northern, uppermost and southern limits of its distribution (Table 1, Fig. 1).

In the Polar and northern Urals sites, sampling took place near the undisturbed treeline ecotone which is situated between 270 m to 450 m a.s.l. and includes larch (*Larix sibirica* Ledeb.) and birch stands (*Betula tortuosa* Ledeb.), shrubs (junipers, *Salix* spp.), and alpine moss–grass–lichen communities. In these remote sites (URT, URF, PU; see Table 1), vegetation has not been heavily disturbed during the last centuries (Shiyatov *et al.*, 2005). Climatic data of the Salekhard meteorological station (66.5°N, 66.7°E, 137 m a.s.l., 55 km south-east of the URF and URT study sites) show a mean annual temperature of -6.4 °C with January (-24.4 °C) and July ($+13.8$ °C) as the coldest and warmest months, respectively. According to climate–growth relationships and based on phenological field observations (needle and shoot elongation, stem wood formation), the growing season lasts from early June to mid-August (J.J. Camarero *pers. observ.*; Devi *et al.*, 2008). Mean annual precipitation is 415 mm, with 50% falling as snow. Maximum snow depth is 200–250 cm (Hagedorn *et al.*, 2014). Soils develop on ultramafic rocks.

In the Italian Alps, the treeline is located between 1800 and 2200 m a.s.l., and vegetation is dominated by larch (*Larix deciduas* Mill.), spruce (*Picea abies* Karst) and stone pine (*Pinus cembra* L.) forests and shrubby (*Juniperus communis* L., *Rhododendron* spp., *Salix* spp.) communities (Pellizzari *et al.*, 2014). Climate is characterized by dry winters, with most of the precipitation occurring from late spring to early autumn; the mean annual temperature is 2.5 °C (coldest and warmest months are usually January and July) and the total annual precipitation is ca. 1800 mm, whilst the growing period lasts from June to early September (Carrer & Urbinati, 2006). Maximum snow depth is usually 250–600 cm. Soils are shallow rendzic leptosols formed over dolomite and limestone to spodosol over crystalline bedrocks. In this region, logging and livestock grazing decreased significantly during the past century and especially after World War II.

In the Mediterranean region, we selected a site (POL) located in southern Italy subjected to wetter conditions than the other two dryer sites (VIL, PEN) situated in eastern Spain

Table 1 Description of the study sites and number of sampled junipers and trees

Region	Site (code)	Latitude (N)	Longitude (W/E)	Elevation (m a.s.l.)	Tree species	No. junipers/trees
Polar	Polar Urals – treeline (URT)	66°51′	65°35′E	320	*Larix sibirica*	24/13
	Polar Urals – forest limit (URF)	66°50′	65°35′E	230	*Larix sibirica*	23/20
	Polar Urals (PU)	66°48′	65°33′E	220	*Larix sibirica*	20/24
	Northern Urals (NU)	61°18′	59°14′E	750	*Larix sibirica*	24/–
Alpine	Devero (DEV)	46°19′	8°16′E	2100	*Larix decidua*	12/18
	Ventina (VEN)	46°18′	9°46′E	2300	*Larix decidua*	17/34
	Sella Nevea (SEL)	46°22′	13°27′E	1800	*Larix decidua*	24/17
Mediterranean	Pollino (POL)	39°09′	16°12′E	2100	*Pinus heldreichii*	16/14
	Peñarroya (PEN)	40°23′	0°40′W	2020	*Pinus uncinata*	13/41
	Villarroya de los Pinares (VIL)	40°34′	0°40′W	1350	*Pinus sylvestris*	12/20
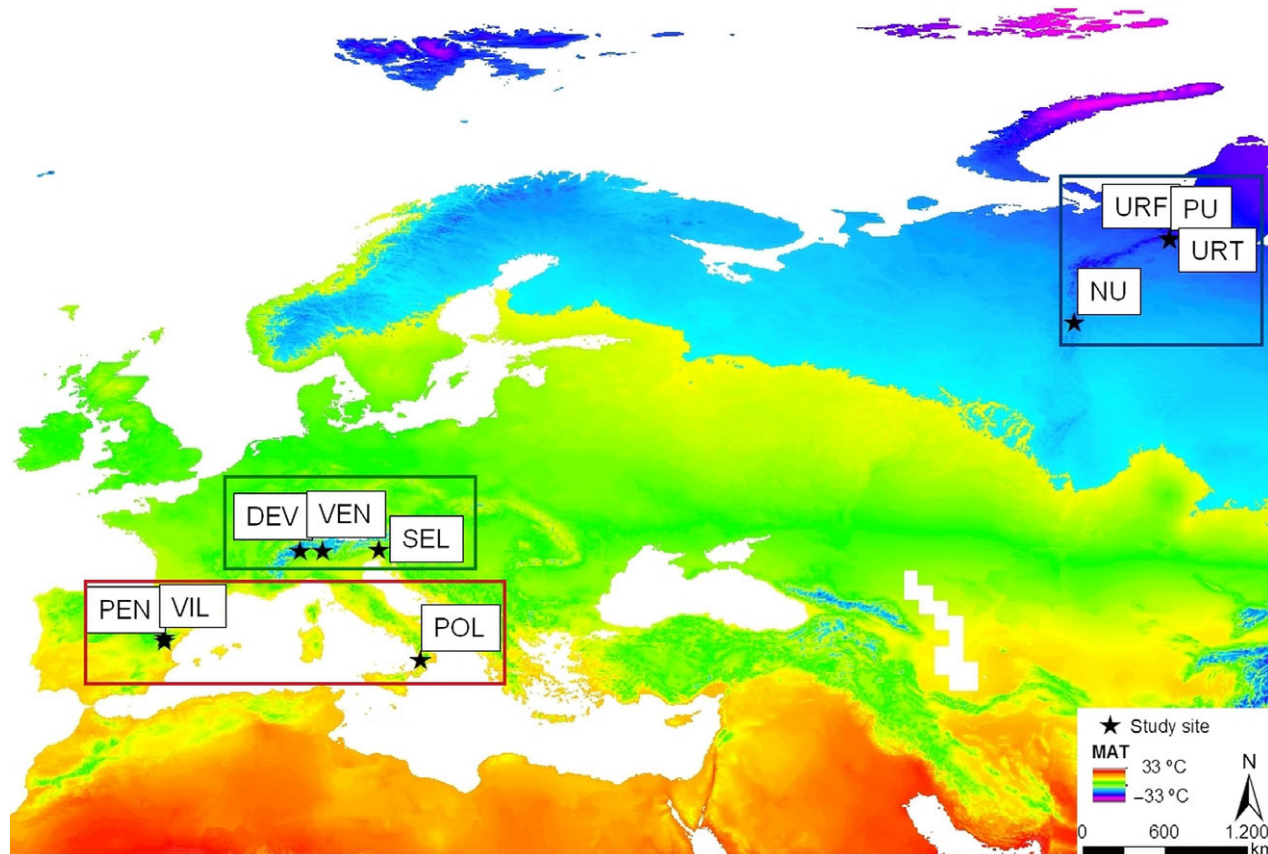
Fig. 1 Juniper tree sample sites. Colour boxes correspond to the three regions: blue for Polar sites (Russian Polar Urals), green for Alpine sites (N. Italy) and red for Mediterranean sites (E Spain, S. Italy). In the case of the NU site, only junipers were sampled. See sites' characteristics in Table 1. Map colours correspond to the annual mean temperature (MAT).

(Camarero *et al.*, 2015a). In POL, forests are dominated by pine (*Pinus heldreichii*) accompanied by junipers and Mediterranean shrubs and grasslands (Todaro *et al.*, 2007). Climate is Mediterranean, humid type, with warm and fairly dry summers and the annual mean temperature is ca. 5.0 °C whilst the precipitation is around 1570 mm mainly concentrated in autumn and winter. Snow cover lasts from November to late May and its maximum depth is 50–150 cm. Soils are shallow

and formed over large outcropping rocks (limestone, dolomites). In the VIL and PEN sites located in Spain, forests are dominated by Scots (*Pinus sylvestris* L.) and mountain pine (*Pinus uncinata* Ram.), whilst shrubby communities are formed by junipers (*J. communis*, *J. sabina* L.) and barberry (*Berberis vulgaris* L.) (Camarero *et al.*, 2015a). Climate is Mediterranean continental with a mean annual temperature of +4.0–9.0 °C and annual precipitation of 510–900 mm. In the low-elevation

VIL site, water deficit occurs in July and drought-induced die-back has been observed in some juniper stands (J.J. Camarero, *pers. observ.*). In the high-elevation PEN site, snow cover lasts from November until March. Soils are shallow and derived from underlying limestone bedrock. The VIL and PEN sites have experienced low land-use pressures (logging, grazing) since the 1950s. Here, the growing season usually starts from early May to early June and ends from late September to late October (Deslauriers *et al.*, 2008). Where the typical Mediterranean summer drought is present, it is possible to observe a resting period within the growing season (Camarero *et al.*, 2010).

Juniper shrubs and trees were usually sampled near the treeline ecotone except at one Mediterranean site (VIL). We collected 350 junipers distributed over the ten study sites and 250 trees, from six different conifer species (Table 1), located at nine of these sites (there were no trees at the Polar NU site, whilst the PU tree-ring chronology was retrieved from the International Tree-Ring Data Bank) (https://www.ncdc.noaa.gov/paleo/study/15341). In the field, we measured the stem diameter of junipers (near the base as close as possible to the root collar) and trees (diameter at breast height measured at 1.3 m). We cut basal discs from the major juniper stems since most of the junipers were multistemmed and prostrate (height <0.5 m) whilst for trees we collected two perpendicular cores at 1.3 m.

Dendrochronological methods

We sanded juniper discs and tree cores with progressively finer sandpapers to better analyse the annual rings. Junipers often present eccentric stems and a high number of wedging rings due to the irregular growth form (Fig. S1). For this reason, we measured 2–4 radii in each disc. The pronounced eccentricity prevented converting radial measurements to area increments (Buras & Wilmking, 2014; Myers-Smith *et al.*, 2014). In trees, 2 radii per individual were measured. Rings were measured to the nearest 0.01 mm using a LINTAB-TSAP (Rinn, Heidelberg, Germany) sliding stage micrometre system and then dated.

We used the COFECHA software (Holmes, 1983) to check the cross-dating. We successfully cross-dated 185 junipers (53% of the samples); in the other cases, irregular growth, wedging and missing rings, especially at the outer part of the cross-sections, made the cross-dating of old individuals challenging (Fig. S1). In junipers, the age was obtained by counting the rings from the bark to the pith, whilst in trees, age was estimated (at 1.3 m) by fitting a geometric pith locator to the innermost rings in the case of cores without pith. Then, tree age was estimated by counting the rings in the oldest core of each tree and adding the estimate length of core missing up to the predicted pith.

To compare ring growth with climate variables, we standardized and detrended the juniper and tree-ring width series using the DPLR (Bunn, 2010) package in the R statistical environment (R Core Team, 2015). In the case of junipers, we chose a spline function with a 50% frequency cut-off at 100 years; in this way, we removed the long-term biological growth trend, maintaining high (annual)- to midfrequency (multidecadal)

growth variability resulting in dimensionless ring-width indices (Helama *et al.*, 2004). Tree chronologies were similarly detrended to remove the typical age-related trend of declining ring-width (often absent in junipers; see Pellizzari *et al.*, 2014) using firstly a negative exponential curve and then applying a 100-year-long spline. Finally, with both growth forms, junipers and trees, the first-order autocorrelation of the standardized ring-width indices was removed through autoregressive modelling. The residual indices were averaged at the individual and site levels using a biweight robust mean to obtain residual individual and site chronologies. Statistical descriptive parameters (Fritts, 2001), including the mean, standard deviation, first-order autocorrelation of raw series, the mean sensitivity (a measure of the year-to-year variability) and the mean correlation between individual series of residual ring-width indices, were also calculated for each site chronology considering the common 1950–2013 period.

Climate data

To analyse climate trends in the three regions, we used the 0.5° gridded CRU climate data set considering monthly data (mean, maximum and minimum temperatures; total precipitation) for the 1901–2013 period (Harris *et al.*, 2014), and also the European-wide E-OBS v12 gridded data set at 0.25° resolution for the 1950–2013 period (Haylock *et al.*, 2008; Van Den Besselaar *et al.*, 2011). We further investigated seasonal values (means in the case of temperatures, totals in the case of precipitation), considering previous year summer, autumn and winter (June to August, September to November and December to current February, respectively) and current spring and summer (March to May and June to August, respectively). Indeed, we also analysed the sum of previous winter and current spring precipitation, considering that snow is present during this period and could affect juniper growth in many sites (Pellizzari *et al.*, 2014). Linear trends of temperature anomalies with respect to the 1981–2010 period were calculated after 1950 considering either the CRU or the E-OBS climate data sets.

Due to a decreasing number of instrumental station records together with an increasing amount of uncertainty associated with climate data before the 1950s (Jones, 2016), and particularly across Mediterranean mountains (e.g. the greater Pyrenees region, cf. Büntgen *et al.*, 2008b), the statistical analyses (climate–growth correlations, models) were restricted to the 1950–2013 period.

Statistical analyses

Climatic drivers of the year-to-year growth variability. All statistical analyses were performed in R environment (R Core Team, 2015). First, to summarize the relationships among juniper and tree chronologies, we calculated Pearson correlations and plotted them as a function of site-to-site distances. We also calculated a principal component analysis (PCA) using the covariance matrices obtained by relating the residual chronologies. Second, we used Pearson correlations and linear mixed-effects models (LMEs; Pinheiro & Bates, 2000) to

quantify the associations between climatic variables and ring-width indices at site and individual scales, respectively. In the correlation analyses, we considered monthly (from April to September) and seasonal climatic variables of the common 1950–2013 period. Moving correlations (25-year-long intervals) were also calculated between growing season mean temperatures (May to August) and juniper and tree site chronologies. Despite that growing season length may differ between regions due to the broad latitudinal difference, parallel elevation variability can counteract this trend. Therefore, having in mind this consideration and looking at the results from the monthly climate/growth associations, we set the common May to August period as the time span expected to cover most of the potential growing season in all regions.

LMEs were fitted for all regions considering regions and individual trees or shrubs nested within sites as random factors and also separately for each region considering again trees or shrubs as random factors. Seasonal and monthly climate variables were considered fixed factors (interactions between climate variables were also considered). The LMEs have the following form:

$$RW_i = X_i\beta + Z_ib_i + \varepsilon_i, \qquad (1)$$

where RW_i represents the shrubs' or trees' ring-width indices of any individual i, β is the vector of fixed effects (climate variables), b_i is the vector of random effects (site or tree/shrub identity), X_i and Z_i are, respectively, fixed and random effects regressor matrices, and ε_i is the within-group error vector. We ranked all the potential models that could be generated with the different explanatory variables according to the Akaike information criterion (AIC). We selected those most parsimonious models, that is the ones with the lowest AIC (Burnham & Anderson, 2002); these models were identified using the MU-MIN package (Barton, 2013). In addition, we used the Akaike weights (*Wi*) of each model to measure the conditional probability of the candidate model assuming it was the best model. Finally, we evaluated the fit of the models by graphical examination of the residual and fitted values (Zuur *et al.*, 2009). The 'lme' function of the NLME package was used to fit the LMEs (Pinheiro *et al.*, 2015).

Growth trends in junipers and trees. To analyse spatiotemporal patterns in juniper and tree-ring width data, we used generalized additive mixed models (GAMMs; Wood, 2006). GAMM is a flexible semiparametric method used to characterize nonlinear patterns observed between a 'response' variable as a function of 'explanatory' variables (Wood, 2006). The final GAMM we used was in the form:

$$RW_i = s(year_i * region_i) + s(age_i) + s(size_i) + Z_iB_i + \varepsilon_i. \quad (2)$$

In this model, the ring widths (RWs) of tree i were modelled as a function of calendar year, age and stem basal area (size). An interaction term between year and region was included to account for different growth trends between regions. Thin plate regression splines (*s*) are used to represent all the smooth terms. The degree of smoothing is determined by internal cross-validation (Wood, 2006). In addition, as RW represents multiple measurements performed on different trees from each site, tree identity (Z_iB_i) was regarded as a random effect.

An error term (ε_i) with an AR1 ($P = 1$) correlation structure was also included in the model. GAMMs were fitted using the *mgcv* library (Wood, 2006).

Results

Climate trends

Unexpectedly, warming trends during the 1901–2013 and 1950–2013 periods were stronger in the Mediterranean and Alpine sites than in the Polar sites (Table S1; Fig. S2). Seasonally, the warming was more intense in summer across Mediterranean sites, particularly in Spain, followed by spring minimum temperatures in the Polar and Alpine sites, particularly in the Polar Urals (Table S1). Few significant trends were detected for seasonal precipitation.

Growth patterns and trends

Junipers were youngest at the Polar and grew more in Mediterranean sites, whereas the oldest individuals (ca. 400- and 1000-year-old junipers and larches, respectively) were sampled in the Alpine sites (Fig. S3). For junipers and trees younger than 200 years, the mean growth rate was always lowest at the Polar region, whilst growth was highest in the Alpine sites. The mean ring widths of junipers (0.30 mm) were significantly lower ($t = -4.41$, $P = 0.001$) than that (0.90 mm) of trees (Table 2). However, neither the first-order auto-correlation nor the mean sensitivity differed between juniper and trees chronologies.

The mean correlation between individuals was also significantly lower ($t = -5.56$, $P = 0.0002$) in junipers (0.26) than in trees (0.54). This also explains why the correlation between trees' chronologies was much stronger than between junipers' chronologies within each biome (Table S2, Fig. S4). Accordingly, the first axis of the PCA accounted for 45% and 32% of the total variance of ring-width indices in the case of tree and juniper sites, respectively (Fig. S5). The PCA allowed grouping sites geographically, that is within each biome, but in the case of the Mediterranean sites, the humid Italian POL site clearly diverged from the dry Spanish PEN and VIL sites. Lastly, positive and significant ($P < 0.05$) correlations between juniper and tree chronologies within each site were found in the Polar and Mediterranean biomes, but not in the Alpine one (Table S2).

The GAMMs demonstrated a long-term growth increase of Polar junipers since the 1950s, which boosted after the 1980s when climate warming intensified (Fig. S2), closely followed by Mediterranean junipers (Fig. 2). In contrast, Mediterranean trees showed a

Table 2 Tree-ring series length and descriptive statistics for the juniper (J) and trees (T) computed over the common period 1950–2013. Values are means except for age data

| Region | Site | Age (years) | | Ring widths | | | | | | Residual indices | | | |
| | | | | Mean (mm) | | Standard deviation (mm) | | First-order autocorrelation | | Mean sensitivity | | Correlation between individual series | |
		J	T	J	T	J	T	J	T	J	T	J	T
Polar	URT	85	210	0.22	0.71	0.11	0.31	0.61	0.54	0.32	0.41	0.27	0.67
	URF	74	331	0.27	0.38	0.17	0.24	0.72	0.63	0.30	0.45	0.30	0.64
	PU	164	162	0.17	0.69	0.09	0.36	0.86	0.72	0.22	0.34	0.27	0.63
	NU	99	–	0.20	–	0.07	–	0.54	–	0.21	–	0.20	–
Alpine	DEV	103	564	0.27	0.77	0.14	0.42	0.59	0.35	0.36	0.32	0.16	0.59
	VEN	171	1000	0.25	0.66	0.11	0.39	0.68	0.72	0.27	0.33	0.23	0.56
	SEL	85	405	0.28	1.17	0.13	0.56	0.60	0.67	0.32	0.27	0.29	0.65
Mediterranean	POL	182	574	0.26	0.83	0.12	0.46	0.65	0.90	0.32	0.16	0.36	0.40
	PEN	95	256	0.57	1.59	0.30	0.70	0.49	0.81	0.38	0.23	0.21	0.33
	VIL	103	123	0.52	1.26	0.28	0.48	0.61	0.75	0.36	0.20	0.29	0.36
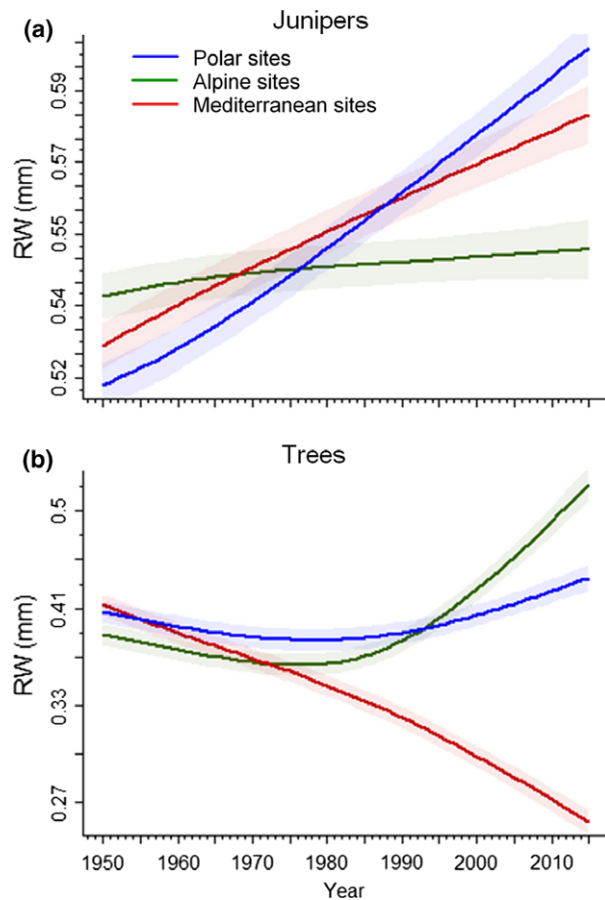
Fig. 2 Ring-width growth (RW, ring-width; values are means ± SE) based on the generalized additive mixed models (GAMM) for (a) junipers and (b) trees in each region (blue, green and red lines refer to the Polar, Alpine and Mediterranean sites, respectively). Trends were assumed for a theoretical individual with mean age and basal area across all the study sites.

rapid declining in growth since the 1980s, whereas Alpine trees followed by Polar ones featured growth acceleration.

Growth associations with climate

Warm summer conditions enhanced growth in cold regions (Polar and Alpine biomes) with stronger temperature–growth correlations in trees than in junipers (Fig. 3).

Specifically, higher June to July maximum temperatures were related to wider ring widths, particularly in treeline trees at the Polar sites. Wet September conditions enhanced juniper and tree growth at several Polar sites. Winter-to-spring wet conditions were negatively associated with Alpine juniper growth. In contrast, cool and wet spring and early summer conditions favoured growth of junipers and trees in the PEN and VIL dry Mediterranean sites, whereas warm spring and
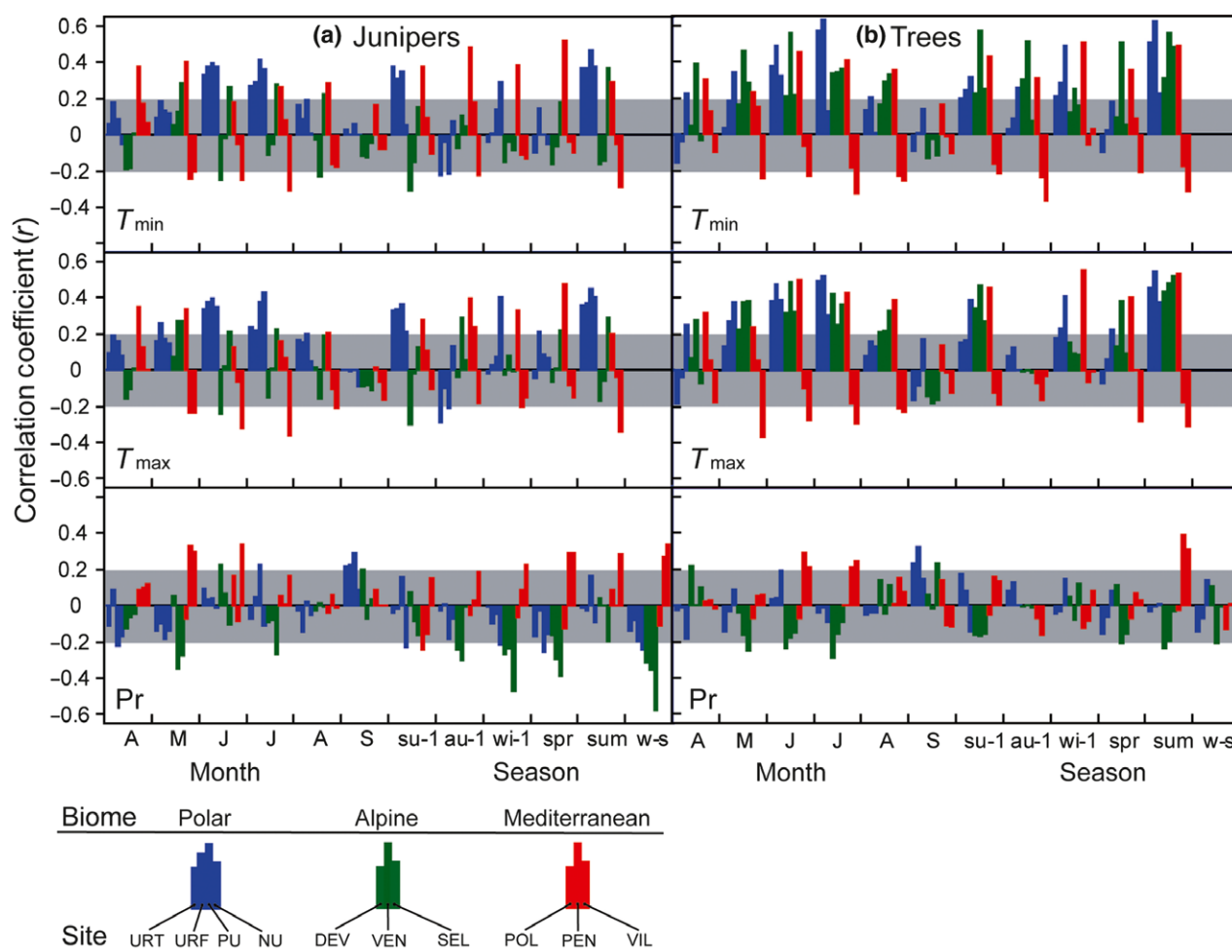
Fig. 3 Site-level climate–growth relationships for the juniper and trees. Bars are Pearson correlation coefficients obtained by relating seasonal or monthly mean minimum (Tmin) or maximum (Tmax) temperatures and precipitation (Pr) with site chronologies of ring-width indices for the common period 1950–2013. Grey boxes indicate nonsignificant values. The temporal window includes monthly climate values from April to September and seasons are indicated by three-letter codes (w-s is the previous winter to spring season). Previous year summer (su-1), autumn (au-1) and winter (wi-1) have also been considered.

summer conditions enhanced tree and juniper growth in the wet POL Mediterranean site (Fig. 3). In the two dry Mediterranean sites, the growth of junipers and trees was enhanced by wet conditions in May–June and June–July, respectively. Previous summer temperatures influence positively juniper growth at Polar Urals and tree growth at some Polar and Alpine sites. These associations at the site level were also reflected by the LMEs fitted at individual level which showed: (i) the dominant role played by summer maximum temperatures for Polar juniper and tree growth; (ii) the negative influence of high winter-to-spring precipitation for Alpine juniper growth; and (iii) the relevance of cool and wet spring and summer conditions to Mediterranean growth (Table 3; see also Table S3).

Growing season temperatures were significantly ($P < 0.05$) and positively related to Polar tree growth

during most of the 1950–2013 period, but in the case of Polar junipers such association decreased to not significant values after the 1990s (Fig. 4). In the case of Alpine trees, temperatures were playing a more important role by enhancing growth since 1970 and turning significant after 1982. In Alpine junipers, positive and significant temperature–growth relationships occurred only during the mid-1960s, following afterwards a reverse trend to that described for coexisting trees. Growth of Mediterranean trees and shrubs did not show significant correlations with temperature.

Discussion

The growth of the two plant forms (shrub and tree), despite featuring even opposite trends, clearly diverges in all the three biomes. This outcome is also

Table 3 Summary of the linear mixed-effects models of juniper and tree growth (ring-width indices) as a function of region and climate variables (mean temperatures, total precipitation). Note that the models' intercepts are not presented for simplicity

Data set or region	Junipers		Trees	
	Parameters	Wi	Parameters	Wi
All regions	$+0.022$ Txaut$_{t-1}$ $+0.012$Txsum $+ 0.001$Tnspr $- 0.002$ PrWS$_{t-1}$	0.88	$+0.072$ Txsum $+ 0.014$ Txsum$_{t-1}$ $+ 0.001$ Prwin$_{t-1}$	0.86
Polar	$+ 0.048$ Tm67 $- 0.001$ PrWS$_{t-1}$	0.97	$+ 0.077$ Tx7 $+ 0.041$ Tm6	0.89
Alpine	$+ 0.013$ Tm5 $- 0.003$ PrWS$_{t-1}$	0.56	$+ 0.118$ Txsum $+ 0.021$ Tx5	0.97
Mediterranean	$- 0.020$ Txsum $+ 0.001$ Pr5	0.77	$- 0.029$ Txsum $+ 0.001$ Pspr	0.83

aut, autumn; Pr, precipitation; spr, spring; sum, summer; Tn, mean minimum temperatures; Tx, mean maximum temperatures; win, winter; Wi, Akaike weights; WS, winter to spring. Numbers after climate variables indicate months, whereas the subscript '$t-1$' indicates the previous year.

corroborated by the climate/growth associations which highlight general higher tree sensitivity to temperature. As assumed, shrubby junipers were less coupled to air temperature and related atmospheric patterns than coexisting tree species across the three biomes in Europe. Unexpectedly, juniper showed enhanced growth at the extreme latitudinal Polar and Mediterranean sites, whereas trees increased their growth rates in Alpine and Polar regions (Fig. 2) and mostly declined in Mediterranean sites. We discuss how this tree–shrub dichotomy could explain these findings by analysing, in space and time, the contrasting macro- and microclimatic influences to which these two growth forms are exposed in different biomes.

The Arctic is rapidly warming because of the climate-albedo feedbacks related to snow dynamics (IPCC, 2014). The effect on plants life is a stronger warming-triggered boosting of growth and productivity at the Polar biome with a widespread shrub expansion and a rapid shift from low to tall shrubs (Arctic 'greening') observed in many tundra ecosystems (Tape *et al.*, 2006; Devi *et al.*, 2008; Macias-Fauria *et al.*, 2012; Myers-Smith *et al.*, 2015). Our results are in line with this picture with tree-ring growth of Polar junipers and trees (Fig. 2) mainly constrained by the short growing season and cold summer conditions (Fig. 3). However, at the study sites, warming trends after 1950 were more pronounced in the Mediterranean and Alpine biomes due to the contribution of increasingly warmer summer conditions (Table S1). This highlights that the typical representation featuring a straight northward or upward growth enhancement, and a growth reduction at the southernmost species' distribution limit (as, e.g., in Matías & Jump 2015 for juniper and Scots pine), is more complex, with the role of precipitation that should not be overlooked.

In our case, the significant positive correlations at Polar treeline sites recorded on both the growth forms for September precipitation (Fig. 3), even though in the region according to current knowledge the vegetative period is almost if not fully ended, could indicate a positive effect of wet conditions in late summer and early autumn. This would suggest a longer growing season than that previously described (Devi *et al.*, 2008) or even a potential late summer drought stress induced by warmer conditions, since many junipers establish on rocky substrates and shallow sandy soils, which intensify water deficit. In addition, at the Polar biome, beside the key role of summer temperature, the expansion of shrubs and trees might be also related to the snow amount and cover (Frost & Epstein, 2014). Previous investigations across the Siberian subarctic, including some of our Polar study sites, detected a post-1960s divergence between tree
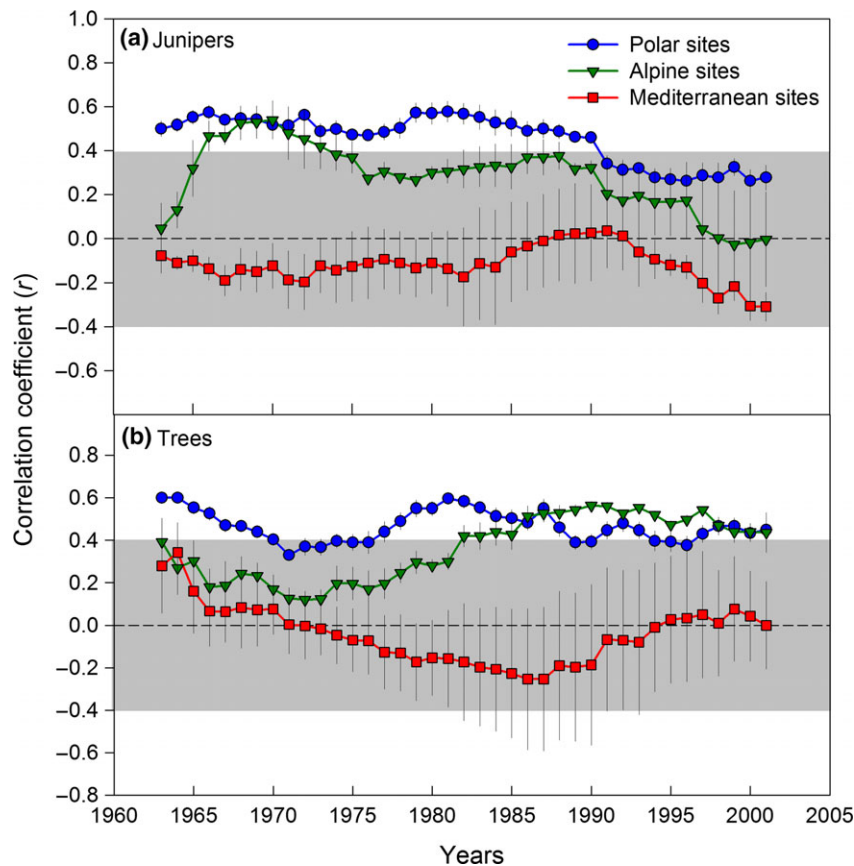
Fig. 4 Moving Pearson's correlations (25-year-long intervals, 1950–2013 period) calculated between growing season mean temperatures (May to August) and the mean ($\pm$ SE) site chronologies of ring-width indices for (a) junipers and (b) trees. The symbols correspond to the midyear of each 25-year-long interval. Values located outside the grey boxes are significant at the 0.05 level. [Colour figure can be viewed at wileyonlinelibrary.com]

growth and summer temperatures which was explained by a delayed snow melt due to increasing winter precipitation (Vaganov *et al.*, 1999). Late snow melting could have postponed the onset of cambial activity, thus leading to slower growth and a loss of growth sensitivity to summer temperatures (Kirdyanov *et al.*, 2003). Similar detrimental effect of snow pack duration on growth has been described for prostrate junipers in the Alps (Pellizzari *et al.*, 2014). In this mountain region, the amount of winter precipitation is at least double compared to the other biomes and could lead to a short growing season due to late snow melt (Fig. 3, Table 3). However, in most northern Russia, consistently with the trend observed across the Northern Hemisphere (Kunkel *et al.*, 2016), the extent and duration of snow cover tends to be shorter because the first snowfall occurs later and spring snow melt arrives earlier due to rising temperatures (Table S1) even if the amount of fallen snow increases (Bulygina *et al.*, 2009). Such widespread reduction in snow cover could lead to a longer growing season through an earlier snow melt together

with the abovementioned relaxation of September conditions and this can explain the rise of Polar juniper growth.

Unsurprisingly, tree growth at cold sites from the Polar and Alpine biomes responded more to temperature than coexisting junipers, and this response has been stable (Polar sites) or got stronger (Alpine sites) after the 1980s when temperatures started rising rapidly (Figs 3 and 4). Juniper growth at these temperature-limited sites is getting uncoupled from warmer conditions even though temperatures have kept rising. This suggests an overwhelming role played by local factors or other indirect effects of climate warming rather than the temperature rise *per se*, such as, as mentioned, a reduced snow cover period or a longer growing season. Other drivers such as changes in light availability (Stine & Huybers, 2013), nitrogen deposition and rising CO_2, biotic interactions, disturbance regime and local adaptations could also affect Polar juniper and tree growth, but their roles have to be further explored (Matías & Jump, 2015).

Our findings, supporting the hypothesis that trees were more coupled with atmospheric conditions and better responded to climate warming than junipers, could also explain why Mediterranean trees showed a decreasing growth trend in the dry Spanish sites (Fig. 2). Here, the warming-induced drought stress (Galván *et al.*, 2015; Gazol *et al.*, 2015) may drive trees to be more responsive to wet spring conditions than junipers (Fig. 3) which, being less exposed to extreme warm temperatures, likely experience lower evapotranspiration rates. In drought-prone areas as the SW of USA and the Mediterranean Basin, warming-induced aridification has been predicted to trigger forest die-off and the replacement of drought-sensitive pine species by junipers (Williams *et al.*, 2013; Camarero *et al.*, 2015b). Nevertheless, cold spells could also cause the die-off of junipers in dry and continental areas (Soulé & Knapp, 2007). It should also be noted the strong differences in climate conditions between POL and the other two more dry and continental Mediterranean PEN and VIL sites which causes a variable growth response to temperature in the case of trees (Fig. 4). This confirms that warming would mainly amplify drought stress in continental Mediterranean sites whilst wetter sites may buffer this aridification trend (Macias *et al.*, 2006). Note also that the climate–growth associations in the dry sites from the Mediterranean biome indicated an earlier onset of xylogenesis in junipers than in trees (see also Garcia-Cervigón Morales *et al.*, 2012), which suggests that drier summer conditions would be less detrimental to early-growing junipers than to late-growing trees. These results not agreeing with other studies that predicted a reduced performance of common juniper in the southernmost distribution limit (Matías & Jump, 2015) highlight the importance of considering multiple proxies of performance and long-term perspectives to understand species range shifts in response to climate warming.

To conclude, tree growth seems more coupled to temperature than juniper growth in cold-limited regions such as the Polar and Alpine biomes. In the Polar and Mediterranean biomes, junipers grow more since the 1950s, and this growth enhancement accelerated in the 1980s. Contrastingly, in the Mediterranean biome, tree growth was negatively associated with climate warming suggesting an increasing importance of drought stress which would explain the observed long-term growth decline. The increased growth observed in cold-limited sites (Polar junipers and Alpine trees) is coherent with an influence of climate warming, but local factors such an extended snow-free period or wetter conditions could also explain the acceleration of growth rates in other places (e.g. Mediterranean junipers).

This contrasting behaviour and sensitivity to climate between different growth forms should be also considered when forecasting current and future vegetation responses to climate change. This study can contribute to improved understanding of carbon sink dynamics of woody communities and improve dynamic global vegetation models which currently do not fully account for the different responses of the shrub and tree growth forms to projected climates.

Acknowledgements

References

Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–673.

Barton K (2013) MUMIn: Multi-model inference. P package version 1.9.5. Available at: http://CRAN. R-project.org/package=MuMI (accessed 1 September 2016).

Bokhorst SF, Bjerke JW, Tømmervik H, Callaghan TV, Phoenix GK (2009) Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology*, **97**, 1408–1415.

Bulygina ON, Razuvaev VN, Korshunova NN (2009) Changes in snow cover over Northern Eurasia in the last few decades. *Environmental Research Letters*, **4**, 45026.

Bunn AG (2010) Statistical and visual crossdating in R using the dplR library. *Dendrochronologia*, **28**, 251–258.

Büntgen U, Frank D, Wilson R, Carrer M, Urbinati C, Esper J (2008a) Testing for tree-ring divergence in the European Alps. *Global Change Biology*, **14**, 2443–2453.

Büntgen U, Frank D, Grudd H, Esper J (2008b) Long-term summer temperature variations in the Pyrenees. *Climate Dynamics*, **31**, 615–631.

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

Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, Vol. 172. 488 pp.

Camarero JJ, Olano JM, Parras A (2010) Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytologist*, **185**, 471–480.

Camarero JJ, Gazol A, Tardif JC, Conciatori F (2015a) Attributing forest responses to global-change drivers: limited evidence of a CO2-fertilization effect in Iberian pine growth. *Journal of Biogeography*, **42**, 2220–2233.

Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM (2015b) To die or not to die: early warnings of tree dieback in response to a severe drought. *Journal of Ecology*, **103**, 44–57.

Carrer M, Urbinati C (2006) Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. *New Phytologist*, **170**, 861–871.

Danby RK, Hik DS (2007) Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology*, **95**, 352–363.

Deslauriers A, Rossi S, Anfodillo T, Saracino A (2008) Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. *Tree physiology*, **28**, 863–871.

Devi N, Hagedorn F, Moiseev P, Bugmann H, Shiyatov S, Mazepa V, Rigling A (2008) Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. *Global Change Biology*, **14**, 1581–1591.

Esper J, Frank D, Büntgen U, Verstege A, Hantemirov R, Kirdyanov AV (2010) Trends and uncertainties in Siberian indicators of 20th century warming. *Global Change Biology*, **16**, 386–398.

Farjon A (2005) *A Monograph of Cupressaceae and Sciadopitys*. Royal Botanic Gardens, Kew.

Forbes BC, Fauria MM, Zetterberg P (2010) Russian Arctic warming and "greening" are closely tracked by tundra shrub willows. *Global Change Biology*, **16**, 1542–1554.

Fritts HC (2001) *Tree Rings and Climate*. Cladwell, NJ.

Frost GV, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology*, **20**, 1264–1277.

Galván DJ, Büntgen U, Ginzler C, Grudd H, Gutiérrez E, Labuhn I, Julio Camarero J (2015) Drought-induced weakening of growth-temperature associations in high-elevation Iberian pines. *Global and Planetary Change*, **124**, 95–106.

Garcia-Cervigón Morales AI, Olano Mendoza JM, Eugenio Gozalbo M, Camarero Martínez JJ (2012) Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses. *Dendrochronologia*, **30**, 279–286.

Gazol A, Camarero JJ (2012) Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. *Plant Ecology*, **213**, 1687–1698.

Gazol A, Julio Camarero J, Gutierrez E *et al.* (2015) Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *Journal of Biogeography*, **42**, 1150–1162.

Grace J, Allen SJ, Wilson C (1989) Climate and the meristem temperatures of plant communities near the tree-line. *Oecologia*, **79**, 198–204.

Hagedorn F, Shiyatov SG, Mazepa VS *et al.* (2014) Treeline advances along the Urals mountain range - driven by improved winter conditions? *Global Change Biology*, **20**, 3530–3543.

Hallinger M, Wilmking M (2011) No change without a cause – why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia. *New Phytologist*, **189**, 902–908.

Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist*, **186**, 890–899.

Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, **34**, 623–642.

Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.

Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M (2008) A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *Journal of Geophysical Research*, **113**, D20119.

Helama S, Lindholm M, Timonen M, Eronen M (2004) Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods. *Theoretical and Applied Climatology*, **79**, 239–254.

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bulletin*, **43**, 69–78.

IPCC (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Barros VR, Field CB, Dokken DJ, Mastrandre MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL), pp. 688. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Jones P (2016) The reliability of global and hemispheric surface temperature records. *Advances in Atmospheric Sciences*, **33**, 269–282.

Kirdyanov A, Hughes M, Vaganov E, Schweingruber F, Silkin P (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees-Structure and Function*, **17**, 61–69.

Kjellström E, Nikulin G, Hansson U, Strandberg G, Ullerstig A (2011) 21st century changes in the European climate: uncertainties derived from an ensemble of regional climate model simulations. *Tellus, Series A: Dynamic Meteorology and Oceanography*, **63**, 24–40.

Körner C (2012a) *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Springer, Basel.

Körner C (2012b) Treelines will be understood once the functional difference between a tree and a shrub is. *Ambio*, **41**, 197–206.

Kunkel KE, Robinson DA, Champion S, Yin X, Estilow T, Frankson RM (2016) Trends and extremes in northern hemisphere snow characteristics. *Current Climate Change Reports*, **2**, 65–73.

Liang E, Lu X, Ren P, Li X, Zhu L, Eckstein D (2012) Annual increments of juniper dwarf shrubs above the tree line on the central Tibetan Plateau: a useful climatic proxy. *Annals of Botany*, **109**, 721–728.

Lu X, Huang R, Wang Y, Sigdel S, Dawadi B, Liang E, Camarero JJ (2016) Summer temperature drives radial growth of alpine shrub willows on the northeastern Tibetan Plateau. *Arctic, Antarctic and Alpine Research*, **48**, 461–468.

MacDonald GM, Kremenetski KV, Beilman DW (2008) Climate change and the northern Russian treeline zone. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 2285–2299.

Macias M, Andreu L, Bosch O, Camarero JJ, Gutiérrez E (2006) Increasing aridity is enhancing silver fir (*Abies alba* Mill.) water stress in its south-western distribution limit. *Climatic Change*, **79**, 289–313.

Macias-Fauria M, Forbes BC, Zetterberg P, Kumpula T (2012) Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nature Climate Change*, **2**, 613–618.

Matías L, Jump AS (2015) Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shifts of two woody species. *Global Change Biology*, **21**, 882–896.

Myers-Smith IH, Forbes BC, Wilmking M *et al.* (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, **6**, 45509.

Myers-Smith IH, Hallinger M, Blok D *et al.* (2014) Methods for measuring arctic and alpine shrub growth: a review. *Earth-Science Reviews*, **140**, 1–13.

Myers-Smith IH, Elmendorf SC, Beck PSA *et al.* (2015) Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, **5**, 1–44.

Pellizzari E, Pividori M, Carrer M (2014) Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps. *Environmental Research Letters*, **9**, 104021.

Pinheiro JC, Bates DM (2000) *Mixed Effects Models in S and S-Plus*. Springer Verlag, New York.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team R (2015) nlme: linear and nonlinear mixed effects models. *R package version 3.1-122*, R package, 1–3.

R Core Team (2015) R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing Vienna Austria*, 0, {ISBN} 3-900051-07-0.

Rixen C, Schwoerer C, Wipf S (2010) Winter climate change at different temporal scales in *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub. *Polar Research*, **29**, 85–94.

Rohde R, Muller R, Jacobsen R, Muller E, Groom D, Wickham C (2013) A new estimate of the average earth surface land temperature spanning 1753 to 2011. *Geoinformatic and Geostatistics: An Overview*, **1**, 1–7.

Salzer MW, Hughes MK, Bunn AG, Kipfmueller KF (2009) Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 20348–20353.

Shiyatov SG, Terent'ev MM, Fomin VV (2005) Spatiotemporal dynamics of forest-tundra communities in the Polar Urals. *Russian Journal of Ecology*, **36**, 69–75.

Soulé PT, Knapp PA (2007) Topoedaphic and morphological complexity of foliar damage and mortality within western juniper (*Juniperus occidentalis* var. *occidentalis*) woodlands following an extreme meteorological event. *Journal of Biogeography*, **34**, 1927–1937.

Stine AR, Huybers P (2013) Arctic tree rings as recorders of variations in light availability. *Nature Communications*, **5**, 3836.

Sturm M, Racine C, Tape K (2001) Climate change. Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.

Suarez F, Binkley D, Kaye MW, Stottlemyer R (1999) Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska. *Ecoscience*, **6**, 465–470.

Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686–702.

Todaro L, Andreu L, D'Alessandro CM, Gutiérrez E, Cherubini P, Saracino A (2007) Response of Pinus leucodermis to climate and anthropogenic activity in the National Park of Pollino (Basilicata, Southern Italy). *Biological Conservation*, **137**, 507–519.

Trahan MW, Schubert BA (2016) Temperature-induced water stress in high-latitude forests in response to natural and anthropogenic warming. *Global Change Biology*, **22**, 782–791.

Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, **400**, 149–151.

Van Den Besselaar EJM, Haylock MR, Van Der Schrier G, Klein Tank AMG (2011) A European daily high-resolution observational gridded data set of sea level pressure. *Journal of Geophysical Research*, **116**, D11110.

Vautard R, Gobiet A, Sobolowski S *et al.* (2014) The European climate under a 2 °C global warming. *Environmental Research Letters*, **9**, 34006.

Vicente-Serrano SM, Lopez-Moreno J-I, Beguería S *et al.* (2014) Evidence of increasing drought severity caused by temperature rise in southern Europe. *Environmental Research Letters*, **9**, 44001.

Williams AP, Allen CD, Macalady AK *et al.* (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, **3**, 292–297.

Wilson C, Grace J, Allen S, Slack F (1987) Temperature and stature: a study of temperatures in montane vegetation. *Functional Ecology*, **1**, 405–413.

Wood SN (2006) Generalized additive models: an introduction with R (ed R. Chapman & Hall U). *Texts in Statistical Science*, **16**, xvii, 392.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM, Ebooks Corporation (2009) *Mixed Effects Models and Extensions in Ecology with R.* Springer, New York, USA.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Shrubby juniper sampled and wedging rings in a juniper cross-section.

Figure S2 Trends in mean annual temperatures in the study sites quantified as temperature anomalies.

Figure S3 Mean ring-width (mrw) of junipers and tree species averaged for 20-year age classes.

Figure S4 Changes in correlation coefficients calculated between site ring-width residual chronologies for junipers and trees as a function of the distance between sites.

Figure S5 Principal Component Analysis calculated on the variance-covariance matrix of the juniper and trees ring-width site chronologies.

Table S1 Seasonal climatic values and trends calculated for the study sites considering the three study biomes.

Table S2 Correlation values of the residual ring-width chronologies between the study sites and between junipers and trees within each site.

Table S3 Summary of the statistics of the most parsimonious linear mixed-effects models fitted to ring-width indices of junipers and trees.
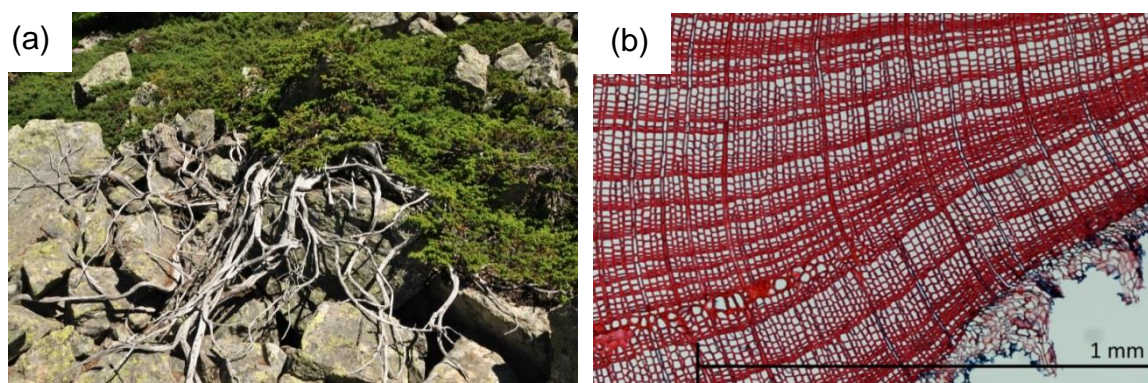
Figure S1. (a) Shrubby juniper sampled at a mountain site located in the Italian Alps and (b) typical wedging rings in a juniper cross-section.
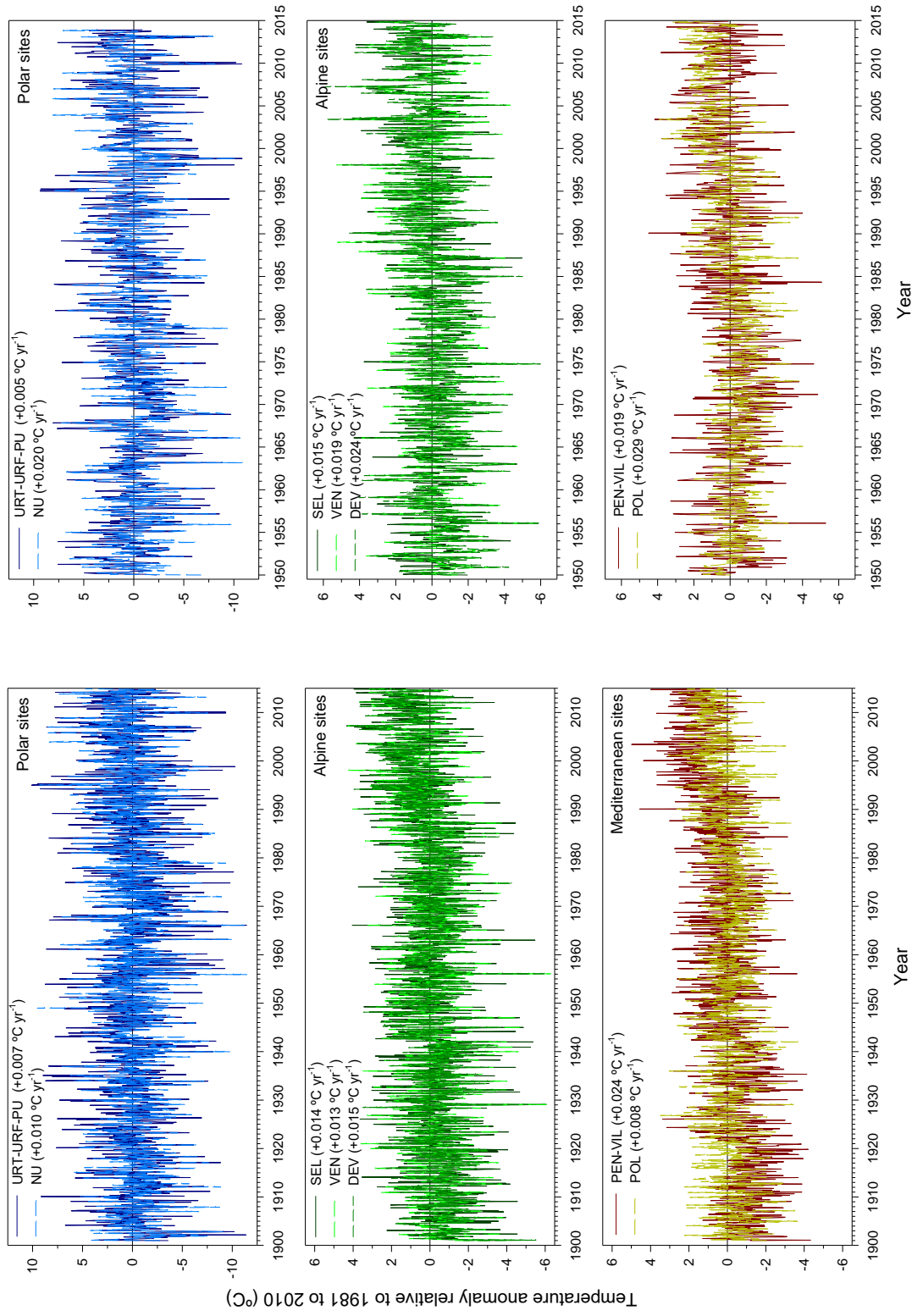
Figure S2. Trends in mean annual temperatures in the study sites for the (a) 1901-2013 and (b) 1950-2013 periods quantified as temperature anomalies with respect to the 1981-2010 average annual cycle for each 0.5° (a, CRU climate dataset) or 0.25° grid (b, E-OBS climate dataset) including each site. See sites' codes in Table 1. Numbers between brackets indicate the annual trends which were significant at the 0.01 level in all cases.
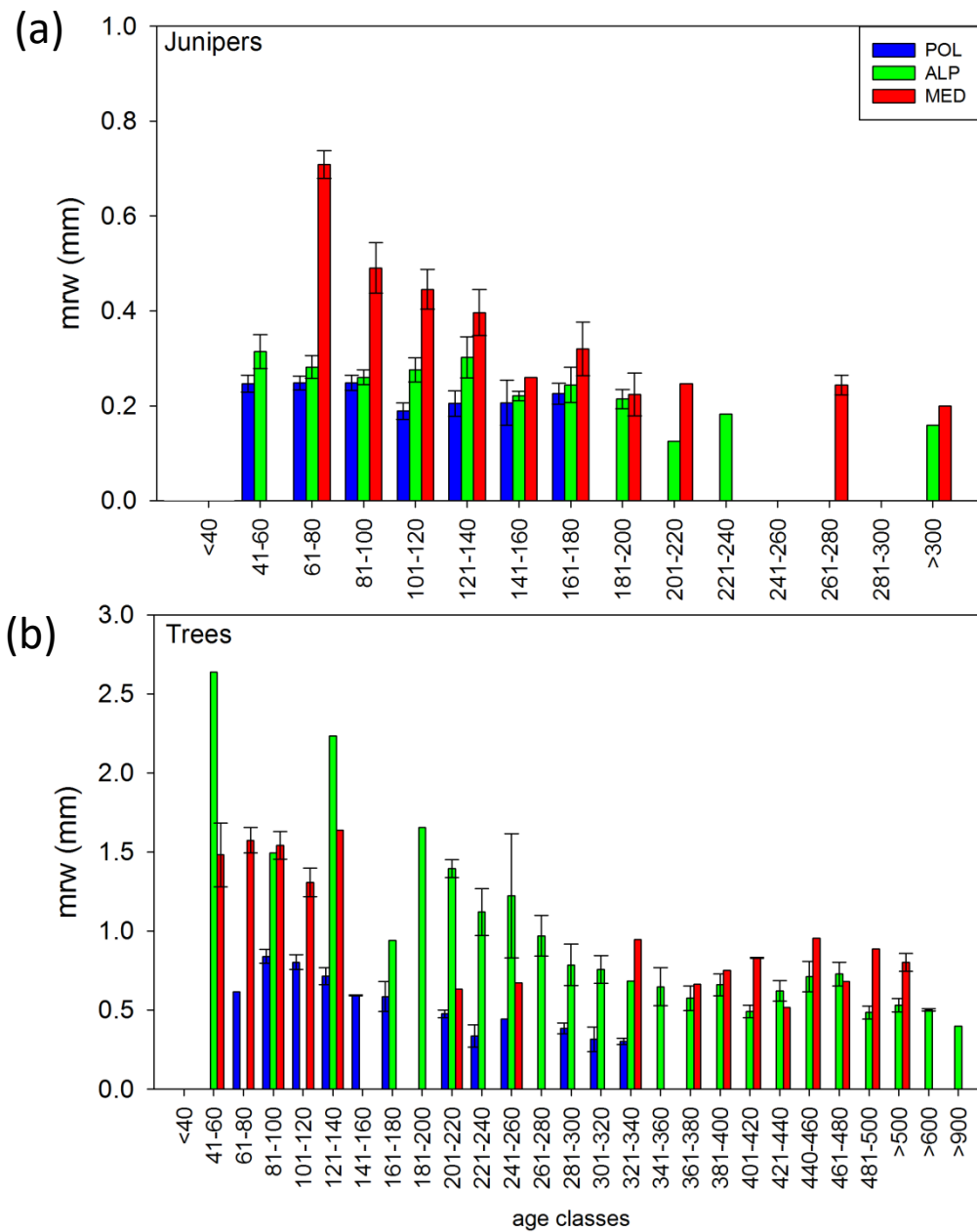
Figure S3. Mean ring-width (mrw) of (a) junipers and (b) tree species averaged for 20-years age classes. Data are plotted considering the three regions: Mediterranean (MED), Alpine (ALP) and Polar (POL). In the case of trees older than 500 years, age classes are presented using wider intervals.
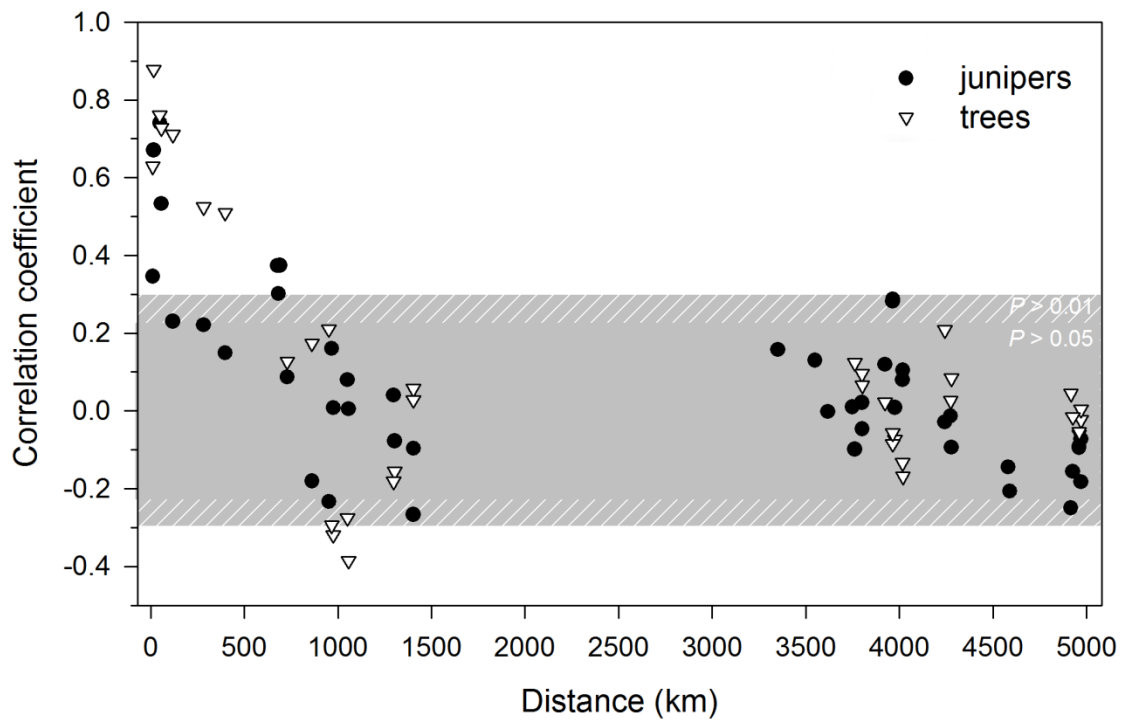
Figure S4. Changes in correlation coefficients (Pearson *r*) calculated between site ring-width residual chronologies for junipers (filled circles) and trees (empty triangles) as a function of the distance between sites. Two significance thresholds ($P > 0.05$, $P > 0.01$) are displayed with different fills. Correlations have been calculated between samples of the same growth form (junipers with junipers and trees with trees).
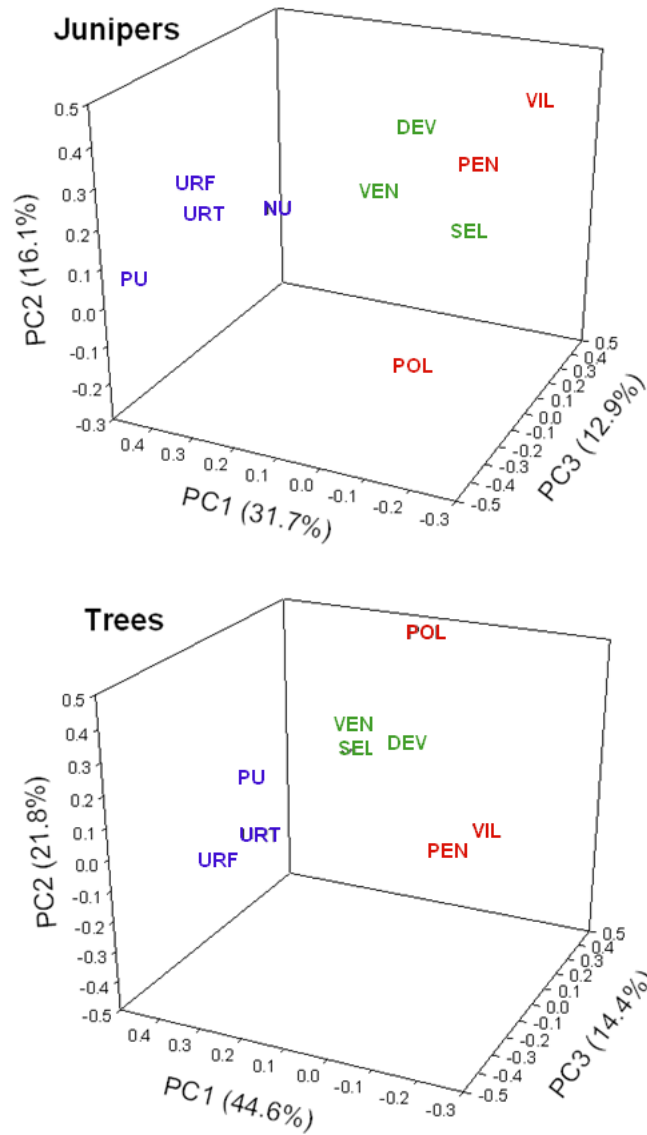
Figure S5. Triplots showing the first three axes (PC1, PC2 and PC3) of a Principal Component Analysis calculated on the variance-covariance matrix of the juniper and trees ring-width site chronologies.

Table S1. Seasonal climatic values (means for temperatures and totals for precipitation) and trends calculated for the study sites considering the three study biomes. Climatic means and trends were calculated for the 1950-2013 period considering the 0.5°-gridded CRU climate dataset. Seasons' abbreviations: Sp, spring; Su, summer; Au, autumn; Wi, winter. Significant ($P < 0.05$) trends are indicated with bold values.

Mean values (°C or mm)													
Region	Site	Mean maximum temperature				Mean minimum temperature				Precipitation			
		Sp	Su	Au	Wi	Sp	Su	Au	Wi	Sp	Su	Au	Wi
Polar	Urt Urf	-2.8	16.6	-0.7	-16.5	-8.7	11.6	-4.7	-22.6	85	182	127	69
	PU	-4.2	14.0	-2.5	-4.8	-12.0	6.6	-7.9	-25.7	82	179	128	65
	NU	2.9	18.0	0.4	-14.7	-8.8	5.8	-7.3	-24.6	133	243	166	88
Alpine	Dev	5.1	13.8	6.8	-1.2	-1.7	6.6	1.0	-6.9	486	628	465	423
	Ven	8.6	18.2	10.4	1.4	2.4	10.9	4.6	-3.5	371	485	442	196
	Sel	14.7	24.5	15.2	4.7	7.6	16.8	9.2	-0.4	470	471	577	363
Mediterranean	Pol	4.4	15.0	7.9	-0.7	0.9	10.7	4.6	-3.5	347	212	523	481
	Pen Vil	17.3	26.3	19.8	12.0	5.7	16.2	8.5	0.5	175	114	158	116

Trends (°C yr⁻¹ or mm yr⁻¹)													
Region	Site	Sp	Su	Au	Wi	Sp	Su	Au	Wi	Sp	Su	Au	Wi
Polar	Urt Urf	**0.04**	0.02	**0.04**	0.02	**0.05**	0.01	**0.04**	0.04	0.48	0.86	-0.24	1.32
	PU	0.03	0.01	0.02	0.01	**0.04**	**0.02**	**0.03**	0.01	-0.04	-0.12	-0.38	-0.20
	NU	0.02	0.00	0.02	0.01	**0.03**	**0.02**	**0.04**	0.02	**0.62**	0.09	0.26	0.04
Alpine	Dev	**0.02**	**0.03**	**0.02**	**0.02**	**0.04**	**0.04**	**0.04**	**0.03**	0.80	0.08	-0.35	-0.51
	Ven	0.01	0.01	0.00	0.02	**0.02**	**0.02**	**0.01**	0.01	0.36	0.49	0.05	0.97
	Sel	**0.03**	0.02	0.01	0.02	0.01	0.01	0.01	0.01	-0.77	-0.76	-0.82	-0.60
Mediterranean	Pol	**0.02**	**0.02**	**0.02**	**0.01**	**0.02**	**0.02**	**0.02**	**0.01**	**1.14**	1.22	1.18	**2.11**
	Pen Vil	**0.02**	**0.04**	0.01	0.00	**0.02**	**0.03**	**0.02**	**0.02**	0.94	0.81	-0.11	1.56

Table S2. Correlation values (Pearson correlation coefficients) calculated of the residual ring-width chronologies (a) between the study sites and (b) between junipers and trees within each site considering the common 1950-2013 period. Significant ($P <$ 0.05) correlations are indicated with bold values.

(a)		Polar sites				Alpine sites			Mediterranean sites	
		Urt	Pu	Nu		Ven	Sel		Pen	Vil
Junipers	Urf	**0.685**	0.251	**0.618**	Dev	**0.242**	0.178	Pol	**0.222**	0.018
	Urt		**0.293**	**0.767**	Ven		**0.219**	Pen		**0.338**
	Pu			**0.485**						
Trees	Urf	**0.889**	**0.766**	––––	Dev	**0.692**	**0.568**	Pol	0.064	-0.05
	Urt		**0.845**	––––	Ven		**0.607**	Pen		**0.592**

(b)	Polar sites				Alpine sites			Mediterranean sites		
	Urt	Urf	Pu	Nu	Dev	Ven	Sel	Pen	Vil	Pol
Junipers-trees	**0.254**	**0.352**	**0.532**	––––	-0.182	0.079	0.115	0.119	**0.417**	**0.293**

Table S3. Summary of the statistics of the most parsimonious linear mixed-effects models fitted to ring-width indices of junipers and trees as a function of monthly and seasonal climate variables for the 1950-2013 period. Abbreviations: AIC, Akaike Information Criterion; Pr, precipitation; spr, spring; sum, summer; Tn, mean minimum temperatures; Tx, mean maximum temperatures; win, winter; *Wi*, Akaike weights; WS, winter to spring. Numbers after climate variables indicate months and the symbol ":" indicates interactions between climate variables. See sites' codes in Table 1.

Region	Site	Junipers			Trees		
		Model parameters	AIC	*Wi*	Model parameters	AIC	*Wi*
POLAR	URF	0.449 +0.049Tm67−0.001PWS	1173	0.42	−1.146 +0.146 Tm67 −0.048Tnspr	519	0.72
		0.384+0.049Tm67+0.001Pspr	1174	0.31	−1.163 +0.147Tm67 −0.049Tnspr+0.001P5	521	0.28
	URT	−0.165−0.021Tnspr+0.068Tnsum−0.010Tnwin+ 0.008Tnaut	893	0.69	−0.460 + 0.112 Tm67 + 0.002 P9	451	0.89
		0.170+0.055Tm67−0.021Tnspr	895	0.31	−0.832 +0.133 Tm67−0.029Tnspr	455	0.11
	PU	0.675+0.068 Tm67−0.002Pspr	1316	0.75	−0.460 + 0.112 Tm67 + 0.002 P9	1529	0.66
		0.672 + 0.068Tnsum − 0.002P9	1319	0.20	−0.135−0.001Tnspr:PWS+0.143Tm67+0.002P9	1530	0.34
	NU	0.441 +0.002Txspr +0.54Txsum +0.029Txwin	1918	0.98	———		
		1.075 −0.015Tnspr +0.074Tnsum +0.026Tnwin	1926	0.01			
ALPINE	DEV	1.052 −0.001Pwin:Tm6+ 0.001 P5:Tm5	633	0.71	−0.33 + 0.139 Txsum −0.035Txspr−0.039Tx9	89	0.65
		1.18−0.001PWS:Tx6 + 0.001 PWS:Tx5	636	0.15	−0.103 + 0.112 Txsum−0.001P6 − 0.034Tx9	91	0.34
	VEN	1.131 −0.001PWS:Tx6 + 0.001PWS:Tx5	836	0.55	−0.653+0.129Txsum −0.001 P5 −0.039Tx9	1686	0.91
		1.069 −0.001PWS − 0.011Tx6 + 0.019Tx5	839	0.17	−0.993+0.117 Txsum+ 0.029Tx5 −0.035Tx9	1691	0.08
	SEL	1.576−0.001Pspr−0.001Psum−0.001Pwin	924	0.84	−1.317 +0.150Txsum −0.045Txspr−0.032 Tx9	593	0.92
		1.367− 0.001PWS:Tm6	928	0.15	−3.11+0.159Txsum+0.001Psum	599	0.05
MEDITERRANEAN	POL	0.770+0.032Tnsum−0.001PWS+0.002Psum	869	0.56	−0.952 + 0.147Txsum + H150.001Txwin:PWS	681	0.83
		1.029 −0.001Pspr:Txspr + 0.001Psum:Txsum + 0.001Pwin:Txwin	870	0.26	−1.011+0.006Txspr+0.133Txsum +0.130Txwin	684	0.17
	PEN	1.346 −0.016Txsum −0.001 P5:Tx5 + 0.001P6	830	0.48	1.409 −0.024Txsum +0.001Pspr+0.002Psum	584	0.50
		1.270 −0.013Txsum + 0.001P5:Tx5 −0.001 P6:Tx6	831	0.34	1.412−0.024Txsum+0.001P5:Tx5 +0.002Psum	585	0.47
	VIL	2.116 −0.052Txsum +0.001PWS:Tnspr+ 0.001Psum	503	0.83	1.741 − 0.031Txsum−0.001P5:Tx5+0.001 Psum	1118	0.51
		1.956 −0.041Txsum + 0.002P5:Tx5 + 0.001P6	507	0.14	1.746−0.031Txsum−0.001Pspr+0.001Psum	1119	0.49

Chapter 6

Changes in plant functional traits in a changing tundra biome (In revision: **Nature**)

Change in plant functional traits across a warming tundra biome

Anne D. Bjorkman[1,2,3*], Isla Myers-Smith[2], Sarah Elmendorf[4,5], Signe Normand[1], Nadja Rüger[3,6], Pieter S.A. Beck[7], Anne Blach-Overgaard[1], Daan Blok[8], J. Hans C. Cornelissen[9], Bruce C. Forbes[10], Damien Georges[11,2], Scott Goetz[12], Kevin Guay[13], Gregory H.R. Henry[14], Janneke HilleRisLambers[15], Robert Hollister[16], Dirk N. Karger[17], Jens Kattge[18,3], Janet S. Prevéy[19], Christian Rixen[19], Gabriela Schaepman-Strub[20], Haydn Thomas[2], Mark Vellend[21], Martin Wilmking[22], Sonja Wipf[19], Michele Carbognani[23], Luise Hermanutz[24], Esther Levesque[25], Ulf Molau[26], Alessandro Petraglia[23], Nadejda A. Soudzilovskaia[27], Marko Spasojevic[28], Marcello Tomaselli[23], Tage Vowles[29], Juha Alatalo[30], Heather Alexander[31], Alba Anadon-Rosell[32,33], Sandra Angers-Blondin[2], Mariska Te Beest[34,35], Logan Berner[12], Robert G. Björk[29], Agata Buchwal[36,37], Allan Buras[38], Katie Christie[39], Laura S Collier[24], Elisabeth J. Cooper[40], Stefan Dullinger[41], Bo Elberling[42], Anu Eskelinen[43,3,44], Esther R. Frei[14], Maitane Iturrate Garcia[20], Oriol Grau[45,46], Paul Grogan[47], Martin Hallinger[48], Karen Harper[49], Monique Heijmans[50], James Hudson[51], Karl Hülber[41], Colleen M. Iversen[52], Francesca Jaroszynska[53,19], Jill Johnstone[54], Rasmus Halfdan Jorgensen[55], Elina Kaarlejärvi[34,56], Rebecca Klady[57], Sara Kuleza[54], Aino Kulonen[19], Laurent J. Lamarque[25], Trevor Lantz[58], Amanda Lavalle[49], Chelsea J. Little[20,59], James David Mervyn Speed[60], Anders Michelsen[61,62], Ann Milbau[63], Jacob Nabe-Nielsen[64], Sigrid Schøler Nielsen[1], Josep Maria Ninot[32,33], Steve Oberbauer[65], Johan Olofsson[34], Vladimir G. Onipchenko[66], Sabine B. Rumpf[41], Philipp Semenchuk[40], **Rohan Shetti[22]**, Lorna Street[2], Katharine Suding[67], Ken Tape[68], Andrew Trant[69], Urs Treier[1], Jean-Pierre Tremblay[70], Maxime Tremblay[25], Susanna Venn[71], Stef Weijers[72], Tara Zamin[47], Noemie Boulanger-Lapointe[14], William A. Gould[73], Dave Hik[74], Annika Hofgaard[75], Inga Svala Jonsdottir[76,77], Janet Jorgenson[78], Julia Klein[79], Borgthor Magnusson[80], Craig Tweedie[81], Philip A. Wookey[82], Michael Bahn[83], Benjamin Blonder[84,85], Peter van Bodegom[86], Benjamin Bond-Lamberty[87], Giandiego Campetella[88], Bruno E.L. Cerabolini[89], F. Stuart Chapin III[90], Will Cornwell[91], Joseph Craine[92], Matteo Dainese[93], Franciska T. de Vries[94], Sandra Diaz[95], Brian J. Enquist[96,97], Walton Green[98], Peter Manning[99], Ruben Milla[100], Ülo Niinemets[101], Yusuke Onoda[102], Jenny Ordonez[103], Wim A. Ozinga[104,105], Josep Penuelas[106,46], Hendrik Poorter[107], Peter Poschlod[108], Peter Reich[109,110], Brody Sandel[111], Brandon Schamp[112], Serge Sheremetev[113], Evan Weiher[114]

1. Ecoinformatics and Biodiversity & Arctic Research Center, Department of Bioscience, Aarhus University, Ny Munkegade 114-116, DK-8000 Aarhus C

2. School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, UK

3. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

4. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA

5. National Ecological Observatory Network, 1685 38th St, Boulder, CO 80301, USA

6. Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa Ancón, Panama

7. European Commission, Joint Research Centre, Directorate D - Sustainable Resources, Bio-Economy Unit, Via Enrico Fermi 2749, 21027, Ispra, Italy

8. Department of Physical Geography and Ecosystem Science, Lund University, Lund S-223 62, Sweden

9. Systems Ecology, Department of Ecological Science, Vrije Universiteit, Amsterdam, The Netherlands

10. Arctic Centre, University of Lapland, FI-96101 Rovaniemi, Finland

11. International Agency for Research in Cancer, Lyon, France

12. Northern Arizona University, Flagstaff, Arizona, USA

13. Bigelow Laboratory for Ocean Sciences, East Boothbay, Maine, USA

14. Department of Geography, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

15. Biology Department, University of Washington, Seattle, USA, 98195-1800

16. Biology Department, Grand Valley State University, 1 Campus Drive, Allendale Michigan USA

17. Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

18. Max Planck Institute for Biogeochemistry, Jena, Germany

19. WSL Institute for Snow and Avalanche Research SLF, 7260 Davos, Switzerland

20. Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

21. Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada J1K 2R1

22. Institute of Botany and Landscape Ecology, Greifswald University, Greifswald, Germany

23. Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze 11/A, I-43124 Parma, Italy

24. Department of Biology, Memorial University, St. John's, Newfoundland and Labrador, Canada A1B3X9

25. Département des Sciences de l'environnement et Centre d'études nordiques, Université du Québec à Trois-Rivières, Trois-Rivières, QC, G9A 5H7, Canada

26. Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

27. Conservation Biology Department, Institute of Environmental Sciences, Leiden University, The Netherlands

28. Department of Evolution, Ecology, and Organismal Biology, University of California Riverside, Riverside, CA.

29. Department of Earth Sciences, University of Gothenburg, P.O. Box 460, SE-405 30 Gothenburg, Sweden

30. Department of Biological and Environmental Sciences, Qatar University, Qatar

31. Department of Forestry, Forest and Wildlife Research Center, Mississippi State University, MS 39762

32. Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Av. Diagonal 643 E-08028 Barcelona

33. Biodiversity Research Institute, University of Barcelona, Av. Diagonal 643 E-08028 Barcelona

34. Department of Ecology and Environmental Science, Umeå University, Sweden

35. Department of Environmental Sciences, Copernicus Institute, Utrecht University, the Netherlands

36. Adam Mickiewicz University, Institute of Geoecology and Geoinformation, B.Krygowskiego 10, 61-680 Poznan, Poland

37. University of Alaska Anchorage, Department of Biological Sciences, 3151 Alumni Loop, Anchorage, Alaska 99508, USA

38. Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising

39. The Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska 99518

40. Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT- The Arctic University of Norway, NO-9037 Tromsø, Norway

41. Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, A-1030 Vienna, Austria

42. Center for Permafrost (CENPERM), Department of Geosciences and Natural Resource Management, University of Copenhagen, DK-1350 Copenhagen, Denmark

43. Department of Physiological Diversity, Helmholz Center for Environmental Research - UFZ, Permoserstrasse 15, Leipzig 04103, Germany

44. Department of Ecology, University of Oulu, 90014 University of Oulu, Finland

45. Global Ecology Unit, CREAF-CSIC-UAB, Bellaterra, Catalonia 08193, Spain

46. CREAF, Cerdanyola del Vallès, Catalonia 08193, Spain

47. Department of Biology, Queen's University, Kingston, ON, Canada

48. Biology Department, Swedish Agricultural University (SLU), Uppsala, Sweden

49. Biology Department, Saint Mary's University, Halifax, NS, Canada

50. Plant Ecology and Nature Conservation Group, Wageningen University & Research, Wageningen, The Netherlands

51. British Columbia Public Service, Canada

52. Climate Change Science Institute and Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA 37831

53. Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, AB24 3UU

54. Department of Biology, University of Saskatchewan, Saskatoon SK S7N 5E2 Canada

55. Department of Geosciences and Natural Resource Management, University of Copenhagen, Denmark

56. Department of Biology, Vrije Universiteit Brussel (VUB), Belgium

57. Department of Forest Resources Management, Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada

58. School of Environmental Studies, University of Victoria, Victoria, BC, Canada

59. Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dubendorf, Switzerland

60. NTNU University Museum, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

61. Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark

62. Center for Permafrost (CENPERM), University of Copenhagen, Oster Voldgade 10, DK-1350 Copenhagen, Denmark

63. Research Institute for Nature and Forest (INBO), Kliniekstraat 25, 1070 Brussels, Belgium

64. Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark

65. Department of Biological Sciences, Florida International University, Miami FL 33199 USA

66. Department of Geobotany, Lomonosov Moscow State University, Moscow, Russia

67. Department of Ecology and Evolutionary Biology, Univeristy of Colorado, Boulder CO

68. Institute of Northern Engineering, University of Alaska Fairbanks, USA

69. School of Environment, Resources and Sustainability, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1

70. Département de biologie, Centre d'études nordiques and Centre d'étude de la forêt, Université Laval, QC, G1V 0A6, Canada

71. Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, VIC, Australia 3125

72. Department of Geography, University of Bonn, Meckenheimer Allee 166, D-53115 Bonn, Germany

73. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, Puerto Rico

74. Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada

75. Norwegian Institute for Nature Research, PO Box 5685 Sluppen, NO-7485 Trondheim, Norway

76. Faculty of Life and Environmental Sciences, University of Iceland, 101 Reykjavík, Iclenad

77. University Centre in Svalbard, N-9171 Longyearbyen, Norway

78. Arctic National Wildlife Refuge, U. S. Fish and Wildlife Service

79. Department of Ecosystem Science & Sustainability, Colorado State University, Campus Delivery 1476, Fort Collins, CO 80523-1476 USA

80. Icelandic Institute of Natural History, Gardabaer, Iceland

81. University of Texas at El Paso, El Paso, Texas, USA

82. Biology and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, Scotland, UK

83. Institute of Ecology, University of Innsbruck, Innsbruck, Austria

84. Environmental Change Institute, School of Geography and the Environment, South Parks Road, University of Oxford, Oxford OX1 3QY, UK

85. Rocky Mountain Biological Laboratory, PO Box 519, Crested Butte, Colorado, 81224 USA

86. Institute of Environmental Sciences, Leiden University, 2333 CC Leiden, the Netherlands

87. Joint Global Change Research Institute, Pacific Northwest National Laboratory, College Park, MD, USA

88. School of Biosciences & Veterinary Medicine - Plant Diversity and Ecosystems Management unit, Univeristy of Camerino, via Pontoni, 5 - 62032, Italy

89. DiSTA - University of Insubria, via Dunant 3, 21100 Varese, Italy

90. Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99709, USA

91. School of Biological, Earth & Environmental Sciences, Ecology and Evolution Research Centre, UNSW Australia, Sydney, NSW 2052, Australia

92. Jonah Ventures, Manhattan KS 66502, USA

93. Department of Animal Ecology and Tropical Biology, University of Würzburg, Biozentrum - Am Hubland, 97074 Würzburg, Germany

94. School of Earth and Environmental Sciences, The University of Manchester, UK

95. Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET and FCEFyN, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina

96. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85719, USA

97. The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA

98. Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138 USA

99. Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, Frankfurt, Germany

100. Área de Biodiversidad y Conservación. Departamento de Biología, Geología, Física y Química Inorgánica. Universidad Rey Juan Carlos, 28933 Móstoles (Madrid), Spain

101. Estonian University of Life Sciences, Kreutzwaldi 1, 51014 Tartu, Estonia

102. Graduate School of Agriculture, Kyoto University, Oiwake, Kitashirakawa, Kyoto, 606-8502 Japan

103. World Agroforestry Centre - Latin America, Av. La Molina 1895, La Molina, Lima, Perú

104. Team Vegetation, Forest and Landscape ecology, Wageningen Environmental Research (Alterra), P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

105. Institute for Water and Wetland Research, Radboud University Nijmegen, 6500 GL Nijmegen, The Netherlands

106. Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, Catalonia 08193, Spain

107. Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, Jülich 52425, Germany

108. Ecology and Conservation Biology, Institute of Plant Sciences, University of Regensburg, D-93040 Regensburg

109. Department of Forest Resources, University of Minnesota, St. Paul, MN 55108 USA

110. Hawkesbury Institute for the Environment, Western Sydney University, Penrith NSW 2751, Australia

111. Department of Biology, Santa Clara University, 500 El Camino Real, Santa Clara, CA, 95053 USA

112. Department of Biology, Algoma University, Sault Ste. Marie, Ontario, Canada

113. Komarov Botanical Institute, Prof. Popov Street 2, St Petersburg 197376, Russia

114. Department of Biology, University of Wisconsin - Eau Claire, Eau Claire, WI 54702, USA

* Corresponding author (current address: Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany, anne.bjorkman@senckenberg.de)

Summary paragraph

Rapid climate warming in Arctic and alpine regions is driving changes in the structure and composition of tundra plant communities[1,2], with unknown consequences for ecosystem functioning. Because plant functional traits are directly related to vital ecosystem processes such as primary productivity and decomposition, understanding trait-environment relationships is critical to predicting high-latitude climate feedbacks[3,4], yet such relationships have never been quantified at the biome scale. Here, we explore the biome-wide relationship between temperature, soil moisture, and key plant functional traits (plant height, leaf area, leaf nitrogen content (leaf N), specific leaf area (SLA), and leaf dry matter content (LDMC), as well as community woodiness and evergreenness. We integrated more than 56,000 trait observations with nearly three decades of plant community vegetation surveys at 117 Arctic and alpine tundra sites spanning the northern hemisphere. We found strong spatial relationships between summer temperature and community height, SLA, and LDMC. Soil moisture had a marked influence on the strength (SLA and LDMC) and direction (leaf area and leaf N) of the temperature-trait relationship, highlighting the potentially important influence of changes in water availability on future plant trait change. Over the past three decades, community plant height increased with warming across all sites, but other traits lagged far behind rates of change predicted from spatial temperature-trait relationships. Our findings highlight the challenge of using space-for-time substitution to predict the consequences of future warming on functional composition and suggest that tundra ecosystem functions tied closely to plant height (e.g., carbon uptake) will show the most

rapid changes with near-term climate warming. Our results reveal the strength with which environmental factors shape biotic communities at the coldest extremes of the planet and will enable improved projections of tundra functional change with climate warming.

Main text

The tundra is warming more rapidly than any other biome on Earth, and the potential ramifications are far-reaching due to global-scale vegetation-climate feedbacks[5]. Up to 50% of the world's belowground carbon stocks are contained in permafrost soils[5], and tundra regions are expected to contribute the majority of warming-induced soil carbon loss over the next century[6]. Plant traits directly impact carbon cycling and energy balance, which can in turn influence regional and global climates[4,7,8]. Traits related to the resource economics spectrum[9], such as specific leaf area, leaf nitrogen content, and leaf dry matter content, affect primary productivity, litter decomposability, and nutrient cycling[3,4,7,10], while changes in size-related traits such as leaf area and plant height influence carbon storage, albedo, and hydrology[11] (Table S1). Quantifying the link between environment and plant functional traits is critical to understanding the consequences of climate change, but such studies rarely extend into the tundra[12,13]. As such, the full extent of the relationship between climate and plant traits in the planet's coldest ecosystems has never been assessed, and the consequences of climate warming for tundra functional change are largely unknown.

Here, we quantify for the first time biome-wide relationships between temperature, soil moisture, and key traits that represent the foundation of plant form and function[14], using the largest dataset of tundra plant traits ever assembled (56,048 measured trait

observations; Fig. 1a and S1, Table S2). We examine five continuous traits related to plant size - including adult plant height and leaf area - and to resource economy - including specific leaf area (SLA), leaf nitrogen content (leaf N), and leaf dry matter content (LDMC) - as well as two categorical traits related to community-level structure (woodiness) and leaf phenology/lifespan (evergreenness). We analyze two underlying components of biogeographic patterns in the five continuous traits: intraspecific variability (phenotypic plasticity or genetic differences among populations) and community-level variability (species turnover or shifts in species' abundances over space; Fig. S2). Intraspecific trait variability is thought to be especially important where diversity is low or where species have wide geographic ranges[15], as in the tundra. We ask: 1) How do plant traits vary with temperature and soil moisture across the tundra biome? 2) What is the relative influence of intraspecific trait variability (ITV) versus community-level trait variation (estimated as community-weighted trait means, CWM) for spatial temperature-trait relationships? 3) Are spatial temperature-trait relationships explained by among-site differences in species abundance or species turnover (presence-absence)?

A major impetus for quantifying spatial temperature-trait relationships is to better predict the potential consequences of future warming[16,17]. Thus, we also estimate realized rates of temporal community-level trait change using nearly three decades of vegetation survey data at 117 tundra sites (Fig. 1a, Table S3). Focusing on interspecific trait variation, we ask: 4) How do community trait changes over three decades of ambient warming compare to predictions from spatial temperature-trait relationships? We expect greater temporal trait change when spatial temperature-trait relationships are a) strong, b) independent of moisture, and c) due primarily to abundance shifts instead of species turnover, given that

species turnover over time depends on immigration and is likely to be slow[18]. Finally, because total realized trait change over time in continuous traits is comprised of both community-level variation and intraspecific trait variation (ITV), we estimated the latter's *potential* contribution to overall trait change (CWM+ITV) using the modeled intraspecific temperature-trait relationships described above (see supplementary methods and Fig. S2). For all analyses we used a novel, generalizable hierarchical Bayesian modeling approach, which allowed us to account for the hierarchical spatial, temporal and taxonomic structure of the data as well as multiple sources of uncertainty.

We found strong spatial associations between temperature and community height, SLA, and LDMC (Fig. 2a and S4) across the 117 survey sites. Both height and SLA increased significantly with summer temperature overall, but the temperature-trait relationship for SLA was much stronger at wet than at dry sites. LDMC was negatively related to temperature overall, and more strongly so at wet than at dry sites. Woodiness decreased overall with warmer temperatures, particularly in wet sites, but the relative proportion of evergreen woody species increased, particularly in dry sites (Fig. S4, Table S5). These spatial temperature-trait relationships suggest that long-term climate warming should cause pronounced shifts toward communities of non-woody, taller plants with more resource-acquisitive leaves (high SLA and low LDMC).

Our results reveal a substantial moderating influence of soil moisture on community traits across spatial temperature gradients[2,19]. Both leaf area and leaf N decreased with warmer temperatures in dry sites but increased with warmer temperatures in wet sites (Fig. 2a). Soil moisture was important in explaining spatial variation in all seven traits investigated

here, even when temperature was not (Fig. 2a and S4). Thus, future warming-driven changes in traits and associated ecosystem functions (e.g. decomposability) will likely depend on current soil moisture conditions at a site[19]. Furthermore, future changes in water availability (e.g., via changes in precipitation, snow melt timing, permafrost, and hydrology[20]) could cause substantial shifts in these traits and their associated functions irrespective of warming.

We found significant intraspecific temperature-trait relationships for all five continuous traits, but these relationships were not always consistent with community-level patterns (Fig. 2b, Table S6). Intraspecific plant height and leaf area showed strong positive relationships with summer temperature (i.e., individuals were taller and had larger leaves in warmer locations). Intraspecific LDMC, leaf N and SLA were significantly related to winter but not summer temperature (Fig. S3). The differing responses of intraspecific trait variation to summer versus winter temperature may indicate that size-related traits better reflect summer growth potential while leaf economics traits reflect cold-stress tolerance. These results, although correlative, suggest that trait variation expressed at the individual or population level is related to the growing environment and that warming may therefore lead to substantial intraspecific trait change in many traits. Thus, the potential for trait change over time is likely to be underestimated by using community-weighted trait means alone. Future work is needed to disentangle the role of plasticity and genetic differentiation in explaining the observed intraspecific temperature-trait relationships, as this will also influence the rate of future trait change[21]. Trait measurements collected over time and under novel (experimental) conditions, as yet unavailable, would enable more accurate predictions of the magnitude of future intraspecific trait change.

Partitioning the underlying causes of community temperature-trait relationships revealed that species turnover explained most of the variation in traits across space (Fig 2c), suggesting that dispersal and immigration processes will play a key role in governing the rate of ecosystem responses to warming. Shifts in species' abundances and intraspecific trait variation contributed only a minor proportion of the overall temperature-trait relationship (Fig 2c). Furthermore, the local trait pool in the coldest tundra sites (mean summer temperature < 3 °C) is constrained relative to the tundra as a whole for many traits (Fig. S5). Together, these results indicate that major community trait shifts with climate change will occur only with the arrival of novel species from warmer climates.

Community plant height was the only trait that changed significantly over the 27 years of the study; it increased rapidly at nearly every survey site (Fig 3 a&b, Fig S4, Table S7). Including potential intraspecific trait variation (ITV) doubled the average estimate of plant height change over time, from ~0.03 to ~0.06 cm/year. Because spatial patterns in ITV can be due to both phenotypic plasticity and genetic differences among populations, this is likely a maximum estimate of the ITV contribution, for example if it is due entirely to phenotypic plasticity. The increase in community height is consistent with a finding of increasing vegetation height in response to experimental warming at a subset of these sites[22] and with studies of increased shrub growth over time[11]. Inter-annual variation in community height was significantly sensitive to summer temperature (Fig. 3c, Fig. S3, Table S8), implying that increases in community height are responding to warming. However, neither the rate of temperature change nor soil moisture predicted the rate of CWM change in any trait (Fig S6, Table S9).

Increasing community height over time was due largely to species turnover (rather than shifts in abundances of resident species; Fig 3b) and was driven by the immigration of taller species rather than the loss of shorter ones (Fig S7, Table S10). The magnitude of temporal change was comparable to that predicted from the spatial temperature-trait relationship (Fig. 4a), indicating that temporal change in plant height does not yet appear to be substantially limited by immigration rates. The importance of turnover in explaining community height change is surprising given the relatively short study duration and long lifespan of tundra plants, but is nonetheless consistent with a previous finding of shifts towards warm-associated species in tundra plant communities[17,23]. Turnover could reflect the movement of tall species upward in latitude and elevation or from local species pools in warmer microclimates. If the observed rate of trait change continues (e.g., if immigration were unlimited), community height (excluding potential change due to ITV) could increase by 20-60% by the end of the century, depending on carbon emission, warming and water availability scenarios (Fig. S8).

Recent (observed) and future (predicted) changes in plant traits, particularly height, are likely to have important implications for ecosystem functions and feedbacks involving soil temperature[24,25], decomposition[4,10], and carbon cycling[26], as the potential for soil carbon loss is particularly great in high-latitude regions[6]. For example, negative feedbacks of increasing plant height to climate could occur with greater carbon storage, increased woody litter production[4], or if shading reduces soil temperatures and thus decomposition rates in summer[5,24,26]. Positive feedbacks are also possible if branches or leaves above the snowpack reduce winter and spring albedo[11] or increase snow accumulation, leading to

warmer winter soil temperatures and increased decomposition rates[5,11]. The balance of these feedbacks and thus the net impact of trait change on carbon cycling may depend on the interaction between warming and changes in water availability[27], which remains a major unknown in the tundra biome.

The lack of an observed temporal trend in SLA and LDMC despite strong temperature-trait relationships over space highlights the limitations of using space-for-time substitution for predicting short-term changes. This disconnect could reflect the influence of unmeasured changes in water availability, e.g. due local-scale variation in the timing of snowmelt or hydrology, that counter or swamp the effect of static soil moisture estimates. For example, we would not expect significant changes in traits demonstrating a significant spatial temperature * moisture interaction (LDMC, leaf area, leaf N or SLA), even in wet sites, if warming over time also leads to drier soils. Perhaps tellingly, plant height was the only continuous trait for which a temperature * moisture interaction was not significant, and was predicted to increase across all areas of the tundra regardless of soil moisture change (Fig. 4c&d). Spatial-temporal disconnects could also reflect dispersal limitation of potential immigrants (e.g., with low LDMC and high SLA), or establishment failure due to novel biotic or abiotic conditions other than temperature to which immigrants are maladapted[18,28]. Furthermore, community responses to climate warming could be constrained by soil properties (e.g., organic matter, mycorrhizae, mineralization) that themselves respond slowly to warming[17] or biotic conditions such as grazing pressure[29].

The patterns in functional traits described here reveal the extent to which environmental factors shape biotic communities in the tundra. Strong temperature- and moisture-related

spatial gradients in traits related to competitive ability (e.g., height) and resource capture (e.g., leaf nitrogen, SLA) reflect tradeoffs in plant ecological strategy[9,14] from benign (warm, wet) to extreme (cold, dry) conditions. Community-level ordination axes are also strongly related to both temperature and moisture, suggesting that environmental drivers structure not only individual traits but also trait combinations and thus lead to a reduced subset of successful functional strategies in some environments (e.g. woody, low-SLA and low-leaf N communities in warm, dry sites; Fig. S9). Thus, warming may lead to a community-level shift toward more exploitative plant strategies[30] at wet tundra sites, but toward more conservative strategies in dry sites as moisture becomes more limiting.

Earth system models are increasingly moving to incorporate trait-environment relationships into modeling efforts, as this can substantially improve estimates of ecosystem change[31,32]. Our results inform these projections of future tundra functional change with warming[31] by explicitly quantifying the link between temperature, moisture, and key functional traits across the biome. In particular, our study highlights the importance of accounting for future changes in water availability, as this will likely influence both the magnitude and direction of change for many traits. In addition, we demonstrate that spatial trait-environment relationships are driven largely by species turnover, suggesting that modeling efforts will need to account for rates of species immigration when predicting the speed of future functional shifts. While the failure of many traits (e.g. specific leaf area) to match expected rates of change suggests that using space-for-time substitution alone may inaccurately represent near-term ecosystem change, the ubiquitous increase in community plant height reveals that rapid functional change is already underway in tundra ecosystems.
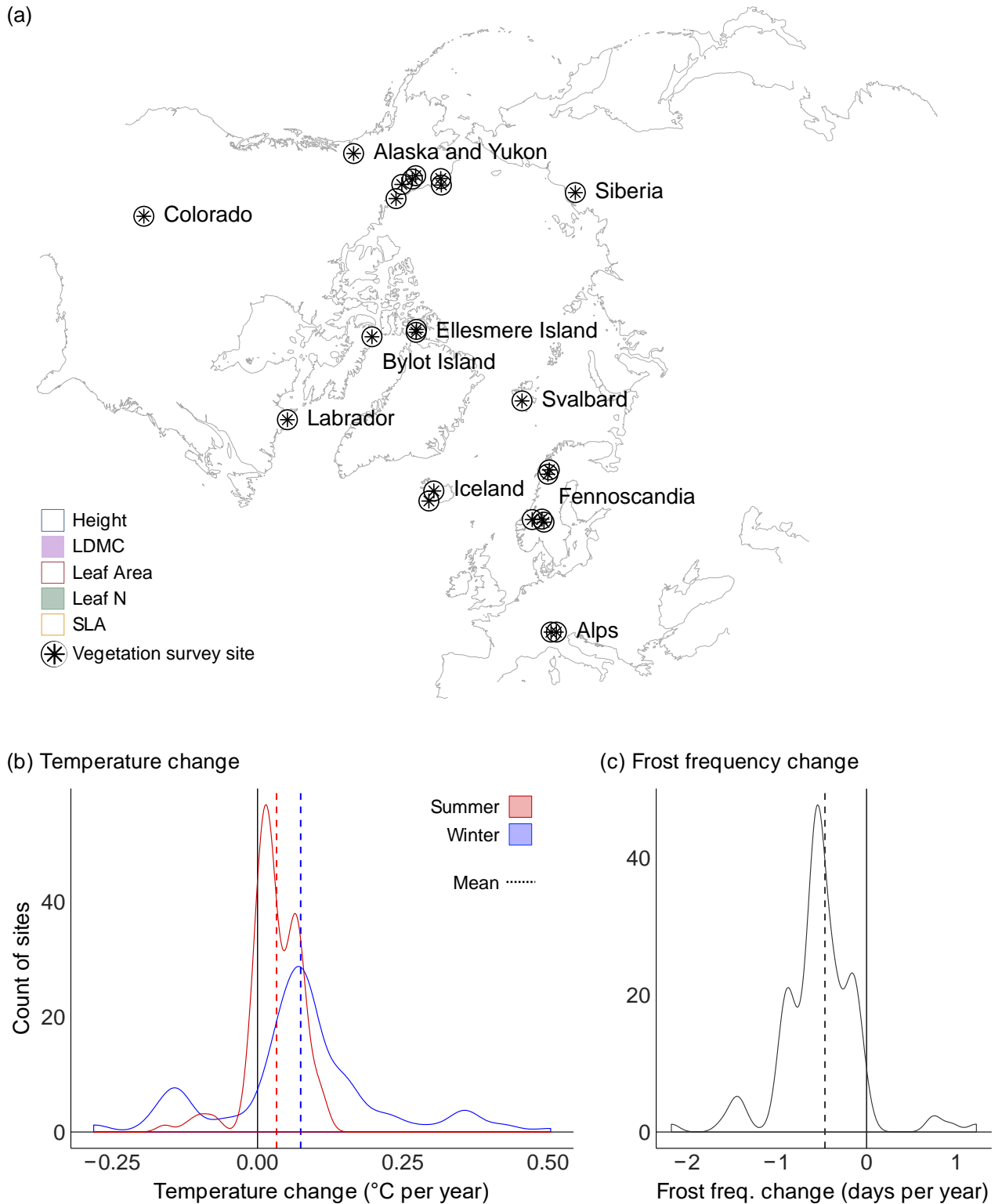
Figure 1. Map of all 56,048 tundra trait records and vegetation survey sites (a) and

climatic change across the period of monitoring at the 117 vegetation survey sites,

represented as mean winter (coldest quarter) and summer (warmest quarter) temperature

(b) and frost day frequency (c). The size of the colored points on the map indicates the relative quantity of trait measurements (larger circles = more measurements of that trait at a given location) and the color indicates which trait was measured. The black stars indicate the vegetation survey sites used in the community trait analyses. Trait data were included for all species that occur in at least one tundra vegetation survey site; thus, while not all species are unique to the tundra, all do occur in at least one tundra site. Temperature change and frost frequency change were estimated for the interval over which sampling was conducted at each site plus the preceding four years in order to best reflect the time window over which tundra plant communities respond to temperature change[17,23].

(a) Temperature – trait relationship: across communities (CWM)
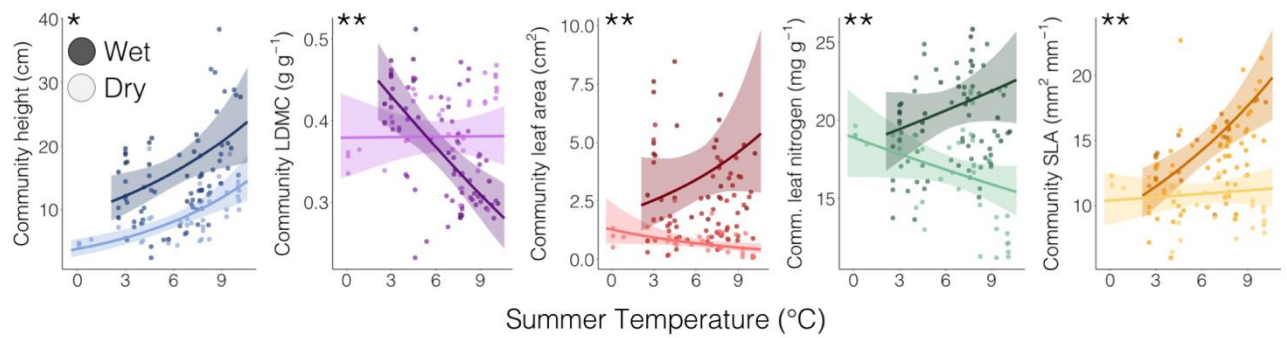
(b) Temperature – trait relationship: intraspecific trait variation (ITV)
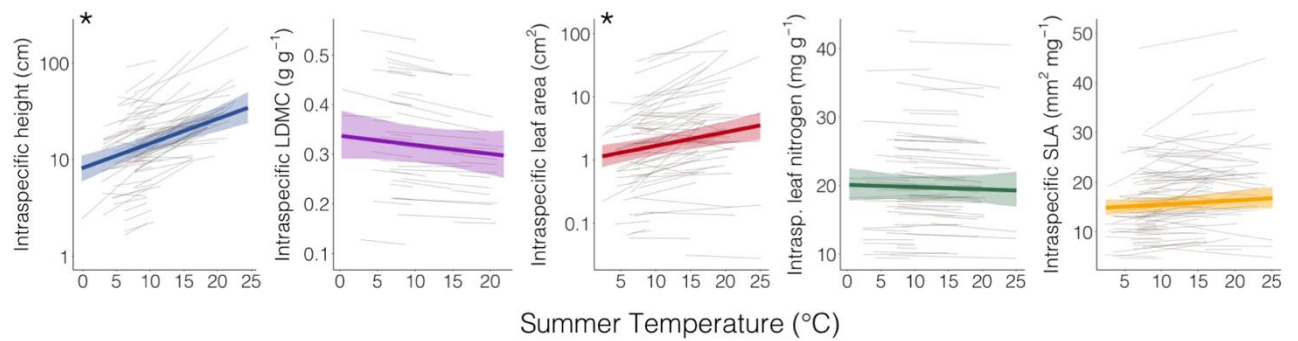
(c) Temperature – trait relationship: standardized effect size
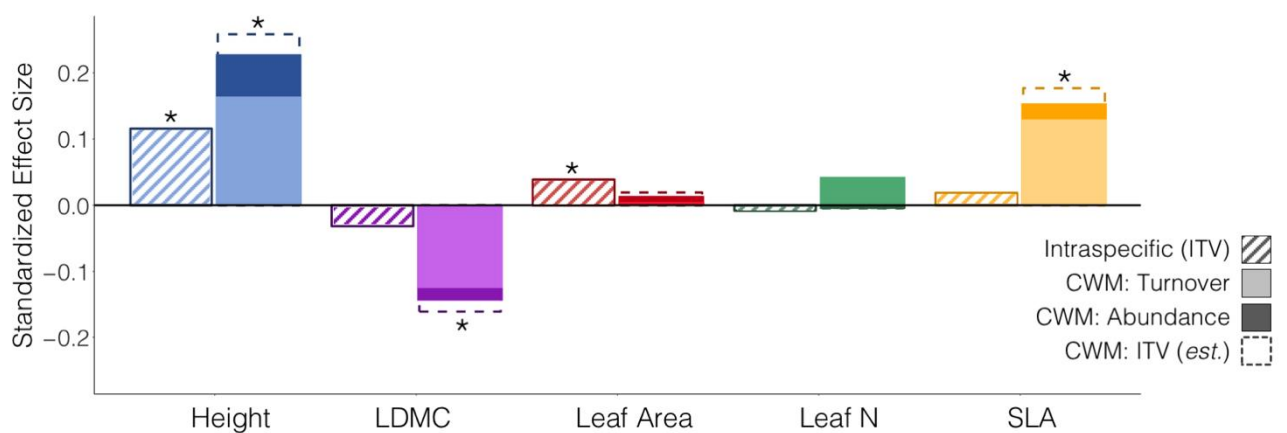
Figure 2. Strong spatial relationships in traits across temperature and soil moisture gradients are primarily explained by species turnover. Community-level (CWM) variation in functional traits across space as related to mean summer (warmest quarter) temperature and soil moisture (ordinal on a scale of 1 to 3; a), and within-species variation (ITV) across space as related to summer temperature (b; note the log scale for height and leaf area). Standardized effect sizes were estimated for all temperature-trait

relationships (c) both across communities (CWM; solid bars) and within species (ITV; striped bars). Effect sizes for CWM temperature-trait relationships were further partitioned into the proportion of the effect driven solely by species turnover (light bars) and abundance shifts (dark bars) over space. Dashed lines indicate the estimated total temperature-trait relationship over space if intraspecific trait variability is also accounted for (CWM: ITV). Effect sizes for CWM estimates were obtained by dividing the slope of the temperature-trait relationship by the standard deviation of the CWM model residuals. Effect sizes for ITV, turnover only, and CWM: ITV were estimated relative to the CWM value for that same trait based on the slope values of each temperature-trait relationship. Transparent ribbons in (a) and (b) indicate 95% credible intervals for model mean predictions. Grey lines in (b) represent intraspecific temperature-trait relationships for each species. In all panels, asterisks indicate that the 95% credible interval on the slope of the temperature-trait relationship did not overlap zero. In panel (a), two asterisks designate a significant interaction between temperature and soil moisture. Winter temperature – trait relationships are shown in Fig. S3. Community woodiness and evergreenness are shown in Fig. S4.
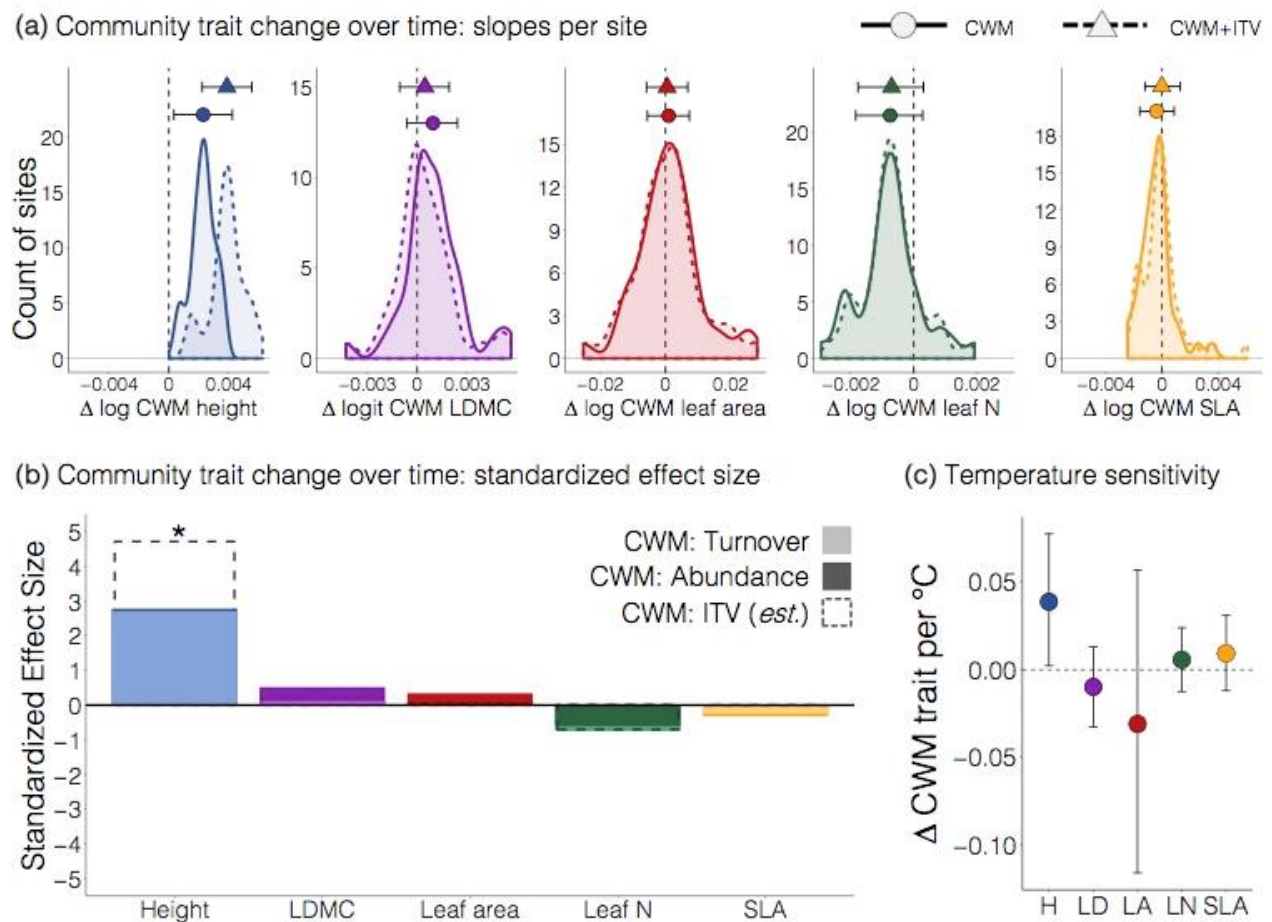
Figure 3. Observed community trait change (transformed units) per site per year (a), with and without estimated intraspecific trait variation (ITV). Solid lines indicate the distribution of community-weighted mean (CWM) model slopes (trait change per site) while dashed lines indicate the community-weighted mean plus potential intraspecific trait variation (CWM+ITV) slopes. Circles (CWM), triangles (CWM+ITV) and error bars indicate the mean and 95% credible interval for the overall rate of trait change across all sites. The vertical black dashed line indicates 0 (no change over time). Standardized effect sizes (b) for CWM change over time were further partitioned into the proportion of the effect driven solely by species turnover (light bars) or shifts in abundance of resident species (dark bars) over time. Dashed lines indicate the estimated total trait change over time if predicted intraspecific trait variability is also included (CWM+ITV).

Effect sizes for CWM estimates were obtained by dividing the slope of overall trait change over time by the standard deviation of the slopes per site. Effect sizes for turnover-only and CWM+ITV change are estimated relative to the CWM change value for that trait based on the slope values of each. Temperature sensitivity (c) of each trait as related to summer temperature (i.e., correspondence between interannual variation in CWM trait values with interannual variation in temperature). Temperatures associated with each survey year were estimated as five-year means (temperature of the survey year and four previous years) because this interval has been shown to be most relevant to vegetation change in tundra[17] and alpine[23] plant communities. Changes in community woodiness and evergreenness are shown in Fig. S4.

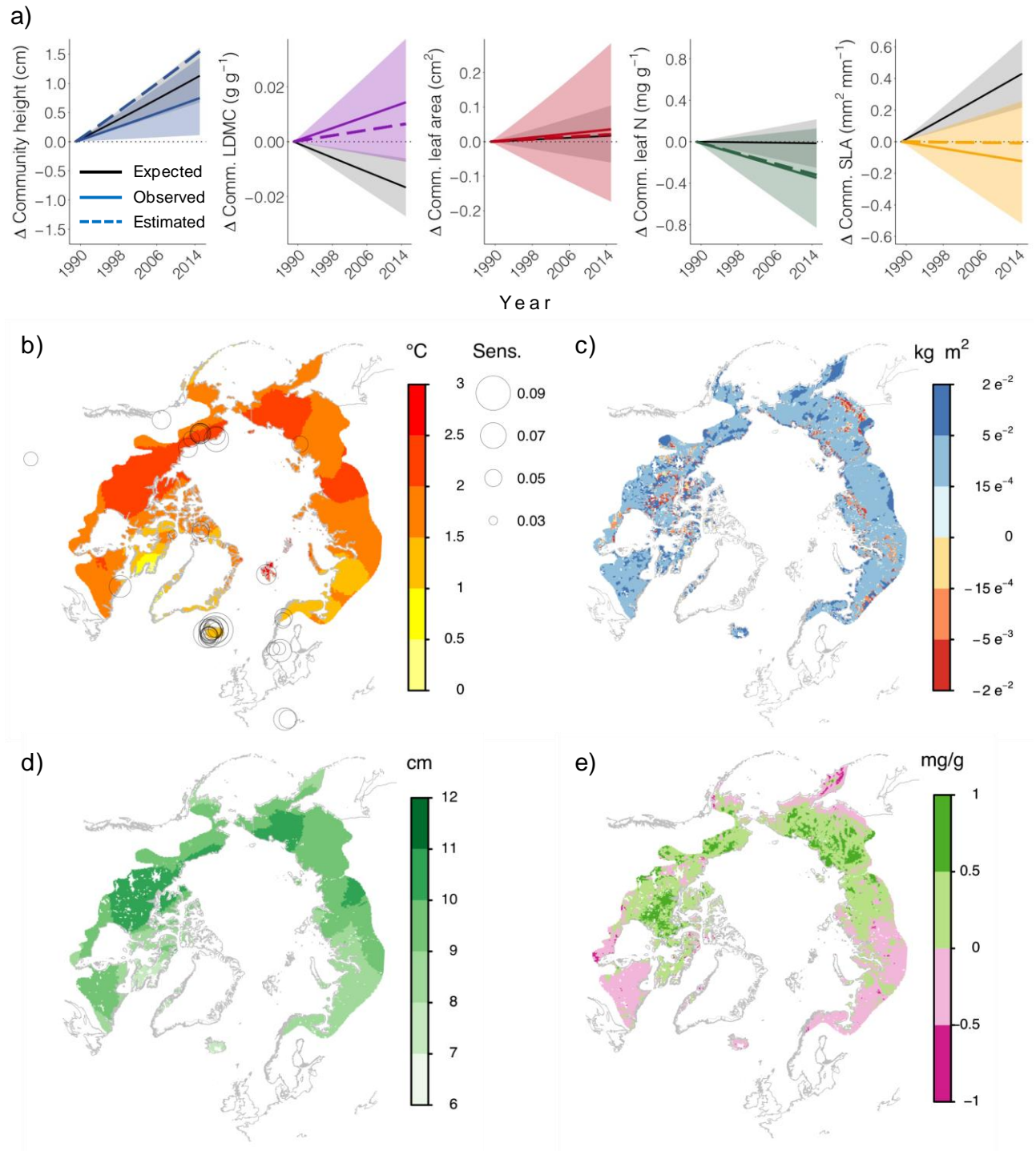Figure 4. Observed community (CWM) trait change over time (colored lines) vs. expected CWM change over the duration of vegetation monitoring (1989-2015) based on the spatial temperature-trait (CWM) relationship and the average rate of recent summer warming across all sites (solid black lines; a). Colored dashed lines indicate the potential change over time if predicted intraspecific trait variability is also included (CWM+ITV).

Values on the y-axis represent the magnitude of change relative to 0 (i.e., trait anomaly), with 0 representing the trait value at t_0. Total recent temperature change (b) and soil moisture change (c) across the Arctic tundra (1979-2016). Temperature change estimates are derived from CRU gridded temperature data, soil moisture change estimates are derived from downscaled ERA-Interim soil moisture data. Circles in (b) represent the sensitivity (cm per °C) of CWM plant height to summer temperature at each site (see Fig. 3c). Areas of high temperature sensitivity are expected to experience the greatest increases in height with warming. Spatial trait-temperature-moisture relationships (Fig. 2a) were used to predict total changes in height (d) and leaf N (e) over the entire 1979-2016 period based on concurrent changes in temperature and soil moisture. Note that (d) and (e) reflect *expected* and not observed trait change. See methods for details of temperature change and soil moisture change estimates. The outline of Arctic areas is based on the Circumpolar Arctic Vegetation Map (http://www.geobotany.uaf.edu/cavm).

References

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

2. Elmendorf, S. C. et al. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2, 453–457 (2012).

3. Díaz, S. et al. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15, 295–304 (2009).

4. Cornelissen, J. H. C. et al. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology Letters 10, 619–627 (2007).

5. Sistla, S. A. et al. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497, 615–618 (2013).

6. Crowther, T. W. et al. Quantifying global soil carbon losses in response to warming. Nature 540, 104–108 (2016).

7. Lavorel, S. & Garnier, E. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545–556 (2002).

8. Pearson, R. G. et al. Shifts in Arctic vegetation and associated feedbacks under climate change. Nature Climate Change 3, 673–677 (2013).

9. Wright, I. J. et al. The worldwide leaf economics spectrum. Nature 428, 821–827 (2004).

10. Cornwell, W. K. et al. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065–1071 (2008).

11. Myers-Smith, I. H. et al. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ. Res. Lett. 6, 045509 (2011).

12. Moles, A. T. et al. Global patterns in plant height. Journal of Ecology 97, 923–932 (2009).

13. Moles, A. T. et al. Global patterns in seed size. Global Ecology and Biogeography 16, 109–116 (2006).

14. Díaz, S. et al. The global spectrum of plant form and function. Nature 529, 167–171 (2016).

15. Siefert, A. et al. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters 18, 1406–1419 (2015).

16. McMahon, S. M. et al. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. Trends Ecol. Evol. 26, 249–259 (2011).

17. Elmendorf, S. C. et al. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proc. Natl. Acad. Sci. U.S.A. 112, 448–452 (2015).

18. Sandel, B. et al. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. New Phytologist 188, 565–575 (2010).

19. Ackerman, D., Griffin, D., Hobbie, S. E. & Finlay, J. C. Arctic shrub growth trajectories differ across soil moisture levels. Global Change Biology (2017). doi:10.1111/gcb.13677

20. Wrona, F. J. et al. Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime. Journal of Geophysical Research: Biogeosciences 121, 650–674 (2016).

21. Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G. & Violle, C. When and how should intraspecific variability be considered in trait-based plant ecology? Perspectives in Plant Ecology, Evolution and Systematics 13, 217–225 (2011).

22. Elmendorf, S. C. et al. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters 15, 164–175 (2012).

23. Gottfried, M. et al. Continent-wide response of mountain vegetation to climate change. Nature Climate Change 2, 111–115 (2012).

24. Blok, D. et al. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Global Change Biology 16, 1296–1305 (2010).

25. Blok, D., Elberling, B. & Michelsen, A. Initial stages of tundra shrub litter decomposition may be accelerated by deeper winter snow but slowed down by spring warming. Ecosystems 19, 155–169 (2016).

26. Cahoon, S. M. P., Sullivan, P. F., Shaver, G. R., Welker, J. M. & Post, E. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. Ecology Letters 15, 1415–1422 (2012).

27. Christiansen, C. T. et al. Enhanced summer warming reduces fungal decomposer diversity and litter mass loss more strongly in dry than in wet tundra. Global Change Biology 23, 406–420 (2017).

28. Bjorkman, A. D., Vellend, M., Frei, E. R. & Henry, G. H. R. Climate adaptation is not enough: warming does not facilitate success of southern tundra plant populations in the high Arctic. Global Change Biology 1–12 (2016). doi:10.1111/gcb.13417

29. Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. Nat Comms 8, 1–8 (2017).

30. Reich, P. B. The world‐wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102, 275–301 (2014).

31. Wullschleger, S. D. et al. Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. Annals of Botany 114, 1–16 (2014).

32. Butler, E. E. et al. Mapping local and global variability in plant trait distributions. Proc. Natl. Acad. Sci. U.S.A. 114, E10937–E10946 (2017).

Acknowledgements

Author contributions

ADB, IMS and SCE conceived the study, with input from the sTundra working group (SN, NR PSAB, AB-O, DB, JHCC, WC, BCF, DG, SG, KG, GHRH, RH, JK, JSP, JHRL, CR, GS-S, HT, MV, MW, and SW). ADB performed the analyses, with input from IMS, SCE, SN, NR. DNK made the maps of temperature, moisture, and trait change. ADB wrote the manuscript, with input from IMS, SCE, SN, NR, and contributions from all authors. ADB compiled the Tundra Trait Team database, with assistance from IMS, HT and SAB. Authorship order was determined as follows: 1) core authors, 2) sTundra participants (alphabetical) and other major contributors, 3) authors contributing both trait (Tundra Trait Team) and community composition (ITEX, etc.) data (alphabetical), 4) Tundra Trait Team contributors (alphabetical), 5) community composition data only contributors (alphabetical), and 6) TRY trait data contributors (alphabetical).

Author Information

Reprints and permissions information is available at www.nature.com/reprints.

The authors declare no competing financial interests.

Correspondence and requests for materials should be addressed to

anne.bjorkman@senckenberg.de.

METHODS

Below we describe the data, workflow (Fig. S2) and detailed methods used to conduct all analyses.

COMMUNITY COMPOSITION DATA

Community composition data used for calculating community-weighted trait means were compiled from a previous synthesis of tundra vegetation resurveys[1] (including many International Tundra Experiment (ITEX) sites) and expanded with additional sites (e.g., Gavia Pass in the Italian Alps and three sites in Sweden) and years (e.g., 2015 survey data added for Iceland sites, QHI, and Alexandra Fiord; Table S3). We included only sites for which community composition data were roughly equivalent to percent cover (i.e., excluding estimates approximating biomass), for a total of 117 sites (defined as plots in a single contiguous vegetation type) within 38 regions (defined as a CRU[2] grid cell). Plot-level surveys of species composition and cover were conducted at each of these sites between 1989 and 2015 (see[1] for more details of data collection and processing). On average, there were 15.2 plots per site. Repeat surveys were conducted over a minimum duration of 5 and up to 21 years between 1989 and 2015 (mean duration = 13.6 years), for a total of 1,781 unique plots and 5,507 plot-year combinations. Plots were either permanent (i.e., staked; 62% of sites) or semi-permanent (38%), such that the approximate but not exact location was resurveyed. The vegetation monitoring sites were located in tree-less Arctic or alpine tundra and ranged in latitude from 40° (Colorado Rockies) to 80° (Ellesmere Island, Canada) and were circumpolar in distribution (Figure 1). Our analyses only include vascular plants because there was insufficient trait data for non-vascular species. Changes in bryophytes and other cryptogams are an important part of the trait and function change

in tundra ecosystems[3,4], thus the incorporation of non-vascular plants and their traits is a future research priority.

Temperature extraction for community composition observations

We extracted summer (warmest quarter) and winter (coldest quarter) temperature estimates for each of the vegetation survey sites from both the WorldClim[5] (for long-term averages; http://www.worldclim.org/) and CRU[2] (for temporal trends; http://www.cru.uea.ac.uk/) gridded climate datasets. WorldClim temperatures were further corrected for elevation (based on the difference between the recorded elevation of a site and the mean elevation of the WorldClim grid cell) according to a correction factor of - 0.005 °C per meter increase in elevation. This correction factor was calculated by extracting the mean temperature and elevation (WorldClim 30s resolution maps) of all cells falling in a 2.5 km radius buffer around our sites and fitting a linear mixed model (with site as a random effect) to estimate the rate of temperature change with elevation.

The average long-term (1960-present) temperature trend across all sites was 0.26 (range -0.06 to 0.49) and 0.43 (range -0.15 to 1.32) °C/decade for summer and winter temperature, respectively.

Soil moisture for community composition observations

A categorical measure of soil moisture at each site was provided by every site PI according to the methods described in Elmendorf et al. 2012 and Myers-Smith et al. 2015 ([1,6]). Soil moisture was considered to be 1) dry when during the warmest month of the year the top 2 cm of the soil was dry to the touch, 2) moist when soils were moist year round, but

standing water was not present, and 3) wet when standing water was found during the warmest month of the year.

Soil moisture change for maps of environmental and trait change (Fig. 4b-e)

We used high-resolution soil moisture observations from ESA CCI SM v04.2. To calculate the mean distribution of soil moisture, we averaged the observations from 1979-2016. Because the ESA CCI SM temporal coverage is poor for our sites, temporal data were instead taken from ERA-Interim (Volumetric soil water layer 1) for the same time period. We downscaled the ERA-Interim data to the 0.05° resolution of ESA CCI SM v04.2 using climatologically aided interpolation (delta change method) [7]. The change in soil water content was then calculated separately for each grid cell using linear regression with month as a predictor variable. To classify the soil moisture data into 3 categories (wet, mesic, dry) to match the community composition dataset, we used a quantile approach on the mean soil moisture within the extent of the Arctic. We assigned the lowest quantile to dry and the highest to wet conditions. For the trends in soil moisture between 1979-2016 we calculated the percentage in change in relation to the mean first, and then calculated the change based on the categorical data (e.g. 5% change from category 1 (dry) to category 2 (mesic)).

Changes in water availability for analysis

Although the strong effect of soil moisture on spatial temperature-trait relationships suggests that change in water availability over time will play an important role in mediating trait change, we did not use the CRU estimates of precipitation change over time because of issues with precipitation records at high latitudes and the inability of gridded datasets

112

to capture localized precipitation patterns (e.g., [8,9]). The CRU precipitation trends at our sites included many data gaps filled by long-term mean values, especially at the high-latitude sites[6]. As a purely exploratory analysis, we used the downscaled ERA-Interim data described above to investigate whether trait change is related to summer soil moisture change (June, July, and August; Fig. S6). However, we caution that soil moisture change in our tundra sites is primarily controlled by snow melt timing, soil drainage, the permafrost table and local hydrology[10], and as such precipitation records and coarse-grain remotely sensed soil moisture change data are unlikely to accurately represent local changes in soil water availability. For this same reason we did not use the ERA-Interim data to explore spatial relationships between temperature, moisture and community traits, as the categorical soil moisture data (described above) were collected specifically within each community composition site and are therefore a more accurate representation of long-term mean soil moisture conditions in that specific location.

TRAIT DATA

Continuous trait data (adult plant height, leaf area (average one-sided area of a single leaf), specific leaf area (leaf area per unit of leaf dry mass; SLA), leaf nitrogen content (per unit of leaf dry mass; leaf N), and leaf dry matter content (leaf dry mass per unit of leaf fresh mass; LDMC); Fig. 1a & S11, Table S2) were extracted from the TRY[11] 3.0 database (available at www.try-db.org). We also ran a field & data campaign in 2014-15 to collect additional in-situ tundra trait data (the "Tundra Trait Team" (TTT) dataset) to supplement existing TRY records. All species names from the vegetation monitoring sites, TRY and TTT were matched to accepted names in The Plant List using the R package Taxonstand[12] (v. 1.8) before merging the datasets. Community-level traits (woodiness and evergreenness)

were derived from functional group classifications for each species (REF). Woodiness is estimated as the proportion (abundance) of woody species in the plot, while evergreenness is the proportion of evergreen woody species abundance out of all woody species (evergreen plus deciduous) in a plot. Because some sites did not contain any woody species (and thus the proportion of evergreen woody species could not be calculated), this trait is estimated only for 98 of the 117 total sites.

Data cleaning - TRY

TRY trait data were subjected to a multi-step cleaning process. First, all values that did not represent individual measurements or approximate species means were excluded. When a dataset within TRY contained only coarse plant height estimates (e.g., estimated to the nearest foot), we removed these values unless no other estimate of height for that species was available. We then identified overlapping datasets within TRY and removed duplicate observations whenever possible. The following datasets were identified as having partially overlapping observations: GLOPNET – Global Plant Trait Network Database, The LEDA Traitbase, Abisko & Sheffield Database, Tundra Plant Traits Database, and KEW Seed Information Database (SID).

We then removed duplicates within each TRY dataset (e.g., if a value is listed once as "mean" and again as "best estimate") by first calculating the ratio of duplicated values within each dataset, and then removing duplicates from datasets with more than 30% duplicated values. This cutoff was determined by manual evaluation of datasets at a range of thresholds. Datasets with fewer than 30% duplicated values were not cleaned in this

way as any internally duplicate values were assumed to be true duplicates (i.e., two different individuals were measured and happened to have the same measurement value).

We also removed all species mean observations from the "Niwot Alpine Plant Traits" database and replaced it with the original individual observations as provided by M.J. Spasojevic.

Data cleaning – TRY & TTT combined

Both datasets were checked for improbable values, with the goal of excluding likely errors or measurements with incorrect units but without excluding true extreme values. We followed a series of data-cleaning steps, in each case identifying whether a given observation (x) was likely to be erroneous (i.e. "error risk") by calculating the difference between x and the mean (excluding x) of the group and then dividing by the standard deviation of the group.

We employed a hierarchical data cleaning method, because the standard deviation of a trait value is related to the mean and sample size. First, we checked individual records against the entire distribution of observations of that trait and removed any records with an error risk greater than 8 (i.e., a value more than 8 standard deviations away from the trait mean). For species that occurred in four or more unique datasets with TRY or TTT (i.e., different data contributors), we estimated a species mean per dataset and removed observations for which the species mean error risk was greater than 3 (i.e., the species mean of that dataset was more than 3 SD's away from the species mean across all datasets). For species that occurred in fewer than 4 unique datasets, we estimated a genus

mean per dataset and removed observations in datasets for which the error risk based on the genus mean was greater than 3.5. Finally, we compared individual records directly to the distribution of values for that species. For species with more than 4 records, we excluded values above an error risk Y, where Y was dependent on the number of records of that species and ranged from an error risk of 2.25 for species with fewer than 10 records to an error risk of 4 for species with more than 30 records. For species with four or fewer records, we manually checked trait values and excluded only those that were obviously erroneous, based on our expert knowledge of these species.

This procedure was performed on the complete tundra trait database – including species and traits not presented here. In total 2,056 observations (1.6%) were removed. In all cases, we visually checked the excluded values against the distribution of all observations for each species to ensure that our trait cleaning protocol was reasonable.

Trait data were distributed across latitudes within the tundra biome (Fig. S1). All trait observations with latitude/longitude information were mapped and checked for implausible values (e.g., falling in the ocean). These values were corrected from the original publications or by contacting the data contributor whenever possible.

Final trait database

After cleaning out duplicates and outliers as described above, we retained 56,048 unique trait observations (of which 18,613 are contained in TRY and 37,435 were newly contributed by the Tundra Trait Team field campaign) across the five traits of interest. Of the 447 identified species in the ITEX dataset, 386 (86%) had trait data available from TRY or TTT

for at least one trait (range 52-100% per site). Those species without trait data generally represent rare or uncommon species unique to each site; on average, trait data were available for 97% of total plant cover across all sites (range 39-100% per site; Table S2).

Temperature extraction for trait observations

WorldClim climate variables were extracted for all trait observations with latitude/longitude values recorded (53,123 records in total, of which 12,380 were from TRY and 33,621 from TTT). Because most observations did not include information about elevation, temperature estimates for individual trait observations were not corrected for elevation and thus represent the temperature at the mean elevation of the WorldClim grid cell.

Data Availability

Data compiled through the Tundra Trait Team will be made available through a public GitHub repository (Bjorkman et al. in revision as a data paper at Global Ecology & Biogeography). The public TTT database will include traits not considered in this study as well as tundra species that do not occur in our vegetation survey plots, for a total of 80,827 trait observations on 834 species.

ANALYSES

All analyses were conducted in JAGS and/or Stan through R (v. 3.3.3) using packages *rjags*[13] (v. 4.6) and *rstan*[14] (v. 2.14.1).

A major limitation of the species mean trait approach often employed in analyses of environment-trait relationships has been the failure to account for intraspecific trait

variation (ITV) that could be as or more important than interspecific variation[15,16]. We addressed this issue by employing a hierarchical analysis that incorporates both within-species and community-level trait variation across climate gradients to estimate trait change over space and time at the biome scale. We used a Bayesian approach that accounts for the hierarchical spatial (plots within sites within regions) and taxonomic (intra- and inter-specific variation) structure of the data as well as uncertainty in estimated parameters introduced through absences in trait records for some species, and taxa that were identified to genus or functional group (rather than species) in vegetation surveys.

Intraspecific trait variation

We subsetted the trait dataset to just those species for which traits had been measured in at least four unique locations spanning a temperature range of at least 10% of the entire temperature range (2.6°C and 5.0 °C for summer and winter temperature, respectively), and for which the latitude and longitude of the measured individual or group of individuals was recorded. The number of species meeting these criteria varied by trait and temperature variable: 108-109 for SLA, 80-86 for plant height, 74-72 for leaf nitrogen, 85-76 for leaf area, and 43-52 for LDMC, for summer and winter temperature, respectively). These species counts correspond to 53-73% of community abundance. The relationship between each trait and temperature was estimated from a Bayesian hierarchical model, with temperature as the predictor variable and species (*s*) and dataset-by-location (*d*) modeled as random effects:

$$traitobs_i \sim logNormal(a_{s,d}, \sigma_s)$$
$$a_{s,d} \sim Normal(\alpha_s + \beta_s \cdot temperature_d, \sigma)$$
$$\beta_s \sim Normal(B, \sigma_1)$$
$$\alpha_s \sim Normal(A, \sigma_2)$$

where A and B are the intercept and slope hyperparameters, respectively. Because LDMC represents a ratio and is thus bound between 0 and 1, we used a beta error distribution for this trait. Temperature values were mean-centered within each species. We used non-informative priors for all coefficients.

We further explored whether the strength of intraspecific temperature-height relationships varied by functional group. We find that all functional groups (including dwarf shrubs, which are genetically limited in their ability to grow upright) show similar temperature-trait relationships (Fig. S12). These results suggest that the intraspecific temperature-trait relationships may not only be a response of individual growth changes, and are not restricted to particular functional groups with greater capacity for vertical growth (e.g., tall shrubs and graminoids versus dwarf shrubs and certain forb species).

Calculation of community weighted mean (CWM) values

We calculated the community-weighted trait mean (i.e., the mean trait value of all species in a plot, weighted by the abundance of each species), for all plots within a site. We employed a Bayesian approach to calculate trait means for every species (s) using an intercept-only model (such that the intercept per species (α_s) is equivalent to the mean trait value of the species) and variation per species (σ_s) with a lognormal error distribution.

$$traitobs_i \sim logNormal(\alpha_s, \sigma_s)$$

Because LDMC is a ratio and thus bound between 0 and 1, we used a beta error distribution for this trait. When a species was measured multiple times in several different locations, we additionally included a random effect of dataset-by-location (*d*) to

reduce the influence of a single dataset with many observations at one site when

calculating the mean per species:

$$traitobs_i \sim logNormal(\alpha_{s,d}, \sigma_d)$$
$$\alpha_{s,d} \sim Normal(\alpha_s, \sigma_s)$$

We used non-informative priors for all species intercept parameters for which there were

four or more unique trait observations, so that the species-level intercept and variance

around the intercept per species were estimated from the data. In order to avoid removing

species with little or no trait data from the analyses, we additionally employed a "gap-

filling" approach that allowed us to estimate a species' trait mean while accounting for

uncertainty in the estimation of this mean. For species with fewer than four but more than

one trait observation, we used a normal prior with the mean equal to the mean of the

observation(s) and variance estimated based on the mean mean-variance ratio across all

species. In other words, we calculated the ratio of mean trait values to the standard

deviation of those trait values per species for all species with greater than four

observations, then took the mean of these ratios across all species and multiplied this

number by the mean of species X (where X is a species with 1-4 observations) to get the

prior σ. For species with no observations, we used a prior mean equal to the mean of all

species in the same genus and a prior variance estimated based on the mean mean-

variance ratio of all species in that genus or 1.5 times the mean, whichever was lower. If

there were no other species in the same genus, then we used a prior mean equal to the

mean of all other species in the family and a prior variance estimated based on the mean

mean-variance ratio of all species in the family or 1.5 times the mean, whichever was lower.

In order to include uncertainty about species trait means (due to intraspecific trait variation,

missing trait information for some species, or when taxa were identified to genus or

functional group rather than species) in subsequent analyses, we estimated community-level trait values per plot by sampling from the posterior distribution (mean +/- SD) of each species intercept estimate and multiplying this distribution by the relative abundance of each species in the plot to get a community-weighted mean (CWM) distribution per plot. This approach generates a distribution of CWM values per plot that propagates the uncertainty in each species' trait mean estimate into the plot-level (CWM) estimate. By using a Bayesian approach, we are able to carry through uncertainty in trait mean estimates to all subsequent analyses and reduce the potential for biased or deceptively precise estimates due to missing trait observations.

Calculation of CWM values: partitioning turnover and estimating contribution of ITV

To assess the degree to which the spatial temperature-trait relationships are caused by species turnover versus shifts in abundance among sites, we repeated each analysis using the non-weighted community mean (all species weighted equally) of each plot. Temperature-trait relationships estimated with non-weighted community means are due solely to species turnover across sites. Finally, we assessed the potential contribution of intraspecific trait variation (ITV) to the community-level temperature-trait relationship by using the modeled intraspecific temperature-trait relationship (described above) to predict trait "anomaly" values for each species at each site based on the temperature of that site in a given year relative to its long-term average.

An intraspecific temperature-trait relationship could not be estimated for every species due to an insufficient number of observations for some species. Therefore, we used the mean intraspecific temperature-trait slope across all species to predict trait anomalies for

species without intraspecific temperature-trait relationships. These site- and year-specific species trait estimates were then used to calculate "ITV-adjusted" community-weighted means (CWM+ITV) for each plot in each year measured, and modeled as for CWM alone. As these "adjusted" values are estimated *relative to each species' mean value*, the spatial temperature-trait relationship that includes this adjustment does not remove any bias in the underlying species mean data. For example, if southern tundra species tend to be measured at the southern edge of their range while northern tundra species tend to be measured at the northern edge of their range, the overall spatial temperature-trait relationship could appear stronger than it really is for species with temperature-related intraspecific variation. This is a limitation of any species-mean approach.

Estimates of temporal CWM+ITV temperature-trait relationships are not prone to this same limitation as they represent relative change, but should also be interpreted with caution as intraspecific temperature-trait relationships may be due to genetic differences among populations rather than plasticity, thus suggesting that trait change would not occur instantaneously with warming. We therefore caution that the CWM+ITV analyses presented here represent estimates of the potential contribution of ITV to overall CWM temperature-trait relationships over space and time, but should not be interpreted as measured responses.

In sum, we incorporate intraspecific variation into our analyses in three ways. First, by using the posterior distribution (rather than a single mean value) of species trait mean estimates in our calculations of CWM values per plot, so that information about the amount of variation within species is incorporated into all the analyses in our study. Second, by

explicitly estimating intraspecific temperature-trait relationships based on the spatial variation in individual trait observations. And finally, by using these modeled temperature-trait relationships to inform estimates of the potential contribution of ITV to overall (CWM+ITV) temperature-trait relationships over space and time.

Spatial community trait models

To investigate spatial relationships in plant traits with summer and winter temperature and soil moisture we used a Bayesian hierarchical modeling approach in which soil moisture and soil moisture x temperature vary at the site level while temperature varies by WorldClim region (unique WorldClim grid x elevation groups). In total, there were 117 sites (*s*) nested within 73 WorldClim regions (*r*). We used only the first year of survey data at each site to estimate spatial relationships in community traits.

$$cwmtrait_p \sim Normal(\alpha_s + \alpha_r, traitsd_p)$$
$$\alpha_s \sim Normal(\gamma_1 \cdot moisture_s + \gamma_2 \cdot moisture_s \cdot temperature_s, \sigma_1)$$
$$\alpha_r \sim Normal(\gamma_0 + \gamma_3 \cdot temperature_r, \sigma_2)$$

Where *cwmtrait_p* is the estimated community-weighted mean (CWM) trait value per plot (*p*) and *traitsd_p* is the standard deviation of the posterior distribution of this mean per plot, as described above.

As woodiness and evergreenness represent proportional data (bounded between 0 and 1, inclusive), we used a beta-Bernoulli mixture model of the same structure as above to estimate trait-temperature-moisture relationships for these traits. Because Arctic and alpine tundra sites might different in their trait-environment relationships due to differences in

e.g. soil drainage, we also present a version of the spatial community trait analyses in which the altitude of each site is indicated (Fig. S13). We do not attempt to separately analyze trait-environment relationships for Arctic and alpine sites due to the ambiguity in defining this cut-off (i.e., many sites can be categorized as both Arctic and alpine, particularly in Scandinavia and Iceland) and the small number of "true" alpine sites (European Alps and Colorado Rockies).

For estimation of the overall temperature-trait relationship, we used a model structure similar to that above but with only temperature as a predictor (i.e., without soil moisture). This model was used for both community-weighted mean (CWM) and non-weighted mean estimates in order to determine the degree to which temperature-trait relationships over space are due to species turnover alone (non-weighted mean) and for CWM+ITV plot-level estimates to determine the likely additional contribution of intraspecific trait variation to the overall temperature-trait relationship, as described above.

Trait change over time

Change over time was modeled at the CRU grid cell (region) level (r), with site (s) as a random effect when there was more than one site per region (to account for non-independence of sites within a region) and plot (p) as a random effect for those sites with permanent (repeating) plots (to account for repeated measures on the same plot over time). We did not account for temporal autocorrelation as most plots were not measured annually (average survey interval = 7.2 years) and did not have more than 3 observations over the study period (average number of survey years per plot = 3.1). Year (y) was centered within each region.

$$cwmtrait_{p,y} \sim Normal(\alpha_p + a_s + a_{r,y}, traitsd_{p,y})$$

For non-permanent plots and for sites that were the only site within a region, α_p or α_s, respectively, were set to 0. Region-level slopes were used to fit an average trend of community trait values over time:

$$\alpha_{r,y} \sim Normal(a_r + \beta_r \cdot year_{y,r}, \sigma)$$
$$\beta_r \sim Normal(B, \sigma_1)$$
$$\alpha_r \sim Normal(A, \sigma_2)$$

where A and B are the intercept and slope hyperparameters, respectively. This model was used for both community-weighted mean (CWM) and non-weighted mean plot-level estimates in order to determine the degree to which temporal trait change is due to species turnover alone (non-weighted mean) and for CWM+ITV plot-level estimates to determine the potential additional contribution of intraspecific trait variation to overall trait change.

For the spatial community trait models, we used a beta-Bernoulli mixture model of the same form described above to estimate change in the proportion of woody and evergreen species. We additionally assessed whether the rate of observed trait change over time was related to the duration of vegetation monitoring at each site (Fig. S10). There was no significant influence of monitoring duration for any trait.

Species gains and losses as a function of traits

We estimated species gains and losses at the site (rather than plot) level to reduce the effect of random fluctuations in species presences/absences due to observer error. Thus, sites with repeating and non-repeating plots were treated the same. A "gain" was defined as a species that did not occur in a site in the first survey year but did in the last survey year, while a "loss" was the reverse. We then modeled the probability of gain or loss separately as a function of the mean trait value of each species. For example, for "gains," all newly observed species received a response type of 1 while all other species in the site received a response type of 0:

$$response_i \sim Bernoulli(\alpha_s + \alpha_r + \beta_r \cdot trait_i)$$
$$\alpha_r \sim Normal(A, \sigma_1)$$
$$\beta_r \sim Normal(B, \sigma_2)$$
$$\alpha_s \sim Normal(0, \sigma_r)$$

We included a random effect for site (s) only when there were multiple sites within the same region (r), otherwise α_s was set to 0. We considered species' responses to be significantly related to a given trait when the 95% credible interval on the slope hyperparameter (B) did not cross 0.

Observed vs. expected trait change

We first calculated the mean rate of temperature change across the 38 regions in our study, and then estimated the *expected* degree of change in each trait over the same period based on this temperature change and the spatial relationship between temperature and CWM trait values. We then compared this *expected* trait change to actual trait change over time, as estimated from the model described above. To create

Fig. 4a we used the overall predicted mean value of each trait in the first year of survey (1989) as an intercept, and then used the expected and observed rates of change (+/- uncertainty) to predict community trait values in each year thereafter. We subtracted the intercept from all predicted values in order to show trait change as anomaly (difference from 0). The difference between the expected (black) and observed (colored) lines in Fig. 4a represents a deviation from expected.

Trait projections with warming

We projected trait change (Fig. S8) for the minimum (2.6) and maximum (8.5) IPCC carbon emission scenarios from the NIMR HadGEM2-AO Global Circulation Model. We used the midpoint years of the WorldClim (1975) and HadGem2 (2090) estimates to calculate the expected rate of temperature change over this time period. We then predicted trait values for each year into the future based on the projected rate of temperature change and the spatial relationship between temperature and community trait values.

These projections are not intended to predict actual expected trait change over the next century, as many other factors not accounted for here will also influence this change. In particular, future changes in functional traits will likely depend on concurrent changes in moisture availability, which are less well understood than temperature change. Recent modeling efforts predict increases in precipitation across much of the Arctic[17], but it is unknown whether increasing precipitation will also lead to an increase in soil moisture/water availability for plants, as the drying effect of warmer temperatures (e.g. due to increased evaporation and/or decreased duration of snow cover[18]) may outweight the impact of increased precipitation. Instead, these projections are an attempt to explore

theoretical trait change over the long-term when using a space-for-time substitution approach.

Temperature sensitivity

Temperature sensitivity (Fig. 3c) was modeled as the variation in CWM trait values with variation in the five-year mean temperature (i.e., the mean temperature of the survey year and the four preceding years). A four-year lag was chosen because this interval has been shown to best explain vegetation change in tundra[19] and alpine[20] plant communities. The model specifics are exactly as shown above for trait change over time, but with temperature in the place of year. Temperatures were centered within each region.

Trait change vs. temperature change and soil moisture

To determine whether the rate of trait change can be explained by the rate of temperature change at a site, the (static) level of soil moisture of a site, or their interaction, we modeled the rate of trait change as described above ("Trait change over time") and compared it to the rate of temperature change over the same time interval (minus a lag of four years) and soil moisture:

$$\beta_r \sim Normal(\gamma_0 + \gamma_1 \cdot temp_r + \gamma_2 \cdot moisture_r + \gamma_3 \cdot temp_r \cdot moisture_r, \sigma)$$

where β_r is the rate of trait change per region (Fig. S6a). When sites within a region were measured over different intervals or contained different soil moisture estimates they were modeled separately in order to match with temperature change estimates over the same interval and soil moisture estimates, which vary at the site level.

We also conducted this analysis using estimates of soil moisture change (with a lag of four years) from downscaled ERA-Interim (volumetric soil water layer 1). This model took the same form as above, but with moisture change in place of static soil moisture estimates

(Fig. S6b). Trait change was modeled at the site (rather than region) level because estimates of soil moisture change vary at the site level. Because ERA-Interim data were not available for every site, this analysis was conducted with a total of 101 rather than 117 sites. We note that the results of this analysis should be interpreted cautiously, as local changes in soil moisture may not be well represented by coarse-scale remotely sensed data, as described previously.

Principal component analysis (PCA)

We performed an ordination of community-weighted trait mean values per plot on all seven traits. Because community evergreenness could only be estimated for plots with at least one woody species, the total number of plots included in this analysis is reduced compared to the entire dataset (1098 plots out of 1520 in total). We used the R package *vegan*[21] (v. 2.4.6) to conduct a principal component analysis of these data. This analysis uses only trait means per plot, and therefore information about CWM uncertainty due to intraspecific trait variation and/or missing species is lost. We extracted the axis coordinates of each plot from the PCA analysis and used the spatial trait-temperature-moisture model described above (section "*Spatial community trait models*") to determine whether plot distributions along both PCA axes varied significantly with temperature, moisture, and their interaction.

Trends in species abundance

In order to provide more insight into the species-specific changes occurring over time in tundra ecosystems, we calculated trends in abundance for the most common (widespread

and abundant) species in the community composition dataset (Fig. SX). We estimated trends for all species that occurred in at least 10 sites at a minimum abundance of 10% cover (mean of all plots within a site) in at least one year and a minimum abundance of 5% across all years. We additionally included species that occurred at low abundance (1% or more) but were widespread (at least 20 sites). Because percent cover is bounded between 0 and 1 (inclusive) we used a beta-Bernoulli mixture model to estimate abundance change over time.

Methods References

1. Elmendorf, S. C. et al. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2, 453–457 (2012).
2. Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. International Journal of Climatology 34, 623–642 (2014).
3. Blok, D. et al. The Cooling Capacity of Mosses: Controls on Water and Energy Fluxes in a Siberian Tundra Site. Ecosystems 14, 1055–1065
4. Soudzilovskaia, N. A., van Bodegom, P. M. & Cornelissen, J. H. C. Dominant bryophyte control over high-latitude soil temperature fluctuations predicted by heat transfer traits, field moisture regime and laws of thermal insulation. Functional Ecology 27, 1442–1454 (2013).
5. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, J. L. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978 (2005).
6. Myers-Smith, I. H. et al. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change 5, 887–891 (2015).
7. Willmott, C. J. & Robeson, S. M. Climatologically aided interpolation (CAI) of terrestrial air temperature. International Journal of Climatology 15, 221–229 (1995).
8. Sperna Weiland, F. C., Vrugt, J. A., van Beek, R. L.). P. H., Weerts, A. H. & Bierkens, M. F. P. Significant uncertainty in global scale hydrological modeling from precipitation data errors. Journal of Hydrology 529, 1095–1115 (2015).
9. Beguería, S., Vicente Serrano, S. M., Tomás Burguera, M. & Maneta, M. Bias in the variance of gridded data sets leads to misleading conclusions about changes in climate variability. International Journal of Climatology 36, 3413–3422 (2016).

10. Wrona, F. J. et al. Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime. Journal of Geophysical Research: Biogeosciences 121, 650–674 (2016).

11. Kattge, J. et al. TRY–a global database of plant traits. Global Change Biology 17, 2905–2935 (2011).

12. Cayuela, L., Granzow-de la Cerda, Í., Albuquerque, F. S. & Golicher, D. J. TAXONSTAND: An R package for species names standardisation in vegetation databases. Methods in Ecology and Evolution 3, 1078–1083 (2012).

13. Plummer, M. rjags: Bayesian graphical models using MCMC. (2016).

14. Stan Development Team. RStan: the R interface to Stan. (2016).

15. Messier, J., McGill, B. J. & Lechowicz, M. J. How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters 13, 838–848 (2010).

16. Violle, C. et al. The return of the variance: intraspecific variability in community ecology. Trends Ecol. Evol. 27, 245–253 (2012).

17. Bintanja, R. & Selten, F. M. Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat. Nature 509, 479–482 (2014).

18. AMAP. Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017. (Arctic Monitoring and Assessment Programme (AMAP), 2017).

19. Elmendorf, S. C. et al. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proc. Natl. Acad. Sci. U.S.A. 112, 448–452 (2015).

20. Gottfried, M. et al. Continent-wide response of mountain vegetation to climate change. Nature Climate Change 2, 111–115 (2012).

21. Oksanen, J., Blanchet, F., Kindt, R. & Legendre, P. Package 'vegan'. (2011).

EXTENDED DATA

Below are all supplementary figures and tables as well as references for the original studies
where trait data contributions were published.
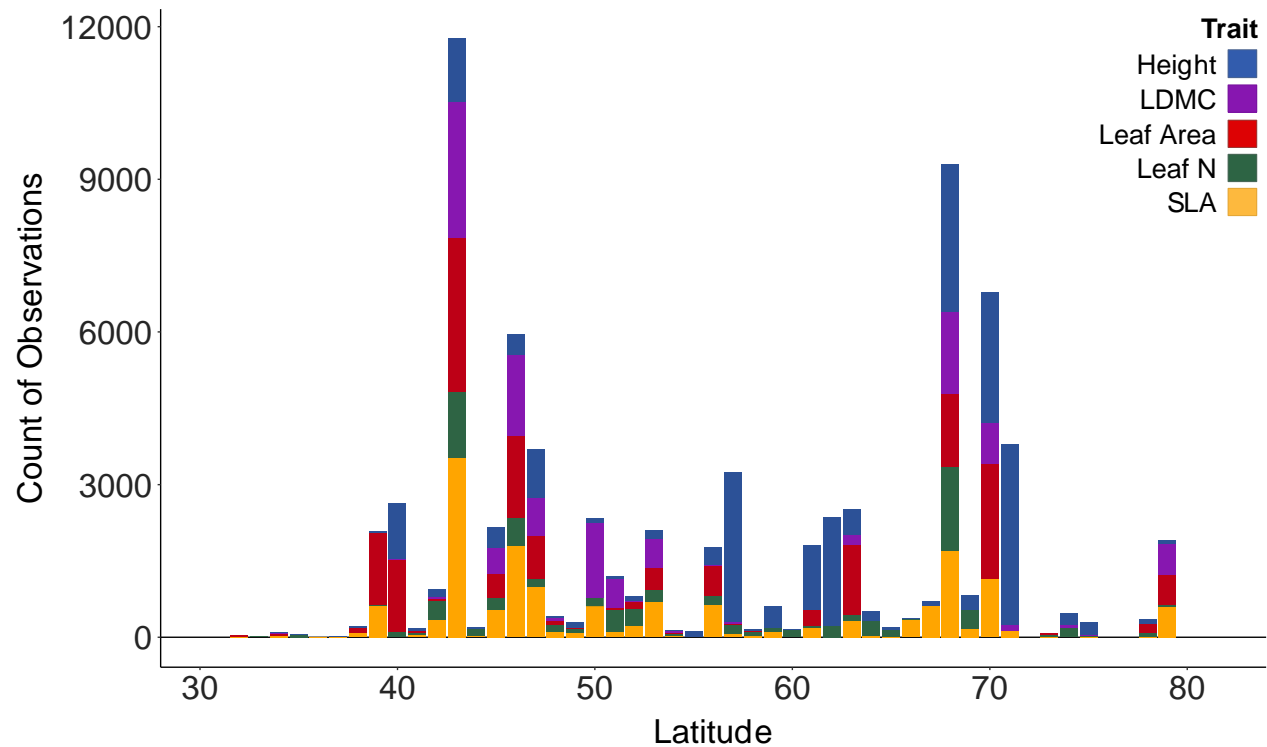
Figure S1. Count of traits per latitude (rounded to the nearest degree) for all georeferenced
observations in TRY and TTT that correspond to species in the vegetation survey dataset.
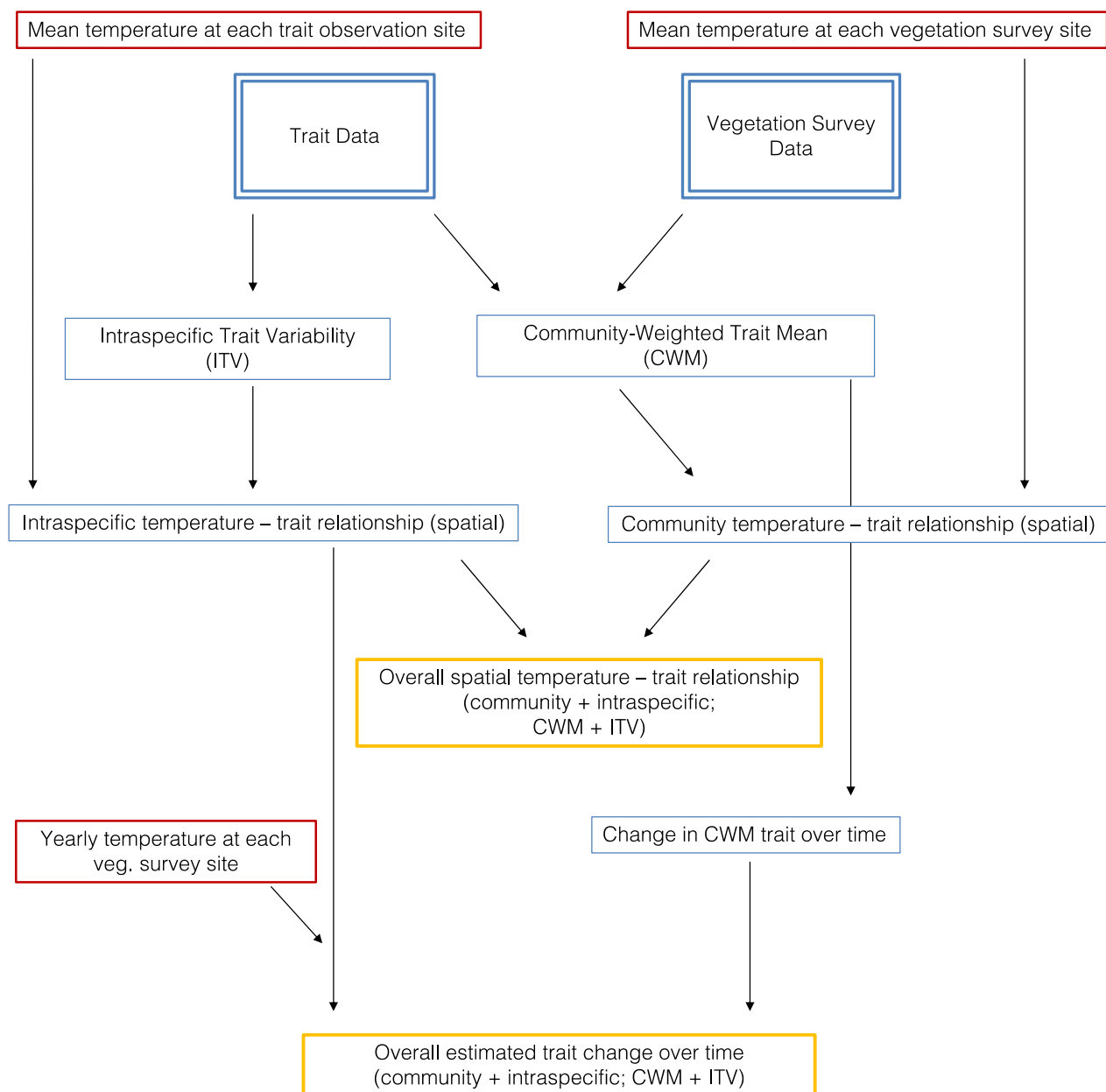
Figure S2. Overview of data, analyses and work flow. Intraspecific temperature-trait relationships over space were used to estimate the potential contribution of ITV to overall temperature-trait relationships over space and time (CWM + ITV) as trait measurements on individuals over time are not available.
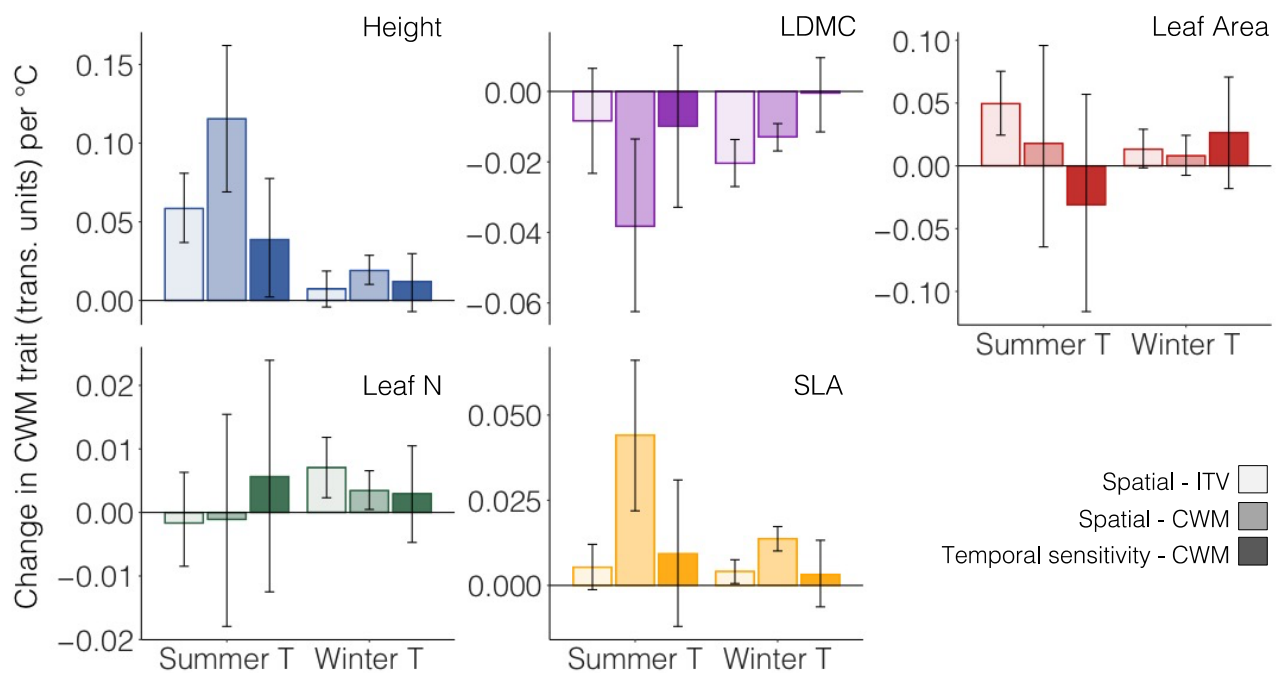
Figure S3. Slope of temperature-trait relationship (log units for all traits but LDMC, logit for LDMC) over space (within-species (ITV) and across communities (CWM)) and with interannual variation in temperature (community temperature sensitivity). Spatial – IPV is the average intraspecific trait variation as related to temperature over space, Spatial – CWM is the relationship between community-weighted trait means and summer temperature, and Temporal sensitivity – CWM is the temperature sensitivity of community-weighted trait means (i.e., correspondence between interannual variation in CWM values with interannual variation in temperature). Error bars represent 95% credible intervals on the slope estimate. We used five-year mean temperatures (temperature of the survey year and four previous years) to estimate temperature sensitivity because this interval has been shown to explain vegetation change in tundra[14] and alpine[15] plant communities. Slope values are in transformed units (inverse logit for LDMC, log for all others).
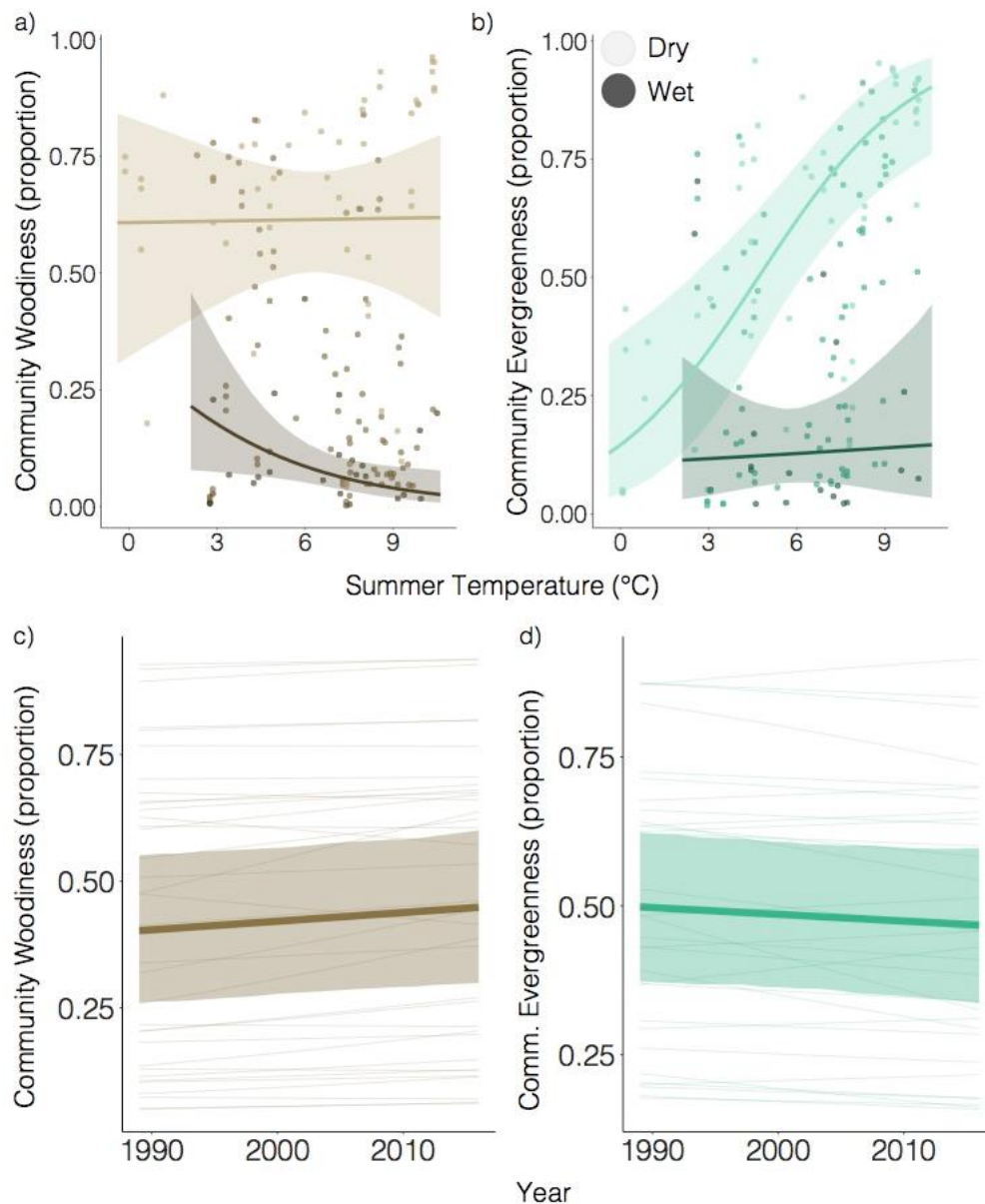
Figure S4. Community woodinesss (a) and evergreenness (b) vary with summer temperature and soil moisture. Community woodiness is the proportion of woody species versus all other plant species in the community. Community evergreenness is the proportion of evergreen shrubs versus all shrub species (deciduous and evergreen). Note that the evergreen model has a reduced number of sites because some sites did not have any woody species (and it was thus not possible to calculate a proportion evergreen). Soil moisture alone was a significant predictor of community woodiness, while both temperature and moisture were significant predictors of community evergreenness. A temperature * moisture interaction was only marginally significant in both models (95% CI on the interaction term: -0.298 to 0.016 and -

0.367 to 0.019 for woodiness and evergreenness, respectively). There was no significant change

over time in woodiness (c) or evergreenness (d).
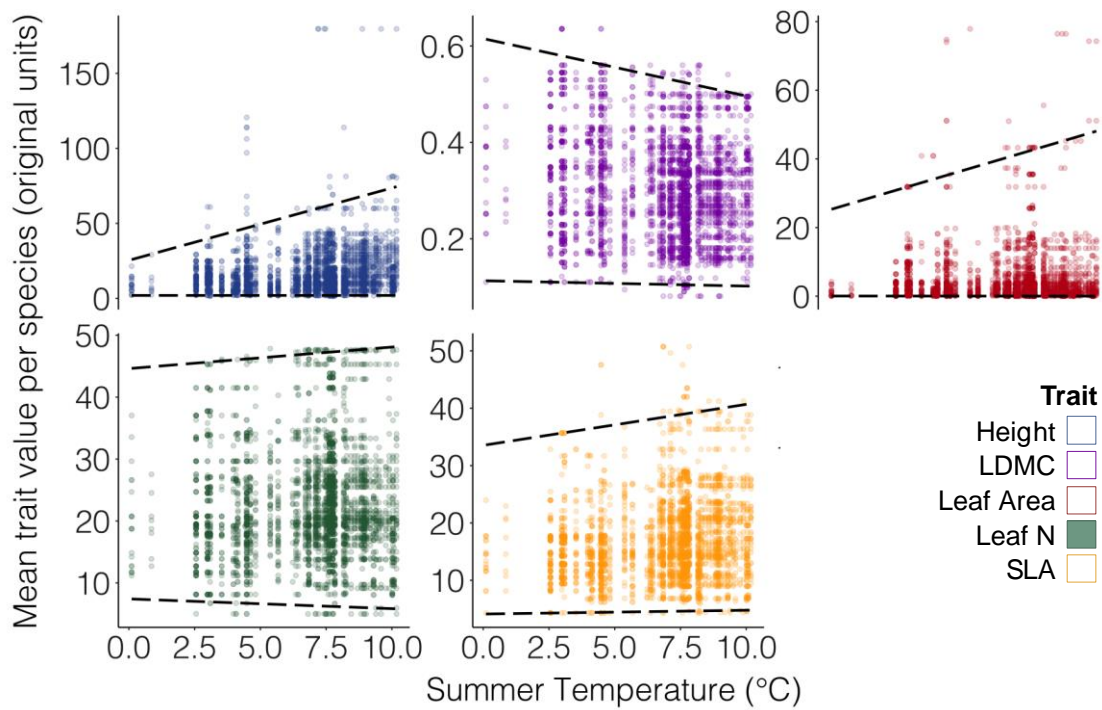
Figure S5. Range in species mean values of each trait by summer temperature. Black dashed lines represent quantile regression estimates for 1% and 99% quantiles. Species mean values are estimated from intercept-only Bayesian models using the estimation technique described in the supplementary methods. All values are back-transformed into their original units (height = cm, LDMC = g/g, leaf area = cm^2, leaf nitrogen = mg/g, SLA = mm^2/mg).
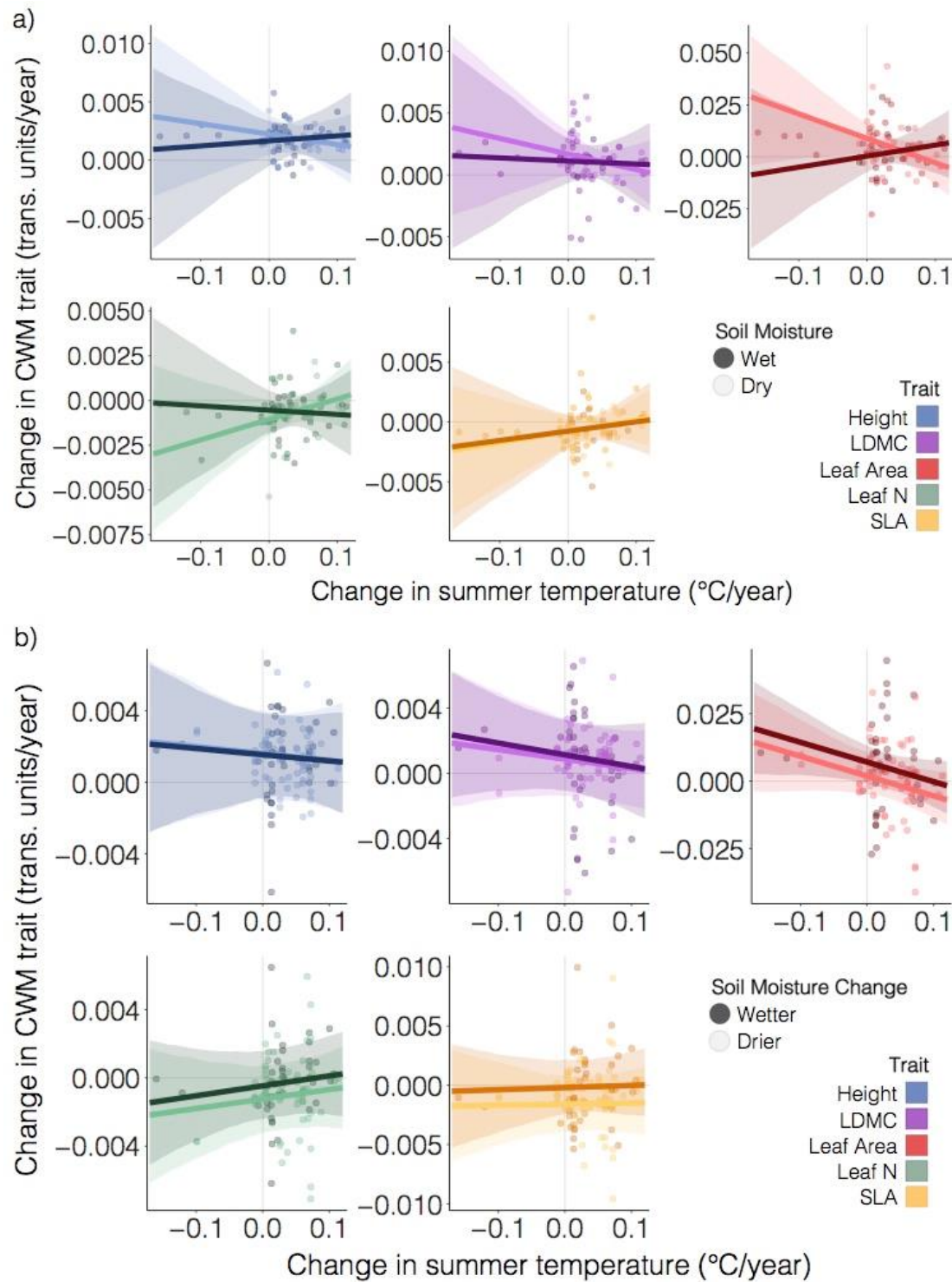
Figure S6. Rate of community-weighted mean change over time per site as related to

temperature change and long-term mean soil moisture (a) or soil moisture change (b) at a site.

The rate of CWM trait change did not vary significantly by temperature change or soil

moisture/soil moisture change for any trait. Points represent mean trait change values for each

site, lines represent the predicted relationship between trait change, temperature change and soil moisture/soil moisture change, and transparent ribbons are the 95% CI's on these predictions. Both mean soil moisture and soil moisture change were modeled as a continuous variables but are shown as predictions for minimum and maximum values/rates of change. Trait change estimates are in transformed units (log for height, leaf area, leaf nitrogen, and SLA, and logit for LDMC).
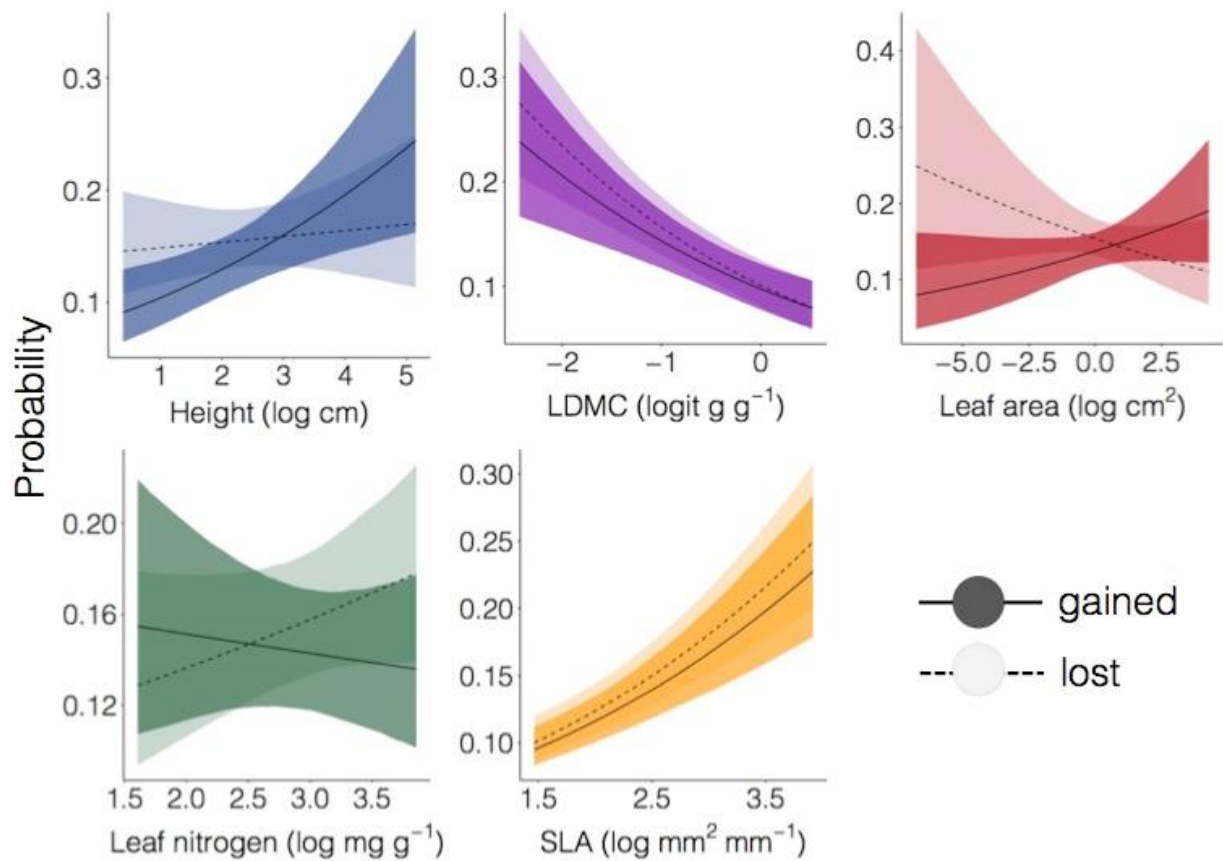
Figure S7. Probability that a species newly arrived in a site ("gained") or disappeared from a site ("lost") as a function of its traits. The probability of gaining a species was significantly related to that species' height (with taller species more likely to gain), but the probability of losing a species was not. Dark ribbons and solid lines represent species gains while pale ribbons and dashed lines represent species losses. Only for plant height was the trait-probability relationship significantly different for gains and losses.
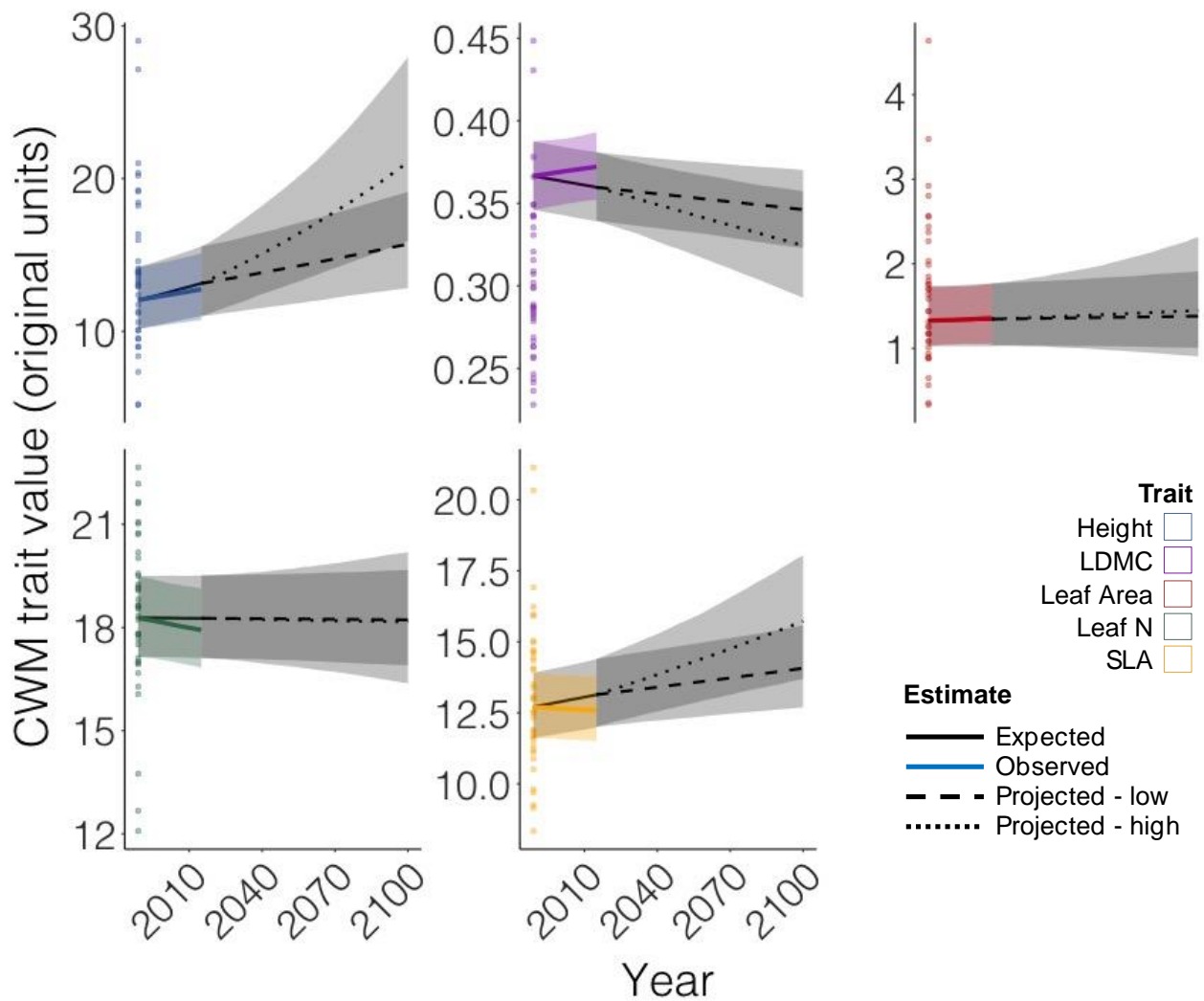
Figure S8. Comparison of the actual (colored lines), expected (solid black lines), and projected (dotted/dashed black lines) CWM trait change over time. Expected trait change is calculated using the observed spatial temperature-trait relationship and the average rate of recent summer warming across all sites. Note that these projections assume no change in soil moisture conditions. The dotted/dashed black lines after 2015 show the projected trait change for the maximum (8.5) and minimum (2.6) IPCC carbon emission scenarios, respectively, from the HadGEM2 AO Global Circulation Model given the expected temperature change associated with those scenarios. Points along the left axis of each panel show the distribution of present-day community-weighted trait means per site. Values are in original units (height = cm, LDMC = g/g, leaf area = cm^2, leaf nitrogen = mg/g, SLA = mm^2/mg).
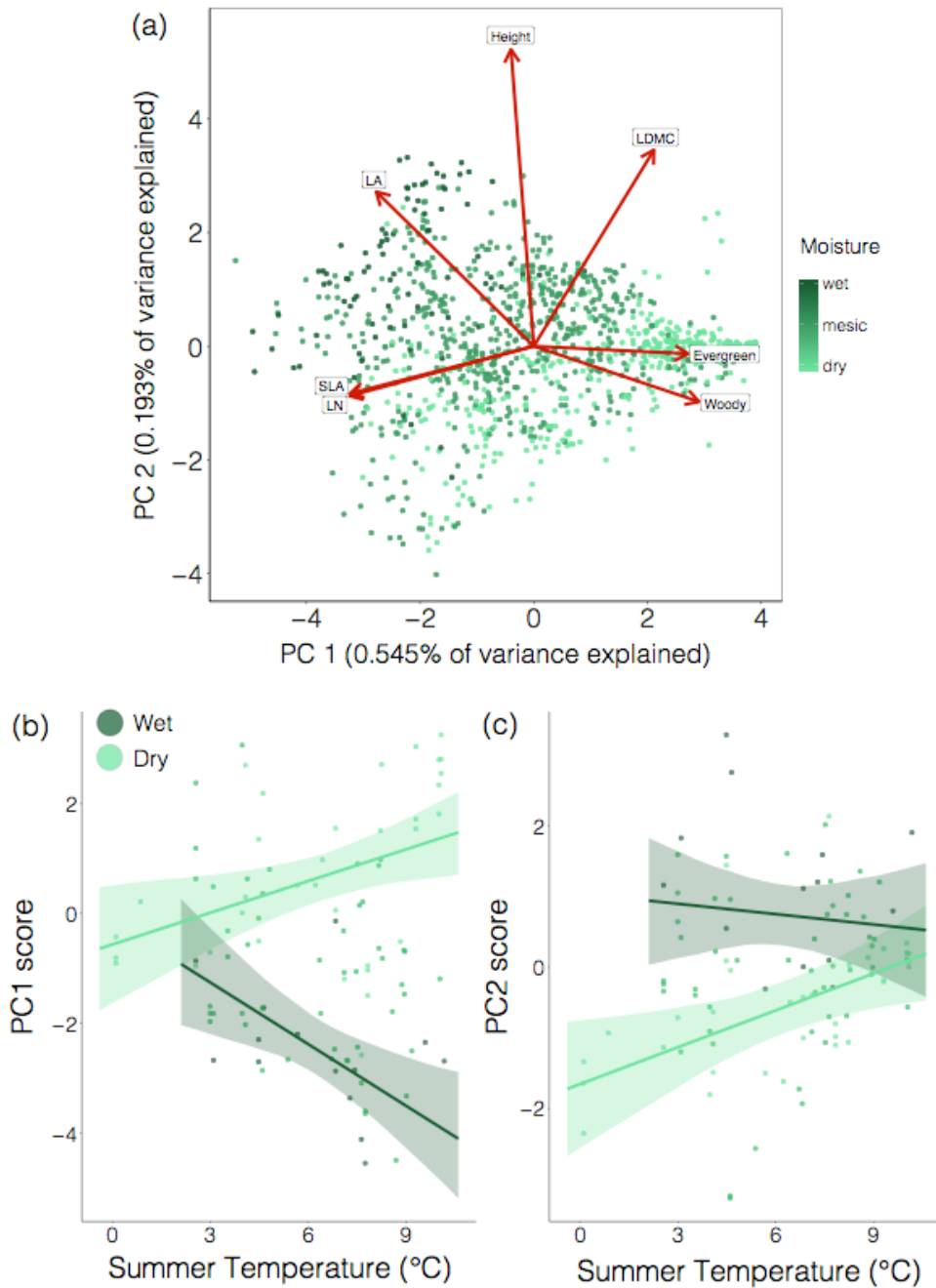
Figure S9. Principal component analysis (a) of plot-level community-weighted traits for the seven key analyzed traits demonstrating how communities vary in multidimensional trait space. Trait correlations are highest for SLA and leaf nitrogen, and evergreenness and woodiness. Variation in SLA, leaf nitrogen, evergreenness and woodiness (PC1) are orthogonal to variation in height (PC2). Variation in leaf area and LDMC are explained by both PC 1 and 2. The color of the points indicates the soil moisture status of each plot at the site-level. PC axis 1 (b) varies significantly with summer temperature, soil moisture, and their interaction

while PC2 varies significantly by soil moisture (c). The color of the points in (b) and (c) indicates the soil moisture of each site. Because not all plots and sites had woody species (and thus proportion evergreen could not be calculated) this analysis was conducted on a subset of 1098 (out of 1520) plots in 98 (out of 117) different sites.
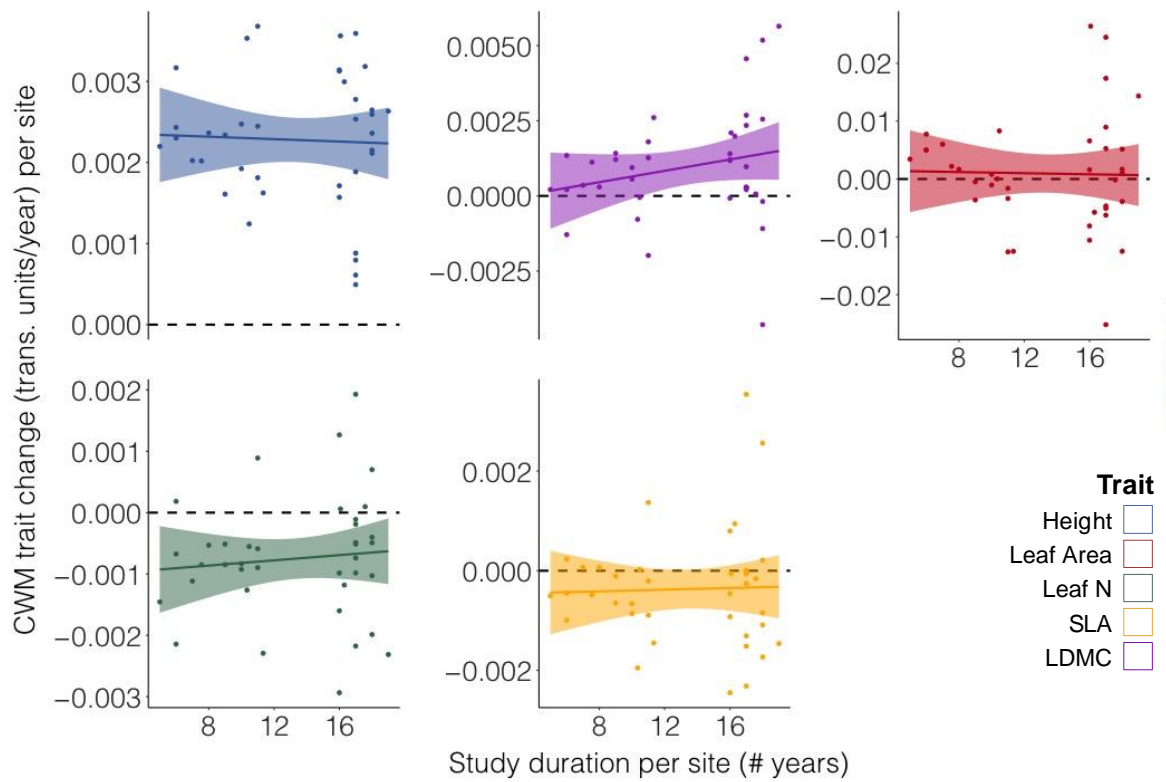
Figure S10. Slope of CWM change at each site vs. the duration of the study at that site. The rate of CWM trait change does not correspond with study duration for any trait. Trait change estimates are in transformed units (log for height, leaf area, leaf nitrogen, and SLA, and logit for LDMC).
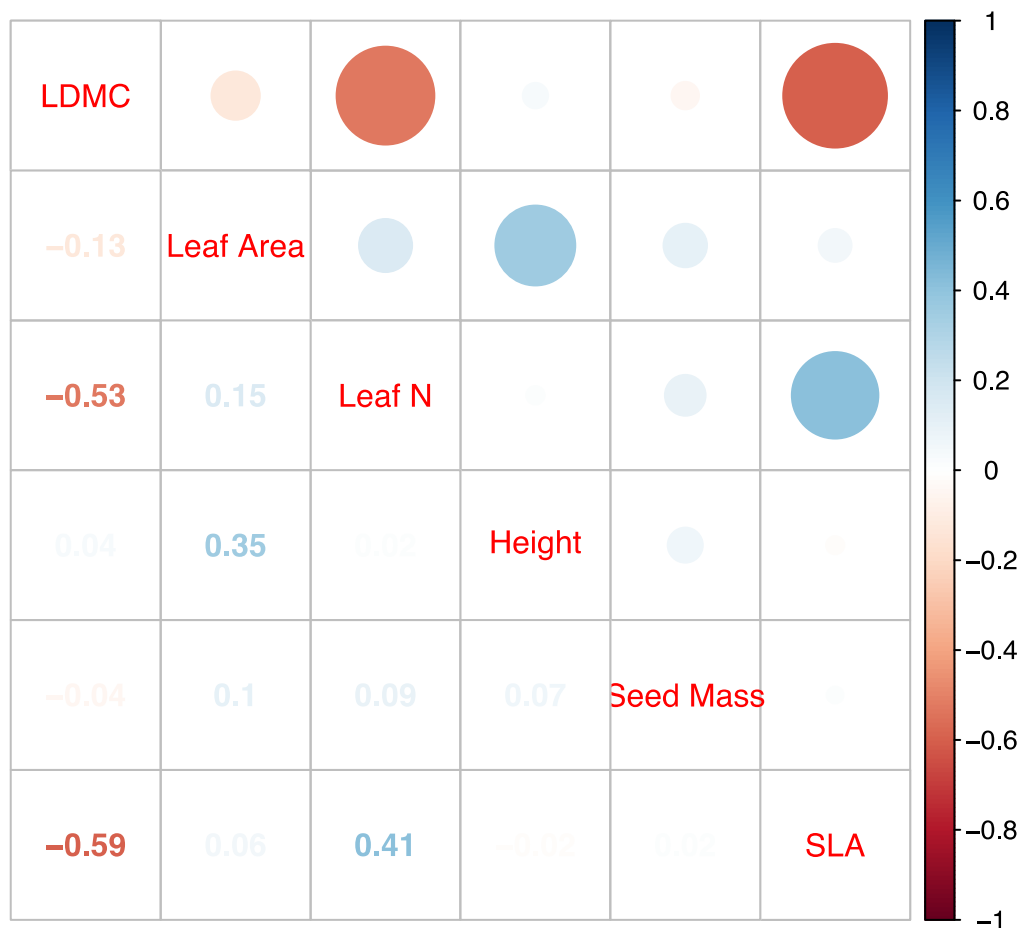
Figure S11. Among-trait correlations (based on species mean values) for all key continuous traits in the analysis. The color and transparency of the correlation numbers indicates the direction and strength, respectively, of the correlations. All trait-trait correlations are below 0.60; however, LDMC, SLA and Leaf N are most highly correlated.
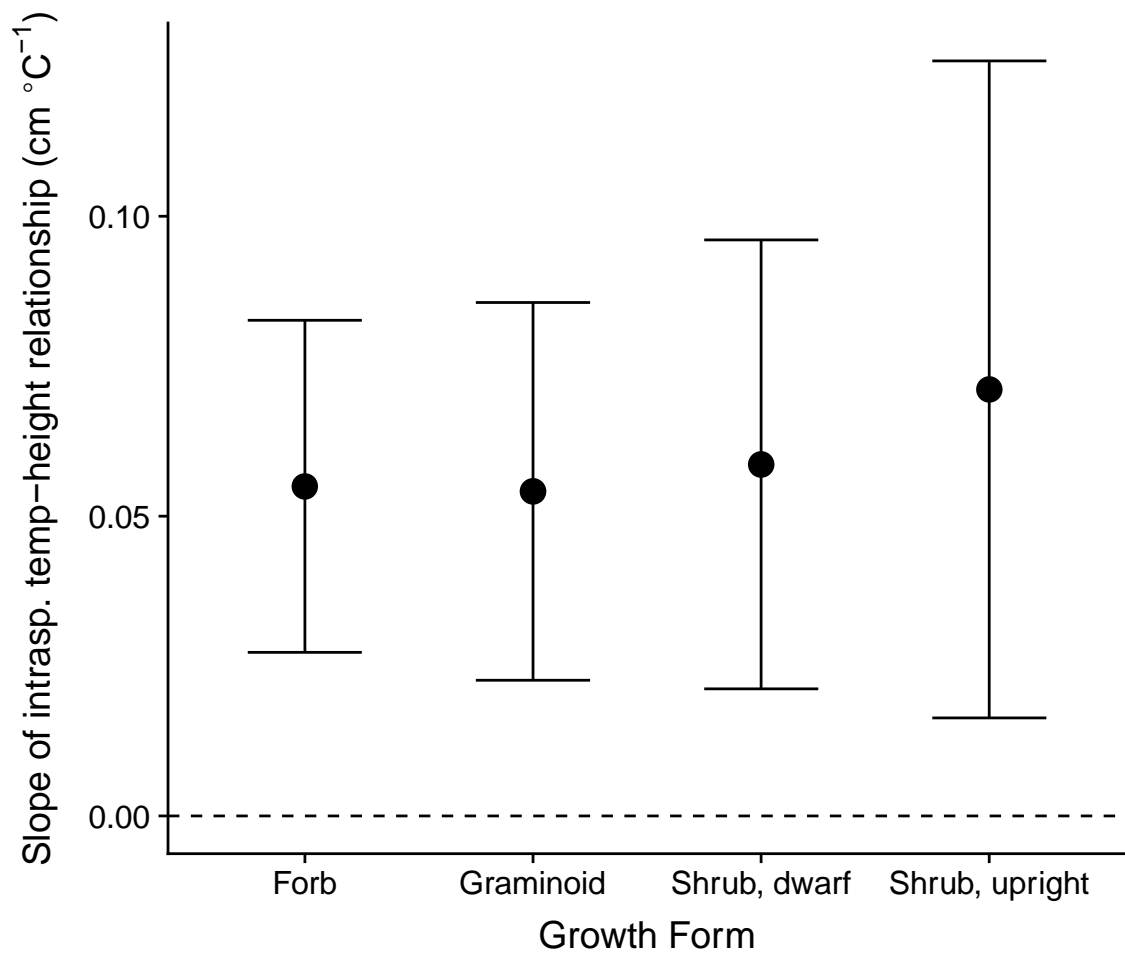
Figure S12. Mean (+/- SD) intraspecific temperature-height relationships per functional group. Dwarf shrubs are defined as those that do not grow above 30 cm in height (as estimated by regional floras: Flora of North America, USDA, Royal Horticultural Society, etc.) and are generally genetically limited in their ability to grow upright. There are no significant differences among functional groups in the magnitude of mean temperature-height relationships.
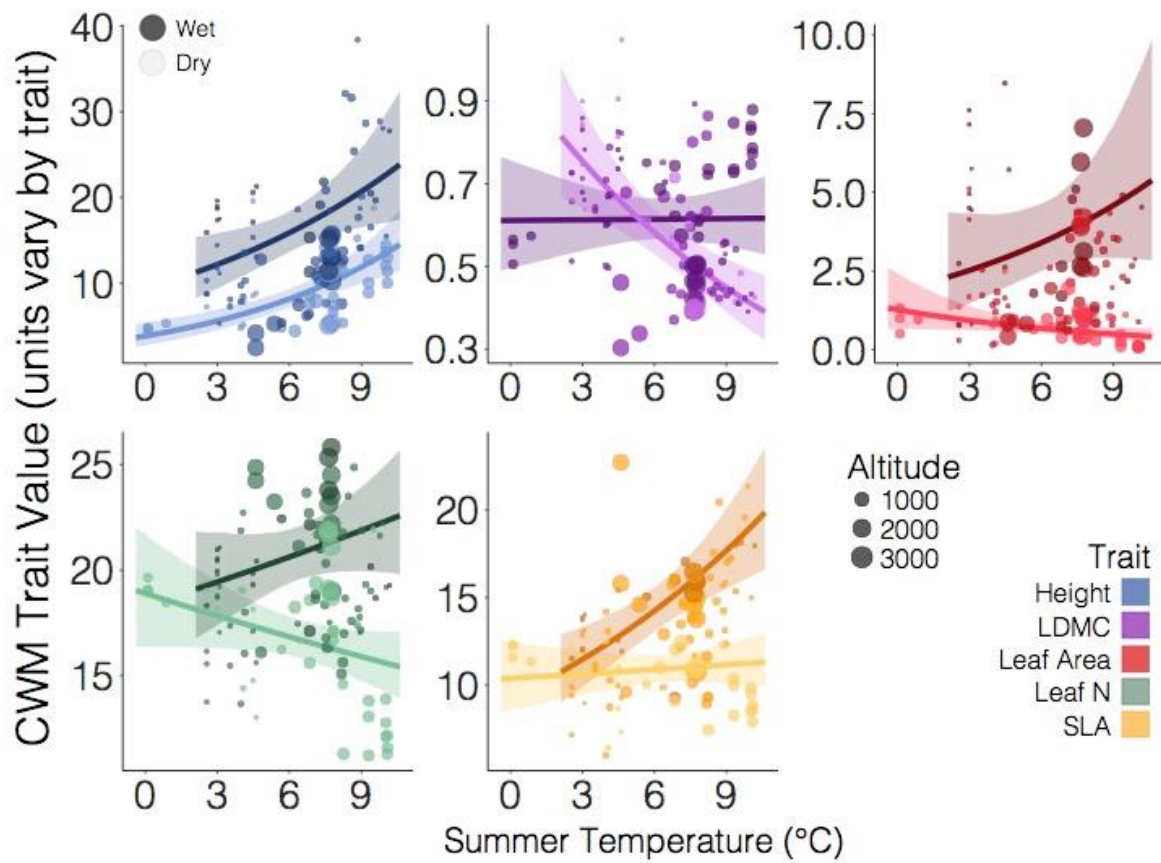
Figure S13. Relationship between community-weighted trait values, summer temperature, and soil moisture across biogeographic gradients. Points represent estimates per site and are sized by the altitude of the site. Ribbons are the overall trait-temperature-moisture relationship across all sites, as in Fig. 2a.

Table S1. Ecosystem functions influenced by each of the seven plant traits investigated here.

Trait	Ecosystem function	Reference
Plant Height	Above ground biomass	(Chapin et al., 1996; Weiher et al., 1999; Lavorel and Garnier, 2002; Violle et al., 2007; Hudson and Henry, 2009)
	Carbon stock	(Lavorel and Garnier, 2002; De Deyn et al., 2008; Moles et al., 2009; Sistla et al., 2013)
	Light Capture	(Moles et al., 2009)
	Competition	(Lavorel and Garnier, 2002) (Kunstler et al., 2016)
	Seed dispersal	(Gaudet and Keddy, 1988) (Westoby et al., 2002) (Moles et al., 2009) (Moles & Leishman 2008)
	Albedo	(Sturm et al., 2001; Sturm, 2005; Loranty et al., 2014)
	Snow cover	(Sturm et al., 2001; Myers-Smith and Hik, 2013;

		DeMarco et al., 2014)
		(Lavorel and Garnier, 2002)
	Disturbance response	(Enquist et al. 1998)
	Maximum population density	
Leaf Area	Above ground biomass	(Street et al., 2007; Poorter et al., 2012; Greaves et al., 2015)
	Albedo	(Westoby and Wright, 2006)
	Light interception	(Niinemets, 2010; Díaz et al., 2016)
	Leaf water balance	(Díaz et al., 2016)
	Leaf energy balance	(Díaz et al., 2016)
Specific Leaf Area	Relative growth rate	(Weiher et al., 1999; Wright et al., 2004; Reich, 2014)
	Decomposition	(Lavorel and Garnier, 2002; Diaz et al., 2004; Cornelissen et al., 2007; Cornwell et al., 2008; Freschet et al., 2012)
	Leaf life span	(Reich, 2014)
		(Wright et al., 2004)
		(Diaz et al., 2004)
Leaf Nitrogen	Decomposition	(Lavorel and Garnier, 2002; Cornelissen et al., 2007; Cornwell et al., 2008; Freschet et al., 2012)

	Primary productivity	(Weiher et al., 1999; Wright et al., 2004; Reich, 2014)
Leaf Dry Matter Content	Decomposition	(Lavorel and Garnier, 2002; Cornelissen et al., 2007; Cornwell et al., 2008; Freschet et al., 2012)
Seed Mass	Regeneration time Dispersal ability Colonisation potential	(Lavorel and Garnier, 2002) (Westoby et al., 1992, 2002) (Thompson, 1987)
Woodiness	Plant architecture Albedo Thermal insulation Decomposition Carbon storage	(Chapin et al., 1996; Iida et al., 2012) (Sturm et al., 2001; Ménard et al., 2014) (Blok et al., 2010; Myers-Smith and Hik, 2013; Nauta et al., 2014) (Hobbie, 1996; Cornelissen et al., 2007; Weedon et al., 2009) (Hobbie, 1996; Myers-Smith et al., 2011; Sistla et al., 2013)
Evergreenness	Decomposition	(Dorrepaal et al., 2005; Cornelissen et al., 2007; Cornwell et al., 2008)

	Nutrient cycling	(Larsen et al., 2012)
	Relative growth rate	(Chapin et al., 1995; Reich et al., 1997)

Table S2. Number of observations per trait overall and with latitude/longitude information. The minimum and mean percent of species per site with at least one trait observation, and the minimum and mean percent cover (abundance) of species per site with at least one trait observation. The maximum % species and % cover is 100 for all traits.

Trait	Num. of observations	Num. obs. w/ coordinates	% species (min)	% species (mean)	% cover (min)	% cover (mean)
Height	23248	22129	48	95.2	38	96.8
LDMC	7331	7123	19	74.2	6	83.3
Leaf Area	10681	10445	20	83.4	10	91.0
Leaf N	4334	3852	29	71.7	30	87.0
SLA	10454	9651	20	77.9	10	87.4

Table S3. Site names, survey duration, and coordinates. Region represents a unique CRU grid cell (0.5 degree grid).

Region	Site Name	Duration (years)	Latitude	Longitude
1	AKUREYRI:GA66	18	65.59	-17.97
2	AKUREYRI:HR58	18	65.56	-18.16
2	AKUREYRI:MD72	18	65.51	-18.08
2	AKUREYRI:SY59	18	65.51	-18.23
2	MODRUVELLIR:LH69	18	65.94	-18.11
2	MODRUVELLIR:ML54	18	65.74	-18.22
2	MODRUVELLIR:MV51	18	65.78	-18.27
2	MODRUVELLIR:MV52	18	65.77	-18.28
3	AKUREYRI:SB63	18	65.45	-18.24
4	ALEXFIORD:CASSIOPE	13	78.87	-75.78
4	ALEXFIORD:DOMEDOLOMITE	14	78.86	-75.9
4	ALEXFIORD:DOMEGRANITE	14	78.86	-75.9
4	ALEXFIORD:DRYAS	21	78.87	-75.78
4	ALEXFIORD:FERT	16	78.87	-75.79
4	ALEXFIORD:LEVDOLOMITE	18	78.86	-75.9
4	ALEXFIORD:MEADOW	16	78.88	-75.81
4	ALEXFIORD:WILLOW	21	78.87	-75.8
5	ANWR:ATIGUN-A	11	68.47	-149.35
5	ANWR:ATIGUN-B	11	68.48	-149.35
5	ANWR:ATIGUN-C	11	68.45	-149.32
6	ANWR:JAGO-A	10	69.7	-143.63
6	ANWR:JAGO-B	10	69.71	-143.62
7	ATQASUK:AD	16	70.45	-157.41
7	ATQASUK:AG	5	70.45	-157.4
7	ATQASUK:AW	16	70.45	-157.4
7	ATQASUK:RATE_BETULA_SHRUB	10	70.46	-157.41
7	ATQASUK:RATE_CAREX_ WET_MEADOW	10	70.46	-157.41
7	ATQASUK:RATE_DRYAS_HEATH	10	70.46	-157.41
7	ATQASUK:RATE_ERIOPHORUM_WET_MEADOW	10	70.46	-157.41
7	ATQASUK:RATE_HIEROCHLOE_DRY_MEADOW	10	70.46	-157.41
8	AUDKULUHEIDI:BETULAHEATH	12	65.22	-19.71
9	BARROW:ARCTOPHILA_POND_ORDINATION	10	71.29	-156.64
9	BARROW:BD	18	71.32	-156.6

9	BARROW:BG	5	71.31	-156.59
9	BARROW:BW	17	71.31	-156.6
9	BARROW:CAREX WET MEADOW_ORDINATION	10	71.29	-156.64
9	BARROW:CAREX_MESIC MEADOW_ORDINATION	10	71.29	-156.64
9	BARROW:CAREX_MOIST MEADOW_ORDINATION	10	71.29	-156.64
9	BARROW:CAREX_MOIST_MEADOW_MICROTOPO	10	71.29	-156.64
9	BARROW:CAREX_WET_MEADOW_MICROTOPO	10	71.29	-156.64
9	BARROW:DRY_HEATH_ORDINATION	10	71.29	-156.64
9	BARROW:DUPONTIA_WET_MEADOW_MICROTOP	10	71.29	-156.64
10	BLONDUOS:SD33	19	65.5	-20.23
10	BLONDUOS:SD34	19	65.5	-20.23
11	BROOKS:SHEEN-B	11	68.57	-143.72
12	BYLOT:MESPOLYGON	7	73.15	-79.95
12	BYLOT:MESPRAIRIE	7	73.15	-79.95
13	DALSMYNNI:AG4	9	65.78	-19.31
13	DALSMYNNI:KD24	9	65.77	-19.03
13	DALSMYNNI:KD25	19	65.77	-19.04
13	DALSMYNNI:KK5	9	65.8	-19.36
14	DOVRE:KUNTSHOE	10	62.3	9.62
15	ENDALEN:BIS-H	7	78.19	15.74
15	ENDALEN:BIS-L	7	78.19	15.74
15	ENDALEN:CAS-H	7	78.19	15.74
15	ENDALEN:CAS-L	7	78.19	15.74
15	ENDALEN:DRY-H	7	78.19	15.74
15	ENDALEN:DRY-L	7	78.19	15.74
16	FURI:FURI4	17	61.64	12.64
16	FURI:FURI5	17	61.64	12.64
16	FURI:FURI6	17	61.64	12.64
17	GAVIA:POL	7	46.34	10.5
17	GAVIA:SAL	7	46.34	10.5
18	HJARDARLAND:HA75	18	64.07	-20.27
18	HJARDARLAND:HF73	18	64.04	-20.28
19	HJARDARLAND:LH92	18	64.22	-20.6
20	HJARDARLAND:SH90	8	63.98	-20.57
21	HOLTAVORDUHEIDI:AH36	19	65.08	-20.55
21	HOLTAVORDUHEIDI:AH37	19	65.07	-20.58
21	HOLTAVORDUHEIDI:AH38	19	65.08	-20.59
22	HOLTAVORDUHEIDI:VH49	19	65.23	-20.44

22	HOLTAVORDUHEIDI:VH50	19	65.24	-20.45
23	KLUANE:PIKA	12	61.22	-138.27
24	KYTALYK:LAKEBED	6	70.83	147.48
25	LATNJA:DRY_HEATH	14	68.36	18.5
25	LATNJA:DRY_MEADOW	19	68.36	18.5
25	LATNJA:TUSSOCK_TUNDRA	20	68.36	18.49
25	LATNJA:WET_SEDGE	14	68.36	18.49
26	LOGH:LOGH2	17	62.1	12.34
26	LOGH:LOGH4	17	62.1	12.34
26	LOGH:LOGH5	17	62.1	12.34
26	LORI:LORI1	17	62.12	12.27
26	LORI:LORI3	17	62.12	12.27
26	LORI:LORI4	17	62.12	12.27
27	NIWOT:BARREN_SADDLE	8	40.05	-105.59
27	NIWOT:DRY MEADOW_SADDLE	8	40.05	-105.59
27	NIWOT:FELLFIELD_SADDLE	8	40.05	-105.59
27	NIWOT:KLEIN	8	40.05	-105.59
27	NIWOT:MOIST MEADOW_SADDLE	8	40.05	-105.59
27	NIWOT:ORDINATION_DRYMEADOW	11	40.05	-105.59
27	NIWOT:ORDINATION_FELLFIELD	11	40.05	-105.59
27	NIWOT:ORDINATION_MOISTMEADOW	11	40.05	-105.59
27	NIWOT:ORDINATION_MOISTSHRUB	11	40.05	-105.59
27	NIWOT:ORDINATION_SNOWBANK	11	40.05	-105.59
27	NIWOT:ORDINATION_WETMEADOW	11	40.05	-105.59
27	NIWOT:SNOW BANK_SADDLE	8	40.05	-105.59
27	NIWOT:WET MEADOW_SADDLE	8	40.05	-105.59
28	OXNADALSHEIDI:SA16	19	65.47	-18.7
28	OXNADALSHEIDI:SA17	19	65.47	-18.69
28	OXNADALSHEIDI:SA19	19	65.48	-18.9
29	QHI:HE	17	69.57	-138.86
29	QHI:KO	17	69.58	-138.87
30	RIRI:RIRI2	17	67.77	17.54
30	RIRI:RIRI4	17	67.77	17.54
30	RIRI:RIRI6	17	67.77	17.54
31	SVERDRUP:SVERDRUP	18	79.14	-79.62
32	THINGVELLIR:MOSS HEATH	12	64.28	-21.07
33	THYKKVIBAER:HH100	18	63.56	-20.17
34	THYKKVIBAER:RT81	18	63.99	-21.16

34	THYKKVIBAER:VE82	18	63.97	-21.17
35	TOOLIK:DRY	14	68.62	-149.61
35	TOOLIK:MOIST	15	68.62	-149.61
35	TOOLIK:TUSSOCKGRID	19	68.62	-149.61
36	TOOLIK:IMNAVAIT	19	68.62	-149.28
37	TORNGATS:NAKVAKDRY	9	58.64	-63.38
37	TORNGATS:NAKVAKWET	9	58.64	-63.38
38	VALBERCLA:ALPINE	20	46.48	9.58

Table S4. Model output for **interspecific** spatial temperature-trait relationships. Bolded rows designate interspecific temperature-trait relationships (slope parameter) for which the 95% credible interval did not cross zero (i.e., the relationship is "significant"). The estimate type indicates the response variable: CWM = community weighted mean (turnover + abundance), NWM = non-weighted mean (due to turnover only), CWM+ITV = the community weighted mean with estimated intraspecific temperature-trait relationships included (see Methods). Climate variable indicates which temperature type was used (bio 10 = summer temperature, bio 11 = winter temperature). Temperature was centered to improve model convergence; thus, the intercept parameter represents the trait value at approximately 6.88 °C for bio 10 and -13.5 °C for bio 11.

Trait	Climate Variable	Estimate Type	Parameter	mean	sd	2.5%	97.5%
Height	10	CWM	Intercept	2.546	0.057	2.434	2.655
Height	10	CWM+ITV	Intercept	2.687	0.054	2.582	2.796
Height	10	NWM	Intercept	2.515	0.042	2.430	2.590
Height	**10**	**CWM**	**Slope**	**0.115**	**0.023**	**0.069**	**0.162**
Height	**10**	**CWM+ITV**	**Slope**	**0.131**	**0.023**	**0.086**	**0.176**
Height	**10**	**NWM**	**Slope**	**0.083**	**0.017**	**0.050**	**0.117**
LDMC	10	CWM	Intercept	-0.549	0.030	-0.608	-0.490
LDMC	10	CWM+ITV	Intercept	-0.576	0.028	-0.631	-0.519
LDMC	10	NWM	Intercept	-0.700	0.031	-0.762	-0.640
LDMC	**10**	**CWM**	**Slope**	**-0.038**	**0.012**	**-0.062**	**-0.013**
LDMC	**10**	**CWM+ITV**	**Slope**	**-0.043**	**0.012**	**-0.066**	**-0.019**
LDMC	**10**	**NWM**	**Slope**	**-0.033**	**0.013**	**-0.059**	**-0.007**
Leaf Area	10	CWM	Intercept	0.446	0.103	0.263	0.649
Leaf Area	10	CWM+ITV	Intercept	0.605	0.102	0.406	0.802
Leaf Area	10	NWM	Intercept	0.394	0.072	0.250	0.537
Leaf Area	10	CWM	Slope	0.018	0.041	-0.065	0.096
Leaf Area	10	CWM+ITV	Slope	0.025	0.043	-0.058	0.111
Leaf Area	10	NWM	Slope	0.006	0.031	-0.055	0.070
Leaf N	10	CWM	Intercept	2.920	0.020	2.880	2.960
Leaf N	10	CWM+ITV	Intercept	2.917	0.020	2.878	2.956
Leaf N	10	NWM	Intercept	2.985	0.020	2.947	3.025
Leaf N	10	CWM	Slope	-0.001	0.009	-0.018	0.015
Leaf N	10	CWM+ITV	Slope	-0.001	0.008	-0.017	0.016

Trait	Climate Variable	Estimate Type	Parameter	mean	sd	2.5%	97.5%
Leaf N	10	NWM	Slope	0.009	0.008	-0.007	0.026
SLA	10	CWM	Intercept	2.559	0.027	2.505	2.611
SLA	10	CWM+ITV	Intercept	2.581	0.027	2.529	2.634
SLA	10	NWM	Intercept	2.635	0.023	2.587	2.680
SLA	**10**	**CWM**	**Slope**	**0.044**	**0.011**	**0.022**	**0.066**
SLA	**10**	**CWM+ITV**	**Slope**	**0.051**	**0.011**	**0.028**	**0.073**
SLA	**10**	**NWM**	**Slope**	**0.037**	**0.010**	**0.017**	**0.057**
Height	11	CWM	Intercept	2.541	0.058	2.425	2.656
Height	11	CWM+ITV	Intercept	2.599	0.057	2.484	2.708
Height	11	NWM	Intercept	2.542	0.040	2.464	2.623
Height	**11**	**CWM**	**Slope**	**0.019**	**0.005**	**0.010**	**0.029**
Height	**11**	**CWM+ITV**	**Slope**	**0.020**	**0.005**	**0.011**	**0.029**
Height	**11**	**NWM**	**Slope**	**0.015**	**0.003**	**0.009**	**0.022**
LDMC	11	CWM	Intercept	-0.616	0.025	-0.666	-0.568
LDMC	11	CWM+ITV	Intercept	-0.872	0.032	-0.933	-0.810
LDMC	11	NWM	Intercept	-0.758	0.034	-0.825	-0.692
LDMC	**11**	**CWM**	**Slope**	**-0.013**	**0.002**	**-0.017**	**-0.009**
LDMC	**11**	**CWM+ITV**	**Slope**	**-0.017**	**0.003**	**-0.022**	**-0.012**
LDMC	**11**	**NWM**	**Slope**	**-0.021**	**0.003**	**-0.027**	**-0.016**
Leaf Area	11	CWM	Intercept	0.457	0.098	0.262	0.643
Leaf Area	11	CWM+ITV	Intercept	0.562	0.101	0.364	0.749
Leaf Area	11	NWM	Intercept	0.572	0.079	0.416	0.727
Leaf Area	11	CWM	Slope	0.008	0.008	-0.008	0.024
Leaf Area	11	CWM+ITV	Slope	0.006	0.008	-0.010	0.022
Leaf Area	11	NWM	Slope	-0.007	0.006	-0.020	0.005
Leaf N	11	CWM	Intercept	2.919	0.019	2.881	2.956
Leaf N	11	CWM+ITV	Intercept	2.949	0.019	2.912	2.987
Leaf N	11	NWM	Intercept	2.997	0.019	2.962	3.033
Leaf N	**11**	**CWM**	**Slope**	**0.003**	**0.002**	**0.000**	**0.007**
Leaf N	**11**	**CWM+ITV**	**Slope**	**0.004**	**0.002**	**0.001**	**0.007**
Leaf N	**11**	**NWM**	**Slope**	**0.005**	**0.002**	**0.002**	**0.008**
SLA	11	CWM	Intercept	2.562	0.022	2.520	2.605
SLA	11	CWM+ITV	Intercept	2.596	0.021	2.555	2.635
SLA	11	NWM	Intercept	2.653	0.019	2.621	2.690
SLA	**11**	**CWM**	**Slope**	**0.014**	**0.002**	**0.010**	**0.017**
SLA	**11**	**CWM+ITV**	**Slope**	**0.014**	**0.002**	**0.010**	**0.017**
SLA	**11**	**NWM**	**Slope**	**0.012**	**0.001**	**0.009**	**0.015**

Table S5. Model output for **interspecific** spatial relationships with both temperature and soil moisture. Bolded rows designate predictors of community weighted trait means (CWM) for which the credible interval did not cross zero (i.e., the relationship is "significant"). All estimates are for summer temperature only (bio 10). Temperature and soil moisture values were centered to improve model convergence; thus, the intercept parameter represents the trait value at approximately 6.88 °C and "mesic" soil moisture.

Trait	Climate Variable	Paramter	mean	sd	2.5%	97.5%
Height	10	Intercept	2.527	0.048	2.435	2.620
Height	**10**	**Moisture**	**0.316**	**0.055**	**0.210**	**0.425**
Height	**10**	**Temperature**	**0.106**	**0.020**	**0.066**	**0.146**
Height	10	Temperature*Moisture	-0.018	0.021	-0.060	0.023
LDMC	10	Intercept	-0.553	0.029	-0.609	-0.497
LDMC	10	Moisture	-0.066	0.035	-0.132	0.003
LDMC	**10**	**Temperature**	**-0.043**	**0.012**	**-0.066**	**-0.018**
LDMC	**10**	**Temperature*Moisture**	**-0.044**	**0.013**	**-0.070**	**-0.017**
Leaf Area	10	Intercept	0.415	0.089	0.243	0.591
Leaf Area	**10**	**Moisture**	**0.896**	**0.118**	**0.668**	**1.126**
Leaf Area	10	Temperature	-0.002	0.037	-0.075	0.072
Leaf Area	**10**	**Temperature*Moisture**	**0.102**	**0.043**	**0.015**	**0.187**
Leaf N	10	Intercept	2.925	0.019	2.889	2.962
Leaf N	**10**	**Moisture**	**0.118**	**0.023**	**0.073**	**0.162**
Leaf N	10	Temperature	0.000	0.008	-0.016	0.016
Leaf N	**10**	**Temperature*Moisture**	**0.019**	**0.009**	**0.001**	**0.038**
SLA	10	Intercept	2.558	0.025	2.509	2.606
SLA	**10**	**Moisture**	**0.162**	**0.033**	**0.096**	**0.228**
SLA	**10**	**Temperature**	**0.040**	**0.010**	**0.020**	**0.061**
SLA	**10**	**Temperature*Moisture**	**0.032**	**0.013**	**0.007**	**0.056**
Woodiness	10	Intercept	-1.067	0.178	-1.409	-0.715
Woodiness	10	Moisture	-0.135	0.070	-0.272	0.003
Woodiness	**10**	**Temperature**	**-1.534**	**0.190**	**-1.918**	**-1.168**
Woodiness	10	Temperature*Moisture	-0.139	0.077	-0.289	0.016
Evergreenness	10	Intercept	-0.599	0.199	-1.005	-0.220
Evergreenness	**10**	**Moisture**	**0.205**	**0.083**	**0.043**	**0.366**
Evergreenness	**10**	**Temperature**	**-1.304**	**0.259**	**-1.809**	**-0.790**
Evergreenness	10	Temperature*Moisture	-0.171	0.100	-0.367	0.019

Table S6. Model output for **intraspecific** spatial temperature-trait relationships. Bolded rows designate intraspecific temperature-trait relationships (slope parameter) for which the 95% credible interval did not cross zero (i.e., the relationship is "significant"). Climate variable indicates which temperature type was used (bio 10 = summer temperature, bio 11 = winter temperature). Temperature was centered within each species to improve model convergence. The "Intercept Temp" column indicates the mean temperature at the intercept for each trait and climate variable.

Trait	Climate Variable	Estimate Type	Parameter	Intercept Temp (°C)	mean	sd	2.5%	97.5%
Height	10	ITV	Intercept	9.71	2.675	0.102	2.471	2.867
Height	**10**	**ITV**	**Slope**		**0.059**	**0.011**	**0.037**	**0.081**
LDMC	10	ITV	Intercept	10.70	-0.767	0.085	-0.932	-0.596
LDMC	10	ITV	Slope		-0.008	0.007	-0.023	0.007
Leaf Area	10	ITV	Intercept	10.61	0.547	0.172	0.211	0.885
Leaf Area	**10**	**ITV**	**Slope**		**0.050**	**0.013**	**0.024**	**0.075**
Leaf N	10	ITV	Intercept	11.19	2.983	0.045	2.896	3.066
Leaf N	10	ITV	Slope		-0.002	0.004	-0.008	0.006
SLA	10	ITV	Intercept	10.93	2.743	0.045	2.656	2.832
SLA	10	ITV	Slope		0.005	0.003	-0.001	0.012
Height	11	ITV	Intercept	-12.82	2.645	0.101	2.453	2.845
Height	11	ITV	Slope		0.007	0.006	-0.004	0.019
LDMC	11	ITV	Intercept	-12.22	-0.750	0.070	-0.890	-0.620
LDMC	**11**	**ITV**	**Slope**		**-0.020**	**0.003**	**-0.027**	**-0.014**
Leaf Area	11	ITV	Intercept	-10.50	0.615	0.173	0.265	0.936
Leaf Area	11	ITV	Slope		0.013	0.008	-0.002	0.029
Leaf N	11	ITV	Intercept	-9.69	2.977	0.047	2.888	3.063
Leaf N	**11**	**ITV**	**Slope**		**0.007**	**0.002**	**0.002**	**0.012**
SLA	11	ITV	Intercept	-9.83	2.744	0.045	2.660	2.835
SLA	**11**	**ITV**	**Slope**		**0.004**	**0.002**	**0.001**	**0.008**

Table S7. Model output for **interspecific** trait change over time. Bolded rows designate slope parameters (change over time) for which the 95% credible interval did not cross zero (i.e., the relationship is "significant"). The estimate type indicates the response variable: CWM = community weighted mean (turnover + abundance), NWM = non-weighted mean (due to turnover only), CWM+ITV = the community weighted mean with estimated intraspecific temperature-trait relationships included (see Methods). CWM+ITV was estimated based on summer temperature change only (bio 10).

Trait	Climate Variable	Estimate Type	Parameter	mean	sd	2.5%	97.5%
Height	-	CWM	Intercept	2.514	0.087	2.341	2.683
Height	10	CWM+ITV	Intercept	2.691	0.087	2.514	2.858
Height	-	NWM	Intercept	2.495	0.072	2.357	2.635
Height	**-**	**CWM**	**Slope**	**0.002**	**0.001**	**0.000**	**0.004**
Height	**10**	**CWM+ITV**	**Slope**	**0.004**	**0.001**	**0.002**	**0.006**
Height	**-**	**NWM**	**Slope**	**0.002**	**0.001**	**0.001**	**0.004**
LDMC	-	CWM	Intercept	-0.535	0.045	-0.624	-0.446
LDMC	10	CWM+ITV	Intercept	-0.569	0.041	-0.649	-0.489
LDMC	-	NWM	Intercept	-0.677	0.044	-0.766	-0.596
LDMC	-	CWM	Slope	0.001	0.001	-0.001	0.002
LDMC	10	CWM+ITV	Slope	0.000	0.001	-0.001	0.002
LDMC	-	NWM	Slope	0.000	0.000	-0.001	0.001
Leaf Area	-	CWM	Intercept	0.292	0.126	0.033	0.526
Leaf Area	10	CWM+ITV	Intercept	0.461	0.125	0.213	0.697
Leaf Area	-	NWM	Intercept	0.337	0.108	0.124	0.550
Leaf Area	-	CWM	Slope	0.001	0.003	-0.006	0.007
Leaf Area	10	CWM+ITV	Slope	0.001	0.003	-0.006	0.007
Leaf Area	-	NWM	Slope	0.003	0.002	-0.001	0.007
Leaf N	-	CWM	Intercept	2.896	0.032	2.833	2.960
Leaf N	10	CWM+ITV	Intercept	2.895	0.031	2.835	2.958
Leaf N	-	NWM	Intercept	2.952	0.031	2.891	3.014
Leaf N	-	CWM	Slope	-0.001	0.001	-0.002	0.000
Leaf N	10	CWM+ITV	Slope	-0.001	0.001	-0.002	0.000
Leaf N	-	NWM	Slope	-0.001	0.000	-0.001	0.000
SLA	-	CWM	Intercept	2.536	0.045	2.448	2.625
SLA	10	CWM+ITV	Intercept	2.573	0.045	2.484	2.660
SLA	-	NWM	Intercept	2.613	0.039	2.535	2.688
SLA	-	CWM	Slope	0.000	0.001	-0.002	0.001
SLA	10	CWM+ITV	Slope	0.000	0.001	-0.001	0.001
SLA	-	NWM	Slope	0.000	0.000	-0.001	0.001

Table S8. Model output for temperature sensitivity of community weighted trait means. Temperature sensitivity represents the correspondence between interannual variation in CWM traits and interannual variation in temperature (i.e., the amount of change in CWM trait per °C). All estimates are for community-weighted mean (CWM) change only. Bolded rows designate slope parameters (sensitivity) for which the 95% credible interval did not cross zero (i.e., the relationship is "significant").

Trait	Climate Variable	Parameter	mean	sd	2.50%	97.50%
Height	10	Intercept	2.518	0.086	2.350	2.679
Height	**10**	**Slope**	**0.039**	**0.019**	**0.002**	**0.078**
LDMC	10	Intercept	-0.535	0.045	-0.625	-0.449
LDMC	10	Slope	-0.010	0.011	-0.033	0.013
Leaf Area	10	Intercept	0.295	0.125	0.041	0.531
Leaf Area	10	Slope	-0.031	0.044	-0.116	0.057
Leaf N	10	Intercept	2.897	0.031	2.836	2.957
Leaf N	10	Slope	0.006	0.009	-0.012	0.024
SLA	10	Intercept	2.535	0.044	2.448	2.623
SLA	10	Slope	0.009	0.011	-0.012	0.031
Height	11	Intercept	2.514	0.086	2.342	2.684
Height	11	Slope	0.012	0.009	-0.007	0.030
LDMC	11	Intercept	-0.595	0.046	-0.684	-0.506
LDMC	11	Slope	-0.001	0.005	-0.011	0.010
Leaf Area	11	Intercept	0.286	0.129	0.023	0.526
Leaf Area	11	Slope	0.026	0.023	-0.018	0.071
Leaf N	11	Intercept	2.896	0.031	2.834	2.956
Leaf N	11	Slope	0.003	0.004	-0.005	0.010
SLA	11	Intercept	2.536	0.045	2.450	2.623
SLA	11	Slope	0.003	0.005	-0.006	0.013

Table S9. Model output for **interspecific** trait change over time with temperature change and soil moisture (static) as predictors of this change. Neither temperature change nor soil moisture was a significant predictor of trait change over time (all credible intervals overlap zero). All estimates are for community-weighted mean (CWM) and summer temperature (bioclim 10) change only.

Trait	Climate Variable	Parameter	mean	sd	2.5%	97.5%
Height	10	Intercept	0.002	0.000	0.001	0.003
Height	10	Moisture	0.000	0.001	-0.002	0.001
Height	10	TemperatureChange	-0.002	0.008	-0.018	0.012
Height	10	TemperatureChange*Moisture	0.007	0.016	-0.022	0.043
LDMC	10	Intercept	0.001	0.000	0.001	0.002
LDMC	10	Moisture	0.000	0.001	-0.002	0.001
LDMC	10	TemperatureChange	-0.008	0.008	-0.023	0.008
LDMC	10	TemperatureChange*Moisture	0.005	0.017	-0.030	0.034
Leaf Area	10	Intercept	0.005	0.002	0.001	0.008
Leaf Area	10	Moisture	-0.004	0.003	-0.011	0.003
Leaf Area	10	TemperatureChange	-0.032	0.039	-0.112	0.045
Leaf Area	10	TemperatureChange*Moisture	0.085	0.077	-0.069	0.225
Leaf N	10	Intercept	-0.001	0.000	-0.001	0.000
Leaf N	10	Moisture	0.000	0.000	-0.001	0.001
Leaf N	10	TemperatureChange	0.005	0.006	-0.007	0.015
Leaf N	10	TemperatureChange*Moisture	-0.007	0.011	-0.027	0.016
SLA	10	Intercept	-0.001	0.000	-0.001	0.000
SLA	10	Moisture	0.000	0.001	-0.001	0.001
SLA	10	TemperatureChange	0.009	0.007	-0.005	0.022
SLA	10	TemperatureChange*Moisture	-0.001	0.014	-0.027	0.027

Table S10. Probability that a species immigrated into ("gain") or disappeared from ("loss") a site as a function of its traits. Only for plant height were the trait values of gained and lost species significantly different – the probability of a species being gained was significantly (positively) related to its height but the probability of a species being lost was not.

Trait	Direction	Parameter	mean	sd	2.5%	97.5%
Height	gained	Intercept	-2.402	0.221	-2.821	-1.948
Height	lost	Intercept	-1.786	0.223	-2.188	-1.358
Height	**gained**	**Slope**	**0.247**	**0.082**	**0.081**	**0.403**
Height	**lost**	**Slope**	**0.039**	**0.080**	**-0.116**	**0.194**
LDMC	gained	Intercept	-2.225	0.127	-2.474	-1.978
LDMC	lost	Intercept	-2.186	0.124	-2.432	-1.944
LDMC	gained	Slope	-0.438	0.100	-0.619	-0.225
LDMC	lost	Slope	-0.501	0.092	-0.666	-0.305
Leaf Area	gained	Intercept	-1.834	0.099	-2.037	-1.644
Leaf Area	lost	Intercept	-1.704	0.099	-1.881	-1.512
Leaf Area	gained	Slope	0.090	0.059	-0.024	0.211
Leaf Area	lost	Slope	-0.089	0.061	-0.207	0.046
Leaf N	gained	Intercept	-1.590	0.418	-2.423	-0.764
Leaf N	lost	Intercept	-2.184	0.377	-2.897	-1.427
Leaf N	gained	Slope	-0.067	0.137	-0.334	0.205
Leaf N	lost	Slope	0.170	0.124	-0.069	0.403
SLA	gained	Intercept	-2.872	0.116	-2.996	-2.569
SLA	lost	Intercept	-2.850	0.133	-2.995	-2.500
SLA	gained	Slope	0.421	0.054	0.302	0.517
SLA	lost	Slope	0.447	0.057	0.317	0.543

164

References for Table S1

1.   Lavorel, S. & Garnier, E. Predicting changes in community composition and ecosystem functioning from plant traits: revisting the Holy Grail. Functional Ecology 16, 545–556 (2002).

2.   Weiher, E. et al. Challenging Theophrastus : A common core list of plant traits for functional ecology. Journal of Vegetation Science 10, 609–620 (1999).

3.   Hudson, J. & Henry, G. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 90, 2657–2663 (2009).

4.   Violle, C. et al. Let the concept of trait be functional! Oikos 116, 882–892 (2007).

5.   Chapin, F. S., Bret-Harte, M. S., Hobbie, S. E. & Zhong, H. L. Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science 7, 347–358 (1996).

6.   Moles, A. T. et al. Global patterns in plant height. J Ecol 97, 923–932 (2009).

7.   Sistla, S. a et al. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497, 615–8 (2013).

8.   De Deyn, G. B., Cornelissen, J. H. C. & Bardgett, R. D. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters 11, 516–531 (2008).

9.   Kunstler, G. et al. Plant functional traits have globally consistent effects on competition. Nature 529, 1–15 (2016).

10.   Gaudet, C. & Keddy, P. A comparative approach to predicting competitive ability from plant traits. Nature1 334, 242–243 (1988).

11.   Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33, 125–159 (2002).

12.   Moles, A. T. & Leishman, M. R. in Seedling Ecology and Evolution 217–238 (2008). doi:10.1017/CBO9780511815133.012

13.   Sturm, M. et al. Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. Journal of … 336–344 (2001). at <http://journals.ametsoc.org/doi/abs/10.1175/1520-0442(2001)014%3C0336:SSIIAT%3E2.0.CO%3B2>

14.   Sturm, M. Changing snow and shrub conditions affect albedo with global implications. Journal of Geophysical Research 110, G01004 (2005).

15. Loranty, M. M., Berner, L. T., Goetz, S. J., Jin, Y. & Randerson, J. T. Vegetation controls on northern high latitude snow-albedo feedback: Observations and CMIP5 model simulations. Global Change Biology 20, 594–606 (2014).

16. Myers-Smith, I. H. & Hik, D. S. Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. Ecology and Evolution 3, 3683–700 (2013).

17. DeMarco, J., Mack, M. & Bret-Harte, M. Effects of arctic shrub expansion on biophysical versus biogeochemical drivers of litter decomposition. Ecology 95, 1861–1875 (2014).

18. Enquist, B. J., Brown, J. H. & West, G. B. Allometric scaling of plant energetics and population density. Nature 395, 163–165 (1998).

19. Greaves, H. E. et al. Estimating aboveground biomass and leaf area of low-stature Arctic shrubs with terrestrial LiDAR. Remote Sensing of Environment 164, 26–35 (2015).

20. Poorter, H. et al. Biomass allocation to leaves , stems and roots : meta-analyses of interspecific variation and environmental control. 30–50 (2012). doi:10.1111/j.1469-8137.2011.03952.x

21. Street, L. E., Shaver, G. R., Williams, M. & Van Wijk, M. T. What is the relationship between changes in canopy leaf area and changes in photosynthetic CO_2 flux in arctic ecosystems? Journal of Ecology 95, 139–150 (2007).

22. Westoby, M. & Wright, I. J. Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution 21, 261–268 (2006).

23. Díaz, S. et al. The global spectrum of plant form and function. Nature 529, 167–171 (2016).

24. Niinemets, Ü. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecological Research 25, 693–714 (2010).

25. Reich, P. B. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. Journal of Ecology 102, 275–301 (2014).

26. Wright, I. J. et al. The worldwide leaf economics spectrum. Nature 428, 821–827 (2004).

27. Diaz, S. et al. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15, 295–304 (2004).

28. Cornelissen, J. H. C. et al. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology letters 10, 619–27 (2007).

29.   Cornwell, W. K. et al. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065–1071 (2008).

30.   Freschet, G. T., Aerts, R. & Cornelissen, J. H. C. A plant economics spectrum of litter decomposability. Functional Ecology 26, 56–65 (2012).

31.   Westoby, M., Jurado, E. & Leishman, M. R. Comparative evolutionary ecology of seed size. Trends in Ecology and Evolution 7, 368–72 (1992).

32.   Thompson, K. Seed and seed banks. New Phytologist 106, 23–34 (1987).

33.   Iida, Y. et al. Wood density explains architectural differentiation across 145 co-occurring tropical tree species. Functional Ecology 26, 274–282 (2012).

34.   Ménard, C. B., Essery, R., Pomeroy, J., Marsh, P. & Clark, D. B. A shrub bending model to calculate the albedo of shrub-tundra. Hydrological Processes 28, 341–351 (2014).

35.   Blok, D. et al. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Global Change Biology 16, 1296–1305 (2010).

36.   Nauta, A. L. et al. Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source. Nature Climate Change 5, 67–70 (2014).

37.   Weedon, J. T. et al. Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? Ecology Letters 12, 45–56 (2009).

38.   Hobbie, S. E. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecological Monographs 66, 503–522 (1996).

39.   Myers-Smith, I. H. et al. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6, 45509 (2011).

40.   Dorrepaal, E., Cornelissen, J. H. C., Aerts, R., Wallén, B. & Van Logtestijn, R. S. P. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? Journal of Ecology 93, 817–828 (2005).

41.   Larsen, K. S., Michelsen, A., Jonasson, S., Beier, C. & Grogan, P. Nitrogen uptake during fall, winter and spring differs among plant functional groups in a subarctic heath ecosystem. Ecosystems 15, 927–939 (2012).

42.   Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J. & Laundre, J. A. Responses of Arctic tundra to experimental and observed changes in climate. Ecology 76, 694–711 (1995).

43.   Reich, P. B., Walters, M. B. & Ellsworth, D. S. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences 94, 13730–13734 (1997).

TRY Data References

1. Atkin, O. K., M. H. M. Westbeek, M. L. Cambridge, H. Lambers, and T. L. Pons. 1997. Leaf respiration in light and darkness - A comparison of slow- and fast-growing Poa species. Plant Physiology 113:961-965.

2. B. Sandel, J. D. Corbin, and M. Krupa 2011. Using plant functional traits to guide restoration: A case study in California coastal grassland. Ecosphere 2:art23. http://d

3. Bahn, M., G. Wohlfahrt, E. Haubner, I. Horak, W. Michaeler, K. Rottmar, U. Tappeiner, and A. Cernusca. 1999. Leaf photosynthesis, nitrogen contents and specific leaf area of 30 grassland species in differently managed mountain ecosystems in the Eastern Alps. Pages 247-255 in A. Cernusca, U. Tappeiner, and N. Bayfield, editors. Land-use changes in European mountain ecosystems. ECOMONT- Concept and Results. Blackwell Wissenschaft, Berlin.

4. Bakker, C., J. Rodenburg, and P. Bodegom. 2005. Effects of Ca- and Fe-rich seepage on P availability and plant performance in calcareous dune soils. Plant and Soil 275:111-122.

5. Bakker, C., P. M. Van Bodegom, H. J. M. Nelissen, W. H. O. Ernst, and R. Aerts. 2006. Plant responses to rising water tables and nutrient management in calcareous dune slacks. Plant Ecology 185:19-28.

6. Blonder, B., Buzzard, B., Sloat, L., Simova, I., Lipson, R., Boyle, B., Enquist, B. The shrinkage effect biases estimates of paleoclimate. American Journal of Botany (2012).

7. Bond-Lamberty, B., C. Wang, and S. T. Gower (2002), Leaf area dynamics of a boreal black spruce fire chronosequence, Tree Physiol., 22(14), 993-1001.

8. Brendan Choat, Steven Jansen, Tim J. Brodribb, Herve Cochard, Sylvain Delzon, Radika Bhaskar, Sandra J. Bucci, Taylor S. Feild, Sean M. Gleason, Uwe G. Hacke, Anna L. Jacobsen, Frederic Lens, Hafiz Maherali, Jordi Martinez-Vilalta, Stefan Mayr, Maurizio Mencuccini, Patrick J. Mitchell, Andrea Nardini, Jarmila Pittermann, R. Brandon Pratt, John S. Sperry, Mark Westoby, Ian J. Wright & Amy E. Zanne (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752-755 doi:10.1038/nature11688

9. Burrascano S., Del Vico E., Fagiani S., Giarrizzo E., Mei M., Mortelliti A., Sabatini F.M., Blasi C., submitted. Environmental filtering of wild boar rooting activity on understorey composition and functional traits. Plant Ecology.

10. Byun C, S de Blois, J Brisson (2012) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. Journal of Ecology, doi: 10.1111/1365-2745.12016

11. Campbell, C., L. Atkinson, J. Zaragoza-Castells, M. Lundmark, O. Atkin, and V. Hurry. 2007. Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. New Phytologist 176:375-389.

12. Campetella, G; Botta-Dukát, Z; Wellstein, C; Canullo, R; Gatto, S; Chelli, S; Mucina, L; Bartha, S (2011): Patterns of plant trait-environment relationships along a forest

succession chronosequence. Agriculture, Ecosystems & Environment, 145(1), 38-48. doi:10.1016/j.agee.2011.06.025

13. Cerabolini B.E.L., Brusa G., Ceriani R.M., De Andreis R., Luzzaro A. & Pierce S. 2010. Can CSR classification be generally applied outside Britain? Plant Ecology 210: 253-261

14. Ciocarlan V. (2009). The illustrated Flora of Romania. Pteridophyta et Spermatopyta. Editura Ceres, 1141 p (in Romanian).

15. Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. Journal of Ecology 84:573-582.

16. Cornelissen, J. H. C., B. Cerabolini, P. Castro-Diez, P. Villar-Salvador, G. Montserrat-Marti, J. P. Puyravaud, M. Maestro, M. J. A. Werger, and R. Aerts. 2003. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? Journal of Vegetation Science 14:311-322.

17. Cornelissen, J. H. C., H. M. Quested, D. Gwynn-Jones, R. S. P. Van Logtestijn, M. A. H. De Beus, A. Kondratchuk, T. V. Callaghan, and R. Aerts. 2004. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. Functional Ecology 18:779-786.

18. Cornelissen, J. H. C., P. C. Diez, and R. Hunt. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology 84:755-765.

19. Cornwell, W. K., J. H. C. Cornelissen, K. Amatangelo, E. Dorrepaal, V. T. Eviner, O. Godoy, S. E. Hobbie, B. Hoorens, H. Kurokawa, N. Pérez-Harguindeguy, H. M. Quested, L. S. Santiago, D. A. Wardle, I. J. Wright, R. Aerts, S. D. Allison, P. van Bodegom, V. Brovkin, A. Chatain, T. V. Callaghan, S. Díaz, E. Garnier, D. E. Gurvich, E. Kazakou, J. A. Klein, J. Read, P. B. Reich, N. A. Soudzilovskaia, M. V. Vaieretti, and M. Westoby. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065-1071.

20. Craine JM, Nippert JB, Towne EG, Tucker S, Kembel SW, Skibbe A, McLauchlan KK (2011) Functional consequences of climate-change induced plant species loss in a tallgrass prairie. Oecologia 165: 1109-1117

21. Craine JM, Towne EG, Ocheltree TW, Nippert JB (2012) Community traitscape of foliar nitrogen isotopes reveals N availability patterns in a tallgrass prairie. Plant Soil 356: 395-403

22. Craine, J. M., A. J. Elmore, M. P. M. Aidar, M. Bustamante, T. E. Dawson, E. A. Hobbie, A. Kahmen, M. C. Mack, K. K. McLauchlan, A. Michelsen, G. B. Nardoto, L. H. Pardo, J. Penuelas, P. B. Reich, E. A. G. Schuur, W. D. Stock, P. H. Templer, R. A. Virginia, J. M. Welker, and I. J. Wright. 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytologist 183:980-992.

23. Craine, J. M., W. G. Lee, W. J. Bond, R. J. Williams, and L. C. Johnson. 2005. Environmental constraints on a global relationship among leaf and root traits of grasses. Ecology 86:12-19.

24. Díaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Martí, J. P. Grime, F. Zarrinkamar, Y. Asri, S. R. Band, S. Basconcelo, P. Castro-Díez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Pérez-Harguindeguy, M. C. Pérez-Rontomé, F. A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martínez, A. Romo-Díez, S. Shaw, B. Siavash, P. Villar-Salvador, and M. R. Zak. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295-304.

25. Dainese M, Bragazza L (2012) Plant traits across different habitats of the Italian Alps: a comparative analysis between native and alien species. Alpine Botany

26. Everwand G, Fry, EL, Eggers T, Manning P (2014) Seasonal variation in the relationship between plant traits and grassland carbon and water fluxes. Ecosystems 17, 1095-1108

27. Fitter, A. H. and H. J. Peat 1994. The Ecological Flora Database. Journal of Ecology 82:415-425.

28. Freschet, G. T., J. H. C. Cornelissen, R. S. P. van Logtestijn, and R. Aerts. 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. Journal of Ecology 98:362-373.

29. Fry, E.L., Power, S.A. Manning, P. (2014) Trait based classification and manipulation of functional groups in biodiversity-ecosystem function experiments. Journal of Vegetation Science, 25, 248-261.

30. Gallagher RV, MR Leishman (2012) A global analysis of trait variation and evolution in climbing plants. Journal of Biogeography 39, 1757-1771.

31. Garnier, E., S. Lavorel, P. Ansquer, H. Castro, P. Cruz, J. Dolezal, O. Eriksson, C. Fortunel, H. Freitas, C. Golodets, K. Grigulis, C. Jouany, E. Kazakou, J. Kigel, M. Kleyer, V. Lehsten, J. Lepš, T. Meier, R. Pakeman, M. Papadimitriou, V. P. Papanastasis, H. Quested, F. Quétier, M. Robson, C. Roumet, G. Rusch, C. Skarpe, M. Sternberg, J.-P. Theau, A. Thébault, D. Vile, and M. P. Zarovali. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. Annals of Botany 99:967-985.

32. Green, W. 2009. USDA PLANTS Compilation, version 1, 09-02-02. (http://bricol.net/downloads/data/PLANTSdatabase/) NRCS: The PLANTS Database (http://plants.usda.gov, 1 Feb 2009). National Plant Data Center: Baton Rouge, LA 70874-74490 USA.

33. Guy, A. L., J. M. Mischkolz, and E. G. Lamb. 2013. Limited effects of simulated acidic deposition on seedling survivorship and root morphology of endemic plant taxa of the

Athabasca Sand Dunes in well watered greenhouse trials. Botany 91:176-181. http://dx.doi.org/10.1139/cjb-2012-0162

34. Han, W. X., J. Y. Fang, D. L. Guo, and Y. Zhang. 2005. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. New Phytologist 168:377-385.

35. Hickler, T. 1999. Plant functional types and community characteristics along environmental gradients on Öland's Great Alvar (Sweden) Masters Thesis, University of Lund, Sweden.

36. Kattge, J., W. Knorr, T. Raddatz, and C. Wirth. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. Global Change Biology 15:976-991.

37. Kerkhoff, A. J., W. F. Fagan, J. J. Elser, and B. J. Enquist. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. American Naturalist 168:E103-E122.

38. Kichenin et al. 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. Functional Ecology, in press.

39. Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. van Groenendael, L. Klimes, J. Klimesova, S. Klotz, G. M. Rusch, Hermy, M. , D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Gözenberger, J. G. Hodgson, A.-K. Jackel, I. Kühn, D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266-1274.

40. Komac, B., C. Pladevall, J. Peñuelas, J. V. Conesa, and M. Domènech. 2015. Variations in functional diversity in snowbed plant communities determining snowbed continuity. Plant Ecology 216:1257-1274.

41. Louault, F., V. D. Pillar, J. Aufrere, E. Garnier, and J. F. Soussana. 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. Journal of Vegetation Science 16:151-160.

42. Loveys, B. R., L. J. Atkinson, D. J. Sherlock, R. L. Roberts, A. H. Fitter, and O. K. Atkin. 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. Global Change Biology 9:895-910.

43. Meziane, D. and B. Shipley. 1999. Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. Plant Cell and Environment 22:447-459.

44. Milla & Reich 2011 Annals of Botany 107: 455Â–465, 2011.

45. Niinemets, U. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82:453-469.

46. Onoda, Y., M. Westoby, P. B. Adler, A. M. F. Choong, F. J. Clissold, J. H. C. Cornelissen, S. Diaz, N. J. Dominy, A. Elgart, L. Enrico, P. V. A. Fine, J. J. Howard, A. Jalili, K. Kitajima, H. Kurokawa, C. McArthur, P. W. Lucas, L. Markesteijn, N. Perez-Harguindeguy, L. Poorter, L. Richards, L. S. Santiago, Jr. E. Sosinski, S. Van Bael, D. I. Warton, I. J. Wright, S. J. Wright, and N. Yamashita. 2011. Global patterns of leaf mechanical properties. Ecology Letters 14:301-312.

47. Ordonez, J. C., P. M. van Bodegom, J. P. M. Witte, R. P. Bartholomeus, J. R. van Hal, and R. Aerts. 2010. Plant Strategies in Relation to Resource Supply in Mesic to Wet Environments: Does Theory Mirror Nature? American Naturalist 175:225-239.

48. Paula, S., M. Arianoutsou, D. Kazanis, Ç. Tavsanoglu, F. Lloret, C. Buhk, F. Ojeda, B. Luna, J. M. Moreno, A. Rodrigo, J. M. Espelta, S. Palacio, B. Fernández-Santos, P. M. Fernandes, and J. G. Pausas. 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90:1420.

49. Peco B., de Pablos I., Traba J., & Levassor C. (2005) The effect of grazing abandonment on species composition and functional traits: the case of dehesa grasslands. Basic and Applied Ecology, 6(2): 175-183

50. Pierce S., Brusa G., Sartori M. & Cerabolini B.E.L. 2012. Combined use of leaf size and economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive strategies. Annals of Botany 109(5): 1047-1053

51. Pierce S., Ceriani R.M., De Andreis R., Luzzaro A. & Cerabolini B. 2007. The leaf economics spectrum of Poaceae reflects variation in survival strategies. Plant Biosystems 141(3): 337-343.

52. Pierce S., Luzzaro A., Caccianiga M., Ceriani R.M. & Cerabolini B. 2007. Disturbance is the principal alpha-scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. Journal of Ecology 95: 698-706.

53. Poorter, H., U. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 182:565-588.

54. Poschlod, P., M. Kleyer, A. K. Jackel, A. Dannemann, and O. Tackenberg. 2003. BIOPOP - a database of plant traits and Internet application for nature conservation. Folia Geobotanica 38:263-271.

55. Prentice, I.C., Meng, T., Wang, H., Harrison, S.P., Ni, J., Wang, G., 2011. Evidence for a universal scaling relationship of leaf CO2 drawdown along a moisture gradient. New Phytologist 190: 169Â–180

56. Price, C.A. and B.J. Enquist. Scaling of mass and morphology in Dicotyledonous leaves: an extension of the WBE model. (2007) Ecology 88(5): 1132Â–1141.

57. Pyankov, V. I., A. V. Kondratchuk, and B. Shipley. 1999. Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tadjikistan. New Phytologist 143:131-142.

58. Quested, H. M., J. H. C. Cornelissen, M. C. Press, T. V. Callaghan, R. Aerts, F. Trosien, P. Riemann, D. Gwynn-Jones, A. Kondratchuk, and S. E. Jonasson. 2003. Decomposition of sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites. Ecology 84:3209-3221.

59. Reich, P. B., J. Oleksyn, and I. J. Wright. 2009. Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. Oecologia 160:207-212.

60. Reich, P. B., M. G. Tjoelker, K. S. Pregitzer, I. J. Wright, J. Oleksyn, and J. L. Machado. 2008. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. Ecology Letters 11:793-801.

61. Schweingruber, F.H., Landolt, W.: The Xylem Database. Swiss Federal Research Institute WSL Updated (2005)

62. Sheremet'ev S.N. (2005) Herbs on the soil moisture gradient (water relations and the structural-functional organization). KMK, Moscow, 271 pp. (In Russian)

63. Shipley B., 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance, Functional Ecology (16) 682-689

64. Shipley, B. 1995. Structured Interspecific Determinants of Specific Leaf-Area in 34 Species of Herbaceous Angiosperms. Functional Ecology 9:312-319.

65. Shipley, B. and M. J. Lechowicz. 2000. The functional co-ordination of leaf morphology, nitrogen concentration, and gas exchange in 40 wetland species. Ecoscience 7:183-194.

66. Shipley, B. and T. T. Vu. 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. New Phytologist 153:359-364.

67. Spasojevic, M. J. and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. Journal of Ecology 100:652-661.

68. Tucker SS, Craine JM, Nippert JB (2011) Physiological drought tolerance and the structuring of tallgrass assemblages. Ecosphere 2(4): 48

69. van Bodegom, P. M., B. K. Sorrell, A. Oosthoek, C. Bakke, and R. Aerts. 2008. Separating the effects of partial submergence and soil oxygen demand on plant physiology. Ecology 89:193-204.

70. Vanessa Minden, Michael Kleyer (2011): Testing the effect–response framework: key response and effect traits determining above-ground biomass of salt marshes. Journal of Vegetation Science 22: 387-401

71. Vanessa Minden, Sandra Andratschke, Janina Spalke, Hanna Timmermann, Michael Kleyer (2012): Plant trait–environment relationships in salt marshes: Deviations from predictions by ecological concepts. Perspectives in Plant Ecology, Evolution and Systematics, 14: 183-192

72. Vergutz, L., S. Manzoni, A. Porporato, R.F. Novais, and R.B. Jackson. 2012. A Global Database of Carbon and Nutrient Concentrations of Green and Senesced Leaves. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/ORNLDAAC/1106

73. Wenxuan Han, Yahan Chen, Fang-Jie Zhao, Luying Tang, Rongfeng Jiang and Fusuo Zhang, 2011, Floral, climatic and soil pH controls on leaf ash content in China's terrestrial plants. Global Ecology and Biogeography, DOI: 10.1111/j.1466-8238.2011.00677.x

74. Wirth, C. and J. W. Lichstein. 2009. The Imprint of Species Turnover on Old-Growth Forest Carbon Balances - Insights From a Trait-Based Model of Forest Dynamics. Pages 81-113 in C. Wirth, G. Gleixner, and M. Heimann, editors. Old-Growth Forests: Function, Fate and Value. Springer, New York, Berlin, Heidelberg.

75. Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M. L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.

76. Yahan Chen , Wenxuan Han , Luying Tang , Zhiyao Tang and Jingyun Fang 2011 Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. Ecography 34, doi: 10.1111/j.1600-0587.2011.06833.x

Ural Mountains
N 61° 17' 19.89"
E 59° 19' 27.13"
Rohan Shetti 2014

Chapter 7

Synthesis and Discussion

Chapter 7: Synthesis and Discussion

In this dissertation, I investigated the potential of shrubs in understanding contemporary climate change in the Arctic, sub-arctic and alpine environments. In **Chapter 2**, I started with quantifying growth differences within a shrub (along the length of the stem) and noted its impacts on site-chronologies developed from ring-width series. We found that heterogeneous growth along the length of the stem has profound effects on climate-growth relationships. Then in **Chapter 3**, I studied if sexual dimorphism - like in trees - has any impact on radial growth in shrubs and should it be a point to be considered while sampling shrubs for dendro-climatological/ecological analysis. In **Chapter 4**, we studied the reconstruction potential of the shrub *Alnus viridis* ssp *crispa.* In our study, we inferred that a combined use of ring-width measurements and serial sectioning can have promising results for climate reconstructions using ring-widths from shrubs. We compared shrub and tree climate sensitivity to contemporary warming in **Chapter 5** and found divergent responses of cohabiting trees and shrubs. We found that shrubs were more sensitive to current warming as compared to trees. This was markedly seen at Mediterranean sites. Finally in **Chapter 6** we studied functional plant traits and their relation with temperature and soil moisture.

In this synthesis, I wish to discuss the potential of shrubs in dendro-ecology, dendro-climatology and as indicators of change in general in the Arctic context. I wish to discuss the current methods used, critically look at the limitations and bring to light new possibilities which could help refine methods in shrub based dendrochronological analysis. At first, I will explain the link between fundamental factors like growth architecture, sexual-dimorphism and climate sensitivity as this is the basis of any dendrochronological analysis. Then, I would like to explain how the use of combinations of methods like wood-anatomy with ring-width analysis could potentially improve data reliability for reconstructions. Further, by discussing a comparison of differences between responses of shrubs and trees to current climate warming, I wish to explain how shrubs and trees have fundamental differences in the growth forms, morphometry and ecological resilience. Then, I will discuss the role of plant traits and their responses to current warming. This chapter encompasses a broader geographical extent and shows how plant traits act as drivers in

ecosystem processes in the Arctic. Lastly, I would like to discuss future scopes of shrub-arctic research which combines dendro-ecology with functional trait biology as changes in shrub functional traits can be used to model Arctic changes. In conclusion, I would explain the limitations of this investigation and suggest future avenues of research.

Growth Architecture and Climate Sensitivity

In the last years, with the rapidly increasing shrub studies, it is evident shrubs are and will be an important part of future investigatio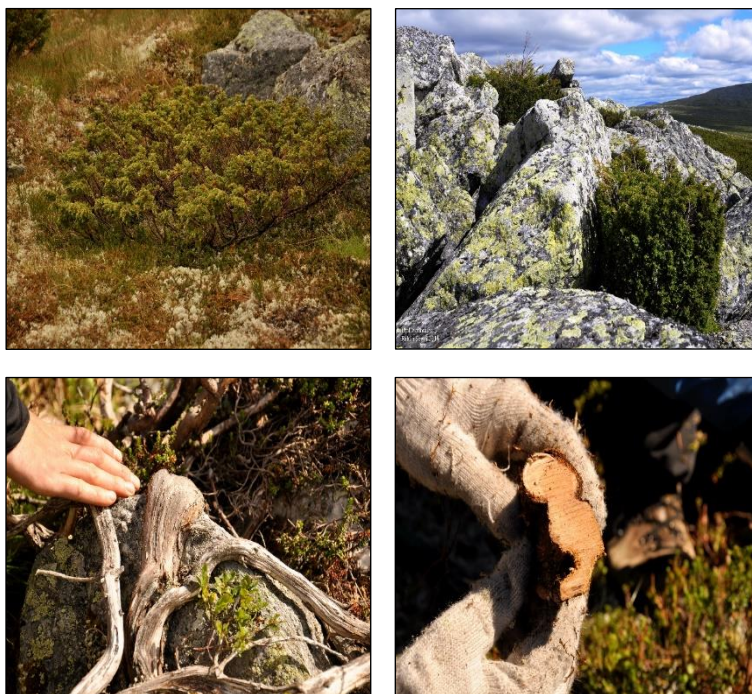ns in the Arctic research. Not only are they important as proxies which can help trace environmental changes but are also crucial in the ecosystem dynamics in the circumpolar Arctic. The alpine tundra and especially areas above the treeline remain the most pristine environments with least anthropogenic impact and hence are of special interest to the scientific community (Körner, 2012a). Shrubs are known to grow in a wide range of environments from low lying river basins (Tape et al., 2012) to areas higher than the treeline (Schweingruber and Poschold, 2005; Hallinger et al., 2010). This wide range of ecological niches is habitable by shrubs because of better adaptability to micro-site conditions (Körner, 2012a). However, this could potentially mean that shrubs might be highly influenced by micro-site conditions as well.

Commonly reported difficulties like hard cross-dating, low inter-series correlations and low EPS values (Woodcock and Bradley, 1994; Bär et al., 2007) are indicative of lack of growth

Figure: 2

Figure 2: Example of irregular growth and influence of microsite conditions on shrub stem growth

synchronicity which is the key aspect for detecting common signals (as environmental response) in dendro-ecology.

Growth irregularities at the root collar and along the length of the stem could be due to a number of reasons; some prominent ones being rocky substrates at high elevations, exposition on the slope, wind direction, snow burial, runoff, precipitation and temperature (example: Fig: 2) (Sonesson and Callaghan, 1991; le Roux and Luoto, 2014; Ropars et al., 2017). These growth irregularities could result in locally missing rings, wedging rings or compression wood, or missing outer rings causing differential growth among different stem heights within an individual (example: Fig 3 A to D) (Wilmking et al., 2012). To select the stem-disk closest to the ground surface (many times root collar itself) has been the most commonly used procedure for sampling shrubs (Gazol and Camarero, 2012; Pellizzari et al., 2014; Beil et al., 2015; Pellizzari et al., 2017). However correct dating and selection of the right stem-disk is critical for climate reconstruction (Rayback and Henry, 2006; Wilmking et al., 2012; Buras and Wilmking, 2014).

Figure: 3

A: SD section root 00cm

B: SD section 10cm

C: SD section at 30 cm

D: SD section 20cm
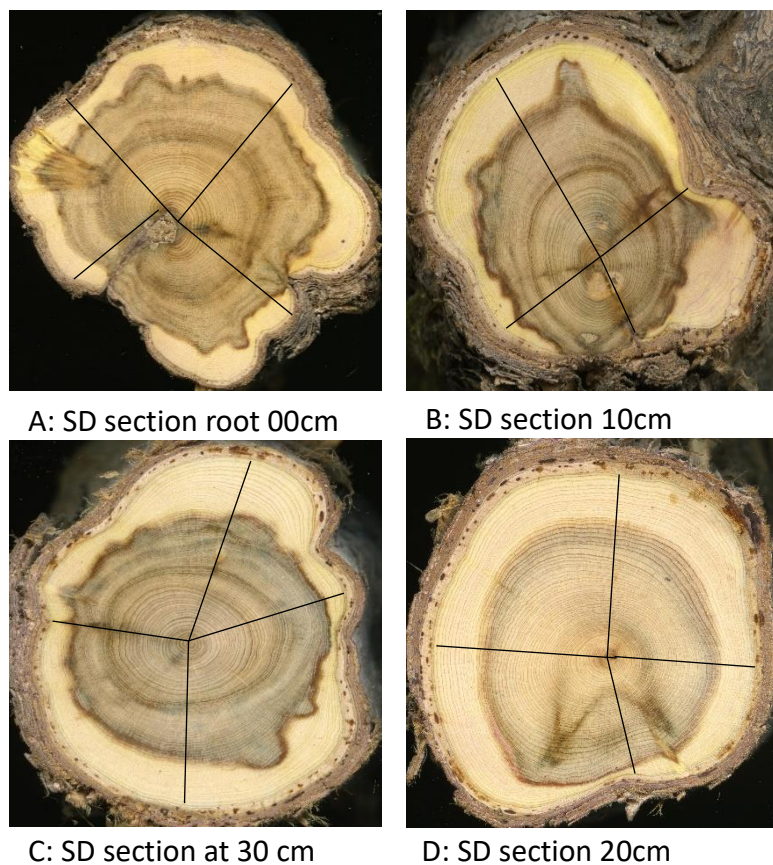
Figure 3: Example of irregular growth from stem-disks from three stem heights from an individual. Black lines show radial pathways.

In **Chapter 2** we analyzed ring-width measurements from three stem-disk sections per individual and tested for growth synchronicity across stem heights. We found that there was significantly differential growth between different stem-disks within an individual shrub (**Chapter 2: Figure 2; Supplement S1**). When we tested site-chronologies from different stem heights for

climate sensitivity we found significantly varying responses clearly suggesting that a single stem-disk does not entirely represent what the shrub individual might be responding to. Asynchronous radial growth was confirmed by significant reduction in inter-series correlation and Gleichläufigkeit among stem heights. Complementary to our findings, a recent study by Ropars et al. (2017) reported the finding that different stem-disks (i.e. from different stem heights) show changes in climate sensitivity. However, their study with *Betula glandulosa* inferred that the root collar shows the highest climate sensitivity, whereas in our study with Juniperus communis we observed stem-disks higher (SD20 i.e. stem-disks at 20 cm from ground level) showed optimal climate sensitivity. These contrasting findings clearly indicate that a single stem-disk represents radial growth for a limited time section and that it can differ substantially along the stem. This raises the question, 'which sampling height is best suited for testing for climate-growth relationships?' which yet remains unanswered. As from the contrasting findings, we can infer that growth architecture can differ within individuals and also among species. A study by Sadras and Denison (2009) showed that even plant parts could compete for resources if it benefits the overall growth of the plant. Therefore, this paves the way for further research to test different stem heights for climate sensitivity from different species. In **Chapter 2** we discussed extrinsic micro-site factors that might affect growth along the length of the stem. As shrubs, grow beyond treelines they are subjected to harsh conditions like wind pressure, snow burial, surface flow and substrate conditions. Intrinsic factors like branching, formation of multiple pits, rot, disease, genotypic factors like differences in responses of different sexes to environmental stresses are also factors that can affect growth and hence ring-width formation.

Sexual dimorphism and Climate Sensitivity

In **Chapter 3,** we studied effects of sex-separated sub-groups of ring-width indices and basal area increments from Juniperus communis on site-chronologies from samples collected across the Ural sites and from Kirkenes, Norway. We assumed that like in dioecious trees, even in shrubs there might be considerable differences in ring-width formation (radial growth) between male and female shrubs. However, we found a borderline to moderate difference between male and female shrub's ring-width series. Differences between male and female shrubs in terms of overall

growth (Lloyd and Webb, 1977), flowering times (Godley, 1976), resistance to disease, pest and herbivory (Ward, 2007), differential resource allocation (Freeman et al., 1976) differing sex ratios in population stands (Gauquelin et al., 2002) is already well established in literature. However, there was a knowledge gap as to how can sexual differences and allied attributes like reproductive effort in females could impact radial growth - which is key to ring-width analysis.

We employed a series of analysis ranging from multivariate statistics like cluster analysis and Principle Component Gradient Analysis (PCGA) to time series analysis like cumulative growth analysis and inter-series correlation with site-chronology. In all the analyses - except an overall comparison of gender-separated sub groups to site-chronologies - we could not find any significant differences between males and females. Retrospectively, we questioned why this might be the case? A probable answer could be that there is reproductive effort in female shrubs but is not consistent over time. These time-inconsistent growth trends appear as noise in the overall dataset. Therefore, we do see a moderate differentiation but cannot attribute it entirely to gender-specific reasons. This differentiation was evidently translated in climate sensitivity as well, as we observed a moderate difference in sensitivity to summer temperatures between males and females (**Chapter 3 Supplement S1**). We saw a pronounced difference however to temperatures at Kirkenes site where females showed stronger correlations as compared to males. A shortcoming of this study is that as discussed in the earlier chapter there is fair amount of heterogeneous growth along the length of the stem of shrubs which could be due to a number of intrinsic and extrinsic factors. We could not differentiate which of the differences we see are gender-specific or an attribute of heterogeneous growth architecture caused by local micro-site conditions. Generally, we recommended that an unbiased sampling of equal males and females is advisable. However, from the moderate differentiation noted in the overall analysis, we cannot deny the possibility that reproductive effort from females causes differential resource allocation which might induce short-term artificial trends in ring-width data, therefore, a female-biased sample set might have more noise in the data. We recommend that such a multifold analysis with other shrub species is essential and can bring a deeper understanding how gender differentiation can influence site-chronologies.

Ecological Responses and Synergy of Methods:

Climate reconstructions and ecological indications are the two main usages of tree-ring data. Numerous studies with climate-reconstructions and eco-sensitivity have based these investigations using tree-rings as proxies. Similarly, annual rings from shrubs have been used for many ecological indications from glacial retreat (Buras et al., 2012; Buras et al., 2017), to establishing climate-growth relationships (Pellizzari et al., 2014) to tracing sea-surface temperatures (Beil et al., 2015). However, there are hardly any reconstructions which are purely based on annual rings from shrubs. This might be so, because of reasons like relatively less age of shrubs as compared to trees and asynchronous or heterogeneous growth, which makes capturing the common signal in a population stand difficult. Prior studies with remote sensing and repeat photography have shown that shrub expansion in the Arctic is heterogeneous and can differ spatially (Myers-Smith et al., 2011; Tape et al., 2012). Therefore, a deep understanding of response mechanisms in shrubs is imperative. Secondly, shrubs being highly influenced by macro-environmental-factors like climate, exposition, the direction of the wind etc. are also greatly influenced by micro-site conditions like the nature of substrate, herbivory and insect outbreaks. Shrub responses to these factors can vary spatially and temporally (Arft et al., 1999; Tape et al., 2006) and is not easy to disentangle and isolate proxy-response relationship. In **Chapter 4** and **Chapter 5** we explored the potential of shrubs for reconstruction using a test case of *Alnus viridis* ssp *crispa* and also compared shrub response to current climate warming as compared to trees using a test case of *Juniperus communis*.

In **Chapter 4** we correlated summer (June-July) temperatures with ring-width data from *Alnus viridis* ssp *crispa* and found significant positive correlations. Initially, when we tested for stability of temperature growth relationships using bootstrapped transfer function stability test (BTFS) for the entire period (1958-2012) the model failed stability tests. However, with the correction of three rings (i.e. from 2004-2007) the model passed all tests. When the stem-disks were closely examined for these years using wood-anatomical procedures of thin sectioning cell-wall abnormalities (exceptionally thin rings) were detected. When corrected for these years the model passed all stability tests. A pointer year analysis confirmed that these years corresponded to a moth larval (*Eurois occulta*) out-break in the sampling area. This showed that a combination

of techniques using ring-width measurements and wood anatomy could present promising results for the use of shrubs in reconstructions. It is true that not in all ecological settings can the effects of micro-site events/conditions be disentangled for a clear growth-response signal however a synergetic approach like this can very much improve data quality and could aid in climate reconstructions from areas where climate data is not available.

Further, in **Chapter 5** we compared the climate-growth sensitivity of trees and Juniper shrubs from a wide range of eco-regions ranging from Polar Urals in the north to the Iberian systems in Mediterranean region. At all sites tree cores and shrub stem-disks were collected from same ecosystems. This was done so that the macro-climate in all individual systems would be the same making the results comparable. We assumed that shrubs being stunted growth-forms with entire growth closer to the ground, would be relatively less sensitive to macro-climatic drivers and would be more influenced by local micro-climates, local topography and ground temperatures. On the contrary, we found that in the Mediterranean biome, shrubs were more sensitive to climate warming in the last decades than trees. A decoupling of climate sensitivity was seen among trees and shrubs throughout the dataset, but was more pronouncedly seen for Mediterranean region. Trees in the Mediterranean, post-1950s, might be induced by a drought stress and hence were less sensitive to climate warming.   This showed that shrubs like trees, do react to environmental changes but have very different responses. These differences could occur because of a variety of reasons like at an individual level – differences in growth within individuals (**Chapter 2**), between sexes of the same species (**Chapter 3**) – to differences at a community level like differing resilience to environmental stresses, differing adaptive mechanisms which might prevail at species distribution margins, or differences in resource consumption within plant communities (Elmendorf et al., 2012a; Myers-Smith et al., 2015a). It is, therefore, necessary to study these relationships using functional plant traits comparing them to abiotic changes. This would improve our understanding of vegetation response mechanisms at a community level.

Plant Traits: An Eco-climatological Response

Studies have shown that shrub response to climate can differ spatially and temporally (Elmendorf et al., 2012a; Tape et al., 2012). From the discussion from **Chapter 2**, **Chapter 3** and **Chapter 5**, it is evident that these changes prevail at various resolutions starting from heterogeneous growth within individuals to entire population stands and communities. Contemporary warming will bring about changes in plant communities and vegetation structure in the Arctic (Post et al., 2009; Elmendorf et al., 2012b). This suggests that if one has to model vegetation response in the Arctic, it is important to study functional responses (plant traits) which encompass a broader spectrum of ecological indications than pure 'radial-growth-response' relationships (Myers-Smith et al., 2015a). In **Chapter 6** we looked at a biome-wide study which encompassed plant trait data from 117 sites in the Arctic. The main objective of this investigation was to understand differences in spatial-temporal responses in plant communities to the current warming. This is a crucial feature as plant traits are directly linked with water balance, carbon-nutrient dynamics, changes in albedo, and subsequent differential surface-heat exchange which influence regional and global climates. As the Arctic has approximately world's 50% of underground carbon reserves in tundra regions under permafrost soils (Osterkamp, 2007; Blok et al., 2010), understanding the response of plant traits is critical as they act as indicators and primers in the primary productivity of a biome. Primary productivity in a biome is directly linked with nutrient turnover and the subsequent carbon cycling. Productivity on one hand is influenced by warming, but on the other also acts in feedback mechanism such as reduction in summer albedo because of increase in crown-covers which traps more heat becoming a driver for "greening" of the Arctic. Plant traits such as leaf nitrogen content, specific leaf area (SLA), and leaf dry matter content (LDMC), affect primary productivity whereas differences in size related traits such as plant height and leaf area influence hydrology, albedo and carbon storage. In our study, we observed that overall, leaf area, intra-specific plant height, SLA and LDMC had a strong link with summer temperature. However these were not consistent at community levels. We observed a significant change in community plant height over the span of 27 years (**Chapter 6 Figure a, Figure b**). Community plant height also showed a strong relationship to temperatures suggesting that it was a response to warming. Soil moisture content also showed a significant impact on the strength and progression of

temperature-trait relationships signifying the importance of water availability as a crucial factor in the future. However, some traits like SLA and LDMC did not show strong temperature-trait relationships on a temporal scale. SLA and LDMC lagged on a bi-decadal time series analysis suggesting differences in responses between intra-specific and inter-specific plant traits.

Overall, we found a complex interlinking between temperature, soil moisture, and plant traits. Not all plant traits responded to temperature and soil moisture (e.g. specific leaf area) suggesting a limitation of the model or other unexplained biotic or abiotic influences impacting specific traits. Another aspect which could influence SLA and LDMC are genotypic factors which cannot be explained from our investigation. Even though the study cannot explain all trait-factor relations entirely, it is clear that plant traits reacting to current warming can be instrumental in future projections of Arctic ecosystem modeling.

Inferences and Future Questions:

From my research with shrubs, I understood that shrubs, now more than ever, are important to be studied because of their role in the Arctic. Shrubs are not only important as indicators of current warming but also as actors in the feedback mechanisms which are set in motion because of shrubification of the Arctic. Shrubs, from a variety of studies as discussed in **Chapter 1** and **Chapter 6** have proven to be good proxies of change, however, there are still knowledge gaps about the growth architecture and shrub responses to environmental factors.

From our investigation, it was evident that even though shrubs are woody species that form annual rings, their environmental response mechanisms seem to differ significantly from that of trees. Most of the shortcomings arising with shrubs-based dendrochronology are due to irregular growth patterns among individuals and even more so from within individuals as seen from the findings of **Chapter 2** and **Chapter 3**. Therefore, currently used methods like using singular stem-disks for investigations need to be revised. From our study in **Chapter 2,** we could not recommend which stem-disk could be used as a standard protocol as our study was confounded to Juniper species and contrasting findings from Ropars et al. (2017) with Betula species confirm that this could be species specific. We found that for the Ural sites, for Junipers, radial

measurements from stem-disks higher up the stem (SD20 in our case: **Chapter 2: Fig 3** and **Fig 4**) showed best climate-sensitivity. Therefore, it remains unanswered what could be the best practice for selection of stem-disks when aimed at tracing climate-sensitivity.

A study by Sadras and Denison (2009) suggested that even within plants various parts can compete for resources if it is beneficial for the overall growth of the plant. This logically means that, if so, then even within shrubs, a single stem-disk just represents a response to specific time section. The influencing factors might change over time resulting in asynchronous growth, for reasons which could also change over time. Similarly, if resource allocation changes within an individual, does gender-specificity play a role in it? How could these interrelated processes be addressed while disentangling climate-growth responses? Are these factors species-specific? From our investigation in **Chapter 3,** we found that gender-specific differences were moderate but our study was limited by low sample size and was only based on *Juniperus communis* species. However, the same could be tested with larger sample size to see if the reproductive effort in females influences site-chronologies. In **Chapter 4,** we saw that reconstructions with annual rings from shrubs could be possible if data quality is improved by using a combination of methods from wood-anatomy and dendrochronology.

In **Chapter 5,** we saw divergent responses of shrubs and trees to current warming. This re-iterates that shrubs could be sensitive to different environmental parameters than trees. This can change spatially and temporally, however, such comparisons could help in devising more robust climate reconstructions. From plant traits itself, it is evident that only some plant traits are responsive to current warming and that this also differs within communities. Therefore, devising multi-proxy models using dendrochronology and plant traits could be a more robust approach for future Arctic modeling.

Deliverables and Learning Outcomes:

This thesis comprehensively reviews the potential use of shrubs in tracing current climate warming in the Arctic and Alpine tundra using dendro-ecology. The following are the major highlights from this study. This investigation looks at -

1. The current methods of stem-disk measurements for ring-widths in shrubs and identifies and highlights knowledge-gaps and shortcomings.

2. Highlights the issue of changing climate sensitivity along the length of the stem questioning the use of only single/lowermost stem-disks for analytical purposes.

3. Investigates the impact of sex-specificity and shows how it could be an influential factor to be considered in sample selection in dioecious shrubs.

4. Looks at the reconstruction potential of shrubs with a case study of *Alnus viridis* ssp *crispa* and proposes the use of combined methods from dendrochronology and wood-anatomy to devise robust reconstructions using ring-width data from shrubs.

5. Compares climate-sensitivity among trees and shrubs in a network of study sites across ecoregions ranging from Polar Urals to the Mediterranean, confirming divergent growth responses to current warming. This study clearly highlights the differing climate sensitivity between trees and shrubs

6. Compares plant traits from 117 sites to show plant traits as useful indicators for tracing current warming and illustrates their role in the carbon-nutrient cycling and vegetation feedback mechanisms.

Overall, this study looks at shrub response to climate change in the Arctic at various scales starting from growth within individual stem-disks of shrubs to biome wide vegetation response to the climate. The study follows a common thread of how, from ring-width to functional traits, can shrubs be instrumental in monitoring changes in the Arctic. It encompasses data from circumpolar Artic in a latitudinal extent from Greenland through Norway to Polar Russia, and from Polar Urals to the Mediterranean in a longitudinal extent, emphasizing the significance of shrubs as auditees and agents of change in the Arctic and alpine tundra.

References:

Adams, R., 2014. Juinpers of the world: The genus Juniperus, 4 ed. Trafford Publishing Co, Bloomington, Indiana.

Anisimov, O.A., D.G. Vaughan, T.V. Callaghan, C. Furgal, H. Marchant, T.D. Prowse, H. Vilhjálmsson, J.E. Walsh, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden, Hanson, C.E., 2007. Polar regions (Arctic and Antarctic). Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 653-685.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jonsdottir, I.S., Laine, K., Vesque, E.L., Marion, G.M., Molau, U., Mølgaard, P., Nordenhäll, U., Rasyhivin, V., Robinson, C.H., Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M., Wookey, P.A., 1999. Responses of Tundra plants to experimental warming: Meta-Analysis of the international tundra experiment. Ecological Monographs 69, 491-511.

Bär, A., Bräuning, A., Löffler, J., 2007. Ring-width chronologies of the alpine dwarf shrub Empetrum hermaphroditum from the Norwegian mountains. International Association of Wood Anatomists (IAWA) 28.

Barradas, M.C.D., Otilia, C., 1999. Sexual dimorphism, sex ratio and spatial distribution in male and female shrubs in dioecious species Pistacia lentiscus Folia Geobotanica 34, 163-174.

Beil, I., Buras, A., Hallinger, M., Smiljanic, M., Wilmking, M., 2015. Shrubs tracing sea surface temperature--Calluna vulgaris on the Faroe Islands. Int J Biometeorol 59, 1567-1575.

Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C., Berendse, F., 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Global Change Biology 16, 1296-1305.

Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M.M.P.D., Sauren, P., Berendse, F., 2011. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences 8, 1169-1179.

Boulanger-Lapointe, N., Lévesque, E., Baittinger, C., Schmidt, N.M., 2016. Local variability in growth and reproduction of Salix arctica in the High Arctic. Polar Research 35, 24126.

Buras, A., Hallinger, M., Wilmking, M., 2012. Can shrubs help to reconstruct historical glacier retreats? Environmental Research Letters 7, 044031.

Buras, A., Lehejček, J., Michalová, Z., Morrissey, R.C., Svoboda, M., Wilmking, M., 2017. Shrubs shed light on 20th century Greenland Ice Sheet melting. Boreas, 667-677.

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

Cavigelli, M., Paulos, M., Lacey, E.P., 1986. Sexual dimorphism in a Temperate Dioecious Tree Ilex montana The American Midland Naturalist 115, 397-406.

Cook, E.R., Kairikustis, L.A., 1992. Methods of Dendrochronology: Applications in the Environmental Sciences. Springer Science+Buisness Media.

D'Arrigo, R.D., Cook, E.R., Jacoby, G.C., Briffat, K.R., 1993. NAO and sea surface temperature signature in tree-ring records from the North Atlantic sector. Quaternary Science Reviews 12, 431-440.

Elmendorf, S.C., Henry, G.H., Hollister, R.D., Bjork, R.G., Bjorkman, A.D., Callaghan, T.V., Collier, L.S., Cooper, E.J., Cornelissen, J.H., Day, T.A., Fosaa, A.M., Gould, W.A., Gretarsdottir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jonsdottir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver, G.R., Stenstrom, A., Tolvanen, A., Totland, O., Troxler, T., Wahren, C.H., Webber, P.J., Welker, J.M., Wookey, P.A., 2012a. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol Lett 15, 164-175.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jónsdóttir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lara, M., Lévesque, E., Magnússon, B., May, J.L., Mercado-Dı´az, J.A., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Martin Schmidt, N., Shaver, G.R., Spasojevic, M.J., Þórhallsdóttir, Þ.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P.J., Welker, J.M., Wipf, S., 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2, 453.

Freeman, D.C., Klikoff, L.G., Harper, K.T., 1976. Differential Resource Utilization by the Sexes of Dioecious Plants. Science 193, 597-599.

Gauquelin, T., Bertaudière-Montès, A., Badri, W., Montès, N., 2002. Sex ratio and sexual dimorphism in mountain dioecious thuriferous juniper (Juniperus thurifera L., Cupressaceae). Botanical Journal of the Linnean Society 138, 237-244.

Gazol, A., Camarero, J.J., 2012. Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. Plant Ecology 213, 1687-1698.

Godley, E.J., 1976. Sex ratio in Clamatis gentianoides. New Zeland Journal of Botany 14, 299-306.

Greenwood, S., Jump, A.S., 2014. Consequences of Treeline Shifts for the Diversity and Function of High Altitude Ecosystems. Arctic, Antarctic, and Alpine Research 46, 829-840.

Haflidason, H., Sejrup, H.P., Kristensen, D.K., Johnsen, S., 1995. Coupled response of the late glacial climatic shifts of northwest Europe reflected in Greenland ice cores: Evidence from the northern North Sea. Geology 23, 1059-1062.

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

Hantemirov, R., Shiyatov, S., Gorlanova, L., 2011. Dendroclimatic study of Siberian juniper. Dendrochronologia 29, 119-122.

Holz, A., Haberle, S., Veblen, T.T., De Pol-Holz, R., Southon, J., 2012. Fire history in western Patagonia from paired tree-ring fire-scar and charcoal records. Climate of the Past 8, 451-466.

Juszak, I., Erb, A., Maximov, T.C., Schaepman-Sturb, G., 2014. Arctic shrub effects on NDVI, summer albedo and soil shading. Remote Sensing of Environment 153, 78-79.

Kolishchuk, V.G., 1990. Dendroclimatological study of prostrate woody plants, in: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Applications in the environmental sciences. Kluwer, Dordrecht, Boston, London, pp. 51-55.

Körner, C., 2012a. Alpine Treelines: Functional Ecology of Global High elevation Tree limits. Springer, Basel.

Körner, C., 2012b. Treelines will be understood once the functional difference between a tree and a shrub is. Ambio 41 Suppl 3, 197-206.

le Roux, P.C., Luoto, M., 2014. Earth surface processes drive the richness, composition and occurrence of plant species in an arctic–alpine environment. Journal of Vegetation Science 25, 45-54.

Lehejček, J., 2015. Dwarf tundra shrubs growth as a proxy for late Holocene climate change. Czech Polar Reports 5, 185-199.

Liang, E., Eckstein, D., 2009. Dendrochronological potential of the alpine shrub Rhododendron nivale on the south-eastern Tibetan Plateau. Ann Bot 104, 665-670.

Liang, E., Lu, X., Ren, P., Li, X., Zhu, L., Eckstein, D., 2012. Annual increments of juniper dwarf shrubs above the tree line on the central Tibetan Plateau: a useful climatic proxy. Ann Bot 109, 721-728.

Lloyd, D.G., Webb, C.J., 1977. Secondary Sex Characters in Plants Botanical Review 43, 177-216.

Lushuang Gao, Chunyu Zhang, Xiuhai Zhao, Gadow, K.V., 2010. Gender-Related Climate Response of Radial growth in dioecious *Fraxinus manshurica* trees. Tree-Ring Research 66, 105-112.

Malik, I., Wistuba, M., 2012. Dendrochronological methods for reconstructing mass movements — An example of landslide activity analysis using tree-ring eccentricity. Geochronometria 39, 180-196.

McKay, N.P., Kaufman, D.S., 2014. An extended Arctic proxy temperature database for the past 2,000 years. Sci Data 1, 140026.

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., Speed, J.D.M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N.M., Baittinger, C., Trant, A.J., Hermanutz, L., Collier, L.S., Dawes, M.A., Lantz, T.C., Weijers, S., Jørgensen, R.H., Buchwal, A., Buras, A., Naito, A.T., Ravolainen, V., Schaepman-Strub, G., Wheeler, J.A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015a. Climate sensitivity of shrub growth across the tundra biome. Nature Climate Change 5, 887-891.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6, 045509.

Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S.A., Weijers, S., J. Trant, A., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Dawes, M.A., A. Wheeler, J., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B.C., Lévesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilmking, M., 2015b. Methods for measuring arctic and alpine shrub growth: A review. Earth-Science Reviews 140, 1-13.

Obeso, J.R., Alvarez-Santullano, M., Retuerto, R., 1998. Sex Ratios, Size Distributions, and Sexual Dimorphism in the Dioecious Tree Ilex aquifolium (Aquifoliaceae). American Journal of Botany 85, 1602.

Ortiz, P.L., Arista, M., Talavera, S., 2002. Sex ratio and reproductive effort in the dioecious Juniperus communis subsp. *alpina* (Suter) Čelak. (Cupressaceae) along an altitudnal gradient. Annals of Botany 89, 205-211.

Osterkamp, T., 2007. Characteristics of the recent warming of permafrost in Alaska. Journal of Geophysical Research-Earth Surface 112, 1-10.

Pellizzari, E., Camarero, J.J., Gazol, A., Granda, E., Shetti, R., Wilmking, M., Moiseev, P., Pividori, M., Carrer, M., 2017. Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. Global Change Biology 23, 3169-3180.

Pellizzari, E., Pividori, M., Carrer, M., 2014. Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps. Environmental Research Letters 9, 104021.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., Aastrup, P., 2009. Ecological Dynamics Across the Arctic Associated with Recent Climate Change. Science 325, 1355-1358.

Rayback, S.A., Henry, G.H.R., 2006. Reconstruction of Summer Temperature for a Canadian High Arctic Site from Retrospective Analysis of the Dwarf Shrub, Cassiope tetragona. Arctic, Antarctic, and Alpine Research 38, 228-238.

Ropars, P., Angers-Blondin, S., Gagnon, M., Myers-Smith, I.H., Lévesque, E., Boudreau, S., 2017. Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. Global Change Biology 23, 3281-3291.

Rozema., J., Boelen, P., Doorenbosch, M., Bohncke, S., Blokker, P., Boekel, C., Broekman, R.A., Konert, M., 2006. A Vegetation, Climate and Environment Reconstruction Based on Palynological Analyses of High Arctic Tundra Peat Cores (5000–6000 years BP) from Svalbard. Plant Ecology 182, 155-173.

Sadras, V.O., Denison, R.F., 2009. Do plant parts compete for resources? An evolutionary viewpoint. New Phytol 183, 565-574.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., Wilmking, M., 2011. Drought matters – Declining precipitation influences growth of Fagus sylvatica L. and

Quercus robur L. in north-eastern Germany. Forest Ecology and Management 262, 947-961.

Scharnweber, T., Manthey, M., Wilmking, M., 2013. Differential radial growth patterns between beech (Fagus sylvatica L.) and oak (Quercus robur L.) on periodically waterlogged soils. Tree Physiol 33, 425-437.

Schweingruber, F.H., 1988. Tree Rings: Basics and Applications of Dendrochronology. Springer, Dordrecht, Netherlands.

Schweingruber, F.H., Poschold, P., 2005. Growth rings in herbs and shrubs life span age determination and stem anatomy Forest Snow and Landscape research 79, 195-415.

Sonesson, M., Callaghan, T.V., 1991. Strategies of survival in plants of the Fennoscandian tundra. Arctic 44, 95-105.

Speer, J.H., 2010. Fundamentals of Tree-ring research. The University of Arizona Press, Tucson.

Sturm, M., Racine, C., Tape, K., 2001. Increasing shrub abundance in the Arctic. Nature 411, 546.

Tape, K.D., Hallinger, M., Welker, J.M., Ruess, R.W., 2012. Landscape Heterogeneity of Shrub Expansion in Arctic Alaska. Ecosystems 15, 711-724.

Tape, K.D., Sturm, M., Racine, C.H., 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12, 686-702.

Ward, L.K., 2007. Lifetime sexual dimorphism in Juniperus communis var. communis. Plant Species Biology 22, 11-21.

Weijers, S., Broekman, R., Rozema, J., 2010. Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub Cassiope tetragona. Quaternary Science Reviews 29, 3831-3842.

Wilmking, M., Hallinger, M., Van Bogaert, R., Kyncl, T., Babst, F., Hahne, W., Juday, G.P., de Luis, M., Novak, K., Völlm, C., 2012. Continuously missing outer rings in woody plants at their distributional margins. Dendrochronologia 30, 213-222.

Woodcock, H., Bradley, R.S., 1994. Salix arctica (Pall.): Its potential for dendroclimatological studies in the High Arctic. Dendrochronologia 12, 11-22.

Hiermit erkläre ich, dass diese Arbeit bisher von mir weder an der Mathematisch-Naturwissenschaftlichen Fakultät der Ernst-Moritz-Arndt-Universität Greifswald noch einer anderen wissenschaftlichen Einrichtung zum Zwecke der Promotion eingereicht wurde.

Ferner erkläre ich, dass ich diese Arbeit selbstständig verfasst und keine anderen als die darin angegebenen Hilfsmittel und Hilfen benutzt und keine Textabschnitte eines Dritten ohne Kennzeichnung übernommen habe.

Unterschrift des Promovenden

Northern Ural Mountains
N 61°17'40.9"
E 059°17'17.9"
Rohan Shetti 2014

Curriculum Vitae and Acknowledgements

Rohan Shetti: Curriculum Vitae

Personal Information:

Name	: Rohan Shetti
Nationality/ Visa	: Indian, (with residence permit to study and work in Germany)
Birth date	: 31.08.1987
Current Position	: Ph.D. researcher at Greifswald University, Germany

---

Education and Work Experience:

Since 2013 - 2018	I. Finishing doctoral (Ph.D.) research at Landscape Ecology and Ecosystem Dynamics (LEED) working group, Greifswald University, Germany. [Modelling climate-growth relationships using dendrochronological data from shrubs in the Arctic; R-platform] II. Honorary post of Vice President at Tribal Mensa Nurturing Program (TMNP: www.tribalmensa.org)
2012	Completed Master Degree in Landscape Ecology and Nature Conservation (LENC) MSc, Greifswald University, Germany. (Grade 1.8)
2011 - 2012	I. Master Thesis: Studying vegetation patterns and comparing biodiversity in a state managed reserve forest and a temple managed sacred grove in Western-Ghats (Indian tropical deciduous forests). Supervisor: Prof. Dr. Konrad Ott II. Summer school in Bolzano-Bozen "Forestry and Agriculture".
2010 – 2011	I. Master Degree coursework Greifswald University (M.Sc). II. Eco-Logic Restoration Services, Ltd. Ocean Springs Mississippi, USA (Restoration Ecologist: Internship)
2008 – 2009	Environmental Educational Assistant: Field Studies Council (FSC), Juniperhall, Surrey, London (Internship).
2006 – 2010	Undergraduate Degree: Environmental Science Specialization: Water Chemistry and Toxicology B.Sc. (Hon). Kingston University, London.

Publications and Research in progress:

Ecology and Environmental Science:

Pellizzari E, Camarero J, Gazol Granda E, **Shetti R**, Wilmking M, Moiseev P, Pividori M,Carrer
M (2017) Diverging shrub and tree growth from the Polar to the Mediterranean
biomes across European continent. – **Global Change Biology**.

Shetti R, Smiljanic M, Buras A, Wilmking M (2018) Climate sensitivity is affected by growth
differentiation along the length of *Juniperus communis* L. shrub stems in the
Ural Mountains.– **Dendrochronologia**

Shetti R, Smiljanic M, Buras A, Hallinger M, Grigoriev A, Wilmking M (2018) Does sex matter?
Gender specificity and its influence on site-chronologies in dioecious shrub
Juniperus sp. – **Dendrochronologia**

Wilmking M, Buras A, Lehejček J, Lange J, **Shetti R,** van der Maten E (2018) Influence of
larval outbreaks on the climate reconstruction potential of an Arctic shrub –
Dendrochronologia

Lehejček J, Buras A, **Shetti R**, Pellizzari E, Wilmking (2017) Call to complete the circumarctic
juniper network – an environmental proxy. - **Biosciences in Polar and Alpine
Research 2017- Abstracts**

2012   Investigating vegetation and ecosystem diversity with respect to
management practices in Indian Tropical deciduous forests (Site: Western
Ghats, India) [Thesis: Greifswald University, Germany].

2010   Developed a bio-indication model to detect phosphate and nitrate pollution
fresh-water diatoms and algae (Site: River Mole and River Thames, London)
Supervisor: Dr. Stuart Downward. [Thesis: Kingston University, U.K.]

Yoga and Neurology

2014   Towards Enlightenment: Translation of book Yogavani
(Siddhayogopadesha) from Marathi / Sanskrit to English. Available at
Vasudevniwas Press, Pune India.

2014   A comparative study between modern discoveries of brain electrical
activity linked with Yoga, Vedas, Tantra as traditional techniques of brain

utilization enhancement. A case study from "Yogarahasya" written by his holiness Vasudevananada Saraswati Tembe Swami. – Pune University

Honors and Awards:

2000	Identified as a MENSAN by MENSA India for a 99+ percentile score of IQ
2010 – 2012	Stifterverband scholarship for postgraduate degree in Landscape Ecology and Nature conservation from Greifswald University.
2013 – 2016	ERA.NET Treeline-Project: Euro-Russian Federation Project to study the effects of climate change on Treeline advances in Russia and circumpolar Arctic
2016 – 2017	DAAD-STIBET scholarship for Ph.D. students, Greifswald University.
2017	Travel grant for TRACE conference in Kaliningrad: Association of Tree-ring research (ATR)

_____

General Skillset and Analytical Expertise:

❖ Data Analytics using R- Platform, Dataset domains: Dendrochronological data; climatological data; environmental informatics; Geo-spatial; QGIS secondary data.

❖ Statistical modeling using-R (Explorative analysis with Advanced Statistical modelling simulation models, projection analysis, testing for model stability).

❖ Designing environmental restoration projects.

❖ Development of restoration strategies based on succession models (reference states to progression).

❖ Dendrochronological / Dendro-ecological analysis / Dendro-climatological analysis.

❖ Cartographic and geo-informatics system (GIS): Arc-GIS / Arc MAP (10.4.1) and Q-GIS (platform).

❖ Development of post-project monitoring systems (system progression analysis e.g. Lake restoration project; eradication of invasive species in forests).

❖ Chemical analysis of Lake and river systems (trophic analysis; geo-chemical analysis)

❖ Toxicological analysis using HPLC (High Performance Liquid Chromatography)

❖ Trace element detection using (Flame Induction Spectrometry)

_____

Other Activities and Interests:

I have been an active practitioner of yoga and meditation for the last decade. It is something which started as a practice and eventually became a way of life. In my spare time I am a photography enthusiast and have published my work in magazines and online galleries. Most of my work is available at http://yourshot.nationalgeographic.com/profile/157394/ and at https://www.flickr.com/photos/rohan-shetti/ , https://www.flickr.com/photos/rohanshetti/

_____

Contact details:

Linkedin	:	https://www.linkedin.com/in/rohan-shetti-40a66756/
Research Gate	:	https://www.researchgate.net/profile/Rohan_Shetti
Greifswald University:		http://t3-temp.botanik.uni-greifswald.de/3708.html
Email	:	rohanshetti@gmail.com
Phone	:	+491606271836

References:

Doctoral Supervisor:

Prof. Dr. Martin Wilmking

Department of Landscape Ecology
and Ecosystem Dynamics Greifswald University Soldmannstrasse-15
17489 Greifswald Germany
Email: wilmking@uni-greifswald.de

Master thesis Supervisor

Prof. Dr. Konrad Ott

Department of Philosophy CAU Kiel
Leibnizstr. 4 | R. 333
24118 Kiel
Email: ott@philsem.uni-kiel.de

Founder Tribal Mensa Project

Dr. Narayan Desai
Executive Director, Society for Ecological Restoration-India
Principal Investigator, Tribal Mensa Nurturing Program

Email: nrd1675@gmail.com

Acknowledgements:

I always like a long walk through the woods as it helps me stray my mind on the lines of being at 'wonder' and being 'lost'. It is those moments which make me aware and fill me with life to wonder and observe the intricacy and beauty of the natural design. Thanks to this investigation I got a chance to visit many pristine places in the Urals and gather many such introspective moments. So, firstly I would like to thank my shrubs who have taught me many lessons, like patience, perseverance, and humbleness at the same time made me travel to wonderful fieldwork expeditions.

I would like to thank my supervisor Prof. Martin Wilmking who throughout my PhD studies has always been motivating and yet patient with me. I appreciate the help of all my colleagues at Greifswald University and our working group who made my study and stay very enjoyable. I would like to thank Rene Fronczek and Ilka Beil who have in times of dire needs "especially with German translations" helped me going out of their way. May it be field work, laboratory analysis, or just day- to-day interactions, all people at our working group made my life experience thoroughly enjoyable.

I would like to thank Dr Allan Buras and Marko Smilijanic who guided me extensively with my analysis. They were very patient with me which helped me lay a good foundation in R programming. As they say "some skills are learnt by choice and some by need", so in my need of learning programming Marko and Allan mentored me well for which I will always be thankful. I would like to specially thank Stefan Busse for helping me with making maps for my sites and also helping me with proofing of this dissertation.

I thank my colleagues in Russia at Russian Academy of Sciences who helped with my field expedition in the Ural Mountains. I highly appreciate all the help extended to me by my parents, wife, friends and all mentors who have helped me with advice and suggestions on this way.

I would like to thank ERA.Net RUS and DAAD-STIBBET for funding my research and providing me with financial support during my fieldwork in the Ural Mountains.

Photography

All the images including the thesis cover are taken by me. Only the images of cell thin sections are taken by Jelena Lange.