Treelines in the Swiss Alps:
Growth dynamics and forest succession in
a changing climate

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Summary

The alpine treeline is one of the most prominent ecosystem boundaries in nature. The two ecosystems that are separated by this ecotone – the subalpine forest and the alpine tundra – provide essential ecosystem goods and services (EGS) in densely populated mountain regions like the European Alps. Ongoing global climate change with its temperature increase affects the major limiting factor of tree growth close to treeline. Moreover, mountain regions have experienced a more pronounced temperature increase than the global average, and this is expected to continue into the future, with far-reaching consequences for forest dynamics at treeline and therefore also for the EGS provided by both ecosystem types. Although the alpine treeline has attracted scientific interest for centuries, understanding the interplay between factors influencing treeline formation and subalpine forest dynamics, especially at the regional to local scale, remains a challenge. To reliably quantify the consequences of global warming for subalpine forests approaching treeline, an in-depth understanding of the large-scale drivers is required, but also of the regional- to local-scale modulators of tree population dynamics.

The aim of this PhD thesis is to enhance this understanding by means of empirical analyses of the past and simulations of future treeline dynamics. In particular, I wanted to (i) identify the climatic drivers of short-term tree growth dynamics, reveal the underlying functional form of the growth-temperature relationship, and elucidate the role of inter- and intra-species variability in modulating the growth response of trees; (ii) scrutinize the relative importance of air and soil temperature variables for determining individual tree growth; (iii) assess treeline dynamics at larger spatial and temporal scales, by exploring the causes of population-wide long-term growth trends, and by isolating important regional- to local-scale drivers of tree population dynamics; and (iv) synoptically validate all these findings regarding their importance as drivers of treeline dynamics, which then allows to robustly explore the development of forest dynamics at and directly below treeline under changing climatic conditions. All analyses of my PhD thesis use the
three study sites Bosco/Gurin, Hohgant and Zermatt. They experience three
distinct climate regimes of the Swiss Alps (Southern, Northern and Central
Alps) and are representative for a variety of prevailing growth conditions.

In Part I, I analyzed the effects of past climate variability on short- to
long-term tree growth dynamics, with a focus on among-tree variability and
potential climate change feedback effects. Even though previous research had
suggested among-tree variability to be of large significance, it has not yet been
systematically considered in studies of tree growth dynamics. Thus, I con-
ducted a dendroecological study of four major tree species (*Picea abies*, *Larix
decidua*, *Pinus cembra*, *Pinus mugo*) and employed linear mixed-effects mod-
els (LMMs) to quantify climate influences on short- and long-term growth
dynamics. LMMs simultaneously capture among-tree variability and feed-
back effects due to inter-species competition. These results were comple-
mented with stand-level analyses of size and age structure using a combina-
tion of remotely sensed and field-sampled data. The LMMs revealed large
amounts of previously unquantified among-tree variability regarding when
and to what extent individual trees invest assimilates into growth. Further-
more, the LMMs indicated strongly positive temperature effects on growth
during short summer periods across all species, and significant contributions
of fall conditions (*L. decidua*). Furthermore, the influence of snow was im-
plicitly indicated by current year’s spring effects (*L. decidua*, *P. abies*). In
the longer term, all species showed positive growth trends at the highest ele-
vations, but indifferent patterns with just slightly decreasing elevation. *Larix
decidua* exhibited even negative growth trends just below treeline, whereas
*P. abies*, *P. cembra*, and *P. mugo* showed a range of positive trends with
decreasing elevation. Clearly, the population-wide positive response at the
highest elevations reflected the effects of ameliorated climatic conditions over
time, but at the same time it revealed the prominent role of among-tree vari-
ability in controlling the response of treeline growth dynamics to climate
change. Due to increased competition, first signs of long-suspected negative
feedback effects of climate change on stand dynamics at treeline emerged.

In Part II, I further scrutinized the role of temperature as the most im-
portant determinant of tree growth as the cold edge of a species’ distribution
is approached. Both radial and height growth of trees are determined by sev-
eral interlinked processes, which exhibit different reactions to temperature.
I unraveled the relative importance of (i) soil vs. air temperature, (ii) abso-
lute temperatures vs. time-integrated temperatures, and (iii) reserves from
the previous growing season for annual radial tree growth, and I attempted
to capture the form of the functional relationship between temperature and
growth. To this end, I measured long-term, high-resolution (both spatially
and temporally) air and soil temperature along elevational transects at each study site and paired them with basal area increment (BAI) data. In addition, I covered the temporal component, i.e. past and present climate variability. Hence, I was able to quantify the growth reactions to temporal as opposed to spatial variability. Close to treeline, BAI of all species depended on integrated rather than absolute temperatures. While BAI was best explained by combining air temperature of the previous and current growing seasons, soil temperature was important only at Bosco/Gurin, a site with extensive snow cover in late winter/spring. When moving down from upper treeline, the temperature-growth relationship was strongly non-linear, showing a rapid decrease of temperature limitation and an increasing importance of other growth-determining factors. For the last 50 years, temperatures have been rising substantially at all sites, with isotherms moving upward 160–260 m in elevation. The threshold-dependence of growth to temperature has led to a positive trend of BAI over time, which consequently was consistent throughout the population only at highest elevations.

In Part III, I employed the dynamic forest succession model ForClim to assess the ecological relevance of different abiotic and biotic factors driving subalpine forest dynamics, which were partly derived from the first two parts. To this end, I evaluated different model variants based on their capability to reproduce observed individual-tree and stand-scale properties derived from (i) my dendroecological data, (ii) forest size structure as remotely sensed and measured in the field, and (iii) in-situ temperature data from the study sites. Subsequently, using the best model and climate change scenarios, I projected the future development of treeline elevation, growth dynamics of the subalpine forest and its species composition. This mechanistic approach revealed a pivotal role of the precipitation regime in modulating growth conditions at treeline. Precipitation mainly controlled incoming radiation and, via the snow melt date, determined the start of the growing season. Projections of subalpine forest dynamics under future climate suggested substantial changes compared to present-day conditions in all three Alpine regions that I studied. Only after a lag of ca. 100 years, the subalpine forest moved uphill by several 100 m even under the low-end climate change scenario. Simultaneously, a strong immigration of montane forest species at the lower end of the present-day subalpine forest became apparent.

Overall, I showed that the reaction of treeline forest dynamics to past and future climates is strongly influenced by temperature variability. At the same time, it is significantly modulated by other abiotic forcings such as the precipitation regime and biotic drivers like the substantial among-tree growth variability or competition effects. These drivers act on different spa-
tial scales, from climatic regions down to the individual tree and tree-specific structures such as roots vs. needles. Consequently, it is a misconception to assume that increased temperatures due to climate change generally ameliorate growth conditions at treeline. The highly non-linear relationship between radial tree growth and temperature leads to a pronounced increase in growth variability, just after the temperature limitation is overcome. This behavior is due to other growth-limiting factors setting in, but also partly founded in the previously unquantified among-tree variability. Declining growth trends with decreasing elevation may indicate negative feedback effects of climate change on tree growth due to increased stem density. In addition, the precipitation regime significantly modulates growth conditions at treeline, first by controlling cloud cover, air humidity and therefore the direct radiation energy available to the trees, and second through the amount of snow, thus restricting the period during which trees can actually grow.

In summary, the growth of trees at treeline reacts strongly to climate variability but is also decisively modulated by regional-to local-scale drivers. This can go as far as reversing the per se positive implications of increasing temperatures for tree growth close to its cold limit. Consequently, considering the above-mentioned population-internal and -external processes on smaller spatial scales allows for a significantly more reliable assessment of climate impacts on tree growth.
Zusammenfassung

Die Baumgrenze ist einer der markantesten Ökotone, die in der Natur vorkommen. Die beiden Ökosysteme, die er trennt – der subalpine Nadelwald und die alpine Tundra – stellen gerade in dicht besiedelten Bergregionen wie beispielsweise den europäischen Alpen lebenswichtige Ökosystemdienstleistungen zur Verfügung. Der fortschreitende globale Klimawandel wirkt sich durch den Temperaturanstieg auf den wichtigsten limitierenden Faktor des Baumwachstums nahe der Baumgrenze aus. Dieser Temperaturanstieg war in den vergangenen Jahrzehnten in Bergregionen sogar stärker ausgeprägt als im globalen Durchschnitt und wird dies höchstwahrscheinlich auch in Zukunft bleiben, was wiederum weitreichende Folgen für die Walddynamik nahe der Baumgrenze und damit auch für die Ökosystemleistungen haben wird.

Obwohl sich die Wissenschaft seit über zwei Jahrhunderten mit dem Phänomen der Baumgrenze befasst, ist das Zusammenspiel verschiedener Einflussfaktoren auf die Bildung der Baumgrenze sowie auf die Bestandesdynamik subalpiner Nadelwälder, insbesondere auf regionaler und lokaler Ebene, nicht abschliessend geklärt. Um die Auswirkungen der globalen Erwärmung auf subalpine Nadelwälder und die Baumgrenze zuverlässig quantifizieren zu können, ist ein besseres Verständnis einerseits von global wirksenden Einflüssen, aber andererseits auch von Prozessen, welche die Bestandesdynamik auf regionaler und lokaler Ebene beeinflussen, erforderlich. Das übergeordnete Ziel dieser Dissertation war deshalb, dieses Verständnis mittels empirischer Analysen bisheriger sowie Simulationen der zukünftigen Bestandesdynamik nahe der Baumgrenze zu vertiefen.

Zentrale Aspekte der vorliegenden Dissertation waren dabei, (i) klimatische Einflüsse auf die interannuelle Variabilität des Baumwachstums quantitativ zu bestimmen, die zugrunde liegende funktionelle Form der Zuwachstemperatur-Beziehung zu eruieren und die Rolle der Zuwachsvariabilität zwischen und innerhalb der Baumarten aufzuzeigen; (ii) die Bedeutung von Luft- und Bodentemperatur für das Wachstum individueller Bäume zu untersu-
(iii) die Walddynamik an der Baumgrenze in räumlich und zeitlich größeren Massstäben zu analysieren. Dies einerseits, um Wachstumstrends auf Bestandesebene sichtbar zu machen, und andererseits, um Prozesse zu identifizieren, welche die Bestandesdynamik auf regionaler und lokaler Ebene beeinflussen, zu identifizieren. Schliesslich (iv) bewerte ich diese Erkenntnisse hinsichtlich ihrer gesamthaften Bedeutung für die Walddynamik, was es mir erlaubt, die zukünftige Entwicklung der Walddynamik an der Baumgrenze unter sich verändernden klimatischen Bedingungen vorherzusagen. Alle Analysen wurden an den drei Standorten Bosco/Gurin, Holgant und Zermatt durchgeführt. Diese Standorte liegen in verschiedenen Klimaregionen der Schweizer Alpen (Süd-, Nord- und Zentralalpen) und repräsentieren damit eine Vielfalt von Wachstumsbedingungen.

P. cembra und P. mugo eher positive Trends mit abnehmender Höhe aufweise. Die positive Reaktion der Bäume an den höchstgelegenen Standorten spiegelt die sich verbessernenden Klimabedingungen an der Baumgrenze wider. Gleichzeitig zeigte sich aber auch die wichtige Rolle von Zuwachsunterschieden innerhalb derselben Baumart. Aufgrund der steigenden Konkurrenz wurden zudem erste Anzeichen der seit langem vermuteten negativen Rückkoppelungseffekte des Klimawandels auf die Walddynamik an der Baumgrenze sichtbar.

ner Bäume, was sich jedoch nur in den höchsten Lagen in einem positiven Zuwachstrend auf Bestandesebene widerspiegelte.


Insbesamt wurde in der vorliegenden Dissertation gezeigt, dass die Bestandesdynamik nahe der Baumgrenze einerseits stark durch die Temperatur bestimmt wird, andererseits aber durch Einflüsse wie dem jeweiligen Niederschlagsregime und biotischen Treibern (wie z.B. der erheblichen Zuwachsvariabilität innerhalb einzelner Baumarten) respektive durch sich ändernde Konkurrenzverhältnisse deutlich modifiziert wird. Alle Einflüsse wirken auf verschiedensten räumlichen Ebenen, angefangen von der Klimaregion bis zur Ebene des einzelnen Baumes und baumsspezifischen Strukturen wie Wurzeln und Nadeln. Folglich ist es ein Trugschluss anzunehmen, dass steigende Temperaturen aufgrund des Klimawandels die Wuchsbedingungen an der Baumgrenze generell verbessern. Die stark nichtlineare Beziehung zwischen Zuwachs und Temperatur führt zu einer deutlichen Zunahme der Wachstumsvariabilität unmittelbar nach Überwindung der Temperaturbegrenzung. Dieses Verhalten ist auf andere wachstumslimitierende Fakto-
ren zurückzuführen, die aber auch teilweise mit der bisher nicht quantitativ erfassten Baum-Gesamtvariabilität begründen lassen. Zunehmend negative Wachstumstrends einzelner Bäume mit abnehmender Höhe sind erste Anzeichen negativer Rückkopplungseffekte des Klimawandels durch eine erhöhte Konkurrenz. Darüber hinaus beeinflusst das jeweilige Niederschlagsregime die Wachstumsbedingungen an der Baumgrenze erheblich, indem es zum einen die Bewölkung, die Luftfeuchtigkeit und damit die direkte Strahlungsenergie, die den Bäumen zur Verfügung steht, zum anderen die Schneemenge steuert und so den Zeitraum begrenzt, in dem die Bäume tatsächlich wachsen können.

Zusammenfassend lässt sich sagen, dass das Wachstum von Bäumen an der Baumgrenze stark von der Temperatur beeinflusst wird, aber ebenso stark von anderen abiotischen und biotischen Prozessen abhängt, die auf regionaler bis lokaler Ebene wirken. Der Einfluss dieser Prozesse kann bis hin zu einer Umkehrung der an sich positiven Auswirkungen steigender Temperaturen auf das Wachstum der Bäume nahe ihrer temperaturbedingten Verbreitungsgrenze führen. Folglich ermöglichte die Berücksichtigung dieser kleinräumig wirkenden Prozesse eine wesentlich zuverlässigere Abschätzung der Auswirkungen des Klimawandels auf das Baumwachstum an der Baumgrenze.
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CHAPTER 1

Introduction

The global climate system is unequivocally changing, and these changes affect numerous aspects of our environment. The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) has confirmed an average global temperature increase by 0.85 K over the last 130 years (IPCC, 2013). It is beyond scientific doubt that the increase in radiative forcing and the net uptake of energy by the climate system are predominantly caused by the anthropogenic input of CO$_2$ and other greenhouse gases (IPCC, 2013). Visible consequences of climate change are numerous, and in addition to higher air temperatures they also include increasing ocean temperatures, rising sea levels and a widespread retreat of snow and ice.

Although the signs of ongoing global changes are pervasive, they are not distributed evenly around the globe. Among the systems that are expected to be affected disproportionally strongly by climate change are high mountain regions (Pepin et al., 2015). For instance, Switzerland, a country covering a considerable fraction of the European Alps, has experienced a more pronounced temperature increase compared to the global average, with an absolute increase of 1.35 K in the 20$^{th}$ century and a mean trend of 0.57 K per decade over the last 30 years (Rebetez and Reinhard, 2008). Rising temperatures and changing precipitation have had clear impacts in the Swiss Alps (CH2014-Impacts, 2014). Major ice losses and decreasing lengths of Alpine glaciers (e.g., Bauder et al., 2007; Lüthi et al., 2010), seasonal shifts of river runoff patterns (CH2014-Impacts, 2014), alterations of biodiversity and range losses of plants in mountain regions (Dullinger et al., 2012) as well as advances in the spring phenology of plants (Güsewell et al., 2017) are just a few climate change impacts that an attentive observer will notice.
Lastly, and for this study most relevant, forest ecosystems depend strongly on climatic conditions, and hence changes in the climate system strongly affect forests by altering the physiology, growth, mortality and reproduction of trees, the interactions between trees and pathogens, and lastly disturbance regimes like windstorms, fires and insect attacks (Bonan, 2008; Bugmann et al., 2014; Millar and Stephenson, 2015; Seidl et al., 2017).

Especially at the upper treeline and in the subjacent subalpine forest, where temperature is thought to be the most important large-scale driver of forest growth (Körner, 1998; Tranquillini, 1979), global warming implies changes in treeline elevation as well as changes in the productivity and species composition of the forest stands (e.g., Camarero and Gutiérrez, 2004; Carrer et al., 1998; Harsch et al., 2009). These changes, in turn, have consequences for the ecosystem services provided by these landscapes (Haslett, 2010): (1) landscape aesthetics will change, which has implications for touristic use (CH2014-Impacts, 2014); (2) different species composition and forest stand density will pose both opportunities and challenges for maintaining protective functions but also affect timber production, surface runoff (Elkin et al., 2013) and non-timber forest products; and (3) an advancing treeline will lead to a considerable increase in carbon sequestration (CH2014-Impacts, 2014; Elkin et al., 2013). Therefore, it is of vital importance to understand the processes that drive the dynamics of subalpine forests approaching treeline if one wants to assess the consequences of climate change and elucidate the fate of these ecosystems and the goods and services they provide. An improved process understanding includes (i) analyzing the connections between past climate variability and tree population dynamics, (ii) scrutinizing the relationship between tree growth and temperature, which is the growth determinant most directly affected by climate change, and (iii) combining this knowledge for a robust assessment of future subalpine forest dynamics under different climate change scenarios.

Drivers of tree population dynamics at upper treeline

Upper treeline is one of the most conspicuous ecosystem boundaries (Körner, 1998; Tranquillini, 1979) and has therefore attracted scientific interest for a very long time (e.g., Brockmann-Jerosch, 1919; Humboldt and Bonpland, 1807). However, despite over two centuries of research, understanding the interplay between the factors influencing treeline formation, especially at the regional to local scale, remains a challenge (Barbeito et al., 2012; Holtmeier and Broll, 2017a; Malanson et al., 2011). These interactions make it difficult to project the future of tree populations at treeline (e.g., Holtmeier and
Broll, 2017b). In addition, while there are many studies on the effects of climate variability on single aspects of forest dynamics at treeline, relatively few studies have determined empirically the potential impacts of currently ongoing and future climate change.

Abiotic and biotic factors on different spatial scales determine subalpine forest dynamics and the limits of the tree life form (Holtmeier and Broll, 2017a). As the treeline is a relatively sharp boundary in an otherwise gradually changing environment and prevalent all over the globe, there must be common and biologically interpretable drivers (Körner, 2012; Körner and Paulsen, 2004). However, differences in treeline elevation at the landscape scale suggest regionally valid, finer-scale drivers that act to modulate global patterns. These regional drivers do not eliminate the global drivers, but are superposed on them (Holtmeier and Broll, 2005; Körner, 2012; Körner and Paulsen, 2004). In addition, processes that vary with temporal scale need to be considered when analysing the sensitivity of treelines to altering environmental conditions (Holtmeier and Broll, 2005). For example, the low growth rates, the long lifespan of treeline-forming species and the resistance of established forest communities to environmental change temporally separate changing climatic conditions (drivers) and changes in treeline positions (Körner, 1998; Wieczorek et al., 2017).

On large spatial scales, treelines are constrained by low temperature (Babst et al., 2013; Holtmeier and Broll, 2005; Humboldt and Bonpland, 1807; Körner, 2012; Paulsen and Körner, 2014). The effect that low temperatures have on trees is not primarily acting via photosynthesis (Körner and Paulsen, 2004; Tranquillini, 1979), but rather the limited investment of assimilates into structural growth (Hoch and Körner, 2003; Körner, 1998; Körner and Paulsen, 2004; Simard et al., 2013). The accumulation of non-structural carbohydrates that is often found at low temperatures implies that growth is not limited by CO₂ uptake, but by the rate at which glucose can be converted into plant tissue (Grace et al., 2002; Simard et al., 2013). Due to their physiognomy, trees themselves contribute to the low temperatures experienced by their tissue at treeline sites (Körner, 1999; Körner and Paulsen, 2004). Their canopy is tightly coupled to atmospheric conditions while their roots are shaded from sun-driven soil heat flux. Therefore, the ground under a closed forest canopy is colder than under low-stature vegetation, which is a major disadvantage because root growth as well as the uptake of water and nutrients depend on soil temperature as a major environmental determinant (Körner and Paulsen, 2004). Therefore, trees that grow close to the upper treeline often show a distinct, shrub-like krummholz physiognomy or a distinct spatial arrangement into clumps with open space in between, where
solar radiation reaches the ground (Holtmeier and Broll, 2005; Körner, 2012). Lastly, low temperatures affect not only tree growth and physiognomy, but also regeneration. Among others, the production of viable seeds depends on a series of subsequent summers with sufficiently high temperatures (Grace et al., 2002; Körner, 2012; Tranquillini, 1979). Thus, both the growth and regeneration of trees operate under severe environmental constraints at upper treeline.

Trees can reach their upper climatic limit only if no other modulating factors act at smaller spatial scales (Holtmeier and Broll, 2005). Regional-, landscape-, local- and site-scale drivers can prevent trees from reaching their climatic elevational limit (Holtmeier and Broll, 2005; Malanson et al., 2011). For example, at cold treelines liquid precipitation only rarely has a limiting influence on tree growth. More important are cloud and snow cover, topography (which modifies wind flow patterns, solar radiation, geomorphological processes, and snow cover duration, to name just a few processes), pathogens and insects (Barbeito et al., 2012; Hagedorn et al., 2014; Holtmeier, 2009; Holtmeier and Broll, 2005; Paulsen and Körner, 2014). Especially in areas like the European Alps that feature high human population densities, the strong human influence often has lowered the treeline ecotone by several hundred meters (Leonelli et al., 2009; Motta and Nola, 2001). For example, anthropogenic fires, timber harvesting and alpine farming have depressed the treeline in Switzerland for centuries to millennia (Schwörer et al., 2014; Vittoz et al., 2008). These aspects need to be considered carefully when analysing forest dynamics at treeline sites, particularly in the European Alps.

1.1 Research context

Climate variability and treeline forest dynamics

Already today, many effects of climate warming can be observed at treeline sites. The timing and rates of tree growth have shifted and increased respectively (e.g., Kipfmueller and Salzer, 2010; Salzer et al., 2009), tree physiognomy changed from krummholz to more upright standing tree statures (Holtmeier and Broll, 2005), latewood density declined (Briffa et al., 1998), establishment of seedlings is favored (Holtmeier and Broll, 2011; Kullman, 2002), an elevational advance of the ecotone was observed (Gehrig-Fasel et al., 2007; Harsch and Bader, 2011; Leonelli et al., 2011) and stand densities increased (Camarero and Gutiérrez, 2004; Wang et al., 2016; Wieczorek et al., 2017). While rising temperatures per se tend to improve the conditions
for trees at high elevations, other aspects of climate change may amplify or dampen direct temperature effects (cf. Körner, 2003). For example, changes in precipitation and cloud cover can alter water availability (Lloyd and Fastie, 2002), pathogen infection rates (Barbeito et al., 2013) and incoming radiation (Grace et al., 2002). Also, growth rates have an influence on tree lifespan (Bigler, 2016; Di Filippo et al., 2012) and can thus alter forest turnover rates (Stephenson and Mantgem, 2005). Increasing stand density modifies canopy cover, thereby affecting tree-to-tree competition and root zone temperatures, which feed back to tree growth rates (Barbeito et al., 2012; Körner, 2012; Malanson et al., 2011; Wang et al., 2016). In spite of a substantial number of studies on single effects of climate variability on forest dynamics at treeline, there is little knowledge on the interplay of these processes. Furthermore, it has been suggested that intra-species among-tree variability is controlling the individual trees’ growth response more strongly than generally thought (cf. Buras et al., 2016; Vanoni et al., 2016). However, the importance of this variability in controlling a tree population’s reaction to climate change remains to be clarified. The entanglement of the aforementioned processes and the feedback reactions that potentially arise make it challenging to predict forest dynamics at the treeline ecotone in a changing climate and require an in-depth reconstruction of past growth dynamics.

**Scrutinizing the role of temperature for tree growth at the upper treeline**

The importance of temperature for tree growth close to the cold limit of tree distribution is undisputed (e.g., Körner, 2012; Tranquillini, 1979). Several warmth-sensitive processes such as meristematic activity, leaf phenology, photosynthesis and nutrient uptake determine both radial and height growth of trees (e.g., Körner, 1998; Rossi et al., 2007; Tranquillini, 1979) and are strongly interlinked. However, neither are those processes synchronized in their reaction to temperature, nor do they take place in the same parts of trees. The relative importance of both the different temperature variables (soil vs. air temperatures) and the different periods of growth (current vs. previous year) has not been clarified conclusively yet. In addition, the entanglement of these processes causes the functional relationship between temperature and tree growth to remain inconclusive, resulting in the use of different functions in terms of form and parameterization (e.g., Lenz et al., 2013; Paulsen et al., 2000; Rickebusch et al., 2007). An aggravating factor for empirically analyzing temperature-growth relationships is the temporal component of temperature variability. To tackle this, an assessment of the
relation between radial growth and temperature should be based on highly resolved, long-term air and soil temperature data along elevation gradients approaching the limit of tree growth. In this way, temperature variability in both space (i.e., along the elevation gradients) and time can be captured.

Modelling forest dynamics at treeline

The treeline ecotone on the current landscape is the result of (i) past variability of many abiotic and biotic driving factors, ranging from the global to the local scale (Holtmeier and Broll, 2005), and (ii) the capability of trees to respond to these factors. Warmth deficiency has been identified as a pivotal driver of treeline formation at the global scale (e.g., Körner and Paulsen, 2004). It restricts the warmth-sensitive processes that determine tree growth and regeneration (e.g., Rossi et al., 2008). In the recent past, an increasing number of simulation studies have projected the response of the treeline ecotone and the subjacent subalpine forest to climate change, and at the same time have tried to quantify the future fate of ecosystem goods and services provided by these ecosystems (e.g., CH2014-Impacts, 2014; Elkin et al., 2013). However, for these simulation results to be meaningfully applicable, the ecosystem response is to be examined at local to regional scale rather than at the global scale (cf. Henne et al., 2017). At such high spatial resolution, regional- to local-scale drivers of forest dynamics need to be considered, which will allow to robustly simulate the response of the present day’s treeline ecotone to climate change and to better understand tree reactions to those drivers (Holtmeier and Broll, 2017a). However, the interplay of drivers on different spatial scales remains unclear, and little is known on the scope of influence of regional- to local-scale climatic factors such as precipitation patterns (Holtmeier and Broll, 2017a), which do not only determine available water holding capacity but also cloud cover or the length of the snowy season and thereby modulate energy availability (Paulsen and Körner, 2014). Previous simulation studies on small spatial scales were capable of portraying essential features of long-term forest dynamics at the subalpine level, but overestimated biomass when approaching treeline (e.g., Heiri et al., 2006; Rickebusch et al., 2007; Schwörer et al., 2014). While this overestimation was mainly attributed to the confounding influence of land use, I assume them to be also caused by neglecting small-scale climatic factors. The consideration of non-climatic influences is of great importance if one wants to understand the causes behind today’s patterns of subalpine forests and their dynamics. These range from land use, pathogen infestations, soil conditions, geomorphological mass movements and nutrient supply to successional trends.
and feedback effects (Holtmeier and Broll, 2005). Due to the complexity of the internal and external factors driving forest dynamics at small scales, it is hardly possible to disentangle all of them and include them in a model. However, by systematically assessing the influence of some of these modulators (e.g., precipitation effects on radiation and snow), while at the same time excluding other modulators (land use, mass movements), at least parts of the causal chain behind present-day patterns in subalpine forest dynamics can be disentangled.

1.2 Objectives and outline of the thesis

The overall objective of this thesis is to quantify the impacts of climate variability on past and future stand- and tree-level growth dynamics, and on tree population dynamics at the treeline in three climatically distinct parts of the Swiss Alps. In particular, I want to

(i) identify climatic drivers of short-term tree growth dynamics, reveal the underlying functional form of the growth-temperature relationship, and elucidate the role of inter- and intra-species variability in modulating the growth response of trees.

(ii) investigate the relative importance of air and soil temperature variables for determining individual tree growth.

(iii) explore treeline dynamics at larger scales, both spatially and temporally, by identifying the causalities behind population-wide long-term growth trends, and by isolating important regional- to local-scale drivers of tree population dynamics along elevation gradients.

(iv) combine and synoptically validate these findings regarding their importance as drivers of treeline dynamics, which then allows to robustly explore the development of forest dynamics at and directly below treeline under changing climatic conditions.

These objectives are addressed in the three main parts of the thesis (Fig. 1.1); each of them is written in the form of a scientific paper, and framed by a general Introduction and an overall Synthesis. In the following, I briefly outline the three main parts.
CHAPTER 1. INTRODUCTION

Analysis of past treeline growth dynamics
Stand + tree level

Scrutinizing temperature-growth relationships
Tree level

Prediction of future population dynamics
Stand + tree level

Figure 1.1: Conceptual overview and methodological framework of the PhD thesis. The three columns contain information on input data, the methods that were applied and the resulting output data of each of the three main parts. In addition, the connections between the three parts of the thesis are visualized by bold arrows.

Part I “Among-tree variability and feedback effects result in different growth responses to climate change at the upper treeline in the Swiss Alps”

Temperature as the main limiting factor of tree growth at the treeline ecotone is increasing due to anthropogenically induced climate change. In the medium to long term, this implies substantial changes of tree population dy-
1.2. OBJECTIVES AND OUTLINE OF THE THESIS

Dynamics at treeline, and corresponding impacts for the ecosystem goods and services provided by mountain landscapes. To fully understand the impact of climate variability on tree growth in both the short and long term, it is necessary to (i) systematically consider intra-species, among-tree variability of growth responses, requiring analyses beneath the population level (e.g., Buras et al., 2016; Holtmeier and Broll, 2017b), and (ii) elucidate potential feedback effects that arise from changes in the interactions of co-existing species (e.g., Wang et al., 2016). Therefore, I explored treeline growth dynamics by means of a comprehensive dendroecological study of four major tree species (Picea abies, Larix decidua, Pinus cembra, Pinus mugo) in three distinct climate regimes of the Swiss Alps (Northern, Central and Southern Alps). To analyze the intra-seasonal influence of temperature on short-term growth variability, I employed an information-theoretic model selection based on linear mixed-effects models with monthly temperatures as predictors. This method allowed me to quantify between- and within-species differences regarding when and to what extent trees invest assimilates into radial growth. The long-term growth variability from 1850 to today was then analyzed in interaction with elevation, providing insights into population-wide growth trends, within-population interactions and resulting feedback effects at the three study sites.

Part II “Tree growth responses to changing temperatures across space and time: a fine-scale analysis at the treeline in the Swiss Alps”

It is undisputed that temperature considerably affects tree growth across the entire tree distribution range (Lenoir and Svenning, 2015; McMahon et al., 2010), but most importantly at the cold limit of a species’ distribution (Körner et al., 2016). Tree growth as a whole – both in diameter and height – is driven by several entangled warmth-sensitive processes. They take place in different parts of the tree (canopy, stem, root zone) and during different times of the annual cycle of growth, leading to distinct reactions of overall growth to temperature (e.g., Lenz et al., 2013; Pregitzer et al., 2000; Rossi et al., 2007). In order to gain new insights into the relative importance of (i) soil vs. air temperature, (ii) absolute temperatures vs. time-integrated temperatures and (iii) reserves from the previous growing season on annual radial tree growth, I compiled long-term, spatially and temporally highly resolved air and soil temperature data along transects at three study sites in the Swiss Alps and combined them with basal area increment data of trees. In addition, I did not only cover elevation-dependent temperature
variability but also the temporal component, i.e. past and present climate system changes. In this way, I was able to also scrutinize the growth reactions to temporal as opposed to spatial variability.

**Part III** “Understanding the past is the key to the future: Combining empirical data and dynamic modeling to predict forest dynamics at treeline under climate change”

The fate of subalpine forests and the ecosystem goods and services they provide is of great public interest, especially in densely populated mountain areas like the European Alps (CH2014-Impacts, 2014; Haslett, 2010). Temperature variability and the trees’ capability to convert energy into growth are the most important large-scale drivers of forest dynamics in the subalpine zone (Körner, 1998). However, if one wants to robustly investigate the impacts of climate change on subalpine forests at the regional level, more complex regional-scale modulators of forest dynamics need to be considered (Holtmeier and Broll, 2017a). In a first step, I therefore combined temporally and spatially fine-scale empirical data from three study sites in the Swiss Alps with simulations from a dynamic forest succession model (ForClim) to identify important regional- and local-scale modulators of subalpine forest dynamics. Specifically, I assessed the model assumptions for the relationship between temperature and tree growth. I analyzed both the stand-scale variables basal area and volume, and the individual-tree variables radial growth and tree height. Second, I used an improved model version of ForClim, incorporating the findings on the key modulators of tree growth, to simulate potential future subalpine forest dynamics under three climate change scenarios as well as under a constant climate.
1.3 References


CHAPTER 1. INTRODUCTION


1.3. REFERENCES


Holtmeier, F.-K. and G. Broll (2017b). “Feedback effects of clonal groups and tree clusters on site conditions at the treeline: implications for treeline dynamics”. In: *Climate Research*.


1.3. REFERENCES


CHAPTER 1. INTRODUCTION


Part I: Among-tree variability and feedback effects result in different growth responses to climate change at the upper treeline in the Swiss Alps

Abstract

Upper treeline ecotones are important life form boundaries and particularly sensitive to a warming climate. Changes in growth conditions at these ecotones have wide-ranging implications for the provision of ecosystem services in densely populated mountain regions like the European Alps. We quantify climate effects on short- and long-term tree growth responses, focusing on among-tree variability and potential feedback effects. Although among-tree variability is thought to be substantial, it has not been considered systematically yet in studies on growth-climate relationships. We compiled tree-ring data including almost 600 trees of major treeline species (Larix decidua, Picea abies, Pinus cembra, Pinus mugo) from three climate regions of the Swiss Alps. We further acquired tree size distribution data using unmanned aerial vehicles. To account for among-tree variability, we employed information-theoretic model selections based on linear mixed-effects models (LMMs) with flexible choice of monthly temperature effects on growth. We isolated long-term trends in ring-width indices (RWI) in interaction with elevation. The

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LMMs revealed substantial amounts of previously unquantified among-tree variability, indicating different strategies of single trees regarding when and to what extent to invest assimilates into growth. Furthermore, the LMMs indicated strongly positive temperature effects on growth during short summer periods across all species, and significant contributions of fall (\textit{L. decidua}) and current year’s spring (\textit{L. decidua}, \textit{P. abies}). In the longer term, all species showed consistently positive RWI trends at highest elevations but different patterns with decreasing elevation. \textit{L. decidua} exhibited even negative RWI trends compared to the highest treeline sites, while \textit{P. abies}, \textit{P. cembra} and \textit{P. mugo} showed steeper or flatter trends with decreasing elevation. This does not only reflect effects of ameliorated climate conditions on tree growth over time, but reveals first signs of long-suspected negative and positive feedbacks of climate change on stand dynamics at treeline.
2.1 Introduction

Investigating plant population dynamics at their distribution limits is a key approach for understanding global change impacts (Luckman, 1996; Motta and Nola, 2001). High-elevation treelines are one of the most prominent ecosystem boundaries (Körner, 2012; Tranquillini, 1979) and have attracted scientific interest for a long time (e.g., Brockmann-Jerosch, 1919; Humboldt and Bonpland, 1807). Temperature is widely recognized as the major large-scale driver determining upper treeline position around the globe (Brockmann-Jerosch, 1919; Holtmeier and Broll, 2005; Humboldt and Bonpland, 1807; Körner, 2012), although some of the detailed processes are still subject to debate (e.g., Takahashi and Furuhata, 2016). Thus, the ongoing increase of global temperature (IPCC, 2013) affects the main limiting factor of tree growth at high elevations and may imply substantial alterations of regional and local forest dynamics.

Global land temperatures are changing, with a global mean increase of $0.85\,^\circ C$ between 1880 and 2012 (IPCC, 2013). In mountain regions such as Switzerland, this trend is even more pronounced with a mean temperature increase of $0.35\,^\circ C$ per decade over the last 30 years (Pepin et al., 2015; Rebetez and Reinhard, 2008). As temperature is the most important driver of treelines, global warming implies changes in treeline elevation and dynamics (Holtmeier, 2009; Körner, 2012; Tranquillini, 1979). Numerous effects of climate warming on upper treelines have been observed such as changes in tree physiognomy (Gehrig-Fasel et al., 2007; Holtmeier and Broll, 2005), changes in establishment rates (Holtmeier and Broll, 2011), an elevational advance of the ecotone (Gehrig-Fasel et al., 2007; Harsch et al., 2009; Leonelli et al., 2011), an increase of stand density (Camarero and Gutiérrez, 2004; Gehrig-Fasel et al., 2007) and increasing growth rates (Graumlich, 1991; Kipfmueller and Salzer, 2010; Motta and Nola, 2001; Salzer et al., 2009).

A prominent consequence of global warming is changing growth rates of trees, which are determined by short- to long-term climate effects on tree growth. Relationships between climate variables and secondary growth rates on the level of tree populations have been studied for a long time (e.g., Fritts, 1976). The effects of monthly or seasonal climate variables on population mean growth at the elevational or latitudinal treeline are well tested (Graumlich, 1991; Kipfmueller and Salzer, 2010), also for the European Alps (Babst et al., 2013; Carrer et al., 1998; Frank and Esper, 2005; Oberhuber et al., 2008). However, some recent studies suggest considerable amounts of variability of the individual trees’ growth response, which is not identifiable with standard analyses based on growth data at the population level.
(c.f., Buras et al., 2016; Carrer, 2011; Graumlich, 1991; Vanoni et al., 2016). To date, this among-tree variability has rarely been accounted for, and the magnitude of its effect on the explanatory power of climate-growth analyses is suspected to be large but remains unclear. Additionally, the timing of growth appears to be temporally fine-scaled (Kirdyanov et al., 2003; Lenz et al., 2013), and thus temporally higher resolved climatic data than only seasonal means should be used.

While rising temperatures \emph{per se} improve life conditions for trees at high elevations, there are aspects of climate change that may amplify or dampen temperature effects on forest dynamics and create feedback effects. Changes in precipitation and cloud cover can alter water availability (Lloyd and Fastie, 2002), pathogen infection rates (Barbeito et al., 2013) and incoming radiation (Grace et al., 2002). Due to the inverse relationship between tree lifespan and growth rate (Bigler and Veblen, 2009; Di Filippo et al., 2012), improved growing conditions may enhance forest turnover (Bugmann and Bigler, 2011; Stephenson and Mantgem, 2005). Finally, changing stand density modifies canopy cover, thereby affecting tree-to-tree competition and root zone temperatures, which feed back to tree growth rates (Barbeito et al., 2012; Malanson et al., 2011; Wang et al., 2016). The interactions of these processes and the potential feedback effects make it challenging to predict tree population dynamics at the treeline ecotone in a changing climate, which in turn are expected to also have consequences for trees at lower elevations (e.g., Holtmeier and Broll, 2005; Seidl et al., 2009). Yet, knowledge about the future development of tree population dynamics may be inferred from past dynamics at the treeline and their temporal variability with respect to changing climatic conditions.

A distinguished feature of many tree-ring chronologies – not only in the Alps but worldwide – is accelerated growth, often starting around the year 1950 (Kipfmueller and Salzer, 2010). While early studies attributed this increase to CO$_2$ fertilization (e.g., La Marche et al., 1984; Nicolussi et al., 1995), more recent work has questioned this hypothesis (Handa et al., 2006). Lately, positive trends in growth rates are mostly ascribed to a direct climatic cause, especially rising temperatures and the extending growing season (Graumlich, 1991; Kipfmueller and Salzer, 2010; Motta and Nola, 2001; Salzer et al., 2009). Although tree-ring data are often available as long time series, which renders them an ideal measure for multi-decadal to centennial growth trend analyses, isolating the low-frequency variability caused by abiotic influencing factors remains challenging. This variability is often confounded with the trees’ age-related trend, and the choice of detrending method for disentangling abiotic influences and age effects can greatly bias the results
2.1. INTRODUCTION

(Peters et al., 2015). Furthermore, the sampling design may induce biases to the data that can void results on growth trends (Bowman et al., 2013; Nehrbass-Ahles et al., 2014). Thus, it is advisable to thoroughly design dendroecological sampling and carefully choose the detrending method when attempting to analyze the long-term effects of increasing temperatures on growth rates of treeline trees and identify feedback effects.

In the European Alps, a large share of the treeline rise can be attributed to the cessation of human activities (e.g., Gehrig-Fasel et al., 2007; Leonelli et al., 2009). When assessing the impact of climate change on treeline forest dynamics, biases due to the confounding influence of this decrease in land use as well as other regional treeline modulators, such as geomorphological processes, wind and snow damages need to be considered. While the cessation of human land use and geomorphological processes mainly affect studies on the establishment of trees above the current tree limits (Gehrig-Fasel et al., 2007; Leonelli et al., 2009), other factors such as wind and snow can also influence short- and long-term tree growth variability. When we try to isolate the impacts of increasing temperatures on tree growth variability, it is therefore necessary to rule out growth-determining factors other than temperature as much as possible.

We carefully selected climatic treeline sites in three major climate regions of the Swiss Alps that are as undisturbed by non-climatic drivers (e.g., land use, geomorphology etc.) as possible, which makes them suitable for the analysis of the effects of recent climate change. The goals of our study were to evaluate the elevational dynamics of these treeline stands using stand structure and age data, analyse short-term temperature-growth relationships of major treeline tree species at the population and individual tree level and quantify longer-term growth trends at the population and tree level. Specifically we ask the following research questions: (i) Are the analysed treeline sites limited by temperature and do they show signs of suspected upward movement? (ii) Which monthly temperature variables control the annual growth of trees at the treeline and how do their effects differ among climate regimes, species and individual trees? (iii) Do long-term growth rates reflect the recently increasing temperatures due to climate change, and can we identify feedback effects on growth rates?
2.2 Materials and methods

Study site selection

The shape of treelines can help to identify sites that are undisturbed by human activities, as it is reasonable to assume that diffuse treelines are limited by temperature during the growing season while abrupt treelines are forced by climatic controls on seedling mortality or frost- and wind-induced growth limitations (Harsch and Bader, 2011; Malanson et al., 2011). Additionally, the recent cessation or extensification of human activities in many regions of the Swiss Alps renders it challenging to differentiate between changes in the functioning and dynamics of treeline ecosystems that are caused by recovery from human land use and those that arise from climate change (Gehrig-Fasel et al., 2007; Leonelli et al., 2009). For these reasons, forest “outposts” at treeline (Körner, 2012) were investigated in this study.

The study sites were chosen using multiple criteria. The regionally highest patches of forest in Switzerland were identified using Swiss land use statistics GEOSTAT (Gehrig-Fasel et al., 2007). Following the assumptions of Körner and Paulsen (2004), these regionally highest patches of forest are most likely limited by temperature and not by anthropogenic activities. The climatic limitation of these sites was checked by examining changes in treeline position between historic and current aerial images and evaluating detailed descriptions of high-elevation treelines from the early 20th century (Brockmann-Jerosch, 1919; Hess, 1923; Imhof, 1900). During preliminary field surveys, the form of these treelines was assessed according to the conceptual model by Harsch and Bader (2011) to confirm temperature as a potential key factor determining tree growth. Still, we cannot exclude that some of the ongoing ingrowth and densification of the forests at the identified treeline sites is due to anthropogenic influences or abiotic treeline modulators other than temperature.

The following treeline sites in the Swiss Alps were selected, each containing multiple forest outposts: (1) Stavel Crastu near Bosco/Gurin (treeline at approximately 2200 m a.s.l., for a photo see Fig. 2.A.1), (2) the Hohgant massif near Schangnau (treeline elevation at approximately 2000 m a.s.l., Fig. 2.A.2), and (3) the Gugle ridge near Zermatt (treeline elevation at approximately 2500 m a.s.l., Fig. 2.A.3; Fig. 2.1 a, Table 2.1). Each study area is located in a distinct climate region of the Swiss Alps: Bosco/Gurin is situated in the Insularian southern Alps with high precipitation and high irradiation (Fig. 2.1 b), Hohgant in the northern Alps experiencing high precipitation and low irradiation (Fig. 2.1 c), and Zermatt in the central Alps with low...
2.2. MATERIALS AND METHODS

Figure 2.1: (a) Location of the three study sites Bosco/Gurin (BOS), Holgant (HOH) and Zermatt (ZER) in Switzerland in the context of regional treeline elevation calculated using the Swiss land use statistics (GEOSTAT) and the method proposed by Gehrig-Fasel, 2007. (b)–(d) Climate diagrams of the study sites employing gridded MeteoSwiss climate data using a 30-year standard period from 1981 to 2010, showing distinct differences in precipitation sum and pattern between the Insularian southern Alpine climate (b), the northern Alpine climate (c) and the central Alpine climate (d).

precipitation and high irradiation (Fig. 2.1 d). These distinct differences in precipitation and radiation patterns enable us to qualitatively assess the impact of precipitation on the short- and long-term growth variability, rather than using interpolated precipitation data, which would potentially introduce a high amount of uncertainty (Daly, 2006).

Sampling design

At each study site, we defined three forest outposts as sampling plots. In each plot, 64 trees equally distributed over the prevailing tree species and four classes of diameter at breast height (DBH; 5-10 cm, >10-15 cm, >15-
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Table 2.1: Summary of the study area characteristics, dendroecological sampling and remote sensing data.

<table>
<thead>
<tr>
<th>Topography</th>
<th>Bosco/Gurin</th>
<th>Holgant</th>
<th>Zermatt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope range [(^{\circ})]</td>
<td>6–70</td>
<td>0–50</td>
<td>0–70</td>
</tr>
<tr>
<td>Expositions</td>
<td>Southwest, south</td>
<td>South, west, east</td>
<td>North, northwest, northeast</td>
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<table>
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<tr>
<th>Dendroecological sampling</th>
<th>Bosco/Gurin</th>
<th>Holgant</th>
<th>Zermatt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampled species</td>
<td>Picea abies, Larix decidua</td>
<td>Picea abies, Pinus mugo subsp. uncinata</td>
<td>Pinus cembra, Larix decidua</td>
</tr>
<tr>
<td>No. of sampled trees</td>
<td>60 (spruce), 95 (larch)</td>
<td>85 (spruce), 83 (mountain pine)</td>
<td>95 (larch), 84 (Swiss stone pine)</td>
</tr>
<tr>
<td>Elevation range of sampled trees [m a.s.l.]</td>
<td>1939–2297</td>
<td>1708–2021</td>
<td>2250–2540</td>
</tr>
<tr>
<td>Tree height range [m]</td>
<td>2.5–26.4</td>
<td>2.2–25.0</td>
<td>2.0–24.0</td>
</tr>
<tr>
<td>Tree diameter at breast height (DBH) range [cm]</td>
<td>5.1–88.0</td>
<td>5.2–92.0</td>
<td>5.0–134.0</td>
</tr>
<tr>
<td>Mean tree age ± standard deviation</td>
<td>upper 36 ± 15</td>
<td>104 ± 55</td>
<td>94 ± 28</td>
</tr>
<tr>
<td></td>
<td>middle 54 ± 36</td>
<td>99 ± 63</td>
<td>68 ± 31</td>
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<tr>
<td></td>
<td>lower 72 ± 55</td>
<td>100 ± 42</td>
<td>115 ± 81</td>
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<table>
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<th>Remote sensing data</th>
<th>Bosco/Gurin</th>
<th>Holgant</th>
<th>Zermatt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation range of data [m a.s.l.]</td>
<td>1658–2140</td>
<td>1698–1975</td>
<td>2129–2492</td>
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<tr>
<td>Area of canopy height model [ha]</td>
<td>68.5</td>
<td>87.5</td>
<td>141.7</td>
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<tr>
<td>Number of detected trees with height &gt;2.5 m</td>
<td>16461</td>
<td>10289</td>
<td>13489</td>
</tr>
</tbody>
</table>

20 cm, >20 cm) were sampled with increment borers, employing a stratified sampling and resulting in a “pseudo-population” design (Nehrbass-Ahles et al., 2014).

The sampled tree species included Norway spruce (Picea abies) and European larch (Larix decidua) at Bosco/Gurin, Norway spruce and mountain pine (Pinus mugo subsp. uncinata) at Hohgant, and Swiss stone pine (Pinus cembra) and European larch at Zermatt. Trees in each DBH class covered the complete elevation range of the plot. Two cores were taken per tree, one at breast height (130 cm) and one as close as possible to the root collar-shoot boundary. During coring, we always attempted to hit the pith. The estimation of tree age and primary growth rate from the stem base to breast height is essential and only possible when the pith is included in the sample. Each tree’s coordinates, tree height, crown length, DBH, elevation, aspect and slope were measured. We further recorded whether the tree grew with a single or multiple stems. In the lab, the increment cores were mounted on wooden supports, sanded and the ring widths measured with a resolution of 0.01 mm on a measurement device (Lintab 5, Rinntech, Heidelberg, Germany) according to standard dendrochronological procedures (Fritts, 1976). The ring-width series were crossdated visually and quantitatively using COFECHA (Holmes, 1983) to ensure correct assignment of
calendar years to each ring (cf. Table 2.A.1 for summary statistics of the tree-ring-width series).

Climate data

For the analysis of climate-tree growth-relationships, gridded HISTALP monthly mean surface temperature (spatial resolution 5 arc minutes) was used (Chimani et al., 2013). To ensure correct representation of treeline temperature conditions in the HISTALP data, a total of 72 (eight per plot) temperature loggers (iButton DS1922L, Maxim Integrated) were installed, which recorded hourly 2m air temperature between May 2014 and November 2015. The temperature loggers were protected from radiation by self-developed Gill screens. A direct evaluation of HISTALP temperatures against in-situ measurements was not possible, since the gridded data were only available until 2008. Therefore, we calculated Pearson correlations ($r$) between tree-line stand monthly mean temperatures and all available monthly mean temperature records of MeteoSwiss climate stations. Stations with the highest correlations and longest time series were selected (station Locarno/Monti for Bosco/Gurin, $r = 0.98$; station Grimsel Hospiz for Hohgant, $r = 0.98$; station Col du Grand St. Bernard for Zermatt, $r = 0.99$) and used to analogously evaluate the HISTALP data (grid cell Bosco/Gurin, $r = 0.97$; grid cell Hohgant, $r = 0.95$; grid cell Zermatt, $r = 0.98$). HISTALP monthly mean temperatures were used from 1850 onwards. We did not use precipitation data for the analysis as (1) temperature is assumed to be the major limiting factor at the study sites (Körner, 2012), and (2) long-term precipitation data are only available from climate stations far from the study sites, which cannot be used due the highly inhomogeneous distribution of precipitation in mountainous terrain (Daly, 2006), and (3) the available water capacity of a tree is not only defined by precipitation but would need to be assessed in combination with soil characteristics and slope (Barij et al., 2007).

Long-term trends of monthly mean temperature at each study site were quantified using time series derived from the nearest grid point of the HISTALP monthly mean surface temperature data set (Chimani et al., 2013). Locally weighted smoothing splines of monthly temperature anomalies with regard to the 30-year mean from 1971–2000 were calculated.

Tree height and age distribution analysis

To capture stand structure, the height distribution of trees in each stand was surveyed by means of 3D surface model reconstructions. We used largely
overlapping high-resolution (<10 cm/px) aerial imagery obtained with an unmanned aerial vehicle. Canopy height models were derived and single trees with a height >2.5 m automatically delineated (Hyppa et al., 2001; Zarco-Tejada et al., 2014). For each stand, the trees were grouped in three elevation classes, using the 25th and 75th percentile as class breaks. Then, tree height distributions were plotted for each elevation class.

To assess tree age distributions of the remote sensing sample, tree heights were converted to tree age employing site-specific linear regressions of tree age and tree height. These linear models were calculated using the dendroecological sample, which included measured tree ages and tree heights (for the age-height relationships see Fig. 2.A.4). Tree ages were estimated by the dating the pith of the cores taken at the base of the trees. Tree ages were then converted to ingrowth times and plotted analogously to the height distributions in three elevation classes. The elevational extent and the size of the stands that were analyzed with remote sensing data was larger than and slightly different to the dendroecological sampling and ranged between 1658–2140 m a.s.l. and approximately 70 ha at Bosco/Gurin, 1698–1975 m a.s.l. and approximately 90 ha at Hohgant, and 2129–2492 m a.s.l. and 140 ha at Zermatt (Table 2.1).

Analysis of short-term temperature-growth relationships

Ring-width indices were calculated from the raw ring-width series. The series were restricted to start in 1850 to match with the climate data; data going longer back in time were not considered. The series were detrended using a 32-year spline to remove the low-frequency components of the data and amplify interannual variability, resulting in annual ring-width indices (RWI$_{st}$). Most previous studies on climate-growth relationships have used correlations between climate variables and tree-ring chronologies representing the whole population (e.g., Carrer et al., 1998; Oberhuber et al., 2008), which do not account for among-tree variability. In our study, we used ring-width indices derived from individual trees and as predictors standardized monthly mean temperature variables of the current and previous year of ring formation (Eq. 2.1) to fit linear mixed-effects models (LMMs; Pinheiro and Bates, 2004) for each tree species and study site. Seasonal mean temperatures were avoided, as previous studies suggest that shorter time periods better account for growth variability (Kirdyanov et al., 2003; Lenz et al., 2013). The initial LMMs were calculated in the following form:

$$RWI_{st}^p = \beta_0 + \sum_{i=1}^k \beta_i \times T_i^M + \sum_{j=1}^l \beta_j \times T_{i-1}^m + b_0 + \epsilon_t$$  \hspace{1cm} (2.1)
with $RWI_{t}^{sp}$ being a spline-detrended $RWI$ in the year $t$, $\beta_i$ being the coefficients of the fixed effects, $T_{t}^{M}$ being monthly mean temperatures from current January until current October, $T_{t-1}^{M}$ from previous August until previous December, $b_0$ being a random intercept with $b_0 \sim N(0, \sigma_{b_0}^2)$ and $\epsilon_t$ being the residual error in year $t$ with $\epsilon_t \sim N(0, \sigma^2)$. All monthly mean temperatures were centered and scaled. Temporal autocorrelation of $RWI_{t}^{sp}$ was accounted for by adding an autoregressive parameter $\phi$ of order 1 (Pinheiro and Bates, 2004) to the model (Eq. 2.2):

$$\epsilon_t = \phi \times \epsilon_{t-1} + \eta_t$$

where $\epsilon_{t-1}$ is the residual error in the previous year, and $\eta_t$ is a noise term with zero mean.

The best-fitting model was inferred from the initial full LMM (Eq. 2.1) using information-theoretic model selection (Burnham and Anderson, 2002). A repeated evaluation of all possible 215 model combinations that included all combinations of variables shown in the full model (Eq. 2.1) was conducted using the Bayesian Information Criterion (BIC; Aho et al., 2014) and maximum likelihood estimation (ML; Burnham and Anderson, 2002). A model with a lower BIC score indicates a better-fitting model.

After identifying the best-fitting model for each species and site, the LMM with the random intercept was extended by adding random effects for those variables, which were selected as fixed effects. This model form was then refitted using restricted maximum likelihood (REML) estimation. The assumptions of the final models were investigated to ensure the validity of the interpretation of model outputs. Model diagnostics included checks for linearity, absence of collinearity and heteroscedasticity, and normality of residuals. All calculations were conducted in the R statistics software (R Core Team, 2016), using the packages dplR (Bunn, 2008), nlme (Pinheiro and Bates, 2004) and MuMIn (Barton, 2016).

**Detection of long-term growth trends**

Trends in tree growth are often affected by biases introduced by the sampling design (Bowman et al., 2013; Brienen et al., 2012; Nehrbass-Ahles et al., 2014) and age trend removal (Peters et al., 2015). A review of past studies on tree growth trends (Bontemps and Esper, 2011; Melvin and Briffa, 2008; Peters et al., 2015) led us to favor regional curve standardization (RCS; Becker, 1989; Briffa et al., 1992) to account for the trees’ age trend. For RCS, the cambial age of the tree at coring height is needed. For cores that did not hit the pith, a geometric method was used to estimate the number
of missing years to the pith based on ring curvature and the average of the first five measurable ring widths (Duncan, 1989). Cores with more than ten missing rings were excluded to restrict uncertainty introduced by this estimation.

Again, LMMs were employed to describe the growth increment per species and site as a function of time. Following the initial hypothesis of temperature being the single most important determinant of growth, elevation was added as a predictor for ring-width indices, which is a proxy for the different long-term mean temperatures experienced by the trees and further climatic and other environmental influences along the elevational gradient. Furthermore, the interaction of time and elevation was added to the model to cover potentially differing trends of growth on different elevation (temperature) levels. To check for other confounding variables, we further tested models with combinations of these variables and any other tree variables (height, DBH, crown length, aspect, and slope) in an information-theoretic model selection approach. The model with the lowest Akaike Information Criterion (AIC) was achieved with only time, elevation and their interaction predicting ring-width indices for all species and sites. The AIC was used in this case because it was undesirable to restrict the model’s size as the objective was to check for the explanatory power of the variables mentioned above. Therefore, the original trend model (Eq. 2.3) was used:

\[
RWI_t^{RCS} = \beta_0 + (\beta_1 + b_1) \times t + (\beta_2 + b_2) \times elev \\
+ (\beta_3 + b_3) \times (t \times elev) + b_0 + \epsilon_t
\]  

(2.3)

with \(RWI_t^{RCS}\) being the regional curve standardized \(RWI\) in year \(t\), \(\beta_0\) to \(\beta_3\) the coefficients of the fixed effects, \(elev\) the tree’s elevation, \(b_0\) a random intercept with \(b_0 \sim N(0, \sigma^2_{b_0})\), \(b_1\) to \(b_3\) random slopes and \(\epsilon_t\) the residual error in the year \(t\) with \(\epsilon_t \sim N(0, \sigma^2)\). Analogously to the climate-growth LMMs, an autoregressive parameter \(\phi\) of order 1 (Pinheiro and Bates, 2004) was added to each trend model (Eq. 2.3). As for the temperature-growth LMMs, compliance with model assumptions was checked. For each site and species, several elevation levels were used for predicting ring-width indices over time in interaction with the elevation of the trees. Elevations were chosen to be the 0th, 20th, 40th, 60th, 80th and 100th percentile of the elevation range (Table 2.1) of the data underlying the LMMs.
2.3 Results

Tree height and age distribution of the forest outposts

The age distribution of the dendroecological samples across the elevation gradients indicates Bosco/Gurin to have the youngest trees overall, whereas Hohgant and Zermatt have trees of similar age (Table 2.1). Bosco/Gurin yields a tree age of $36 \pm 15$ years (mean ± standard deviation) at the highest 25% and an increase to $72 \pm 55$ years when going down to the lower end of the sample. At Hohgant and Zermatt, the trees across the gradient are older, with tree ages at the upper 25% of 104 ± 55 years and 94 ± 28 years, respectively. At Hohgant, the mean ages are similar across the entire gradient, and at Zermatt there is a decrease in mean age in the middle 50% and again an increase in the lower 25% of the gradient.

Average stand density across the entire elevational gradient was 277 trees/ha at Bosco/Gurin, 128 trees/ha at Hohgant and 153 trees/ha at Zermatt; for the highest 25%, densities were 129, 89 and 48 trees/ha, respectively. At all study sites, the absolute number of trees in the highest 25% of the gradients was lower than within the lowest 25% or the central portion (25-75%) of the elevation gradients (Fig. 2.2). However, tree height distributions varied across study sites and elevation gradients. With increasing elevation, the distributions prominently shifted towards lower tree heights (Fig. 2.2 a). The age distribution of the remotely sensed trees in the highest 25% of the elevation gradients approximated a negative J-shaped curve of ingrowth time at Bosco/Gurin and Zermatt, while at Hohgant it was closer to a right-skewed unimodal shape (Fig. 2.2 b). The lower parts of the stands at Hohgant also showed unimodal, bell-shaped ingrowth time distributions. The distributions of the lower quantiles at Bosco/Gurin featured multiple modes and were right-skewed, while at Zermatt they were close to negative J-shaped curves.

Linear regressions of tree age and tree height in the tree-ring dataset (Table 2.1) revealed highly significant (p-values $< 10^{-10}$) positive relationships between age and height at all sites (Fig. 2.A.4). The strength of the relationship varied and was strongest at Bosco/Gurin ($R^2 = 0.48$), moderate at Hohgant ($R^2 = 0.43$) and lowest at Zermatt ($R^2 = 0.27$).

Analysis of short-term temperature-growth relationships

The number of temperature variables affecting growth variability that were included in the LMMs showed considerable variability between species and sites (Fig. 2.3), ranging from six monthly variables for spruce at Hohgant to
eleven variables for larch at Bosco/Gurin. Also, the absolute values of the coefficients varied considerably, with larch having fixed effect values mostly $>0.1$ while spruce, mountain pine and Swiss stone pine had values mostly $<0.1$ (Fig. 2.3). Still, only two fixed effects were not significant (previous August for larch and current April for Swiss stone pine at Zermatt); all other coefficients featured p-values $<0.01$ (Fig. 2.3). Since our approach included multiple tests, the standard errors and p-values were biased to some extent. Still, in most cases the absolute p-values lie at least one magnitude below the most rigorous significance level of $p<0.001$ (Fig. 2.A.5). As the temperature variables were centered and scaled in the LMMs, a fixed effect of 0.1 indicates a 10\% increase in ring-width indices with a temperature increase by one standard deviation.

Larch showed a pattern of four clearly distinguishable seasonal periods at
both Bosco/Gurin and Zermatt: positive fixed effects for previous year’s late summer and fall temperatures (previous August, September and October at both sites), negative fixed effects for current year’s late winter and spring (February, March and April at Bosco/Gurin, February and April at Zermatt), positive fixed effects for current year’s midsummer (June and July at both Bosco/Gurin and Zermatt), and negative fixed effects for current year’s late summer and fall (August, September and October at Bosco/Gurin and August only at Zermatt). The highest positive values for both Bosco/Gurin (0.22) and Zermatt (0.25) resulted for current year’s July, and the lowest negative values (−0.19 and −0.12, respectively) were found for current year’s April (Fig. 2.3).

Similar to larch, spruce featured significant seasonal periods for current year’s late winter and spring, mid and late summer as well as fall at both Bosco/Gurin and Hohgant (Fig. 2.3). However, there were no clear seasonal effects for previous year’s fall. The majority of absolute effect values for spruce at both sites was considerably lower, mostly below 0.1. As for larch, the highest positive fixed effects were found for July with 0.12 at Bosco/Gurin and 0.21 at Hohgant (Fig. 2.3). For Swiss stone pine and mountain pine, there were no clear seasonal patterns (Fig. 2.3). While for mountain pine, current year’s July temperature effect was notably higher (0.21) than the other fixed effects, the Swiss stone pine model featured generally low absolute values of coefficients with the highest positive coefficient in current year’s May.

With the inclusion of random intercepts and slopes in the LMMs, among-tree variability may be quantified in relation to the fixed effects. The standard deviations of the random effects showed considerable variability due to individual tree characteristics and tree-specific environmental conditions (Fig. 2.3). Similar to the fixed effects, larch exhibited the highest among-tree variability. However, for current year’s July (highest positive fixed effect), the standard deviation of the random effect was notably low, i.e. tree growth responded in a similar way to temperature. This is also true for spruce and mountain pine, showing standard deviations of a comparable magnitude as the fixed effects in most months, except for July. Swiss stone pine, with its differing behavior featuring May as the month with the highest positive fixed effect, also has the relatively lowest standard deviation of the random effect in May.

Model diagnostics showed compliance of all temperature-growth LMMs with the assumptions of linearity, absence of collinearity and heteroscedasticity, as well as independence of the predictor variables. Still, the residuals partly exhibited a heavy-tailed distribution, which was due to a small number of trees in each model causing large residuals, mostly towards the right
CHAPTER 2. RECONSTRUCTION OF GROWTH DYNAMICS

Detection of long-term growth trends

The predictions of tree-ring-width index ($RW_{t}^{RCS}$) using LMMs (cf. Eq. 2.3, Table 2.2) revealed a positive growth trend across all species, sites and elevations, although its strength varied considerably (Fig. 2.4, Table 2.2). For larch, a strong positive trend at the highest elevations at both Bosco/Gurin and Zermatt was evident, but declined with decreasing elevation at both sites (Fig. 2.4 a and b, Table 2.2). There was a weak negative trend for predicted ring-width index ($RW_{t}^{RCS}$) at the lower end of the elevation range at Zermatt. Note that the elevation range of the sampled trees and therefore also the range of elevations for the predictions was twice as large at Zermatt compared to Bosco/Gurin. For larch, time, elevation and their interaction were significant at the levels of $p<0.05$ (Bosco/Gurin) and $p<0.001$ (Zermatt), respectively. Among-tree variability was generally low for larch as indicated by the standard deviation of the random effects relative to the fixed effects (Fig. 2.4 a and b, Table 2.2).
Figure 2.3: Temperature-growth relationships as calculated with LMMs (Eqs. 2.1 and 2.2). Numbers and tile colors represent the fixed effect sizes of the best-fitting temperature-growth models (lowest BIC) of Larix decidua, Picea abies, Pinus cembra and Pinus mugo at all study sites. Significance levels of the fixed effects are indicated by * for p<0.05, ** for p<0.01 and *** for p<0.001; for the absolute p-values see Fig. 2.A.5. The smaller numbers in brackets are the standard deviations of the random effects.
Table 2.2: Summary of the model parameters of the LMMs for growth trend analysis for European larch (*L. decidua*), Norway spruce (*P. abies*), Swiss stone pine (*P. cembra*) and mountain pine (*P. mugo*) (cf. Eq. 2.3). The coefficients relate to the intercept ($\beta_0$) and the slopes of the time ($\beta_1$), the elevation ($\beta_2$) and the interaction of time and elevation ($\beta_3$). SE refers to the standard error, SD to the standard deviation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sampling site</th>
<th>$\beta_0$</th>
<th>$\beta_1$</th>
<th>$\beta_2$</th>
<th>$\beta_3$</th>
<th>$\phi$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. decidua</em></td>
<td>Bosco/Gurin</td>
<td>$259 \pm 106$</td>
<td>$-0.127 \pm 0.053$</td>
<td>$-0.126 \pm 0.050$</td>
<td>$6 \times 10^{-5} \pm 2 \times 10^{-5}$</td>
<td>0.184</td>
</tr>
<tr>
<td></td>
<td>Zermatt</td>
<td>$281 \pm 48$</td>
<td>$-0.149 \pm 0.024$</td>
<td>$-0.123 \pm 0.020$</td>
<td>$6 \times 10^{-5} \pm 1 \times 10^{-5}$</td>
<td>0.084</td>
</tr>
<tr>
<td><em>P. abies</em></td>
<td>Bosco/Gurin</td>
<td>$27 \pm 132$</td>
<td>$-0.010 \pm 0.066$</td>
<td>$-0.022 \pm 0.062$</td>
<td>$1 \times 10^{-5} \pm 3 \times 10^{-5}$</td>
<td>2.245</td>
</tr>
<tr>
<td></td>
<td>Hohgant</td>
<td>$-250 \pm 231$</td>
<td>$0.126 \pm 0.117$</td>
<td>$0.126 \pm 0.119$</td>
<td>$-6 \times 10^{-5} \pm 6 \times 10^{-5}$</td>
<td>0.224</td>
</tr>
<tr>
<td><em>P. cembra</em></td>
<td>Zermatt</td>
<td>$-203 \pm 128$</td>
<td>$0.107 \pm 0.064$</td>
<td>$0.077 \pm 0.052$</td>
<td>$-4 \times 10^{-5} \pm 3 \times 10^{-5}$</td>
<td>0.017</td>
</tr>
<tr>
<td><em>P. mugo</em></td>
<td>Hohgant</td>
<td>$-42 \pm 114$</td>
<td>$0.022 \pm 0.058$</td>
<td>$0.019 \pm 0.059$</td>
<td>$-1 \times 10^{-5} \pm 3 \times 10^{-5}$</td>
<td>0.33</td>
</tr>
</tbody>
</table>

Fixed effects (estimate ± SE [p-value])
2.3. RESULTS

For spruce at Bosco/Gurin, the LMM revealed weaker effects of time and elevation, featuring a stable positive growth trend on all elevation levels and decreasing absolute ring-width indices with elevation (Fig. 2.4 c), but the standard deviation of the random effect for the intercept was high relative to the fixed effect intercept (Table 2.2). Conversely, the LMM for spruce at Hohgant showed weaker effects of time and elevation but a stronger interaction, resulting in a strengthening of the positive trend with decreasing elevation (Fig. 2.4 d). Both spruce LMMs did not indicate any highly significant effects.

For Swiss stone pine at Zermatt, the LMM yielded overall increasing ring-width indices over time and a decreasing intercept of ring-width indices with elevation (Fig. 2.4 e). The interaction term caused a strengthening of the positive growth trend with decreasing elevation. P-values for the fixed effects were nearly significant (Table 2.2). Among-tree variability for all effects was low.

For mountain pine at Hohgant, the low fixed effects of time and elevation (Table 2.2) caused a rather weak positive trend of ring-width indices and decreasing base level of ring-width indices with increasing elevation (Fig. 2.4 f). There was a constant positive growth trend across elevations. However, p-values indicated that the trend was not significant.

Monthly mean temperature anomalies over time

To assess whether growth trends were associated with trends in climate variables, monthly mean temperature anomalies relative to the 1971–2000 reference period were calculated for 1850 to 2008, showing increasing temperatures at all sites and in all months (Fig. 2.5). Patterns and strength of the temperature trends varied considerably among individual months, but only little between sites. All months except September exhibited a clear increase in temperature, starting around 1950 at the latest. The strongest temperature increase for all sites was found for June, featuring relatively constant temperatures around the 1971–2000 June mean until shortly after 1950, followed by a pronounced rise of almost 2°C. The weakest warming was evident for September, with mean temperatures staying relatively constant over the entire time period. The absolute increase of September mean temperature amounted to approximately 0.5°C since 1850.
Figure 2.4: Ring-width indices over time of the four tree species at the study sites Bosco/Gurin (BOS), Hohgant (HOH) and Zermatt (ZER) (a–f). The first row shows predictions based on the fixed effects coefficients at five different levels of elevation (0%, 20%, 40%, 60%, 80% and 100% of the elevation range covered by the sampled trees at each study site, cf. Table 2.1). The second row shows predictions based on the random effects for each tree included in the model. The third row contains the original detrended ring-width series that the models are based on. Both the predictions using the random effects and the ring-width series are colored according to the elevation class of the individual trees.
Figure 2.5: Locally weighted smoothing of monthly temperature anomalies with regard to the 30-year mean from 1971 to 2000 (due to the length of the used HISTALP data, the new WMO standard reference period 1981–2010 could not be used). For each site (Bosco/Gurin: BOS; Hohgant: HOH; Zermatt: ZER), only the months that were included in the temperature-growth LMMs (Fig. 2.3) are displayed. The grey shading indicates the 95% confidence intervals. For the sake of clarity, the single months are displayed in seasonal facets (rows).
2.4 Discussion

**Tree height and age distribution of forest outposts: implications for population dynamics and migration**

Stand size and age structure analyses can reveal developmental patterns and may therefore provide evidence whether the sampled stands are largely free of anthropogenic disturbance, and can inform about their successional phase (Veblen, 1986). In our study, stand densities were uniformly low, especially in the highest parts of the stands, and similar to undisturbed treeline sites in the Polar Ural Mountains and interior Alaska (Lloyd and Fastie, 2003; Mazepa, 2005). Both the distribution of tree heights and ingrowth times in the uppermost 25% of the elevation gradient at Bosco/Gurin and Zermatt feature uneven age distributions and reverse J-shaped height distributions (McCarthy and Weetman, 2006; Shorohova et al., 2009). Thus, we conclude that these stands are forest outposts that have established prior to the beginning of the current warming trend, and do not appear to be moving uphill yet (cf. Harsch et al., 2009). At Zermatt, this is additionally backed by the mean ages of the trees included in the sample, indicating the trees to have grown at the highest elevations also before the beginning of the pronounced temperature increase (cf. Fig. 2.5). However, the dendroecological sample of Bosco/Gurin yields trees at the highest elevations that are younger on average, which may indicate more recent ingrowth and a beginning advance of this treeline.

At Hohgant, however, the stands at the highest elevations are rather even-aged, but still have relatively more trees with recent ingrowth time than in the lower elevation quantiles. This relative abundance of young trees and the lack of older trees at the highest elevation quantiles may be caused either by a rising treeline or due to harsh environmental conditions that promote fast turnover rates caused by frequent dieback (Lloyd and Fastie, 2003). While the latter would provide evidence for a climatic (i.e., anthropogenically undisturbed) treeline (Harsch and Bader, 2011), the former cause could indicate a combined effect: treeline rise due to ameliorating growth conditions and the recent cessation of human activities. The age distribution of the dendroecological sample rather points to the latter, yielding a mean tree age exceeding the start of the pronounced temperature increase (cf. Fig. 2.5). Also, in case of the cessation of e.g. pasturing, one would expect many young trees to establish, but also the presence of a few remaining large old trees, thus leading to a bimodal distribution. This was not evident for any of the highest stands at the three study sites.
2.4. DISCUSSION

Analysis of short-term temperature-growth relationships

The quantification of among-tree variability and an analytical zooming in, below the population level, has long been stressed to be important (Carrer, 2011; Graumlich, 1991; Vanoni et al., 2016), but has hitherto been neglected in the analysis of climate-growth relationships. In other studies, temperatures of many and quite different months were found to be related to population mean growth across tree species at treeline in the European Alps, even with large differences for single species. Still, there is a stronger tendency of larch growth to be determined by temperatures over longer periods in the current year as well as in the year preceding growth ring formation (King et al., 2013b) compared to other species at treeline in the Alps. Based on ‘classical’ correlation analyses, growth of Swiss stone pine and mountain pine, for example, tends to be explained by mean temperatures of only one or two months or summer seasonal means (Carrer et al., 1998; Lenz et al., 2013; Oberhuber et al., 2008). These findings are partly supported by our results, showing larch at Bosco/Gurin to include the largest number of monthly temperature variables in the LMM (Fig. 2.3). However, our use of an information-theoretic model selection of LMMs resulted in a substantially higher number of significant covariates also for spruce, Swiss stone pine and mountain pine. This can largely be ascribed to the capacity of LMMs to explain not only a mean population signal, but also to account for among-tree variability in the estimation of relevant covariates by employing tree-specific random effects.

The species- and site-specific temperature-growth LMMs showed common patterns, but also slightly differing findings. The fixed effects exhibited clear seasonal periods for larch and spruce growth at both sites, but somewhat less clear patterns for Swiss stone pine and mountain pine (Fig. 2.3). Still, all LMMs yielded a strong positive effect of temperature in June/July (larch, spruce) and May/July (Swiss stone pine, mountain pine), forming periods of strong positive effects of summer temperature regardless of tree species and site. This generally agrees with previous studies using correlation analyses (Carrer et al., 1998; Graumlich, 1991; King et al., 2013a; Kirdyanov et al., 2003; Oberhuber et al., 2008). Growth of Swiss stone pine and mountain pine does not seem to be driven by temperatures during a continuous period of summer months, as for both species the positive effects of May and July were interrupted by weak negative effects in June. In their study on mountain pine, Lenz et al. (2013) explained this pattern with temperatures early in the growing season to determine the width of the cambium and therefore to be the main determinant of ring width. Temperatures later in the growing season were assumed to determine the earlywood-latewood ratio. Given the similar
pattern in our study, this explanation may also apply to Swiss stone pine, but with a somewhat higher impact of cambium formation on ring width than on the earlywood-latewood ratio. For all species and sites, the random effects of these months exhibited low standard deviations relative to the fixed effects, thus indicating low among-tree variability and the high importance of summer temperatures for synchronizing tree growth at treeline, regardless of tree characteristics and other abiotic growth modulators.

The climatic determinants of larch deviated systematically from those of the other species. Both at Bosco/Gurin and Zermatt, the LMMs for larch included periods of significantly positive effects for previous year’s August to October temperatures, with high absolute effects. Although the LMMs for spruce, Swiss stone pine and mountain pine also contained fall months, the period affecting growth occurred later, was shorter, and its absolute effects were smaller. This key difference between larch and the other species may be due to the deciduous nature of larch, relying much on stored carbohydrates to start the new growing season and producing a complete new set of needles (Kagawa et al., 2006; King et al., 2013a,b). On the contrary, the other species retain their needles for several years. Random effects in relation to the fixed effects of previous late summer/fall temperature were high for all species and sites. Unlike previous correlation analyses, these findings suggest that the need for stored reserves may differ substantially among trees.

The amount of snow cover and the timing of snow melt are key factors determining growth processes at upper treeline (Hagedorn et al., 2014). The period of negative effects of spring temperatures on growth of larch at both sites, but also of spruce (even though less distinct and with p-values higher by several magnitudes) is likely due to a combination of temperature and the amount of snow during late winter/spring. Respiratory carbon losses were found to be directly linked to air temperature, as long as the root zone is too cold to permit the uptake of water (Wieser, 2012; Wieser and Bahn, 2004). Carbon balance analyses at treeline have shown losses during the late winter/spring for evergreen conifers but also for larches, which feature pronounced net carbon losses as late as June (Havranek, 1985; Wieser, 2012). This is especially the case because larches have no needles at the beginning of the growing season and therefore cannot counteract the carbon loss, unlike evergreen conifers (Wieser, 2012). The differences between larches at Bosco/Gurin and Zermatt presumably are a consequence of the sites’ different precipitation regimes, with Bosco/Gurin having twice the annual precipitation sum and experiencing more extensive late winter snow than Zermatt (Blanchet et al., 2009). On the contrary, snow cover is believed to also have beneficial effects for tree growth under certain conditions.
Although low temperatures in late spring shorten the growing season, the subsequent long-lasting snow cover can provide greater water availability at the start of the growing season (Barbeito et al., 2012; Hättenschwiler and Smith, 1999). This hypothesis allows to explain the longer period of negative effects of spring temperature on tree growth at Hohgant compared to Bosco/Gurin. Trees at Hohgant grow on calcareous bedrock, which is heavily dominated by karst formations and lacks surface runoff. Therefore, they may depend more on water stored as snow than trees at Bosco/Gurin, which are situated on siliceous bedrock. In addition, deeper snow cover causes the trees to be better protected from freezing air temperatures. In a study on dwarf shrubs above treeline, low temperatures causing longer snow cover outweighed the positive effect of higher temperatures in spring that would result in a longer growing season (Wipf et al., 2009). Low temperatures favoring snow cover further minimize the exposure of trees to wind abrasion, snow and ice damage, and winter desiccation (Holtmeier, 2009), and promote nutrient availability (Mack et al., 2004; Sveinbjornsson et al., 2002). Another important factor controlled by spring temperatures are various forms of snow fungi (Gremmeniella abietina, G. laricina, Phacidium infestans, Herpotrichia juniperi). They have been shown to strongly influence growth and mortality particularly of young trees (Barbeito et al., 2013), but possibly also to lead to a reduction of the photosynthetically active needle surface of larger trees, which may also lead to reduced growth rates.

Carbon allocation to growth vs. reserves is a key strategic decision, especially for treeline trees (Felten et al., 2007; Landhausser et al., 2012). All tree species experienced conspicuously negative effects in late summer, paired with a high standard deviation of the corresponding random effects (Fig. 2.3). The cambial activity of trees at treeline finishes around the end of July, however cell-wall thickening and therefore the completion of the tree ring formation can last until mid-October, even at treeline (e.g., Rossi et al., 2007). Although the share of the total ring width attributed to xylem differentiation is relatively smaller compared to cambial activity, it was found that up to 15% of the total ring width was produced during the cell wall thickening phase (Gruber et al., 2009). Larch at Bosco/Gurin stood out with a three-month period of negative effects and the highest absolute values across all sites. This phenomenon can be understood by examining the among-tree variability (random effects). As mentioned above, the positive effects of previous fall temperatures reveal that some trees, most prominently larches, allocate a substantial amount of assimilates to reserves. The trees that deviated positively from the population mean in previous fall showed a negative deviation in the same months of the current year. This potential trade-off
applies to trees that allocate more assimilates to the carbohydrate reserves for the next year rather than to growth for the current year, provided that temperatures are favorable late in the growing season. The absolute values of the fixed effects emphasize again the high importance of reserve storage for the deciduous conifer larch compared to spruce, Swiss stone pine and mountain pine. Still, it has to be noted, that the p-values of the negative effects of current year’s late summer are by several magnitudes higher than those of current and previous year’s summer and still larger than those of current year’s late winter/spring (Fig. 2.A.5).

Detection of long-term growth trends

The growth rate trends at the uppermost part of the elevational gradients across all four treeline species were positive, but significant for larch at Bosco/Gurin and Zermatt only, and nearly significant for Swiss stone pine at Zermatt. Spruce and mountain pine did not yield significant trends in growth rates over time. Following the general hypothesis of temperature being the most important factor limiting tree growth at the treeline (e.g., Körner, 2012), as well as our findings regarding the relationship of temperature and growth (Fig. 2.3) in conjunction with rising temperatures in months that affect tree growth (Fig. 2.5), these trends are likely induced by improved growth conditions due to recent climate change. Although some studies suggest elevated atmospheric CO₂ levels or increased nitrogen deposition to account for positive trends in tree growth rates of some species (e.g., Dawes et al., 2013), the timing of the growth increase at our study sites favors temperature as the key factor since the start of the positive trend (approximately 1950) does not coincide with a pronounced increase of CO₂ (Bigler, 2016). Furthermore, the study sites are located in areas that experienced relatively small amounts of nitrogen deposition (Thimonier et al., 2010). Thus, our findings confirm the results of studies on the impact of climate change on tree growth in the Alps, attributing accelerated growth of Swiss stone pine (Motta and Nola, 2001; Vittoz et al., 2008) and larch (Motta and Nola, 2001) to a rise in temperature.

Larch exhibits high climate sensitivity (Carrer and Urbinati, 2004), exceeding the one of Swiss stone pine, spruce and mountain pine. This is well reflected in the temperature-growth LMMs (Fig. 2.3) and may cause the species to profit more strongly from rising temperatures during the growing period (Fig. 2.5) than the other species, and thus result in significant positive growth trends. On the contrary, Swiss stone pine, spruce and mountain pine exhibited rather small effect sizes and therefore lower temperature
sensitivity (Fig. 2.3), leading to non-significant growth reactions to the long-
term trend of increasing temperatures. However, these species still feature
positive growth trends. Unlike the short-term temperature-growth relations-
ships, the long-term development of growth over time showed relatively little
among-tree variability (Table 2.2). This may indicate that, regardless of the
period affecting the growth of single trees, the general warming trend in all
but one month (September) led to a low variability in growth trends over
time and elevation. This hypothesis is confirmed by some larch trees, which
strongly depend on reserve building, that feature a weaker positive trend as
mean September temperatures show a less pronounced increase (Fig. 2.5)
compared to other monthly mean temperatures.

Besides the temporal trends in ring widths, predictions based on the fixed
effects also suggest overall smaller ring widths of trees growing at higher el-
evations (Fig. 2.4). This decrease validates the use of elevation as a proxy
in Eq. 2.3 for varying temperature conditions experienced by the trees. Al-
though this effect is significant for larch only, it reflects the temperature
limitation of growth, which is valid for all trees (e.g., Körner, 2012) as tem-
perature and length of the growing season decrease when approaching upper
treeline. The small amount of among-tree variability indicates a homoge-
neous pattern of decreasing ring widths with elevation across the populations
at different sites.

In contrast to the similar growth trends across all four species at the
upper limit of their range, they show a somewhat different trend at lower
elevations, i.e. further away from treeline. The predictions for larch showed
decreasing growth trends, which may be due to the increasing stand density
and thus higher competition (Fig. 2.2). Improved growing conditions lead to
higher stand density (Gehrig-Fasel et al., 2007; Mazepa, 2005), which ham-
pers growth of the early-successional shade-intolerant larch (Motta and Nola,
2001). In this context, the strengthening of the growth trend with decreasing
elevation for spruce at Bosco/Gurin and Swiss stone pine at Zermatt can be
related to the decrease of larch. Both Swiss stone pine and spruce are ev-
ergreen and relatively shade-tolerant (Anfodillo et al., 1998), and they thus
may substitute for larch at the lower end of the treeline ecotone. At the upper
end of the treeline ecotone, the ability of larch to achieve high productivity
throughout the growing season due to osmoregulation (Badalotti et al., 2000;
Carrer and Urbinati, 2004) is advantageous with regard to its competitors.
Although some studies suggest that larch may suffer from drought even at
high elevations (Vittoz et al., 2008), it is unlikely to cause the diminishing
positive growth trend with decreasing elevation observed in our study. De-
spite large differences in precipitation between the two sites (cf. Fig. 2.1 a,
b and d), we found very similar patterns for larch growth at Bosco/Gurin and Zermatt (Table 2.2), suggesting that drought can be ruled out as a major cause for this interaction. The decline of larch is likely to be the first evidence of long-suspected feedback effects due to climate change (cf. Wang et al., 2016). It must be noted, however, that also the cessation of human activity may result in forest densification (Gehrig-Fasel et al., 2007) that negatively influences the performance of a shade-intolerant species such as larch. A definite disentanglement of the causes for the stand densification is not possible with the data at hand. However, based on our rigorous approach to search for study sites it is unlikely that changes in land use have caused an increase in stand density.

Detecting long-term tree growth trends by means of dendroecological analyses poses a number of challenges, including biases that may be introduced by the sampling design (Bowman et al., 2013; Nehrbass-Ahles et al., 2014) and the removal of biological growth trends (Bowman et al., 2013; Bribien et al., 2012; Peters et al., 2015). When sampling older trees in uneven-aged stands like those at Bosco/Gurin, Holgant and Zermatt, the trees’ trade-off between growth rate and longevity (cf. Bigler and Veblen, 2009) tends to create a false positive growth trend due to the older trees in the sample being probably slow-growing (“slow-grower survivorship bias”) and young trees in the sample being mostly fast-growing, as young slow-growing trees are likely to be too small to be considered for sampling (“big tree-selection bias”; Bowman et al., 2013; Brienen et al., 2012). We tackled these issues by firstly employing a stratified sampling design to obtain a “pseudo-population” (Nehrbass-Ahles et al., 2014), including selecting trees with DBHs as small as 5 cm, and secondly starting the trend analysis in the year 1850 only. Although Nehrbass-Ahles et al. (2014) found a random sampling design to best address tree growth trends, in our case this would have led to a proportional representation and thus increased number of small and potentially young trees, which would carry limited and very similar information about the recent past. The “pseudo-population” design was found to be also suited for growth trend analysis (Bowman et al., 2013; Nehrbass-Ahles et al., 2014). Choosing the year 1850 as starting point arose from (i) the timespan being equal to that of the temperature-growth analyses, where this date was chosen due to the availability of climate data; (ii) ensuring a reasonable sample depth; and (iii) choosing a timeframe well below the known longevity across all tree species included in this study. Thus, these measures should limit the effects of both sampling biases.

For detrending the individual tree-ring series, RCS was used, which is highly sensitive and reliable in detecting long-term growth trends (Peters
2.4. DISCUSSION

et al., 2015). Even though RCS tends to dampen the slope of trends, the probability of false positives and negatives is small (Peters et al., 2015). In addition, the robustness of LMMs based on growth trend was investigated by ruling out predictive capabilities of supplementary site and tree parameters (cf. Methods section), i.e. the long-term growth trends contained in the ring-width series were still best explained by time and elevation only.

In summary, we analyzed climatic treeline sites that do not currently show any strong evidence for an upward movement. The analysis of short-term temperature-growth relationships using LMMs revealed a considerable amount of previously unquantified among-tree variability, indicating differing strategies both between and within tree species related to the time when temperature actually affects ring-width formation. Beyond this, the temperature effects on short-term tree growth at natural treeline in three distinct regions of the Swiss Alps obtained from LMMs revealed a pattern that is consistent with findings from previous studies, regardless of the climate regime and tree species. In recent decades, positive growth trends across all study sites and species became evident, but they were significant for larch only, which is the most temperature-sensitive species. The significant positive growth trend was most pronounced at the highest elevations of the study sites, which reflect the effects of ameliorated growth conditions. The observed declining growth trend with decreasing elevation that is most likely due to neighborhood interactions may indicate negative feedback effects of climate change on tree growth at these high-elevation sites.
2.5 Acknowledgements

This research was funded by the Swiss State Secretariat for Education, Research and Innovation (project number C13.0056) in the context of the European Cooperation in Science and Technology (COST) Action “Enhancing the resilience capacity of SENSitive mountain FORest ecosystems under environmental change (SENSFOR)” (project number ES1203). We thank Flavian Tschurr, Alexander Eichenberger, Marius Rüetschi and Lukas Wunderle for their invaluable help with the field campaign and sample processing. We gratefully acknowledge discussions with Dario Martin Benito and Maxime Cailleret about dendroecological analyses and statistical methods.

2.6 Author’s contributions

- Matthias Jochner: Design of the study, acquisition, analysis and interpretation of data for the study; writing of the manuscript and revising it; final approval of the version to be published; agrees to be accountable for all aspects of the study.

- Harald Bugmann: Substantial contributions to the conception of the study, analysis and interpretation of data; revising the manuscript and approving the final version to be published; agrees to be accountable for all aspects of the study.

- Magdalena Nötzli: Contributions to the acquisition and analysis of data; revising the manuscript and approving the final version to be published; agrees to be accountable for all aspects of the study.

- Christof Bigler: Design and conception of the study, acquisition, analysis and interpretation of data for the study; revising the manuscript; final approval of the version to be published; agrees to be accountable for all aspects of the study.
2.7 References


2.7. REFERENCES


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2.A Supplementary information

Figure 2.A.1: Treeline ecotone approaching treeline at Stavel Crastu, Bosco/Gurin. Photo: M. Jochner
Figure 2.A.2: Typical spruce tree cluster outpost at the treeline of the Hohgant study site. Photo: M. Jochner

Table 2.A.1: Summary statistics of the tree-ring-width series. These include the number of trees of the species at each site, the mean series intercorrelation (± standard deviation; SD), the expressed population signal (EPS) and the mean series autocorrelation (± standard deviation).

<table>
<thead>
<tr>
<th>Study site</th>
<th>Species</th>
<th>Number of trees</th>
<th>Mean series intercorrelation ± SD</th>
<th>EPS*</th>
<th>Autocorrelation ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bosco/Gurin</td>
<td>Larix decidua</td>
<td>95</td>
<td>0.52±0.2</td>
<td>0.9</td>
<td>0.45±0.2</td>
</tr>
<tr>
<td></td>
<td>Picea abies</td>
<td>60</td>
<td>0.44±0.18</td>
<td>0.87</td>
<td>0.68±0.21</td>
</tr>
<tr>
<td></td>
<td>Picea abies</td>
<td>85</td>
<td>0.46±0.16</td>
<td>0.91</td>
<td>0.76±0.14</td>
</tr>
<tr>
<td></td>
<td>Pinus mugo</td>
<td>83</td>
<td>0.43±0.15</td>
<td>0.93</td>
<td>0.61±0.24</td>
</tr>
<tr>
<td>Hohgant</td>
<td>Larix decidua</td>
<td>95</td>
<td>0.52±0.16</td>
<td>0.85</td>
<td>0.55±0.22</td>
</tr>
<tr>
<td>Pinus cembra</td>
<td>84</td>
<td>0.40±0.19</td>
<td>0.90</td>
<td>0.74±0.16</td>
<td></td>
</tr>
</tbody>
</table>

* Wigley et al., 1984 suggest an EPS value of 0.85 as an acceptable statistical quality.
Figure 2.A.3: Swiss stone pine at a forest outpost below the Gugle ridge at Zermatt at approximately 2500 m a.s.l.; this is one of the highest tree stands of Switzerland. Photo: M. Nötzli
Figure 2.A.4: Age-height relationships of the individual species and both species combined per site, for Bosco/Gurin (BOS), Hohgant (HOH) and Zermatt (ZER). The lines represent linear models of the form $Age_{tree} = b_0 + b_1 \times height_{tree}$.
Figure 2.A.5: Parameter p-values of the species- and site-specific temperature-growth relationships as calculated with LMMs (Eqs. 2.1 and 2.2). Numbers are the respective p-values, tile colors represent the fixed effect sizes of the single months. Additionally, significance levels of the fixed effects are indicated by * for p<0.05, ** for p<0.01 and *** for p<0.001.
CHAPTER 3

Part II: Tree growth responses to changing temperatures across space and time: a fine-scale analysis at the treeline in the Swiss Alps

Abstract

Forest dynamics and particularly tree growth rates are considerably affected by temperature. Hence, global warming is expected to have large impacts on the growth and distribution of trees, especially at the cold distribution limit. While the influence of interannual temperature variability on tree growth has been described intensely, only few studies have analyzed how growth rates of trees decline along a fine-scale temperature gradient close to treeline. We compiled temporally and spatially highly resolved long-term air and soil temperature variables (degree-day sum, growing season length, growing season mean temperature) at three study sites comprising nine elevation gradients in the Swiss Alps. These temperature variables were paired with basal area increment data of the four major treeline species growing along these transects. Close to treeline, basal area increment of all species depended primarily on degree-day sums or growing season length, rather than on growing season mean temperature. While basal area increment was best explained by combining air temperature of the current and previous growing seasons,

the importance of soil temperature for tree growth was site-specific. When moving down from upper treeline, the temperature-growth relationship was strongly non-linear, showing a rapid decrease of temperature limitation and an increasing importance of factors other than temperature. Over the last 50 years, temperatures have increased substantially at all sites, with isotherms moving upward 160–260 m in elevation. The threshold-dependence of growth to temperature that we identified has led to an increase of high basal area increments over time, which, however, was consistent throughout the population only at the highest elevations.
3.1 Introduction

Trees are exposed to free atmosphere conditions due to their physiognomy, and thus their growth rates are affected by ambient temperatures (Körner, 2012). Consequently, the 0.85 K rise of global land surface temperatures over the past 100 years (IPCC, 2013) is expected to have considerable impacts on tree growth (McMahon et al., 2010) and thus also on forest dynamics and the distribution limits of tree species. These effects, in turn, have implications for the services provided by forest ecosystems (Elkin et al., 2013). While changing temperatures are expected to have impacts across the entire distribution range of a species (Lenoir and Svenning, 2015), they have particularly far-reaching consequences at the cold edge of a species’ distribution, where temperature acts as a key limiting factor (Körner, 2016). Although the influence of low temperature on tree growth in cold environments is undisputed, the interplay between different complementary processes affecting tree growth is challenging to disentangle, and the diverse reactions of these processes to temperature render it difficult to predict future growth patterns induced by increasing temperatures.

Both radial and height growth of trees are determined by several interconnected warmth-sensitive processes that exhibit different reactions to temperature. Meristematic activity underlying the growth of fine roots and aboveground tissue comes to a halt at mean temperatures of around 5° C (Körner, 1998; Rossi et al., 2008). At this temperature, however, photosynthesis and nutrient uptake are not strongly limited yet, but function even at substantially lower temperatures (Kimmins, 2004; Tranquillini, 1979). As these processes take place in different parts of a tree, they depend on different temperature variables. Belowground processes such as nutrient uptake and root growth are determined by soil temperature (Körner, 2012; Pregitzer et al., 2000; Tranquillini, 1979), whereas aboveground meristematic activity and photosynthesis rather depend on air temperature (Lenz et al., 2013). Although some studies found root-zone soil temperature to be a more important determinant for aboveground growth than air temperature (Hoch and Körner, 2003; Holtmeier, 2009; Pregitzer et al., 2000), the relative importance of air versus soil temperature for tree growth remains to be quantified.

Although the instantaneous rate and efficiency of ecophysiological processes underlying tree growth are coupled with temperature, annual growth increments result from the integration over the entire growing season. For some species it was shown that the number of hours above a certain temperature threshold is more important than the absolute temperatures during that period (Alvarez-Uría and Körner, 2007). Further, net ecosystem pro-
duction of forests was found to be highly correlated with the length of the growing season and to exhibit a step-like response of tree growth to temperature (White et al., 1999). However, radial stem growth of deciduous trees along elevation gradients showed higher correlations with growing season mean temperature than with the length of the growing season (Lenz et al., 2014). These temperature variables tend to be highly correlated with each other and with the sum of growing degree-days, such that disentangling their individual contribution to tree growth remains challenging.

For some tree species, not only the environmental conditions during the year of ring formation but also those of the previous year have an important influence on current year’s growth (e.g., Jochner et al., 2017a). This holds true for deciduous species (Kagawa et al., 2006; King et al., 2013a,b) as well as for evergreen and deciduous conifers (Hoch and Körner, 2003; Jochner et al., 2017a). It is therefore necessary to consider the previous year’s environmental conditions when assessing the relationship between radial stem growth and temperature, which complicates disentangling the limiting effect of temperature on tree growth. Thus, determining a functional form of this relationship that is valid for a broad range of species and sites is not trivial (cf. Rickebusch et al., 2007). Along elevation transects and therefore temperature gradients, the form of this function has often been described as being log-linear for deciduous trees (Lenz et al., 2014), rather threshold-like for conifers (Paulsen et al., 2000), or asymptotic (Rickebusch et al., 2007). Thus, to better quantify the relationship between radial stem growth and temperature, it is necessary to (i) employ fine-scale and tree-specific temperature data, (ii) consider several temperature variables influencing above- and belowground tree growth processes, and (iii) refrain from an a priori definition of a functional form of the relationship.

Temperatures, however, change not only across elevation but also in time. Given the general temperature dependency of tree growth at the upper treeline ecotone (e.g., Körner, 2012; Tranquillini, 1979), increased growth rates due to global warming have long been expected (e.g., Holtmeier and Broll, 2005), but were found to be ambiguous (Wilmking et al., 2004). It remains unclear whether trees can directly translate higher temperatures to growth or whether the warming just implies a suspension of the temperature limitation at the present-day treeline, which results in highly individual growth trends that are controlled by factors other than temperature. By disentangling the spatial component of the temperature-growth relationship of trees growing along elevation gradients versus the temporal components of both temperature and growth data, we will be able to elucidate the individual and population reaction of tree growth to increasing temperatures.
To this end, we analyze the variability in radial stem growth of four major treeline species along elevation gradients at the upper treeline in three climate regions of the Swiss Alps. Trees were chosen to face similar conditions regarding soil and present-day competition, i.e., temperature can be assumed to be the most important environmental variable varying among trees. We quantify the relation between radial growth and temperature based on highly resolved, long-term air and soil temperature data along these gradients. Thus, we capture and analyze temperature variability both in space (i.e., along the elevation gradients) and in time.

Specifically, we aim at answering the following questions: (i) What is the relative importance of different air and soil temperature variables on the growth variability of tree species across elevation gradients at natural treeline? (ii) Do absolute tree growth rates differ between tree species as a function of temperature? (iii) What is the functional relationship between key temperature variables and tree growth at these sites, and does it differ across species and sites? (iv) Do long-term growth trends differ along elevation gradients, across species and among individual trees, and do they conform to the expected relationship between growth and temperature?

3.2 Materials and methods

Site selection

Elevational transects are considered powerful for investigating climate-driven changes of tree growth (King et al., 2013b). The selection of transects for the analysis of temperature effects on tree growth should focus on forest stands approaching treelines that are undisturbed by local- and regional-scale modulators (Holtmeier and Broll, 2005). However, the recent cessation or extensification of human activities in many regions of the European Alps renders it challenging to differentiate between changes that are caused by recovery from human land use vs. those that arise from climate change (Gehrig-Fasel et al., 2007; Leonelli et al., 2009). Therefore, our search for study sites was based on multiple criteria. First, we identified the regionally highest patches of forest (“forest outposts”) in Switzerland using Swiss land use statistics GEOSTAT (Gehrig-Fasel et al., 2007), as they are most likely limited by temperature (Körner and Paulsen, 2004). Second, in preliminary field surveys the treeline form of candidate sites was assessed according to the conceptual model by Harsch and Bader (2011) to confirm temperature as the limiting factor of growth of these forest outposts. Third, we selected transects at three study
sites approaching forest outposts (Körner, 2012) in the Swiss Alps: the Ho-
hgant massif at Schangnau (treeline elevation at approximately 2000 m a.s.l.),
Stavel Crastu at Bosco/Gurin (treeline at approximately 2200 m a.s.l.) and
the Gugle ridge at Zermatt (treeline elevation at approximately 2500 m a.s.l.;
Fig. 3.1, Table 3.1). Each study site is located in one of the distinct cli-
mate regions of the Swiss Alps: Hohgant in the northern Alps experiencing
high precipitation and low irradiation; Bosco/Gurin in the Insubrian South-
ern Alps with high precipitation and high irradiation; and Zermatt in the
continental Central Alps with low precipitation and high irradiation.

Figure 3.1: Location of the three study sites Bosco/Gurin (BOS), Hohgant
(HOH) and Zermatt (ZER) in Switzerland in the context of regional treeline ele-
vation calculated using the Swiss land use statistics and the method proposed by
Gehrig-Fasel et al., 2007. Blue circles show the MeteoSwiss climate stations San
Bernardino (SBE), Säntis (SAE) and Col du Grand St. Bernard (GSB) that were
used to compile long time series of in-situ tree temperature conditions. Black lines
symbolize these connections and are labelled with the overall mean \( R^2 \) of all air
temperature transfer models (Eq. 3.1) per site as an estimate of how well in-situ
temperatures are modelled.
3.2. MATERIALS AND METHODS

Table 3.1: Summary of the study site characteristics, dendroecological sampling and temperature data.

<table>
<thead>
<tr>
<th>Topography</th>
<th>Slope range [°]</th>
<th>Bosco/Gurin (BOS)</th>
<th>Hohgant (HOH)</th>
<th>Zermatt (ZER)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspect</td>
<td></td>
<td>6–70</td>
<td>0–50</td>
<td>0–70</td>
</tr>
<tr>
<td></td>
<td>Southwest,</td>
<td></td>
<td>South, west,</td>
<td>North, northwest,</td>
</tr>
<tr>
<td></td>
<td>south</td>
<td></td>
<td>east</td>
<td>northeast</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Dendroecological sampling</th>
<th>Sampled species</th>
<th>1943–2185</th>
<th>1707–1974</th>
<th>2216–2505</th>
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</thead>
<tbody>
<tr>
<td>No. of sampled trees</td>
<td>Picea abies,</td>
<td>53 (spruce), 41 (larch)</td>
<td>50 (spruce), 58 (mountain pine)</td>
<td>Pinus cembra, Larix decidus, 40 (larch), 40 (Swiss stone pine)</td>
</tr>
<tr>
<td>Elevation range of sampled trees (m a.s.l.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree height range [m]</td>
<td>5.1–28.5</td>
<td>5.2–25.0</td>
<td>4.0–24.6</td>
<td></td>
</tr>
<tr>
<td>Tree diameter at breast height (DBH) range [cm]</td>
<td>20.1–91.0</td>
<td>20.3–92.0</td>
<td>20.9–108.5</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Temperature data</th>
<th>Timespan covered by the logger data</th>
<th>[2014-06-14, 2016-10-31]</th>
<th>[2014-05-29, 2016-10-31]</th>
<th>[2014-06-20, 2016-10-31]</th>
</tr>
</thead>
</table>

Dendroecological sampling

At each site, we set up three transects (for the layout see Fig. 3.2 and Figs. 3.A.1 and 3.A.2), ranging from treeline to approximately 320 m in elevation below treeline. Along each transect, we sampled a minimum of 20 trees with increment borers. Trees had a diameter at breast height (DBH, i.e. at a height of 130 cm measured along the stem) >20 cm, equally distributed over the prevailing tree species and along the elevation gradient.

Tree species included Norway spruce (Picea abies) and European larch (Larix decidua) at Bosco/Gurin, Norway spruce and mountain pine (Pinus mugo ssp. uncinata) at Hohgant, and Swiss stone pine (Pinus cembra) and European larch at Zermatt. We sampled two cores at breast height per tree if possible and always attempted to hit the pith. The sampled trees were chosen to face as similarly low competition and equal soil conditions as possible. Each tree’s coordinates, elevation, tree height, and DBH were measured. In the lab, the increment cores were mounted on wooden supports, sanded and the ring widths measured with a resolution of 0.01 mm on a measurement device (Lintab 5, Rinntech, Heidelberg, Germany) according to standard dendroecological procedures (Fritts, 1976). We cross-dated the ring-width series visually and quantitatively using COFECHA (Holmes, 1983) to ensure correct assignment of calendar years to each tree ring.
Compilation of in-situ tree air and soil temperature

To capture fine-scale differences in temperature along the transects, eight temperature loggers per transect (iButton DS1922L, Maxim Integrated), attached to trees, were recording hourly 2 m air temperature between May 2014 and October 2016 (see Hohgant transect layouts in Fig. 3.2, and Figs. 3.A.1 and 3.A.2 for the layouts at Bosco/Gurin and Zermatt). In addition to the placement on the north side of the trees, Gill screens were protecting the air temperature loggers from direct radiation. This way, we ensured measurement conditions close to the standard meteorological approach that made our measurements comparable with those of climate stations. At the same trees on the north-facing side of the stem, eight additional loggers were recording hourly 10 cm soil temperature per transect. In total, $2 \times 8 \times 9 = 144$ loggers were deployed at the nine transects. The hourly temperature measurements of each logger were then aggregated to daily mean temperatures ($T_{air}$, $T_{soil}$).
3.2. MATERIALS AND METHODS

Figure 3.2: Example of the study site layout, showing the three transects at the Hohgant (for maps of the other two sites see Figs. 3.A.1 and 3.A.2). Along each transect, air and soil temperature loggers were installed and trees with a diameter at breast height (DBH) >20 cm were sampled. The dotted black line depicts the 800 degree-day isotherm using the data of 1980–2010, the continuous black line 1930–1960, respectively, demonstrating the strong temperature increase over time. Digital elevation model produced with own aerial imagery.
To obtain long time series of air temperature, all available MeteoSwiss climate stations from Switzerland providing daily mean air temperatures \( T_{\text{air}} \) were checked regarding their Pearson correlation with \( T_{\text{air}} \). For each study site, we selected the respective MeteoSwiss climate station yielding the highest correlation, i.e. between Bosco/Gurin and the San Bernardino station (elevation 1638 m a.s.l.), between Hohgant and the Säntis station (2502 m a.s.l.), and between Zermatt and the Col du Grand Saint Bernard station (2472 m a.s.l.; Fig. 3.1). Using the overlapping timespan of measurements, linear air temperature transfer models for daily mean temperatures of the form

\[
T_{\text{air}}(m) = b_0 + b_1 \times T_{\text{station}}
\]  

(3.1)

were calculated. Separate daily mean air temperature transfer models were calculated for each month, with \( m = \{\text{January} \ldots \text{December}\} \), as lapse rates vary considerably throughout the year (Kollas et al., 2014). Using these models, we transferred the entire time series of the climate stations to logger temperatures, resulting in estimated daily \textit{in-situ} air temperature series going back to 1864 (Bosco/Gurin), 1882 (Hohgant) and 1864 (Zermatt). During the overlapping measurement period 2014–2016, measured and modelled \textit{in-situ} air temperatures showed mean absolute errors of 1.05 K, 1.63 K and 1.37 K, and a mean bias of 0.07 K, 0.24 K and -0.14 K, respectively.

Soil temperature \( T_{\text{soil}} \) is tightly coupled to air temperature \( T_{\text{air}} \) but has a much smaller amplitude and lags behind air temperature (Gehrig-Fasel et al., 2008). Cross-correlograms for each air-soil temperature logger pair revealed significant correlations of \( T_{\text{soil}} \) with \( T_{\text{air}} \) up to five days prior to the current day. Therefore, multiple linear regressions of the form

\[
T_{\text{soil}}(t) = b_0 + b_1 \times T_{\text{air}}(t) + b_2 \times T_{\text{air}}(t - 1) + b_3 \times T_{\text{air}}(t - 2) + b_4 \times T_{\text{air}}(t - 3) + b_5 \times T_{\text{air}}(t - 4) + b_6 \times T_{\text{air}}(t - 5)
\]  

(3.2)

with \( T_{\text{soil}}(t) \) and \( T_{\text{air}}(t) \) being mean soil and air temperatures of loggers at the same location on day \( t \) were fitted, which were employed for air-to-soil temperature transfer models. Using the modelled air (Eq. 3.1) and soil (Eq. 3.2) temperature time-series per logger, we calculated individual air and soil temperature models per day and transect:

\[
T(t) = b_0 + b_1 \times Elev
\]  

(3.3)
with $T(t)$ representing either modelled daily mean air or soil logger temperature on day $t$ and $Elev$ the elevation of the loggers along the transects. Using these daily transect models and the measured elevations of the sampled trees, we predicted tree-specific time series of daily mean temperatures, thus reflecting the fine-scale differences in ambient temperatures experienced by the trees due to their differences in elevation (cf. Fig. 3.2).

To assess the functional form between annual tree growth rates and temperature, we aggregated the daily mean temperatures to annual variables. We calculated annual degree-day sums of both air and soil temperature ($DDSum_{air}$, $DDSum_{soil}$). For $DDSum_{air}$, $5\, ^\circ C$ was used as the development threshold (Körner and Paulsen, 2004; Seo et al., 2008; Sitch et al., 2003), for $DDSum_{soil}$ $3.2\, ^\circ C$ (Körner and Paulsen, 2004). Furthermore, growing season length ($GSL$) and growing season mean temperature ($GSM$), both based on air temperature and a development threshold of $5\, ^\circ C$, were calculated. All these variables were calculated for the current year’s growing season as well as for the current and previous year’s growing season combined to capture carry-over effects in tree carbon relations.

Relative contribution of air and soil temperatures to growth

To reduce geometric- and age-related effects on ring widths, the tree-ring-width series were converted to basal area increment ($BAI$) starting from the pith. For cores that did not hit the pith, a geometric method was used to estimate the number of missing years to the pith based on ring curvature and the average of the first five measurable ring widths (Duncan, 1989). Other detrending methods such as RCS (Becker, 1989) and starting from the bark were also tested and found to yield highly similar and consistent results (Fig. 3.A.3). Finally, starting from the pith was selected for further analysis because it retains growth units unlike indices such as RCS, which produce unit-less indices. Using Spearman’s rank correlations ($\rho$), we assessed the relative contributions of the temperature variables to $BAI$ by means of $\rho$- and p-values.

Functional relationship between air and soil temperature and growth

We further used the annual air and soil temperature variable with the highest $\rho$-values to assess the functional form of the temperature-growth relationship
by plotting the temperature variable against BAI. To obtain interpretable coefficients and to test for statistically significant relationships without imposing a functional form \emph{a priori} between temperature variables and BAI, we employed a two-way unbalanced repeated measures ANOVA per study site, with both $DDS_{\text{air}}$ and $DDS_{\text{soil}}$ as predictors and the individual tree IDs as grouping variable for the random intercept:

$$BAI_{ijk} = \mu + \alpha_i + \beta_j + (\alpha_i \times \beta_j) + b_k + \epsilon_{ijk} \quad (3.4)$$

with $\mu$ being the grand mean of $DDS_{\text{air}}$ or $DDS_{\text{soil}}$, $\alpha$ being the effect of $DDS_{\text{air}}$ or $DDS_{\text{soil}}$ on three levels ($i$), $\beta$ being the effect of the species on two levels ($j$), $b$ a random intercept with $b_k \sim N(0, \sigma_b^2)$ for each individual ($k$) and $\epsilon_{ijk}$ the residual error with $\epsilon_{ijk} \sim N(0, \sigma^2)$. We stabilized the residuals by using a log-link function.

As the ANOVAs are robust for quantifying the significance and strength of the functional relationship but are unable to grasp its form, we furthermore plotted predictions of site- and species-specific linear mixed effects models with spline-smoothed $DDS_{\text{sums}}$ (4 degrees of freedom). These models are flexible enough to visually reveal patterns in the data. All calculations were conducted in the R statistics software (R Core Team, 2016), using the packages dplR (Bunn, 2008) and lme4 (Bates et al., 2015).

### 3.3 Results

**Relative contribution of temperature variables to growth**

Temperature variables calculated based on the current growing season and the season preceding tree ring formation showed a higher influence on annual BAI compared to variables based on the current growing season alone. This pattern was indicated by Spearman’s rank correlation, which yielded higher population median $\rho$-values for the former than the latter for all species and at all sites (Fig. 3.3). The difference of $\rho$ was around 10% (average over all four temperature variables) for mountain pine at Hohgant and Swiss stone pine at Zermatt, around 20% for spruce at Bosco/Gurin and Hohgant as well as larch at Zermatt, and almost 30% for larch at Bosco/Gurin.

Comparing sites and species, there was some agreement as to which temperature variables showed the relatively highest correlation with BAI (Fig. 3.3), as indicated by the $\rho$-values and the percentage of significantly
3.3. RESULTS

positive correlations: $DDSum_{\text{air}}$ (larch at Zermatt, $\rho = 0.61$; mountain pine at Hohgant, $\rho = 0.53$), $DDSum_{\text{soil}}$ (larch at Bosco/Gurin, $\rho = 0.50$; spruce at Bosco/Gurin, $\rho = 0.49$; Swiss stone pine at Zermatt, $\rho = 0.41$) and $GSL$ (spruce at Hohgant, $\rho = 0.59$) yielded almost equally high median-values. For all species at all sites, $GSM$ showed a consistently lower median correlation than the other temperature variables. This is also reflected in the $p$-values of the single trees’ correlations with the temperature variables. In all but one case (spruce at Bosco/Gurin), the percentage of significant ($p < 0.05$) relationships was lower for $GSM$ compared to the other variables (Fig. 3.3). Notably, the variability in $\rho$-values was comparable for all species but mountain pine at Hohgant, which featured particularly high variability (Fig. 3.3).

**Relationship between air and soil degree-day sums and basal area increment**

Since $DDSum_{\text{air}}$ and $DDSum_{\text{soil}}$ of the current and previous growing season showed the highest $\rho$-values for the median in all but one case (spruce at Hohgant), the relationship and functional form between temperature and $BAI$ were assessed for these two variables. A wide range of temperature conditions was covered by combinations between $DDSums$ and $BAI$. $DDSum_{\text{air}}$ ranged from 280.5 K·d (highest tree at Zermatt in the year 1913) to 1845 K·d (lowest tree at Hohgant in the year 2012; Fig. 3.4). $DDSum_{\text{soil}}$ ranged from 700 K·d (highest tree at Zermatt in the year 1925) to 2898 K·d (lowest tree at Bosco/Gurin in the year 1947). The gradients of $DDSums$ spanned comparable ranges at the three sites, but they differed substantially in the absolute values.

Across all species and sites, the average population growth rate ($BAI$) increased invariably when moving towards warmer conditions, be it air or soil temperature (Fig. 3.4). Site-specific ANOVAs revealed highly significant positive effects of higher $DDSum_{\text{air}}$ and $DDSum_{\text{soil}}$ on $BAI$ (Table 3.2). For example, if air degree-days increased by 600 K·d (the base class of $DDSum_{\text{air}}$ differs per site, adhering to the different ranges in $DDSum_{\text{air}}$ at the three sites; Table 3.3), the mean population increase of growth ranged from 136% (spruce at Bosco/Gurin) to 338% (larch at Zermatt). While there were no significant differences between the tree species at the lowest $DDSum$ levels at Bosco/Gurin in the ANOVA, the differences between spruce and mountain pine (mountain pine grew faster) at Hohgant, and larch and Swiss stone pine (Swiss stone pine grew faster) at Zermatt were significant. On the contrary, when moving from cooler to warmer conditions, the sampled tree species...
Figure 3.3: Spearman’s rank correlations ($\rho$) between basal area increment ($BAI$) and $DDSum_{air}$ (for temperatures above 5°C; $DDSumAir$), $DDSum_{soil}$ (for temperatures above 3.2°C; $DDSumSoil$), the growing season length ($GSL$) and the growing season mean temperature ($GSM$) calculated as a combination of the current year’s growing season and the previous year’s growing season no earlier than August (top) as well as for the current year only (bottom). The columns represent the four species (LADE: Larix decidua; PIAB: Picea abies; PICE: Pinus cembra; PIMU: Pinus mugo) at the three sites (BOS: Bosco/Gurin; HOH: Hohgant; ZER: Zermatt). Percentages above the boxes indicate the fraction of significant (p-value<0.05) $\rho$-values.

differed significantly in $BAI$ increases at Bosco/Gurin and Zermatt, while the difference was barely significant at Hohgant (Table 3.3, Figs. 3.4 and
3.3. RESULTS


Table 3.2: Summary statistics of the $DDSum$-$BAI$ ANOVAs. $DDSumClass$ levels were chosen to have equal inter-class distances for all sites (cf. Table 3.3 for the exact levels).

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Bosco/Gurin (BOS)</th>
<th>Hohgant (HOH)</th>
<th>Zermatt (ZER)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Summary statistics</strong></td>
<td>$DDSum_{air}$</td>
<td>$DDSum_{soil}$</td>
<td>$DDSum_{air}$</td>
</tr>
<tr>
<td>Species</td>
<td>$\chi^2$</td>
<td>df</td>
<td>$p$-value</td>
</tr>
<tr>
<td></td>
<td>4.13</td>
<td>1</td>
<td>$4.2 \times 10^{-2}$</td>
</tr>
<tr>
<td>$DDSumClass$</td>
<td>$&lt;2 \times 10^{-16}$</td>
<td>2</td>
<td>***</td>
</tr>
<tr>
<td>Species x $DDSumClass$</td>
<td>17.5</td>
<td>2</td>
<td>$1.6 \times 10^{-4}$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>$DDSum_{soil}$</th>
<th>$DDSum_{air}$</th>
<th>$DDSum_{soil}$</th>
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</thead>
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<tr>
<td><strong>Summary statistics</strong></td>
<td>$DDSum_{soil}$</td>
<td>$DDSum_{air}$</td>
<td>$DDSum_{soil}$</td>
</tr>
<tr>
<td>Species</td>
<td>$\chi^2$</td>
<td>df</td>
<td>$p$-value</td>
</tr>
<tr>
<td></td>
<td>2.16</td>
<td>1</td>
<td>$1.4 \times 10^{-1}$</td>
</tr>
<tr>
<td>$DDSumClass$</td>
<td>$&lt;2 \times 10^{-16}$</td>
<td>2</td>
<td>***</td>
</tr>
<tr>
<td>Species x $DDSumClass$</td>
<td>28.13</td>
<td>2</td>
<td>$7.8 \times 10^{-7}$</td>
</tr>
</tbody>
</table>

Significance codes: $p <0.001$ (***) , $p < 0.01$ (**), $p <0.05$ (*); df = degree of freedom

Functional form of the relationship between air and soil degree-day sums and basal area increment

For all four species at the three study sites, the population signal of the $DDSum_{air}$- and $DDSum_{soil}$-$BAI$ relationships resembled a sigmoidal curve (Fig. 3.4): After relatively flat-angle slopes on the low side of $DDSums$, $BAI$ increased strongly during a steep transition phase. The pronounced $BAI$ increase around the middle of each site’s $DDSums$ range was then again followed by a levelling off of the $BAI$ population signal. Predictions on the level of the individual trees revealed considerable among-tree variability, primarily at higher $DDSums$. While the single trees’ $BAI$ values were relatively close together at the low end of the temperature ranges, they fanned out after the steep transition phase.
### Table 3.3: Coefficients and statistics of the DDSum-BAI ANOVAs

The three DDSumClass levels were chosen to have equal inter-class distances for all sites. Still, the absolute values of each class differed per site according to the differences in DDSumair ranges.

<table>
<thead>
<tr>
<th>Summary statistics</th>
<th>Bosco/Gurin (BOS)</th>
<th>Hohgant (HOH)</th>
<th>Zermatt (ZER)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fixed effects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>6.33</td>
<td>5.49</td>
<td>5.5</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.15</td>
<td>0.15</td>
<td>0.12</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
</tr>
<tr>
<td>Species^1</td>
<td>-0.14</td>
<td>0.76</td>
<td>0.77</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.22</td>
<td>0.19</td>
<td>0.18</td>
</tr>
<tr>
<td>p-value</td>
<td>5.34 x 10^{-1}***</td>
<td>4.34 x 10^{-5}***</td>
<td>1.99 x 10^{-5}***</td>
</tr>
<tr>
<td>DDSumClass II^2</td>
<td>0.68</td>
<td>1.12</td>
<td>1.22</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.07</td>
<td>0.11</td>
<td>0.01</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
</tr>
<tr>
<td>Species x DDSumClass II</td>
<td>-0.3</td>
<td>-0.27</td>
<td>-0.4</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.09</td>
<td>0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>p-value</td>
<td>2.88 x 10^{-4}***</td>
<td>4.06 x 10^{-2}a</td>
<td>&lt;2 x 10^{-16}***</td>
</tr>
<tr>
<td><strong>Fixed effects</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>6.31</td>
<td>5.73</td>
<td>5.53</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.15</td>
<td>0.11</td>
<td>0.13</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
</tr>
<tr>
<td>Species^1</td>
<td>-0.15</td>
<td>0.66</td>
<td>0.74</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.22</td>
<td>0.15</td>
<td>0.21</td>
</tr>
<tr>
<td>p-value</td>
<td>4.91 x 10^{-1}</td>
<td>9.35 x 10^{-6}***</td>
<td>4.41 x 10^{-4}***</td>
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<tr>
<td>DDSumClass II^3</td>
<td>0.24</td>
<td>0.73</td>
<td>0.5</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.04</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>p-value</td>
<td>3.81 x 10^{-9}***</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
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<tr>
<td>DDSumClass III^3</td>
<td>0.68</td>
<td>1.19</td>
<td>1.05</td>
</tr>
<tr>
<td>Std. error</td>
<td>0.05</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
<td>&lt;2 x 10^{-16}***</td>
</tr>
<tr>
<td>Species x DDSumClass II</td>
<td>-0.12</td>
<td>-0.21</td>
<td>-0.33</td>
</tr>
<tr>
<td>Std. error</td>
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<td>0.04</td>
<td>0.08</td>
</tr>
<tr>
<td>p-value</td>
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<td>1.72 x 10^{-6}***</td>
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<tr>
<td>Species x DDSumClass III</td>
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<td>-0.51</td>
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<td>0.05</td>
<td>0.1</td>
</tr>
<tr>
<td>p-value</td>
<td>3.00 x 10^{-7}***</td>
<td>1.08 x 10^{-13}***</td>
<td>2.11 x 10^{-7}***</td>
</tr>
</tbody>
</table>

^1 Species levels: **Bosco/Gurin** base species *Larix decidua*, 2nd species *Picea abies*; **Hohgant** base species *Picea abies*, 2nd species *Pinus mugo*; **Zermatt** base species *Larix decidua*, 2nd species *Pinus cembra*

^2 Class levels DDSumair: **Bosco/Gurin** base class 800–900, class II 1100–1200, class III 1400–1500; **Hohgant** base class 600–700, class II 900–1000, class III 1200–1300; **Zermatt** base class 400–500, class II 700–800, class III 1000–1100

^3 Class levels DDSumsoil: **Bosco/Gurin** and **Hohgant** base class 1800–2000, class II 2200–2400, class III 2600–2800; **Zermatt** base class 1000–1200, class II 1400–1600, class III 1800–2000

^4 Significance codes: p <0.001 '***', p <0.01 '**', p <0.05 '*'
3.3. RESULTS

Temporal patterns within the growth-temperature relationships

The temporal course of both the BAI and temperature data was assessed in a combined way, i.e. by identifying patterns of BAI-temperature pair occurrences along time. Both $DDSum_{air}$ (Fig. 3.5 a, b) and BAI (Fig. 3.5 b) exhibited a positive trend. From the beginning of the temperature time series (i.e., before 1900) until 2016, the average $DDSum$s experienced by the sampled trees increased by between approximately 50% at Bosco/Gurin and nearly 100% at Hohgant and Zermatt (Fig. 3.5 a). A first peak occurred in $DDSum_{air}$ at all sites around 1950, followed by a temporary decrease until around 1975 and a subsequent increase to the highest values in the most recent time. Between 1960 and 2010, 30-year average $DDSum_{air}$ isotherms moved upwards by approximately 160 m in elevation at Bosco/Gurin, and approximately 260 m at Hohgant and Zermatt (Figs. 3.2, 3.A.1, 3.A.2).

To better isolate the temporal component, we divided the data into three elevation bands per site. Absolute elevations of the elevation bands differed per site, however the range was similar as all transects covered approximately 320 m in elevation, starting at treeline. At all transects, small BAI values occurred over almost the entire range of $DDSum$s and throughout the entire time period (Fig. 3.5 b). Only at the very highest $DDSum$s and in most recent times, small BAI values became less frequent. This pattern occurred most prominently in the lower thirds of all transects and species, but it was also recognizable at higher elevations, especially at Bosco/Gurin. On the contrary, both the maximum BAI and its variability increased strongly with rising $DDSum$s and also with time (Fig. 3.5 b). This was true along the entire gradients and for all species and sites, except for spruce at Hohgant and Swiss stone pine at Zermatt where distinct increases in maximum BAI and variability occurred only in the upper thirds of the transects.
Figure 3.4: Relationship between $DDSum_{air}$ and $DDSum_{soil}$ of the current and previous growing season combined, and BAI. The black curves in the background are the raw data, blue curves are predictions using the random effects of species- and site-specific linear mixed effects models with spline-smoothed $DDSums$ (4 degrees of freedom), and the red lines visualize the population mean reaction by representing the fixed effects prediction. The rows are arranged according to species (LADE: Larix decidua; PIAB: Picea abies; PICE: Pinus cembra; PIMU: Pinus mugo) and sites (BOS: Bosco/Gurin; HOH: Hohgant; ZER: Zermatt).
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Figure 3.5: Temporal components in the growth and temperature data. a) Range of $DDSum_{air}$ of the previous and current growing season along the elevation gradient of each tree species (i.e. there are slight differences between the $DDSum_{air}$ ranges of the two species at one site, as the elevational extent was slightly different) over time as indicated by the grey ribbon. The black line depicts the smoothed mean. b) Relationship between $BAI$ and $DDSum_{air}$, coloured with the year of occurrence of the data pairs. Data points are semi-transparent to allow for differentiation of colours of overlapping points. The data are divided into elevation bands (lower, middle and upper third of each transect). The columns are arranged by species (LADE: Larix decidua; PIAB: Picea abies; PICE: Pinus cembra; PIMU: Pinus mugo) and sites (BOS: Bosco/Gurin; HOH: Hohgant; ZER: Zermatt).
3.4 Discussion

Relative contribution of different temperature variables to growth

The storage of carbohydrate reserves for the next growing season – in the past mostly attributed to deciduous trees but more recently regarded to be similarly important for conifers (e.g., Barbaroux and Breda, 2002; Hoch and Körner, 2003; Jochner et al., 2017a) – plays a substantial role in determining annual radial growth rates at the three study sites. Predictions of annual growth variability of all four tree species were improved when the temperature conditions of the previous growing season were considered, compared to only the current season’s temperatures. The largest increase in correlation was found for larch, the only conifer that generates a full set of new needles every year and thus relies most strongly on stored carbon for setting off into the new growing season (Kagawa et al., 2006). However, also spruce at Bosco/Gurin and Hohgant depends on stored reserves, acting to (i) support new growth in spring, (ii) provide the energy expended in winter maintenance respiration (Barbaroux and Breda, 2002), and (iii) allow for an adaptive response to pathogen attacks and herbivory (Oren et al., 1988). Mountain pine and Swiss stone pine depend least on the temperature conditions of the previous growing season. This may be caused by these species’ patterns of intra-seasonal variation of non-structural carbohydrates that are the most important compounds for reserve storage, which diverge from those of other species such as larch. In a study of three *Pinus* species including Swiss stone pine, Hoch and Körner (2003) found little intra-seasonal variation in non-structural carbohydrates, i.e. no significant build-up of reserves was observed at the end of the growing season. This is in contrast to larch, for example, which allocates carbohydrates to aboveground growth early in the season and to storage late in the season, leading to substantial variations in non-structural carbohydrate concentrations throughout the growing period (Kagawa et al., 2006). Also at our study sites, our findings suggest that mountain pine and Swiss stone pine depend less on carbon reserves and therefore are least sensitive to variations in environmental conditions of the previous year’s late growing season.

When assessing the temperature conditions that trees experience throughout the growing season, both the absolute values and their duration affect annual tree growth (e.g., Bouriaud et al., 2005; King et al., 2013a). Therefore, it is plausible that annual radial growth is in all but one case (spruce at Hohgant) best explained by $DDSum_{air}$ above 5°C or $DDSum_{soil}$ above
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3.2 °C, which both integrate absolute temperatures and the duration of the growing season and therefore quantify best the total energy that is available for a tree to grow (Seo et al., 2008). However, for all species at the three study sites, GSL (i.e., the number of days with mean temperatures above 5 °C) showed similar correlations with tree growth. On the contrary, GSM (growing season mean temperature) correlated far less with annual growth, especially at Bosco/Gurin. GSM and GSL are highly correlated at Hohgant and Zermatt, unlike at Bosco/Gurin. A higher variability in the amplitudes of seasonal temperature at Bosco/Gurin compared to the other two sites results in high seasonal mean temperatures with short GSLs and vice versa. This indicates that the period of time a tree experiences temperatures above a certain development threshold (i.e., number of days with mean temperatures above 5 °C) is more important than the absolute temperature above that threshold (e.g., growing season mean temperature). This pattern was previously observed for Smith Fir at treeline in Tibet (Li et al., 2017) and also confirmed by the form of the functional relationship, which features a levelling off of BAI after a steep transition when moving towards higher temperatures (cf. Fig. 3.4). The less variable amplitudes in seasonal temperature at Hohgant and Zermatt and therefore higher correlation between GSL and GSM may mask this effect. This is in contrast to the findings of Lenz et al. (2014) for deciduous trees approaching their upper range limit, who found the length of the growing season to have a negligible effect on stem growth compared to mean temperature. The observed disproportionate increase in the growth of deciduous trees at higher temperatures may not apply to the conifers studied here, which were found to reach a growth maximum slightly above the development threshold (Rossi et al., 2007).

Soil temperatures are important determinants of root growth and nutrient availability (Alvarez-Uria and Körner, 2007). Still, there was no significant difference in the correlation between growth and air versus soil temperatures at Hohgant and Zermatt. As nutrient availability is still sufficient at temperatures below the inhibition temperature of meristematic activity (Pregitzer et al., 2000), soil temperatures seem to influence root growth in the same way as air temperatures influence shoot growth, namely by limiting the structural carbon sink capacity of trees (Alvarez-Uria and Körner, 2007; Körner, 2012). At Hohgant and Zermatt, soil temperatures are therefore representing a dampened version of air temperature and thus do not strongly differ in ρ-values. Only at Bosco/Gurin ρ-values of air and soil temperature differed significantly, with soil temperature exhibiting higher correlations. It is rather unlikely that this difference occurs due to a limitation in nutrients, as soils do not differ substantially from those at Zermatt and as both sites fea-
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ture crystalline bedrock (Swisstopo, 2012). Cold soils were found to inhibit root formation although air temperatures may be favorable (Alvarez-Uria and Körner, 2007). The Insubrian climate at Bosco/Gurin entails considerably larger amounts of snow in late winter/early spring than at Hohgant and Zermatt (Blanchet et al., 2009). High snow cover is known to have a substantial influence on the length of the growing season and thus on growth at treeline (Paulsen and Körner, 2014), as it leads to a long snowmelt period with soil temperatures at 0°C, while air temperatures would permit growth with temperatures exceeding 5°C. This underlines the importance of the late winter snowfall regime for the determination of the key temperature variables controlling growth at Bosco/Gurin.

Relationship between temperature and tree growth

The temperature effect on growth rates may be confounded with other influences such as the onset of drought at higher temperatures, differences in nutrient availability or differences in the competitive situation. We systematically tried to avoid these issues. First, we only analyzed the cold upper end of the species’ ranges. Second, our sampling was designed to be consistent throughout each transect, choosing similar soil conditions (and therefore nutrient availability) and among-tree competition for all sampled trees. Furthermore, we fitted two-way ANOVAs with the individual trees as grouping variable for the random intercepts, allowing to capture both among-tree variability and the population signal (cf. Jochner et al., 2017a). Thus, we did not define any functional form \textit{a priori}, but rather focused on revealing significant patterns in the data.

Temperature-limited treelines were found to occur under comparable temperature conditions (e.g., Körner, 1998). Therefore, the substantial differences between the boundaries of the \textit{DDSum} \textit{air} and \textit{DDSum} \textit{soil} ranges at the three sites seem to be counter-intuitive at first and would suggest that tree growth at least at Bosco/Gurin and Hohgant is limited by factors other than temperature. Still, the treeline elevation conforms to the general pattern of treeline elevations across Switzerland (cf. Fig. 3.1) and other mountain regions (e.g., Körner, 2012), commonly attributed to the ‘mass elevation effect’, which postulates equal temperatures at different elevations across a mountain range. Thus, the temperatures measured in our study appear not to be those experienced by the active tree tissues. Trees at Zermatt with its very low \textit{DDSums} compared to Bosco/Gurin and Hohgant may benefit from little cloud cover and little air humidity and therefore high irradiation, possibly experiencing similar tissue temperatures as trees at the other two
sites. However, these temperatures are not measurable with the standard meteorological approach. This is confirmed when assessing the hourly temperature measurements from our campaign, which clearly show a higher daily amplitude during the growing season at Zermatt compared to both Hohgant and Bosco/Gurin (cf. Fig. 3.A.5; not to be confused with the higher seasonal amplitudes at Bosco/Gurin as discussed earlier in this paper). However, the long time series that were compiled are based on daily mean temperatures. Thus, the higher daytime temperatures at Zermatt are equalized by lower nighttime temperatures. To truly capture the differences in temperature-related continentality between sites, it would therefore be necessary to work with long-term sub-daily resolution temperature data.

The temperature dependency of the processes contributing to tree growth is well reflected in the reaction of $BAI$ to increasing $DDSums$ for both air and soil temperature. The influence on $BAI$ variability is substantial when moving from the cold to the warm end of the temperature gradient, with statistically highly significant increases in $BAI$ throughout all species, sites and $DDSum$ levels. It is noteworthy that the increase from the base to the first $DDSum$ level (for the levels, cf. Table 3.3) in most cases is only about half as large as the increase from the first to the second $DDSum$ level. This suggests a highly non-linear relationship between radial stem growth and temperature, possibly indicating a threshold temperature that, once exceeded, induces disproportionally high growth rates. This conforms to previous findings for conifers at high elevations and latitudes (Paulsen et al., 2000; Rossi et al., 2007) and is also confirmed by the visualized data (cf. Fig. 3.4).

The large increase in $BAI$ variability and model residuals (cf. Figs. 3.4 and 3.A.4) with increasing $DDSums$ suggests a rapid decline of the limiting effect of temperature. The large span of the individual trees’ reactions under warmer conditions suggests that those trees that feature less pronounced growth increases are limited by environmental factors other than temperature, which has been observed for root and shoot growth slightly below treeline (e.g., Lenz et al., 2014; Salzer et al., 2014). Another reason may be intra-seasonal temperature variability, which is also believed to exert a substantial influence on annual ring width (Jochner et al., 2017a; Lenz et al., 2013; Li et al., 2017) but is not captured in the $DDSums$ representing total energy. The statistically indistinguishable low levels of growth of the two species at the low end of the $DDSum$ ranges at Bosco/Gurin can be interpreted as an indication that the upper end of the transects are the low-temperature limit of tree growth for both species indeed, while at Hohgant and Zermatt one species reaches the limit of its range faster than the other.
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Functional form of the relationship between temperature and tree growth

The sigmoid-like shape of the $DDSum_{air}/DDSum_{soil}$-$BAI$ relationships of all four species suggests a threshold behavior of growth including a lower growth asymptote. The steep transition phase of the populations’ responses conforms to the finding of $GSL$ correlating better with growth than $GSM$ and the necessity for trees to acquire a certain amount of energy to accomplish a full annual growing cycle (Seo et al., 2008). Once a threshold of $DDSums$ is passed, higher growth rates are much more likely to occur than below that threshold. For example, for all four species in this study and based on our definition for $DDSum_{air}$ of the previous and current growing season, we expect this threshold to be at approximately 1000 K·d, thus confirming the observations of abrupt tree growth decreases when approaching the treeline (Paulsen et al., 2000) and matching those for seedling root growth of both deciduous and coniferous trees (Alvarez-Uria and Körner, 2007). However, more than one process is controlling growth, as the individual trees of all four species show a steep transition phase at approximately the same $DDSums$ but different levels of growth under conditions above the threshold temperature. This could be due to intra-seasonal temperature variability, which is thought to exert a substantial influence on ring width (Jochner et al., 2017a; Lenz et al., 2013) but is not captured in the $DDSums$ representing total energy, or it may be an indication for different limiting processes setting in as soon as the temperature threshold is passed, possibly including nutrient or water availability.

Temporal patterns within growth-temperature relationships

Increasing temperatures reported on a global scale (IPCC, 2013) are well reflected in the long-term course of modelled $DDSums$ at our study sites. The greater temperature rise reflected in the modelled long-term tree temperatures at Hohgant and Zermatt compared to Bosco/Gurin matches the patterns found by Rebetez and Reinhard (2008) in a study of temperature trends of many climate stations across Switzerland, showing a less pronounced increase for Alpine valleys opening towards the south compared to the rest of Switzerland, especially in spring and fall.

The temporal patterns of paired observations between $DDSum$ and $BAI$ showed that this relationship contains not only $BAI$ variability between trees experiencing different temperatures along transects, but also variabil-
3.4. DISCUSSION

ity within trees due to long-term changes in temperature. The temperature increase over time at the three sites appears to have led to distinct rises of maximum $BAI$ in the upper third of all transects, and rises of the minimum $BAI$ values in their lower thirds. This pattern provides further evidence for a lifting of the temperature limitation of tree growth at present-day tree-line (cf. Motta and Nola, 2001; Vittoz et al., 2008). At the same time, the trends in maximum $BAI$ further downslope are much more variable, with partly consistent rises throughout the transects (larch at Bosco/Gurin and spruce at Hohgant) or with no evident changes in variability over time (e.g., spruce at Bosco/Gurin). As the sampled trees were selected to face equally low competition (at least at the present time), a growth feedback caused by denser stand structure due to increased temperatures can be ruled out (but see Jochner et al., 2017a, where a stratified “pseudo-population” sampling design at the same sites revealed competitive feedback effects; also cf. Wang et al., 2016). Potential explanations may relate to the differences in climate warming patterns of the study sites, as explained below.

Despite the general increase in global temperatures (IPCC, 2013), there is considerable spatial heterogeneity as to the exact patterns (e.g., CH2011, 2011). Although the net temperature increase over time is lower at Bosco/Gurin compared to the other sites, it started off at a higher level compared to Hohgant and especially Zermatt (Fig. 3.5 a; Rebetez and Reinhard, 2008). This pattern may explain the constancy of maximum $BAI$ values of spruce at Bosco/Gurin, where the temperature threshold was passed already at the beginning of the study period in the middle and lower thirds of the transects, while at Hohgant there was a positive trend in maximum $BAI$ also in the middle and lower thirds. Furthermore, spruce growth was found to be particularly sensitive to June and July temperatures at these sites (Jochner et al., 2017a). Long-term trends in monthly temperatures reveal a much larger increase of June and July temperatures north of the Alps compared to the south (Rebetez and Reinhard, 2008). Monthly temperature trends may also explain the contrasting behavior of larch at Bosco/Gurin, which did in fact show a consistent trend of maximum $BAI$ across the entire elevation gradient and even more than larch at Zermatt. At both sites, larch growth is substantially influenced by the build-up of reserves in September and October of the previous growing season (Jochner et al., 2017a). These two months, in turn, have seen similar temperature changes in both regions between 1900 and 2000 (Rebetez and Reinhard, 2008).

We found the form of the functional relationship between temperature and tree growth to feature a threshold behavior rather than a gradual increase in growth rates when moving to higher temperatures. The temporal component
in our data reveals that this threshold is passed more frequently after 1950 than before. Consequently, the varying levels of growth after passing the threshold have led to positive trends for some trees, but rather unclear growth trends at the population level, as other limiting factors set in. However, trees growing at the highest elevation are still close to the temperature threshold and thus may still profit from a further temperature increase due to climate change.

In summary, the general temperature rise has induced a positive trend in BAI of all species in the upper thirds of the transects at Bosco/Gurin, Hohgant and Zermatt. Moving down from treeline, intra-seasonal variability and the threshold dependency of the temperature-growth relationship cause differing temporal trends of BAI.

3.5 Conclusions

Based on the findings of our study, we draw the following conclusions:

(i) The degree-day sums (DDSums) of air temperature and soil temperature were best predicting the growth of trees. In all cases, taking into account the previous year’s growing season explained growth much better, thus demonstrating the importance of reserves of the previous year. This finding plays a role also for evergreen conifers, not only for deciduous species such as larch. In general, soil temperatures exhibited a relative contribution to growth that was equal to that of air temperature, but only at the site with excessive snow cover in late winter/spring (Bosco/Gurin) they showed a higher correlation with annual growth increment than air temperature.

(ii) The relationship between radial growth and key temperature variables revealed a highly non-linear increase of growth of all species at all sites when moving down from the treeline. Soon after the temperature limitation was overcome, growth-limiting factors other than temperature set in, leading to a pronounced increase in growth variability.

(iii) The form of the temperature-growth relationship also supports its non-linear nature, revealing a steep transition phase but varying maximum levels of growth under conditions above the threshold temperature. This is due either to intra-seasonal temperature variability or the importance of other limiting processes.
(iv) The temporal component in our data (1864 to 2015 AD) revealed positive long-term growth trends at the treeline. However, with decreasing elevation below treeline, the site-specific monthly temperature trends rather than the absolute amount of climate warming and other growth limiting factors caused variable reactions of the same species at different sites. This finding matches the patterns expected from the temperature-growth relationship with its sigmoid-like shape.
3.6 Acknowledgements

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3.7 Author’s contributions

- Matthias Jochner: Design of the study; acquisition, analysis and interpretation of data for the study; writing of the manuscript and revising it; final approval of the version to be published; agrees to be accountable for all aspects of the study.

- Harald Bugmann: Substantial contributions to the conception of the study; analysis and interpretation of data; revising the manuscript and approving the final version to be published; agrees to be accountable for all aspects of the study.

- Magdalena Nötzli: Contributions to the acquisition and analysis of data; revising the manuscript and approving the final version to be published; agrees to be accountable for all aspects of the study.

- Christof Bigler: Design and conception of the study; acquisition, analysis and interpretation of data for the study; revising the manuscript; final approval of the version to be published; agrees to be accountable for all aspects of the study.
3.8 References


air-to-soil temperature transfer model”. In: *Ecological Modelling* 213.3-4, pp. 345–355.


3.8. REFERENCES


3.8. REFERENCES


3.A Supplementary information

Figure 3.A.1: Study site layout showing the transects at Bosco/Gurin. Along each transect, air and soil temperature loggers were installed and trees with a DBH >20 cm were sampled. Digital elevation model (c) 2016 swisstopo (JD100042).
Figure 3.A.2: Study site layout showing the transects at Zermatt. Along each transect, air and soil temperature loggers were installed and trees with a DBH >20 cm were sampled. Digital elevation model (c) 2016 swisstopo (JD100042).
CHAPTER 3. TEMPERATURE-GROWTH RELATIONSHIPS

Figure 3.A.3: Comparison of the $DD_{\text{Sum}_{\text{air}}}$ – growth relationships calculated with different detrending methods: (i) basal area increment (BAI, unit mm$^2$) from outside with bark included, (ii) BAI from outside without bark, (iii) BAI from the pith and (iv) regional curve standardization (RCS, unit-less ring-width index). The columns represent the four species (LADE: *Larix decidua*; PIAB: *Picea abies*; PICE: *Pinus cembra*; PIMU: *Pinus mugo*) at the three study sites (BOS: Bosco/Gurin; HOH: Hohgant; ZER: Zermatt).
Figure 3.A.4: Predictions of the site-specific ANOVAs (cf. Table 3.3) fixed effects (red lines) and random effects (blue lines) on three levels of DDSums and for the two species per site. The boxplots resemble the underlying data for calculating the ANOVAs. The small numbers below the boxes indicate the number of observations included in the respective DDSum classes. Classes were chosen to have equal inter-class distances for all sites. The columns represent the four species (LADE: *Larix decidua*; PIAB: *Picea abies*; PICE: *Pinus cembra*; PIMU: *Pinus mugo*) at the three study sites (BOS: Bosco/Gurin; HOH: Hohgant; ZER: Zermatt).
Figure 3.A.5: Mean daily air (A; first row) and soil (S; second row) temperature amplitudes for the growing season months. The grey ribbon indicates the standard deviation. The columns are arranged according to the three study sites Bosco/Gurin (BOS), Hohgant (HOH) and Zermatt (ZER). We used our temperature logger data for these calculations (cf. Table 3.1).
Part III: Understanding the past is the key to the future: Combining empirical data and dynamic modeling to predict forest dynamics at treeline under climate change

Abstract

Mountain forests provide many ecosystem goods and services and thus are of vital importance in densely populated mountain regions. Temperature is commonly thought to be the most important large-scale driver of forest growth at and directly below treeline. Therefore, global warming is expected to have far-reaching consequences for mountain forests and treeline. To predict the future development of these forests, it is important to understand the drivers underlying today’s patterns. Yet, the interplay of abiotic and biotic determinants of forest succession renders this task challenging. We apply a mechanistic approach to elucidate the ecological causalities behind treeline and subalpine forest dynamics in three case study regions of the Swiss Alps. To this end, we assess different variants of the dynamic forest gap model ForClim against an extensive set of empirical data. Besides the importance of growing season temperature for determining subalpine forest dynamics and treeline elevation, we reveal a pivotal role of the site-specific precipitation regime that significantly moderates the growth conditions in two ways: (i)

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cloud cover and air humidity control the direct radiation available to trees, and (ii) snow cover duration restricts the period when trees can actually grow. We then employ the model variant that best portrays past forest dynamics to simulate future development under downscaled climate change scenarios. Simulations show the largest absolute increase of stand basal area at the highest elevations, regardless of the climate change scenario, while stands as little as 200 m below current treeline experience minor changes in basal area only. However, lower-elevation stands show a pronounced species shift from subalpine to montane site types. Differences between the climate change scenarios become visible only after 200 years, due to the large inertia in the reaction of tree population dynamics. These species shifts and potential ingrowth of trees into highest elevations will pose new challenges but also opportunities for the exploitation of ecosystem services provided by mountain forests.
4.1 Introduction

Mountain forests approaching upper treeline ("subalpine" in a European context; cf. Ellenberg and Strutt, 2009) provide important ecosystem goods and services (EGS) in densely populated areas such as the European Alps (Barbeito et al., 2012; Elkin et al., 2013; Grace et al., 2002; Greenwood and Jump, 2014). This includes provisioning services such as timber production, but at least as importantly cultural and regulating services as they contribute to landscape aesthetics, mediate surface runoff and shelter human infrastructure from gravitational natural hazards such as avalanches or rock fall (Haslett, 2010). In addition, subalpine forests play an important role in the carbon cycle and, if advancing (Gehrig-Fasel et al., 2007), are a significant carbon sink at the landscape scale.

Over more than a century, global land temperatures have been increasing (0.85 K on a global average between 1880 and 2012; IPCC, 2013) with important impacts on EGS. In mountain regions such as the European Alps, this trend is even more pronounced with a mean temperature increase of 0.35 K per decade over the last 30 years (Pepin et al., 2015; Rebetez and Reinhard, 2008). Temperature variability is the most important large-scale driver of forest dynamics close to treeline, and therefore global warming implies changes in treeline elevation, productivity and species composition of subalpine forests (Holtmeier, 2009; Körner, 2012; Tranquillini, 1979). This, in turn, has consequences for EGS (CH2014-Impacts, 2014; Elkin et al., 2013). For example, changing landscape aesthetics have implications for touristic use, altered species composition and forest structure will pose challenges for maintaining protective functions, and an advancing treeline will lead to considerable carbon sequestration. Still, the knowledge about the interplay of different drivers of subalpine forest and treeline dynamics is highly incomplete (Holtmeier and Broll, 2017), and recent studies have demonstrated feedback effects that may even reverse the per se positive effect of increasing temperature on growth (e.g., Jochner et al., 2017a; Wang et al., 2016; Wieczorek et al., 2017). Therefore, the development of treeline and subalpine forests under different climate change scenarios, especially at the regional and local scale, is highly uncertain (cf. Barbeito et al., 2012; Holtmeier and Broll, 2017; Körner, 2012).

To robustly assess the response of subalpine forests in a changing climate, a detailed understanding and consideration of regional-scale modulators of forest dynamics is required, beyond just considering air temperature (Holtmeier and Broll, 2017). Especially precipitation patterns and cloud cover are powerful modulators of global patterns. Although a limiting effect of
water availability has been demonstrated (Lloyd and Fastie, 2002), there is rarely such a shortage of liquid precipitation that it would reduce tree growth in cold subalpine environments in Europe (Holtmeier, 2009; Holtmeier and Broll, 2005). More importantly, cloud cover and air humidity control the surface radiation balance (Grace et al., 2002), which is of key importance for determining the actual energy the trees can utilize, but it is not captured well by standard air temperature data (Körner, 2016). Furthermore, the multiple influences of snow on tree regeneration and growth at high elevations are quite important (Barbeito et al., 2013; Kirdyanov et al., 2003; Paulsen and Körner, 2014; Wieser, 2012). For example, as long as there is substantial snow cover, root zone temperatures do not normally exceed 0 °C, regardless of air temperature (Gehrig-Fasel et al., 2008). During this time, root growth is inhibited, whereas enhanced tree respiration during warm, but still snow-covered periods in late winter/spring reduces annual growth (Jochner et al., 2017a; Wieser and Bahn, 2004). This shortening of the growing season also increases the interannual variability of growth conditions due to the larger variability of precipitation compared to temperature, which has been found to distinctly influence subalpine forest biomass and treeline elevation (Bugmann and Pfister, 2000). We posit that assessing the influence of these regional- to local scale drivers of forest dynamics with a mechanistic modelling approach is a viable solution to quantify their relative importance for shaping current subalpine forests, and to improve the quality of predictions of the impacts of climate change.

Several interlinked warmth-sensitive processes that show slightly different responses to temperature, such as meristematic activity, photosynthesis, or nutrient uptake determine tree growth (Pregitzer et al., 2000; Rossi et al., 2008; Tranquillini, 1979). Hence, elucidating the functional relationship between annual tree growth and temperature for a broad range of species and sites is not trivial (cf. Rickebusch et al., 2007). Still, such knowledge is a prerequisite to reliably predict future forest dynamics, especially for sites that are close to the cold edge of species’ distributions because there even small differences in temperature may yield large differences in growth (Lenz et al., 2014; Paulsen et al., 2000). Both the form of this function and its parameterization were described in diverse, partly conflicting ways, particularly towards the low end of the temperature range (Lenz et al., 2014; Paulsen et al., 2000; Rickebusch et al., 2007).

For studying the impact of climate change on forest structure and species composition, dynamic forest gap models have proven to be valuable, and they were applied successfully to simulate forest dynamics at a wide variety of sites, including the treeline ecotone. The model ForClim, which employs
4.2. MATERIALS AND METHODS

simple but reliable mechanisms of climatic influences on ecological processes (Bugmann, 1994, 1996), and the derived landscape model LandClim are capable of portraying essential features of long-term forest dynamics across a wide range of environmental conditions in the European Alps (Elkin et al., 2013; Heiri et al., 2006; Risch et al., 2009), including the border between subalpine forest and alpine tundra (e.g., Bugmann and Pfister, 2000; Colombaroli et al., 2010; Heiri et al., 2006; Schwörer et al., 2014).

In the present study, we address the following research questions: (i) what aspects of the regional climate regime with its implications for snow cover, cloud cover and air humidity are pivotal for determining the simulated response of subalpine forests to climate variability? (ii) How sensitive is simulated forest succession to different assumptions regarding the temperature-growth relationship? (iii) How do these factors affect the simulation of present-day undisturbed treeline stands compared to observations? (iv) How do species composition and forest productivity develop along elevation gradients in subalpine forests in response to scenarios of future climate change? To answer these questions, we assess the importance of various driving factors of subalpine forest dynamics at the individual-tree and stand scale by comparing a range of variants of ForClim with a set of empirical data collected at three case study sites in the Swiss Alps. Then, using the best-fitting model and locally adapted climate change scenarios, we simulate future forest dynamics at the upper end of the subalpine zone.

4.2 Materials and methods

Case study sites

Elevational transects at three study sites in the Swiss Alps were selected that represent natural treelines (for a detailed description of the identification process of these sites, cf. Jochner et al., 2017a): the Hohgant massif at Schangnau (treeline elevation at approx. 2,000 m a.s.l.), Stavel Crastu at Bosco/Gurin (treeline elevation at approx. 2,200 m a.s.l.) and the Gugle ridge at Zermatt (treeline elevation at approx. 2,500 m a.s.l.; Fig. 4.1, Table 4.1). Each study site is located in a distinct climate region of the Swiss Alps: Hohgant in the Northern Alps experiencing high precipitation and low irradiation; Bosco/Gurin in the Insubrian Southern Alps with high precipitation and high irradiation; and Zermatt in the continental Central Alps with low precipitation and high irradiation. For more information on the study sites, see Jochner et al. (2017a) and Jochner et al. (2017b).
Empirical growth, stand and temperature data

To assess and validate different model variants for their suitability in portraying essential features of the subalpine forest approaching treeline, we acquired both tree-scale and stand-scale variables in the field and by means of remote sensing.

Radial growth data

At each site, we set up three transects ranging from treeline to approximately 320 m in elevation below treeline (cf. Jochner et al., 2017b). Along each tran-
sect, we acquired radial growth data of the dominant tree species: Norway spruce (*Picea abies*) and European larch (*Larix decidua*) at Bosco/Gurin, Norway spruce and mountain pine (*Pinus mugo ssp. uncinata*) at Hohgant, and Swiss stone pine (*Pinus cembra*) and European larch at Zermatt (Table 4.1). For a detailed description of the dendroecological sample and its acquisition, see Jochner et al. (2017b).

### Table 4.1: Summary of the study site characteristics and empirical data including the dendroecological sampling, the remotely sensed stand characteristics and the temperature logger data.

<table>
<thead>
<tr>
<th>Topography</th>
<th>Slope range [°]</th>
<th>Aspect</th>
<th>Bosco/Gurin (BOS)</th>
<th>Hohgant (HOH)</th>
<th>Zermatt (ZER)</th>
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<td>0-50</td>
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<th>Elevation range of sampled trees [m a.s.l.]</th>
<th>Tree height range [m]</th>
<th>Tree diameter at breast height (DBH) range [cm]</th>
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<td></td>
<td><em>Picea abies, Larix decidua</em></td>
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<td><em>Pinus cembra, Larix decidua</em></td>
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<th>Temperature data</th>
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<td>[2014-05-29, 2016-10-31]</td>
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<td></td>
<td>1864–2016</td>
<td>1864–2016</td>
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</tbody>
</table>

### Tree height data and stand basal area

To capture stand structure, tree height distribution at each site was surveyed by means of 3D surface model reconstructions using largely overlapping high-resolution (<10 cm/px) aerial imagery obtained with an unmanned aerial vehicle, as well as field measurements (Table 4.1). We compiled canopy height models and automatically delineated single trees with a height >2.5 m (Hyypa et al., 2001; Zarco-Tejada et al., 2014). We developed allometric equations from field-sampled DBH and height measurements to derive tree DBH (Eq. 4.1) from remotely sensed tree heights:

$$\log(DBH) = b_0 + b_1 \times \log(height_{tree})$$  \hspace{1cm} (4.1)

We derived site-specific but not species-specific allometric equations, as we could not reliably distinguish the individual species from each other in the
remotely sensed canopy height model. Still, the field-measured data allowed to accurately differentiate between the species. The $R^2$ of the allometric equations was 0.76 for Bosco/Gurin, 0.53 for Hohgant and 0.65 for Zermatt. P-values never exceeded $7.8 \times 10^{-39}$. After converting remotely sensed tree heights to DBH, we calculated tree volumes using DBH, tree height and a geometric model (Eq. 4.2, Kramer and Akça, 2008):

$$volume = f \times height_{tree} \times DBH^2 \times \frac{\pi}{4}$$

with $f$ being a form factor of 0.5 that approximates stem shape and is analogous to the form factor used to calculate volume in the dynamic forest model (Schmid et al., 2015).

In-situ temperature measurements

To capture fine-scale differences in temperature along the elevation gradients at the three case study sites, we recorded hourly 2m air temperature with eight temperature loggers per transect (iButton DS1922L, Maxim Integrated), attached on the north-facing side of selected trees between May 2014 and October 2016. Gill screens were protecting the air temperature loggers from direct radiation. In total, 72 loggers were deployed at the nine transects. We then aggregated the hourly temperature measurements of each logger to monthly mean temperatures to match the time resolution of the model ForClim.

The dynamic forest succession model ForClim

For the simulations of past, present and future subalpine forest dynamics, we used version 3.3 of the forest gap model ForClim as the reference model (Mina et al., 2017). According to the standard approach of gap models (Botkin et al., 1972), establishment, growth and mortality of tree cohorts are considered on an annual basis. ForClim consists of three basic submodels. First, the weather submodel (Bugmann, 1996), which generates monthly average temperature and precipitation data, and from these derives annual values of bioclimatic variables (minimum winter temperature, annual and seasonal degree-day sums). Second, the water submodel (Bugmann and Solomon, 2000), which combines these bioclimatic variables with site-specific parameters accounting for soil water holding capacity (“bucket size”) and radiation (correction of evapotranspiration based on latitude, slope and aspect) for the calculation of a seasonal and an annual drought index. And third, the plant submodel, which takes the outputs of the weather and water submodels to
simulate tree regeneration, growth and mortality based on species-specific tolerances regarding abiotic factors (e.g., minimum growing degree-day sum, minimum and maximum winter temperature, drought) and biotic processes (e.g., competition for light, browsing). ForClim does not incorporate seed dispersal but considers all species to be potentially present at every location. Growth and regeneration are simulated for cohorts of trees with an initial DBH of 1.27 cm and an annual radial growth that depends on annual variations in biotic (competition for light) and abiotic conditions (degree-day sum and soil moisture). Mortality is simulated for individual trees as the result of a constant background mortality, which is parameterized using maximum age, and a stress-induced mortality, which is driven by slow radial growth. Maximum tree height (a proxy for site index) and height growth are modelled dynamically based on abiotic and biotic conditions (Rasche et al., 2012): the species-specific maximum height is reduced by unfavorable environmental conditions (temperature and drought), and the ratio between diameter and height increment is modulated by competition. A detailed description of ForClim version 3.3, including a list of parameters can be found in Huber et al. (in revision), together with a Europe-wide sensitivity analysis of the model.

Testing of ecological assumptions by means of model variants

To elucidate the processes that shape today’s patterns in subalpine forest dynamics, we modified all three submodels (cf. Table 4.2 for all model variants) to test different ecological assumptions regarding (i) the impact of snow on the growing season, (ii) the species-specific growth response to temperatures at the cold edge, and (iii) the importance of the daily temperature amplitude on tree growth. The relevance of these different assumptions was tested by comparing and assessing the individual model variants regarding their ability to reproduce key aspects of measured subalpine tree growth and forest structure. On the individual-tree level, this included maximum radial growth and maximum tree height. On the stand level, we assessed basal area as well as volume, as it combines the two individual-tree variables radial growth and height. To compare simulated variables with empirical stand data, we used root mean squared errors (RMSE) as well as mean absolute errors (MAE), which are less biased by outliers than RMSE (Willmott and Matsuura, 2005).
Impact of snow cover on soil moisture and growing season length

To assess the influence of snow on the growing season, we implemented a simple snow module. It was originally developed by McCabe and Wolock (2009) and already used by Schwörer et al. (2016) in LandClim, a landscape model derived from ForClim. Precipitation above a monthly mean temperature of $3\, ^\circ\text{C}$ is considered to fall as rain only, whereas below $-1\, ^\circ\text{C}$ it is considered to fall completely as snow. Between these threshold temperatures, the proportion of rain and snow varies linearly. Analogously, snowmelt is a function of monthly mean air temperature and occurs above $-1\, ^\circ\text{C}$. We further considered canopy interception of snow, which has been shown to reduce snow cover on the forest floor considerably (Moeser et al., 2016). We assumed intercepted snow to amount to 30% of precipitation, a reasonable value for subalpine conifer forests (Pomeroy et al., 1998). In LandClim, the snow module is used to enhance water availability during the summer months by providing melt water (Schwörer et al., 2016). We additionally implemented a shortening of the growing season in spring and early summer: when snow is present, soil temperature rarely exceeds $0\, ^\circ\text{C}$ (Gehrig-Fasel et al., 2008), and hence little biological activity is possible for the trees. We thus restrict the period in which the sum of degree-days is calculated to those months without snow cover. This restriction depends on elevation, and it greatly enhances the interannual variability of degree-day sums due to the larger interannual variability of precipitation compared to temperature (Fig. 4.A.1). In the following assessment, we compared variants of ForClim with (Snow on) and without (Snow off) the snow module.

Responses of tree growth to temperature variability at the cold edge

In ForClim version 3.3, the temperature-growth relationship is represented by an asymptotic function (Bugmann and Solomon, 2000). Subsequently, this function will be called the Normal (in terms of being the default) variant. The parameters that define the individual species’ responses in the Normal function were estimated theoretically (Bugmann and Solomon, 2000). Rickebusch et al. (2007) adjusted and reparametrized it using tree-ring data. We will refer to this function as the Rickebusch variant. It should be noted that we did not use our set of empirical data for any parameterization of the temperature-growth asymptote, but only for validation purposes.
4.2. MATERIALS AND METHODS

The importance of the diurnal cycle of air temperature

ForClim features a correction function for degree-day sums, which reduces the error arising from their calculation using monthly mean temperatures (Botkin et al., 1972), in contrast to the more accurate sine-wave method (Allen, 1976), which requires sub-daily temperature data. We assessed the suitability of the ForClim correction function at our sites using data from nearby MeteoSwiss climate stations to compare the degree-day sums calculated from monthly mean against those calculated with locally available sub-daily data. While the original correction function worked well for the case study sites Bosco/Gurin and Hohgant, it did not perform well for the continental site Zermatt (Fig. 4.A.2) due to the significantly higher daily temperature amplitudes (Fig. 4.A.3). We therefore re-fitted the correction function for Zermatt with the method derived by Bugmann (1994) using (i) the average difference (model variant Zermatt Localized mean), and (ii) the maximum difference (model variant Zermatt Localized max) between the degree-day calculation methods based on sub-daily temperature data (Allen, 1976) vs. monthly average temperature (Botkin et al., 1972). A full description of the original correction function can be found in Bugmann (1994).

Simulation experiments

Model initialization using pre-climate change data

For each case study, we defined transects with 100 m elevation steps ranging from 1,400 m a.s.l., which is far below treeline at every site, to the locally highest elevation. This resulted in 15 elevation levels at Bosco/Gurin (1,400–2,800 m a.s.l.), 13 levels at Hohgant (1,400–2,600 m a.s.l.) and 19 levels at Zermatt (1,400–3,200 m a.s.l.). We initialized the model for each site and elevation step by simulating potential natural vegetation from bare ground with the different ForClim variants over a spin-up period of 800 years to reach a stable pseudo-equilibrium. For each site, we compiled 800-year climate series by randomly sampling temperature and precipitation data from the pre-climate change era (i.e., 1801-1950) from the closest grid point in the HISTALP surface climate data set for the greater Alpine region (Fig. 4.2, Auer et al., 2007). For precipitation, we did not account for any further orographic precipitation effects other than those included in the HISTALP data set (Auer et al., 2007) as we did not have any reliable in-situ precipitation data to assess the magnitude of these effects. We scaled monthly mean temperatures individually for each elevation step at the three sites. To this end, we used fine-scale empirical temperature measurements from our case
study sites to calculate month-specific temperature lapse rates for each case study site, and then scale monthly mean temperature to the elevation steps. To account for the stochasticity in the climate data, we repeated the spin-up process 200 times per site and elevation step, and averaged the simulation trajectories to calculate average stand characteristics.

Simulation of present forest characteristics

Following the initialization and averaging of the 200 trajectories per site and elevation step, we continued the simulations with “real” weather data for the recent time period, i.e. with the climate data from the HISTALP data set for the period 1801–2014 (Fig. 4.2). As for the spin-up simulation, temperatures were adapted to each elevation level using the site-specific lapse rates. For the assessment of the model variants against the empirical data, we used the simulation state in the year 2014.

Projections of future forest characteristics

We continued the simulation from 2014 into the future with the best-fitting ForClim variant under four climatic scenarios, including a “no change” scenario and three climate change scenarios. The “no change” scenario assumed temperature and precipitation to remain constant at the level of the period 1980–2009 and was used to predict long-term stand characteristics in equilibrium with current climate conditions. For simulations under climate change, we utilized locally adapted climate change scenarios provided by the CH2011 and CH2011+ projects (Bosshard et al., 2015; CH2011, 2011), which are available for every MeteoSwiss station in Switzerland. They consist of daily temperature and precipitation changes with respect to the period 1980–2009 for the A2, A1B and RCP3PD emission scenarios (CH2011, 2011). For each study site, we selected the MeteoSwiss station yielding the highest correlation with our locally measured temperature data, i.e. between Bosco/Gurin and the San Bernardino station (elevation 1,638 m a.s.l.), between Hohgant and the Säntis station (2,502 m a.s.l.), and between Zermatt and the Col du Grand Saint Bernard station (2,472 m a.s.l.; Fig. 4.1). The climate change scenarios were applied to our site climate data following the approach by Elkin et al. (2013). The scenario data apply until 2085, and from then on we continued the simulation with a constant climate until the year 2300 to evaluate the long-term response to climate change of the simulated forests. Again, we created 200 trajectories per site, elevation step and climate change scenario (Fig. 4.2) and averaged the simulation results.
Figure 4.2: Annual mean temperatures (a) and annual precipitation sums (b) for the simulation runs for the exemplary elevation level 2100 m a.s.l. at the three study sites. For the other elevation levels, temperature data were scaled accordingly. The displayed data are cropped both in the beginning (series start in the year 800) and in the end (series end in the year 2300). The ribbons indicate the minimum and maximum values of the data that were averaged. Each time series consists of three parts: (i) the years 800–1800 were filled with 200 times randomly sampled and averaged years from the period 1801–1950 (before the beginning of climate change), (ii) 1801–2014 are empirical data, and (iii) 2015–2300 follow the four climate change scenarios A2, A1B and RCP3PD (CH2011, 2011) as well as a “no change” scenario.
4.3 Results

Development of stand characteristics and tree growth along the elevation gradient

All model variants featured a decline in tree growth with increasing elevation at all sites: all stand variables (basal area and volume; Fig. 4.3 a and b) and individual-tree variables (maximum radial growth and maximum tree height; Fig. 4.4 a and b) decreased with increasing elevation. This pattern was consistent with observations, which also exhibited a decrease in stand stocking with increasing elevation. Measured basal area dropped from 60.1 m$^2$/ha at 1,830 m to 0.5 m$^2$/ha at 2,120 m at Bosco/Gurin; from 28.1 m$^2$/ha at 1,730 m to 1.9 m$^2$/ha at 1,960 m at Hohgant; and from 28.0 m$^2$/ha at 2,200 m to 0.1 m$^2$/ha at 2,450 m at Zermatt (Fig. 4.3 a). However, simulation results exhibited large variations in both the shape of the decline and the elevation range where the decline occurred, depending on model variant, site and tree species. Furthermore, the differences between model variants increased along the elevation gradients.

Simulated stand characteristics

Simulated basal area at 1,400 m varied between 59 m$^2$/ha to 71 m$^2$/ha at Bosco/Gurin, 55 m$^2$/ha to 69 m$^2$/ha at Hohgant and 47 m$^2$/ha to 65 m$^2$/ha at Zermatt, while differences up to 60 m$^2$/ha could be observed between the different variants at 2,200 m at every site (Fig. 4.3 a). As a result, the predicted elevation of the highest trees (i.e., where basal area approaches 0 m$^2$/ha) strongly varied between model variants for each site. The highest trees were predicted between 2,000–2,200 m with the most “pessimistic” model variant (Snow on x Normal growth function; 2,000 m at Hohgant, 2,100 m at Zermatt and 2,200 m at Bosco/Gurin). With the most “optimistic” model variant (Snow off x Rickebusch growth function), the highest trees were predicted at 3,200 m at Zermatt, and at the highest point of the elevation range at Bosco/Gurin (2,800 m) and Hohgant (2,600 m), the upper limit of tree distribution was not even reached (i.e. basal area not approaching 0 m$^2$/ha). The variations in simulated volume along the elevation gradient and between model variants (Fig. 4.3 b) exhibited similar patterns as basal area, with slight differences due to the additional consideration of tree height. Compared to the empirical data, it was evident that most model variants overestimated stand stocking at high elevations and mispredicted the position of the treeline at Hohgant (observed at 2,000 m) and Bosco/Gurin.
(observed at 2,200 m), while the low-end model variant (Snow on x Normal growth function) appeared fairly close to observations (Fig. 4.3 a). In Zermatt, all model variants either over- or underestimated treeline elevation (2,500 m).

**Figure 4.3:** The performance of different ForClim variants regarding stand-scale characteristics of subalpine forests approaching treeline at the three study sites: a) basal area and b) volume across the elevation gradient. Field data are shown as well. The model variants include variations of the temperature-growth function (the Normal ForClim asymptotic function and the one reparametrized by Rickebusch et al., 2007) as well as two new degree-day-sum (DDSum) correction functions for Zermatt (Localized mean: ZER mean; Localized max: ZER max).

### Simulated individual-tree characteristics

On the individual-tree level, the elevation-dependent divergence of model variants was generally analogous to the stand-scale variables and consistent
across sites and species (Fig. 4.4). Simulated, field-measured and remotely sensed maximum tree heights were coherently declining with increasing elevation (Fig. 4.4 b). Yet, observed tree heights were lower than simulated ones for spruce and larch at Bosco/Gurin and Hohgant, where the low-end variant (\textit{Snow on} x \textit{Normal} growth function) was closest to the actual tree height profile. On the contrary, tree height of mountain pine at Hohgant was considerably underestimated by this variant, whereas the high-end variants were closer to measurements. In Zermatt, the model variants either over- or underestimated tree height for Swiss stone pine and larch, with the exception of two variants (\textit{Snow on} x \textit{Rickebusch} and \textit{Snow on} x \textit{Normal} x \textit{Zermatt Localized max}) for the latter.

Regarding maximum radial growth, the simulation results featured a consistent decrease with elevation for larch and spruce only, whereas mountain pine and Swiss stone pine featured low levels of basal area increment across the entire simulated elevation gradient (Fig. 4.4 a). Although the empirical data of maximum radial growth per elevation level did exhibit a less clear pattern as a function of elevation, there was still a decreasing trend with increasing elevation (Fig. 4.4 a), which was more pronounced for spruce and larch than for mountain pine and Swiss stone pine. It has to be noted that individual-tree scale comparisons were restricted to the four species sampled in the field, whereas the model predicted the presence of additional species.

**Impact of external and internal drivers of tree growth at and below treeline**

**Snow as external forcing**

There was a large difference between the simulation results by the model variants with the snow module being active (\textit{Snow on}) or not (\textit{Snow off}). For both the individual-tree and stand-scale variables, the snow module shifted the curves towards lower elevations (Figs. 4.3 and 4.4), bringing them usually closer to the empirical curves. It also improved the shape of the curves by rendering the declines steeper with increasing elevation, especially for maximum radial growth and tree height (Fig. 4.4). As a result, MAE and RMSE values were usually lower for the model variants with \textit{Snow on} (Table 4.2).
4.3. RESULTS

Figure 4.4: The performance of different ForClim variants regarding individual-tree characteristics of subalpine forests approaching treeline at the three study sites: a) Maximum radial growth and b) maximum tree height across the elevation gradient. Field measurements and remote sensing data are shown as well. For an explanation of the model variants, see Fig. 4.3.
Table 4.2: ForClim model variants tested during the simulation runs. The gray highlighted lines mark the overall “best” model variant for each site, which was subsequently used to predict potential future development. Mean absolute errors (MAE) and root mean squared errors (RMSE) between the simulation outputs and the validation variables basal area, volume, tree growth and tree height (tree height data comes from both field measurements and remotely sensed data) are listed. The asymptotic temperature-growth function as implemented in ForClim since version 2.7 (Bugmann and Solomon, 2000) is referred to as Normal, the readjusted and reparametrized variant by Rickebusch et al. (2007) is called Rickebusch. For Zermatt, results are presented for the Standard and two alternative variants (Localized mean and Localized max) of the calculation of monthly degree-day sums.

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<td>66.6</td>
<td>66.6</td>
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¹ against field measurements
² against remote sensing data
4.3. RESULTS

Temperature-growth relationship as a tree-internal process

By enhancing the response of tree growth at the low end of the temperature range, the alternative Rickebusch temperature-growth function systematically predicted higher values than the original ForClim version 2.7 variant (Normal) for both stand and individual tree variables. When assessing the simulation results against empirical data (Fig. 4.3, Table 4.2), the Normal temperature-growth function featured the lowest MAE and RMSE in most cases (for a given variant of the snow module), while the Rickebusch temperature-growth function considerably overestimated basal area and volume, except at Zermatt. The Normal function also better predicted maximum radial growth for larch and spruce, but not for Swiss stone pine and mountain pine (Fig. 4.3 a). For the latter two species, even the high-end model variants considerably underestimated the empirical data on maximum basal area increment. Results were similar for maximum tree height, but the differences between simulated and observed height of Swiss stone pine and mountain pine were smaller (Fig. 4.3 b).

Radiation via degree-day correction as an external forcing

After further investigations regarding the simulation results in Zermatt, it became evident that the large discrepancy to empirical data was due to the different radiation regime and the pronounced daily temperature amplitudes compared to the other sites (Figs. 4.A.2, 4.A.3). With such a climate regime, the air temperatures experienced by the trees during the day can be quite high in spite of a low daily mean temperature. The degree-day correction functions specifically developed for Zermatt (Localized max and Localized mean, cf. Fig. 4.A.2) considerably improved MAE and RMSE compared to the Standard function for all tested variables (Figs. 4.3 and 4.4, Table 4.2), with the Zermatt Localized max correction function reducing both error measures slightly more (Table 4.2).

Defining the best model variant for each site

The combination of the Normal temperature-growth relationship with the implementation of a negative impact of snow cover on degree-day sums (Snow on) led to the overall smallest MAE and RMSE of simulation results compared to the empirically measured data for Bosco/Gurin and Hohgant (Table 4.2). For Zermatt, the best predictions were obtained when additionally using the Zermatt Localized max degree-day correction function or with the Rickebusch variant including the snow module (Table 4.2). For the projections into
the future, we decided to choose the former because of the plausibility of the importance of the daily temperature amplitude (Figs. 4.A.2 and 4.A.3).
4.3. RESULTS

Projections of subalpine forest dynamics from 1801 to 2300 AD

Changes of basal area

In the past (i.e., years 1801–2014), simulated basal area at all sites was almost constant at lower elevations and increasingly featured decadal-scale fluctuations when approaching treeline (Fig. 4.5). The fluctuations were lowest for Hohgant and highest for Zermatt, as was treeline elevation. At all three sites, simulated basal area first increased towards a peak around the year 1880 and then decreased to a minimum around 1975. Afterwards, it increased again until 2014.

For the future (i.e., years 2015–2300), the projections of basal area showed common patterns but also site- and scenario-specific peculiarities (Fig. 4.5). The projected increase of basal area was earlier and proportionately larger at higher elevations than at the lower end of the simulated transects (Fig. 4.5). For example, the maximum elevation change of the 45 m²/ha isoline between the years 2014 and 2200 amounted to just +100 m. Only after the year 2200 and only for the high-end climate change scenarios A1B and A2, pronounced elevational advances of this isoline were simulated. Even under the “no change” climate, there was an increase of basal area over time, and albeit being marginal at Hohgant, it was clearly visible for Bosco/Gurin and Zermatt. This indicated a disequilibrium between climate and the current status of these treeline forests. Under the climate change scenarios, simulated increases were considerably larger, but quite similar until the year 2100. Only after 2100, the increases of basal area began to fan out according to the magnitude of the temperature change: smallest changes occurred for the RCP3PD, intermediate for the A1B, and largest for the A2 scenario. Between 2015 and 2300, the elevation of, e.g., the 15 m²/ha basal area isoline increased from approximately 1,950 m a.s.l. to 2,250 m (“no change”), to 2,500 m (RCP3PD) and exceeded the highest elevation in the landscape (>2,800 m) for the A1B and A2 scenarios. At Hohgant, the 15 m²/ha isoline was located at approx. 1,750 m today and increased to 1,900 m (“no change”), 2,200 m (RCP3PD), 2,500 m (A1B) and 2,600 m (A2). At Zermatt, the increase started at 2,000 m, topped off between 2,250 m (“no change”), 2,600 m (RCP3PD), 3,100 m (A1B), and presumably just above 3,200 m (A2) at the end of the simulations.
Changes in species composition along the elevation gradient over time

Simulated species composition after model initialization (1800–1830) as well as for the present day (1980–2010) showed a strong dominance of Norway spruce (*Picea abies*) along the elevation gradient at all three study sites (Fig. 4.6 a and b), together with a small share of European larch (*Larix decidua*). In addition, at the very lowest elevation at Bosco/Gurin, individual European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) cohorts complemented the stands. In Zermatt, Swiss stone pine (*Pinus cembra*) was present at elevations higher than 1,700 m. It is noteworthy that the shape of the basal area profile along elevation changed somewhat after model initialization: the decline of total basal area with increasing elevation was rather gradual for the spin-up period (Fig. 4.6 a), while for the present state it exhibited a steeper and more abrupt, even step-like decrease (Fig. 4.6 b). This development was the result of changes in past climate variability (from 1801 until 2014). Due to the strong inertia of forest dynamics, its long-term impact became apparent under the “no change” scenario by 2100 and 2300 only (Fig. 4.6 c and d). The current, step-like decrease of basal area was developing towards a gradual decrease in the future (Fig. 4.6 b vs. d) due to the colonization by larch at mid and high elevations.

For all three study sites, an upward expansion of the forested area as well as changes in species composition and dominance were observed (Fig. 4.6 c and d). The newly forested area above present-day treeline was colonized mainly by spruce and larch at all sites in the medium term (i.e., by 2100; Fig. 4.6 c), with a clear dominance of the latter. This colonization continued in the long term (i.e., by 2300; Fig. 4.6 d), with a strong increase in the basal area of both species.

Colonization by broadleaved species at the lower and mid-elevations was also predicted and mostly visible in the long term. It also varied strongly depending on the site and climate change scenario (Fig. 4.6 c and d). Although there was an increasing number of other species growing in from further below, most of them contributed only a small share of total basal area at any elevation. In fact, European beech appeared to be the only species to succeed as a co-dominant species. This was the case for Bosco/Gurin under all climate change scenarios, although the forest state after 100 years of climate change was not strongly different to the “no change” scenario (Fig. 4.6 c). For Hohgant and Zermatt, the colonization by broadleaves was visible after 300 years of changed climate only, and was yet quite limited for the scenario RCP3PD (Fig. 4.6 d). On the contrary, the ingrowth of beech was substantial
at Bosco/Gurin, especially for the A2 scenario, under which it took over the role as dominant species up to an elevation of approximately 1,800 m a.s.l. in the year 2300.
Figure 4.5: Development of basal area over time and across the elevation gradients of the three study sites (columns) under different climate scenarios (rows). The ForClim variant with negative impact of snow cover on growing season and the original variant of the growth response to temperature (Snow on x Normal) was used and, in the case of Zermatt, the additional correction of the degree-day calculation (Zermatt Localized max). The black lines are isolines of basal area. Simulation results are displayed up to the highest elevation encountered at each site (dotted line), above which the grey shading indicates “no results”. 
Figure 4.6: Simulated species composition by basal area along the transects at the study sites: a) directly after model initialization (1800–1830 mean), b) present-day conditions (1980–2010 mean), c) directly after the end of the four climate scenarios (2080–2110 mean) and d) approximately 200 years after the completion of climate change (2270–2300 mean). The group “Other” combines all species that do not exceed a 5% share of the current total basal area at any point in time (Taxus baccata, Corylus avellana, Sorbus aria, Quercus pyrenaica, Quercus pubescens, Salix alba, Quercus ilex, Acer campestre, Alnus glutinosa, Tilia cordata, Quercus robur, Fraxinus excelsior, Castanea sativa, Tilia platyphyllos, Acer platanoides and Carpinus betulus).
CHAPTER 4. SIMULATING TREELINE DYNAMICS

4.4 Discussion

Below, we first evaluate the relative importance of the tested ecological processes for shaping present-day subalpine forests and second, review the development of treeline dynamics at the three study sites under future climate change.

Ecological processes that shape current subalpine forests

The decline of both stand-scale and individual-tree variables with increasing elevation reflects the importance of temperature as external forcing of subalpine forest dynamics (e.g., Tranquillini, 1979). However, the considerable differences in overall stand productivity and the performance of individual species along the elevation gradients between both the individual model variants, and between simulated and empirical data, indicate biotic and abiotic modulating processes acting at the regional to local scale (Holtmeier and Broll, 2017). Inter- and intra-species differences in growth reactions to temperature as well as feedback effects induced by competition (Jochner et al., 2017a; Wang et al., 2016; Wieczorek et al., 2017) in addition had a large impact on the outcome of our mechanistic simulations and how closely they matched reality.

Influence of snow on the length of the growing season

The precipitation regime of a macroclimatic region is an important abiotic determinant of forest dynamics, even at treeline and in European subalpine forests, where water availability only rarely has a limiting influence (e.g., Holtmeier, 2009). A very important facet of the precipitation regime at this elevation is snow, which has been confirmed to have great influence on tree growth and regeneration (e.g., Hagedorn et al., 2014; Kirdyanov et al., 2003; Wieser, 2012). At our three study sites, snow plays a pivotal role in shaping the subalpine forest along the elevation gradient. Without considering the effects of snow, biomass was overestimated systematically, especially at the upper end of the transects. This overestimation has often been found in modelling studies (Heiri et al., 2006; Rickebusch et al., 2007; Schwörer et al., 2014) and, although frequently confounded with anthropogenic treeline depressions (cf. Gehrig-Fasel et al., 2007), suggests that snow is an essential ecological forcing factor for these forests. Soil temperatures are of great importance for tree growth (Pregitzer et al., 2000) and if lower than 6°C, do not permit root growth (Alvarez-Uria and Körner, 2007). As long as there
is snow on the ground, the radiation energy that hits the ground is used for melting, and soil temperatures stay at 0°C. At the same time, air temperatures may reach favorable values for growth, but root activity is inhibited and even negative effects due to uncompensated respiration and frost desiccation can arise (Wieser, 2012; Wieser and Bahn, 2004). In addition, Bugmann and Pfister (2000) found high interannual variability of growth conditions to have a large (lowering) impact on the treeline due to dieback effects. In fact, enabling snow to limit the growing season in our simulations substantially increased the interannual variability of degree-day sums and by this also contributed to realistically reproducing present-day patterns of subalpine forest dynamics (cf. Fig. 4.A.1). The largest differences between the model variants with and without the snow module were found for Bosco/Gurin, the site with the largest late winter/spring precipitation (Blanchet et al., 2009, cf. also Fig. 4.A.4).

Besides reducing the length of the growing season, snow can have other negative influences on trees, such as exerting mechanical stress, favoring pathogen attacks on young trees, but also positive aspects like protecting young trees from harsh winter conditions and supplying additional water from the melting snow in spring (Barbeito et al., 2013, 2012; Hagedorn et al., 2014; Wieser, 2012). These factors are not currently considered by the snow model. For the future, it would be desirable to extend it to cover additional snow-driven processes, and to evaluate the sensitivity of simulated long-term subalpine forest dynamics to these processes.

**Influence of air humidity and cloud cover on the surface radiation balance**

In addition to shortening the length of the growing season via snow, our study confirmed the importance of the macroclimatic characteristics in terms of cloud cover and air humidity, which influence the radiation energy available to the trees. This process has long been known, and the extra available energy in areas with little cloud cover, e.g. in the interior rain shadow of a mountain range, has been referred to as the *mass elevation effect* (Imhof, 1900; Körner, 2012). It is however not a static state, but as climate change affects cloud cover, this phenomenon can also amplify or dampen the effects of rising temperatures on growth, not only of trees but of all plants (Maclean et al., 2017). Because our case study sites are situated in three distinct precipitation regimes, the energy that is available on the same elevation differs between the sites. From the climate data we derive that the available energy is lowest in the north at Hohgant, highest in the Central Alps at Zermatt and
intermediate in the south at Bosco/Gurin due to a more convective precipitation regime. In Zermatt, which is the driest and most continental of the three sites (cf. Figs. 4.2 and 4.A.4), the model variant with the standard degree-day sum correction function fails to reproduce empirical patterns of basal area along elevation (Fig. 4.A.2). Only after we utilized sub-daily temperature data to compile a locally valid correction, we were able to approximate the energy that the trees have at their disposal. On the contrary, for Bosco/Gurin and Hohgant, the standard correction did work well, suggesting that under certain conditions standardized and averaged air temperature measurements are able to convey the actually available energy. In the future, this mismatch should be scrutinized by means of empirical measurements.

Yet, we kept underestimating basal area and volume at Zermatt, even with the adapted correction function. This leads us to conclude that we are still missing part of the energy in the sub-daily temperature data. It has been found for small stature plants like herbs and grasses but also for seedlings of trees that tissue temperatures are partly decoupled from air temperatures (cf. Grace et al., 2002; Körner, 2016). This, in conjunction with our results, indicates that the potential divergence between averaged standardized air temperature measurements and the energy that is actually available to a plant to grow potentially also applies to larger statured plants and should be reconsidered.

Tree-internal growth reactions to temperature

Our study revealed a strong sensitivity of forest dynamics at treeline to changes in the relationship of tree growth and temperature. With the function as implemented in ForClim version 3.3, we did get reasonable results for the stand scale at all three study sites, and for two of the four tree species on the individual-tree scale. This backs the assumptions of an asymptotic form originally made by Bugmann and Solomon (2000) and confirms the results on the functional form by Rickebusch et al. (2007). Our initial aim was to balance the strong reduction in degree-day sums due to snow by an enhanced internal response of tree to temperature at the colder range of the species distribution. However, the alternative model variant proposed by Rickebusch et al. (2007) led to an overestimation of treeline elevation and stand stocking at Bosco/Gurin and Hohgant. Although at Zermatt simulation results with the Rickebusch growth function (and the standard degree-day correction) were in agreement with observed data, we are convinced that this does not reflect the true causality but rather is an example of “getting the right answer for the wrong reason”. The simulations with the enhanced growth
response *sensu* Rickebusch et al. (2007) has approximately the same effect on stand-scale results as the introduction of the *Localized max* correction function at Zermatt. Given the peculiarities in temperature data that we found (Figs. 4.A.2, 4.A.3), the use of a localized degree-day correction is more plausible than assuming a specific growth-temperature relationship of trees growing at Zermatt.

Although the parametrization of Rickebusch et al. (2007) employing tree-ring data appeared promising, they faced difficulties when fitting the asymptotic function to a wide range of tree-ring width series from the International Tree-Ring Data Bank (ITRDB). Non-climatic effects on growth like competition and site conditions made it challenging to identify potential growth rates in relation to temperature. In addition, coarse climate data may have failed to trace essential thresholds in temperature for tree growth. Both challenges were overcome with the sampling design in our study regarding selecting trees and measuring temperature and therefore provided us with a robust set of validation data. The validation showed the parameterization with theoretically derived species parameters of the original ForClim function to perform better than the empirically derived ones.

The fact that simulation results only matched empirical data well for spruce and larch may partly be an artefact related to underlying modeling assumptions. The substantial underestimation of mountain pine growth is probably driven by its simulated outcompetition for light by larch and spruce, which are favored in the model by both a higher potential growth and a higher maximum height (cf. Table 4.A.1). In addition, the presence of mountain pine at Hohgant is in reality based upon the very special site requirements of this species: especially at very poor microsites it can outcompete more demanding species like spruce (Ellenberg and Strutt, 2009). The Hohgant range does feature rather extreme microsite conditions due to the calcareous bedrock (Swisstopo, 2012) and karst phenomena, which are, however, not incorporated in ForClim. The difficulties of Swiss stone pine to grow at Zermatt may arise from too small trees being simulated. In reality, both species present at Zermatt, larch and Swiss stone pine, feature equal maximum tree heights along the elevation gradient (cf. Fig. 4.4 b). In the model, however, the respective parameters that determine tree heights (cf. Bugmann, 1994, 1996, Table 4.A.1) favor larch over Swiss stone pine, leading to enhanced competition for the smaller species, which in turn results in reduced growth. To solve this problem, the parameters should potentially be re-estimated using empirically measured tree height data.
Important ecological processes for simulating forest dynamics at and below the treeline

The shortening of the growing season due to snow paired with a continentality adaption and increase of degree-days in the case of Zermatt, resulted in simulated degree-day patterns that matched the observed patterns of treeline elevation, stand-scale biomass and to a certain extent also individual-tree height and growth. Therefore, our study confirmed that precipitation patterns play a major role as modulators in determining the regional-scale variability of subalpine forest and treeline, although not limiting in the sense of water availability. Our results show that if we consider these two pivotal factors in a mechanistic model, we can improve the simulations of overall productivity of subalpine forest stands approaching treeline substantially and portray the real situation reasonably well. This supplies us with a valuable tool for predicting the development of subalpine forest dynamics under scenarios of future climate.

Projections of subalpine forest dynamics under climate change scenarios

Elevation dependency of forest sensitivity to increasing temperatures

Treelines are said to be one of the most useful places to study the impacts of climate change due to their high sensitivity compared to lower elevations (Luckman, 1996; Motta and Nola, 2001). Considering the course of simulated basal area over time – both in the past and in the future – it is safe to say that there is a clear elevation dependency of forest sensitivity to increasing temperatures: the highest and least dense forest stands were very much susceptible to temperature variability, as far as overall stand productivity is concerned. At the same time, above a certain temperature threshold there were almost no changes. This seems logical, as the internal processes that drive forest dynamics (regeneration, growth and mortality) both in reality (Elliott, 2012; Lenz et al., 2014; Paulsen et al., 2000) and in the model (Bürgmann, 1996; Rickebusch et al., 2007) do not depend linearly on temperature. Moreover, the highest forest stands operate close to their limitation threshold. Thus, small changes of temperature can have large effects on forest dynamics at the upper end of the treeline ecotone. Additionally, threshold-dependent processes like snowfall modulate temperature as a provision of energy for the trees to grow and regenerate. This high sensitivity of the border zone between subalpine forest and alpine tundra, paired with the expected amplified
increase in temperature at highest elevations (Pepin et al., 2015), suggests substantial changes to the structure of today’s treeline ecotone as well as treeline elevation. These changes can be observed in our simulations, but also in simulations at other sites in the Alps (Bugmann and Pfister, 2000). The non-linearity in both the external forcing and the internal reaction created a characteristic shape of stand basal area along elevation. The rather abrupt decrease of simulated basal area after model initialization and at the present day is in agreement with our empirical evidence (cf. Fig. 4.3 a) as well as with findings on other treeline ecotones that are controlled by a single environmental gradient (Cairns and Waldron, 2003). Interestingly, the simulation results predicted a transformation to a rather gradual decrease of basal area with elevation for the future. This is presumably due to the inertia of the forest stand to the changed growth conditions, such that the abrupt decrease in basal area was not simply shifted, but the gradient formed anew as a new equilibrium was reached. Consequently, a steep decrease of basal area became apparent for the simulated state of the year 2300 only (cf. Fig. 4.6 d).

Temperatures do not only change along the elevation gradient, but have varied over time in the past and are predicted to change substantially in the near future (CH2011, 2011; IPCC, 2013). The decrease of simulated basal area in the second half of the 20th century coincides with the period of so-called “global dimming” (Stanhill and Cohen, 2001), which may provide an explanation for this pattern. As mentioned before, large interannual climate variability resulting in a few years with unfavorable growth conditions can create pronounced dieback effects, which are capable of substantially lowering the treeline (Bugmann and Pfister, 2000). This decrease of basal area may indeed be caused by pronounced diebacks in single climatically unfavorable years, but might also partly be an artefact due to the change from 200 replicated simulations averaged until 1800, to a single trajectory using the instrumental data. The averaging of the simulation runs for the model initialization presumably smoothed emerging dieback effects and produced an initial simulation state that overestimated basal area.

**Forest productivity under future climate change**

The climate change scenarios A2, A1B and RCP3PD resulted in substantially different growth conditions compared to the present-day situation, but they are also largely different among each other (CH2011, 2011, cf. Figs. 4.2 and 4.A.4). Hence, it does not come as a surprise that the predictions of basal area for the future differed strongly among each other. Yet, the predicted
slight increase in basal area and upward shift of the treeline under the “no change” scenario suggests that today’s treeline ecotone is not in equilibrium with the current growth conditions and, again, due to the inertia in the trees’ reactions, lags behind. If one assumed a constant climate based on present day conditions, it would take at least another 100 years for the treeline ecotone to adapt fully to the current growth conditions. This lag conforms to the findings of both empirical (Camarero and Gutiérrez, 2004; Gehrig-Fasel et al., 2007) and simulation studies (Bugmann and Pfister, 2000) on treeline fluctuations. It is presumably the same lag in treeline reaction that caused the similar development of basal area across the elevation gradient under climate change until approximately the year 2100. Under all three scenarios, the limiting effect of temperature at the very top is lifted with rising temperatures. Therefore, the forest first reacted similarly under all three scenarios, regardless of the magnitude of change. Only after 2100, the basal area levels at the newly ingrown elevations reached their temperature-specific limit, first under RCP3PD and last, of course, under the A2 scenario.

In terms of the reaction speed of the treeline to changed growth conditions, it has to be noted that ForcLIM does not simulate seed dispersal. However, this is an important component of the natural regeneration process and known to considerably delay the advance of treelines (Payette, 2007). Thus, modeling seed dispersal would increase the treeline inertia even more than in the current simulations. Therefore, the missing representation of seed dispersal in the model renders the prediction of future treeline elevation to be the theoretically uppermost point where trees will be able to grow under the respective growth conditions, rather than showing a realistic rate of treeline advance in the near future.

The three climate change scenarios do not only predict large increases in temperature, but also changes in the amounts and seasonal course of precipitation (CH2011, 2011, Fig. 4.A.4). Previous simulation studies report increasing drought stress due to reduced summer precipitation in the lower and intermediate elevations of especially central Alpine valleys even under the moderate RCP3PD emission scenario and an associated decrease in biomass (CH2014-Impacts, 2014; Elkin et al., 2013). Although there were substantial decreases in summer precipitation, especially at Bosco/Gurin, drought stress, at least in terms of stand productivity, was not observable in any of the three case study sites. It seems, that even at the lowest simulated elevation level (1,400 m a.s.l.) at the overall driest site Zermatt, there was enough precipitation during the growing season to at least sustain the current level of basal area, even under the high-end emission scenario A2. It is however likely that changes in winter precipitation regimes and spring temperature
would indirectly impact subalpine forest dynamics through reduced snow cover in spring, thus strongly increasing the length of the growing season (cf. Fig. 4.A.4).

**Predicted shifts in species composition under climate change**

Shifts in stand species composition can be the result of both natural succession (e.g., Risch et al., 2009) and the failure of a species to cope with changed growth conditions and its substitution by a better suited species (e.g., Elkin et al., 2013). The colonization of elevation zones above the present-day treeline follows rather a clear successional course. With increasing temperatures, the early successional species larch and, a little later, Swiss stone pine form the first forest stands at the top. Shortly thereafter, they are followed by the later successional spruce, which then outcompetes larch and Swiss stone pine. On the contrary, preexisting stands of spruce and larch at the former treeline ecotone experience both a successional shift to more spruce dominated stands but also an immigration of beech and other deciduous species from below. Our results suggest that this increased amount of deciduous species is the consequence of higher temperatures in combination with a reduced amount of moisture due to changes in the seasonal course of precipitation under the climate change scenarios (cf. Fig. 4.A.4). The differences between the three case study sites can be explained by differences in seasonal precipitation patterns and their changes (cf. Fig. 4.A.4). The shifts to a more montane forest type at the present day low end of the subalpine forest is in agreement with simulations at other alpine study sites (Elkin et al., 2013; Schwörer et al., 2014) but also empirical findings on the impacts of climate change on long-term growth variability at two of the three case study sites, where larch is actually present (Bosco/Gurin and Zermatt; Jochner et al., 2017a). At these sites, larch exhibits a positive trend at the present day treeline but features conspicuously negative growth trends at lower elevation, whereas other species (spruce at Bosco/Gurin, Swiss stone pine at Zermatt) show positive trends.

### 4.5 Conclusions

Our mechanistic simulation approach revealed and quantified important external forcings of subalpine forest dynamics at the regional and local scale, and it identified an ecologically meaningful tree growth reaction to temperature. The sensitivity to all the ecological processes tested by us was substantial. Especially the precipitation regime and its effects on incoming radiation
and, via snow cover, on the length of the growing season had large effects on
the stand scale, but also the individual tree scale. Only by including these
pivotal external forcings were we able to realistically simulate present-day
regional patterns of subalpine forest dynamics. Considering these processes
in the model provided us with an improved tool to evaluate subalpine forest
dynamics under climate change scenarios.

Substantial changes of forest structure and composition compared to
present-day conditions are to be expected in all three study regions. Sub-
alpine forests will expand upwards by several hundred meters even under the
low emission climate change scenario, while at the same time there will be
a strong immigration of montane-zone species (such as beech) at the lower
growths of the present-day subalpine forest. The large increases in basal area at
the highest elevations and the compositional shifts throughout the elevation
gradients will have considerable implications for the ecosystem goods and ser-
vices provided by forests along such elevation gradients. There are ambiguous
implications like an accelerated disappearance of alpine meadows, which often
are of high recreational value, on top of the ongoing forest ingrowth due
to the cessation of subalpine farming. However, these implications stand
against positive consequences like substantial carbon sequestration by newly
forested areas, increased timber production at higher elevations, and higher
tree species diversity at the low edge of current subalpine forests, which will
help to facilitate the maintenance of vital protective functions.
4.6 Acknowledgements

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4.7 Author’s contributions

- Matthias Jochner: Design of the study; acquisition, analysis and interpretation of data for the study; writing of the manuscript and revising it; final approval of the version to be published; agrees to be accountable for all aspects of the study.

- Valentine Lafond: Contributions to the design of the study; interpretation of data for the study; revising the manuscript; final approval of the version to be published; agrees to be accountable for all aspects of the study.

- Christof Bigler: Contributions to the design of the study; contributions to the analysis of data; revising the manuscript and approving the final version to be published; agrees to be accountable for all aspects of the study.

- Harald Bugmann: Substantial contributions to the conception of the study; analysis and interpretation of data; revising the manuscript and approving the final version to be published; agrees to be accountable for all aspects of the study.
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4.A Supplementary information

Figure 4.A.1: Interannual variability of degree-day sums calculated with and without the snow module (Snow on, Snow off) at the three case study sites (horizontal facets) and calculated for selected elevation levels (vertical facets).
4.A. SUPPLEMENTARY INFORMATION

Climate station Bosco/Gurin (1486 m a.s.l.)
Climate station Pilatus (2106 m a.s.l.)
Climate station Zermatt (1638 m a.s.l.)

Figure 4.A.2: Error between the precise sine-wave method of degree-day sum calculation (Allen, 1976) that requires sub-daily resolution temperature data and the method developed by Botkin et al. (1972) that utilizes monthly mean temperatures. The error is displayed in dependence of monthly mean temperatures. Also shown is the standard ForClim correction function that is supposed to account for these errors (Bugmann, 1994), as well as the two adjusted correction functions Zermatt Localized mean (ZER mean) and Zermatt Localized max (ZER max). As precipitation conditions are known to be much more spatially heterogeneous (Daly, 2006), we did not choose the same MeteoSwiss climate stations as for the climate change scenarios, as they are rather distant from the case study sites. To best cover the precipitation conditions at the three sites, we chose the climate stations Bosco/Gurin (not directly at the study site but at the valley floor), Pilatus (for Hohgant) and Zermatt (again at the valley floor) that all offered sub-daily resolved temperature data.
Figure 4.A.3: Mean daily amplitude of air (A; first row) and soil (S; second row) temperature for the growing season months. The grey ribbon indicates the standard deviation of the amplitude. The columns are arranged according to the three study sites Bosco/Gurin (BOS), Holgant (HOH) and Zermatt (ZER). We used our temperature logger data for these calculations (cf. Table 4.1).

Table 4.A.1: Values of relevant model parameters and their variation between species and model variants (original ForClim version 3.3 parametrization vs. Rickebusch variant).

<table>
<thead>
<tr>
<th>Species</th>
<th>Min. degree-day sums</th>
<th>Min. winter temp. (°C)</th>
<th>Max. growth (cm/year)</th>
<th>Max. Height (m)</th>
</tr>
</thead>
<tbody>
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<td></td>
<td>ForClim v3.3</td>
<td>Rickebusch</td>
<td>ForClim v3.3</td>
<td>Rickebusch</td>
</tr>
<tr>
<td>European larch</td>
<td>Larix decidua</td>
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<td>225</td>
<td>-11</td>
</tr>
<tr>
<td>Norway spruce</td>
<td>Picea abies</td>
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<td>300</td>
<td>-99</td>
</tr>
<tr>
<td>Swiss stone pine</td>
<td>Pinus cembra</td>
<td>323</td>
<td>225</td>
<td>-11</td>
</tr>
<tr>
<td>Mountain pine</td>
<td>Pinus mugo</td>
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<td>-</td>
<td>-99</td>
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<tr>
<td>European beech</td>
<td>Fagus sylvatica</td>
<td>723</td>
<td>-</td>
<td>-4</td>
</tr>
</tbody>
</table>
4.A. SUPPLEMENTARY INFORMATION

Figure 4.A.4: Seasonal course of a) monthly mean temperature and b) monthly precipitation sum for the exemplary elevation level 2100 m a.s.l. at all three case study sites. The individual lines represent the spin-up period (1000–1800 mean), present day (1980–2010 mean) and the 2100–2300 mean for the three emission scenarios RCP3PD, A1B and A2.
CHAPTER 5

Synthesis

The aim of my PhD thesis was to quantify the impacts of past and potential future climate variability on growth dynamics and forest succession at upper treeline in the Swiss Alps. An integral component of the three major parts of my thesis was to disentangle the roles of (i) large-scale drivers of subalpine forest dynamics like temperature, and (ii) inter- and intra-species variability, competition-induced feedback effects and regional- to local-scale abiotic drivers in determining the overall response of treeline and subalpine forest dynamics to changing environmental conditions. In the first part, a reconstruction and quantification of past short- and long-term tree growth variability revealed the role of abiotic drivers and biotic interactions in shaping tree growth dynamics. In the second part, I investigated the dependence of tree growth on different aspects of temperature, as this relationship is considered to be the most important driver of individual-tree growth dynamics. And in the third part, I implemented and assessed parts of the findings from the first two parts on the drivers of short- and long-term tree growth variability in the dynamic forest gap model ForClim, which I subsequently used to simulate the development of treeline and the subjacent subalpine forest under changing climatic conditions.

Below, I will first synoptically evaluate the main findings of the three main parts and discuss how they contribute to an advance of our knowledge in the respective field of research. This is followed by a critical evaluation of the methodological and content-related limitations and uncertainties of this study, paired with recommendations for future research. Lastly, I will conclude with some thoughts on how my PhD thesis contributes to the overall research on upper treeline and the impacts of climate change on our environ-
CHAPTER 5. SYNTHESIS

5.1 General evaluation of the findings

Site selection

If one wants to robustly analyze the impact of climate and its changes on treeline forest dynamics, one either has to account for all confounding influences in any statistical or mechanistic model used (e.g., human activities, geomorphological processes, wind, etc.), or systematically exclude their influence in the first place. I made a considerable effort in the latter context, attempting to identify sites that cover distinctly different climate regimes but exclude many local confounding factors. The three study sites Bosco/Gurin, Hohegg and Zermatt were chosen because (i) they are situated in distinctly different climate regimes of the Alps, (ii) they were found to be the regionally highest patches of forest in Switzerland according to the Swiss land use statistics GEOSTAT (cf. Gehrig-Fasel et al., 2007) and are therefore most likely limited by abiotic conditions (including but possibly not restricted to temperature) rather than by confounding factors (Körner and Paulsen, 2004), and (iii) field surveys showed that the treeline form in these areas indicates that temperature is likely the limiting environmental factor (Harsch and Bader, 2011). Although it is quite difficult in a densely populated mountain region like the European Alps to find treeline sites that are not influenced by land use at all (Gehrig-Fasel et al., 2007), I am confident that this approach provided me with data that are well suited for the analysis of climate variability on growth dynamics at treeline and the subjacent subalpine forest. This is additionally supported by the stand structure data analyzed in Part I of my thesis, indicating the stands to be forest outposts according to the definition by Körner (2012).

The influence of temperature on tree growth

Temperature is regarded as the most important limiting factor for growth when approaching the natural upper treeline (e.g., Körner, 1998; Tranquillini, 1979), and therefore interannual growth variability should be controlled mainly by the variability of certain temperature variables (e.g., monthly mean temperatures, growing season mean temperature, degree-day sums). My findings are very much in agreement with this assumption and qualitatively confirm the results of previous studies (Carrer et al., 1998; Graumlich, 1991; King et
5.1. GENERAL EVALUATION OF THE FINDINGS

al., 2013; Kirdyanov et al., 2003): both the significant fixed effects of various combinations of monthly mean temperatures on short-term growth variability (Part I) and Spearman’s rank correlation between basal area increment and integrative temperature variables (i.e., air and soil degree-day sum, growing season mean temperature, growing season length; Part II) underline the substantial warmth-dependence of the processes that determine annual radial growth at the treeline ecotone. Moreover, both analyses revealed a decisive influence of the previous year’s conditions on current year’s growth for all species, albeit this was previously ascribed mostly to larch (Kagawa et al., 2006). According to my analyses, reserves also play a substantial role in determining the annual growth increment of spruce, mountain pine and Swiss stone pine. On the contrary, soil temperatures, which are typically regarded as equally, if not more important than air temperatures for tree growth at treeline (e.g., Hoch and Körner, 2003), stood out at Bosco/Gurin only. I surmise that this pattern resulted from the influence of snow cover duration, which, compared to the other two sites, is quite long in the climatic region of Bosco/Gurin (Blanchet et al., 2009). I will discuss the influence of snow in more detail further below. At this point, I would also like to mention that, unlike the “classical” climate-growth correlation and response function analyses as performed in many previous studies, the statistical models developed in Part I permit both quantitative statements and predictions.

Although annual radial growth was explained well by a species-specific combination of monthly mean temperatures, basal area increment was in general best related to the combined degree-day sums of the current and previous year based on air temperature. It thus appears that it is rather the integration of the total energy above a certain temperature threshold than absolute temperature that determines annual growth, at least at my three study sites. Considering the basal area increment along a fine-scale elevational (and hence also degree-day sum) gradient across treeline, the form of the functional relationship between the two was clearly non-linear. Therefore, growth variability strongly increased after the passing of a certain degree-day threshold. While the growth of some trees increased strongly also beyond the threshold, other trees were not able to profit from the higher temperatures. This result prepares the ground for the next major finding of my PhD thesis.
Among-tree growth variability, long-term growth trends and climate change feedbacks

More surprising than the qualitatively well-known influence of temperature on growth was the discovery of considerable amounts of both inter- and intra-species variability in the growth reactions to monthly mean temperature. While it was previously known that different species vary substantially with regard to the length of the period and the specific months in which radial growth occurs (e.g., larch vs. spruce; Carrer et al., 1998), the analyses beneath the population level in Part I showed that even within a species, there are massive differences between individual trees regarding when and to what extent they invest assimilates into growth and reserves. Although recent studies have confirmed the existence of such strong among-tree variability (Buras et al., 2016; Vanoni et al., 2016), to date this has rarely been accounted for, especially with regard to its potential effects on long-term growth trends. In fact, it turned out that among-tree growth variability has considerable consequences for growth trends on the individual-tree level, and subsequently on the population level as well. Common wisdom suggests that global warming will lead to increased growth rates of all trees growing close to their cold limit. However, as the temperature increase due to climate change is not distributed equally either in its seasonal course or in space, the growth differences of conspecific trees within and among sites show different long-term trends. These patterns are closely related to the months in which trees invest carbon into growth or reserves, and the temperature changes occurring in these months. In terms of the reaction of the treeline ecotone, which per se is sensitive to temperature, i.e. to climate change, the among-tree growth variability has large implications for the magnitude of potential changes in forest dynamics and consequently also for the ecosystem goods and service provided by high-elevation forests.

Besides the influence of differences among trees, the analyses of long-term trends also revealed an elevation-dependence of the strength and sign of the trends, and even some inverse, counter-intuitive reactions. Larch showed highly positive trends over time at the highest elevations in contrast to spruce and pine. This is most probably due to increasing competition with decreasing elevation for larch, which commences already a few dozen meters below treeline, where higher stand density is a great disadvantage for this very light-demanding species. This first sign of a climate change-induced negative feedback effect confirms recent findings of similar nature in both empirical and modelling studies (Wang et al., 2016; Wieczorek et al., 2017). It also conforms to the outcome of our simulation study in Part III of my thesis.
In this study, larch in present-day’s upper edge of the subalpine forest was going to be more and more substituted by spruce in the simulated future. This fact was also reflected in the long-term trends of the empirical data of Part I.

The influence of snow on growth and treeline dynamics

Subalpine forest, alpine tundra and thus also the treeline ecotone are zones that experience large amounts of snow in the temperate and boreal zones. This has strong implications for trees growing in this ecotone (e.g., Barbeito et al., 2012; Hagedorn et al., 2014; Kirdyanov et al., 2003; Wieser, 2012). The linear mixed-effects models for the relationship of short-term growth variability and monthly temperatures (Part I) implicitly suggested a major role of snow for determining annual growth rates, especially at Bosco/Gurin, a site heavily affected by late winter snowfall (Blanchet et al., 2009; Marty and Blanchet, 2012). I concluded this from the conspicuously negative effects of late winter/spring temperatures on annual growth and explained it by the trees’ carbon losses due to uncompensated respiration (Wieser, 2012; Wieser and Bahn, 2004) during the often occurring warm, but still snow-covered periods at Bosco/Gurin. At the same time, the correlation analysis of soil temperatures and annual tree growth (Part II) confirmed the high importance of snow at a site experiencing high snow depths: soil temperatures at Bosco/Gurin showed a higher correlation with annual growth than the other two sites, which feature less snow in late winter.

The results from both Parts I and II were thus congruent and they propagated logically in the mechanistic modelling approach in Part III of my thesis. While the simulation of snow was previously found to be important for a correct estimation of local treeline elevation (Paulsen and Körner, 2014), I found it to be crucial also for reproducing actual growth dynamics and succession on a regional to local scale. When, on the contrary, the snow model was not used and the calculation of degree-days was not restricted to the snow-free period, treelines were simulated to be located at far too high elevations. Moreover, the snow influence led to a more abrupt decrease of stand basal area with increasing elevation, a pattern that perfectly matches the real-life situations at my study sites and the findings of other studies on natural treelines (e.g., Cairns and Waldron, 2003). The negative influence of snow cover on annual growth may even be underestimated in the simulations, as the only effect that was included is the shortening of the growing season. If a growth reduction due to respiratory carbon losses in warm, but still snow-covered spring months was considered, the influence of snow on overall growth
as simulated by ForClim at high elevations would be even more important. Considering the relevance of snow in the results of all three parts of my thesis as compared to the literature, I suggest that the influence of snow, not so much in terms of small-scale processes such as pathogen infestations or snow gliding, but rather in terms of a general influence on the energy available for tree growth, has received too little attention in dynamic forest succession modelling in the past.

**Influence of continentality on treeline elevation**

Treelines at the three study sites occur on significantly different elevations (approximately 2000 m a.s.l. at Hohgant, 2200 m a.s.l. at Bosco/Gurin and 2500 m a.s.l. at Zermatt). These differences have been observed and analyzed for a long time (e.g., Imhof, 1900) and attributed to the so-called *mass elevation effect* (Imhof, 1900; Körner, 2012). Still, according to world-wide studies of treeline positions (Körner and Paulsen, 2004), climatic treelines are expected to occur at roughly equal temperature conditions. However, the treeline air temperature measurements at my three study sites revealed treeline temperatures that considerably differed among each other. Especially Zermatt featured lower average temperatures at treeline compared to the other sites. The analyses in *Parts II* and *III* of my PhD thesis identified two factors that may be responsible for this discrepancy in either treeline temperature or elevation. First, snow cover restricted the growing season and contributed substantially to equalize the degree-day sums between the three sites (as demonstrated quantitatively in *Part III*). The overall low precipitation at Zermatt, which is due to its more continental climate, allows high air temperatures to contribute to the annual degree-day sum much earlier in spring than at Bosco/Gurin and Hohgant. Second, also due to its continentality, the daily amplitude of air temperature in Zermatt were, especially during the summer months June, July and August, much higher than those of Bosco/Gurin (intermediate amplitude) and Hohgant (smallest amplitude). However, long-term temperature series were only available as monthly mean temperatures for the analyses in all three parts, which did not reflect the information on these differences in amplitude as the higher daytime temperatures at Zermatt are equalized by lower nighttime temperatures (*Part III*). Trees at Zermatt appear to benefit strongly from less cloud cover and low air humidity and therefore high irradiation, experiencing similar average tissue temperatures during daytime compared to trees growing at the other two study sites.
5.2 Limitations, uncertainties and recommendations for future research

In spite of thorough planning and execution of field and lab work, data analysis and discussion of the results, my thesis is prone to limitations and uncertainties, part of which could potentially be resolved in future research. Below, I discuss those shortcomings of the three parts of my thesis that are most important from my point of view and present potential approaches to address them.

Human influence at the study sites

For the analyses in all three parts of my PhD thesis, it was an essential prerequisite that the treelines at the three case study sites are natural and thus primarily temperature-limited. However, it is almost impossible to find natural treeline sites in the Swiss Alps. For example, Gehrig-Fasel et al. (2007) found 96% of the upward moving treelines in Switzerland to be due to the cessation of human activities. In spite of the comprehensive search that I adopted to find suitable sampling sites that are unaffected by past or present land use, it is hardly possible to completely exclude any anthropogenic influence on stand density and species composition at the sampling sites Bosco/Gurin, Hohgant and Zermatt. Of all aspects of treeline dynamics, I would expect fluctuations in treeline elevation to be most strongly biased by the cessation of grazing, while growth dynamics should be less influenced. In the first two parts of my thesis I did not focus on treeline elevation, and therefore, the results should not be strongly biased by potential human influences. However, the validation of the simulation outputs heavily depends on the ‘naturalness’ of the treelines under study. Assuming that all ecological processes in the dynamic forest succession model are well represented, the simulated treeline upward shift that was simulated even under a continuation of today’s climate revealed a non-equilibrium state of current treeline. This could be due to either solely inertia in the treeline’s reaction to changing environmental conditions going back to the Little Ice Age (Camarero and Gutiérrez, 2004; Gehrig-Fasel et al., 2007), a human-induced depression of the treeline, or an interaction of the two processes. However, I am confident that, due to my search approach and also due to indications in the stand and age structure data that I acquired in the field, chances are low that my data include heavy biases due to land use. The only viable solution to completely rule out any anthropogenic influence would be to acquire empirical
data in mountain regions that are much less populated than the European Alps, and to conduct comparable mechanistic modelling studies. In this way, the influence of climate change on forest dynamics at treeline and the subjacent subalpine forest could be isolated even better without the possible confounding influence of human activities.

The question arises how sensible analyses of the response of natural treeline sites to climate change are, given that the vast majority of the treelines in the European Alps are human-induced. The results of my thesis contribute to a basic ecological understanding of the key processes driving short-term and long-term growth variability at climatic treeline. However, it is not clear whether these findings also apply to anthropogenic treelines. If this was not the case, from an applied perspective analyses of the reaction of anthropogenic treelines would be of higher value for the estimation of the fate of ecosystem goods and services provided by these ecosystems in densely populated mountain regions. Therefore, I recommend a systematic exploration of differences between the pace and pattern of changes of climatic vs. anthropogenic treelines.

The issue of local-scale precipitation data

Although treeline dynamics are, on a global scale, governed mainly by temperature (Körner, 2012), water availability may act as a limiting factor on smaller scales (e.g., Holtmeier and Broll, 2017; King et al., 2013) and therefore influence forest dynamics. I have shown this in my investigation on the role of snow cover duration (Part III). My approach of identifying the regionally highest forest patches for the field studies has ensured a high probability of strong temperature limitation, which is, however, demonstrably affected by the precipitation as it modulates the temperature conditions through cloud cover and snow (Part III). Therefore, it would have been highly desirable to have precipitation (or at least long time series of snow cover) data in the statistical models of Parts I and II. In Part III, I utilized gridded precipitation data as I assumed that they reflect the general temporal precipitation patterns at the three study sites reasonably well. However, I am rather skeptical whether including precipitation data inferred from a nearby (or, actually, not-so-nearby) climate station or gridded data as proxy for water availability would have yielded useful results in Parts I and II, where I analyzed the distinct interannual variability of growth dynamics. In terms of interannual variability, data from the nearest climate station has been shown to be far off for precipitation in mountainous terrain (e.g., Daly, 2006), especially in areas with predominantly convective precipitation regimes (e.g.,
Bosco/Gurin). Furthermore, soil properties have an important influence on water availability. Hence, if one has access to appropriate precipitation data, also data on soil characteristics should be acquired, which influence the available water capacity for each individual tree together with precipitation and slope steepness. Including precipitation in analyses of interannual growth variability will only make sense if it is possible to understand the complexity behind its spatio-temporal distribution and the trees’ capabilities to use it.

Although I had chosen a different approach to consider precipitation (i.e. by assessing its influence on a qualitative basis by comparing the three study sites, which are located in different precipitation regimes), my analyses would have been more robust if actual in-situ precipitation and soil moisture data had been available, especially considering the high importance of winter precipitation as revealed throughout my thesis. Of course, it would be rather demanding, expensive and lengthy to generate long time series of precipitation data at such remote places. A perhaps more feasible approach might be to employ satellite remote sensing techniques to quantify the interannual variability of the length of the snow-covered period (e.g., Hüsler et al., 2014; Macander et al., 2015). Suitable satellite data are becoming available over considerable periods of time (>30 years; e.g., Landsat, AVHRR) and these, paired with empirical data on forest dynamics and perhaps a space-for-time approach, could (i) yield insights on the role of (winter) precipitation in shaping today’s subalpine forests, and (ii) help to develop a more advanced version of the snow model that is being used in the most recent version of ForClim.

Mean air temperatures vs. bioclimatically meaningful temperature variables

Particularly in Part III of this thesis, I found a considerable mismatch between daily or longer-term average air temperatures at treeline and the bioclimatic conditions experienced by the trees. On the one hand, the above-mentioned shortening of the growing season by snow cover is not reflected in measured air temperatures. On the other hand, diurnal temperature cycles are cancelled out in the averaging procedures. Due to the large differences in cloud cover between the three regions of my study (Northern, Central and Southern Alps), both incoming and outgoing radiation vary substantially from site to site. Thus, Zermatt is characterized by large daily amplitudes, quite in contrast to Hohgant. However, the long-term nature of my analyses required long time series of temperature data, which were only available at daily or even coarser temporal resolution. In addition, air temperatures
measured according to the WMO standard, with the sensor being screened from radiation, do not necessarily reflect actual tissue temperatures, which further depend on the size of the respective plant (Körner, 2016). However, it is eventually the tissue temperatures that are bioclimatically meaningful and determine tree growth (Körner, 2012), not 2 m screen temperatures. Again, the difference between tissue temperature vs. air temperature most likely depends on continentality. At more continental sites I conclude that this difference is largest.

For future research on temperature-growth relationships – common in many dendroecological and dendroclimatological studies – I recommend a more thorough examination of the temperature variables that are used to explain tree growth and other aspects of forest dynamics. This concerns mostly the temporal resolution of the data. The commonly used monthly averages may lead to inconclusive or even misleading results, and higher-resolution data may be pivotal. On the one hand, the models for explaining short-term growth variability (Part I) featured large differences between tree species regarding the number and combination of months that are important for assimilation and investment into growth. On the other hand, the higher the resolution, the smaller the loss of information regarding climatic peculiarities. I am aware that it is not possible to increase the measuring frequency of climate stations a posteriori. However, the compilation of site-specific correction functions for monthly mean temperature-derived, bioclimatically meaningful temperature variables in Part III of my thesis, which were based on only relatively few years of sub-daily data, have the potential to improve our understanding of differences in empirical studies of tree growth dynamics under otherwise seemingly identical growth conditions.

Causalities behind the among-tree variability

One of the major findings from Parts I and II of my thesis was the substantial amount of intra-species among-tree variability that affected not only short-term growth variability but also long-term growth responses of tree populations to changing environmental conditions. This confirms the existence and importance of such variability as found by Buras et al. (2016) and Vanoni et al. (2016). Yet, the mere identification of this phenomenon does not explain its origin. Unfortunately, the tool set and data base of my thesis did not allow for further investigations on this matter. Although there are hypotheses as to what causes this among-tree variability (e.g., microsite conditions, genetic differences, tree size, competition; Buras et al., 2016; Merian and Lebourgeois, 2011), the exact underlying causes are far from being un-
understood. Recently, Buras et al. (2016) proposed a new method to analyze ecological gradients in tree-ring data. They used a so-called principal component gradient analysis that could help to disentangle the population-internal (e.g., age, competition, genetics) from the population-external effects (e.g., soil conditions, bioclimate) that lead to the highly variable growth reactions of trees of the same species. If one systematically quantified the differences in these factors within a population and applied the proposed method, the consequences of changing environmental conditions for growth dynamics could be better understood. This would also increase the reliability of projecting forest growth dynamics under future climate change.

**Tree-height parameters in ForClim**

Finally, I want to spend some thoughts on uncertainties and limitations in the model that I used for the simulations of past and future forest dynamics in *Part III* of this thesis. The process-based forest succession model ForClim is based on rather simple ecological assumptions and, in most cases, robust parameterizations (Bugmann, 1996). In the past, this model was applied under a wide range of conditions, including the subalpine vegetation zone (e.g., Elkin et al., 2013; Risch et al., 2003) and even upper treeline (Bugmann and Pfister, 2000; Heiri et al., 2006). While the majority of the parameters are founded in empirical data and should apply for the conditions prevailing in subalpine forests, there are a few parameters that are questionable in the context of the cold edge of a species’ distribution. Specifically, the formula to determine maximum tree height given certain temperature conditions is based on yield table data (Rasche et al., 2012), and it appears to work well for many elevations. However, it did not seem realistic for the upper edge of the subalpine forest. As treeline is approached, the height of all species but mountain pine was strongly overestimated in the model. It is not surprising that the data from yield tables, which originate from stands anywhere but near the cold limit of growth (cf. Rasche et al., 2012) do not cover such extreme conditions. In my thesis, I have identified a promising approach that may be suitable for an improvement of the tree height parameters at the cold edge of tree growth: close-range remote sensing techniques (Hyppa et al., 2001; Zarco-Tejada et al., 2014) combined with data acquisition using newly arising small unmanned aerial vehicles have permitted me to rather easily assess forest stand structure of my study sites, the results of which I used in *Parts I* and *III* of my thesis. The compilation of canopy height models, an automated tree detection and subsequent tree height calculation as employed in my thesis would also allow for a spatially fine-scale analysis of tree height...
along, e.g. transects and hence temperature gradients that would be highly suited for a parameterization of maximum tree heights. Of course, this would require equally fine-scale temperature data and a thorough consideration of the critical points regarding temperature variables that I discussed further above. As an additional benefit, this approach would yield high-quality validation data on the stand scale (e.g., stand basal area, volume), as shown in Part III of the thesis.

5.3 Significance of the thesis in general

The interface between the subalpine forest and the alpine tundra has attracted scientific interest for a long time. Already Alexander von Humboldt and Aimé Bonpland, on their scientific voyage to South America, noticed the treeline as a globally occurring phenomenon that must be controlled by a common (bio-)climatic driver (Fig. 5.1). Right from the beginning of the research on this phenomenon (Humboldt and Bonpland, 1807) until recently (e.g., Körner and Paulsen, 2004), low temperature as the most important global-scale driver of treeline dynamics was the dominant topic regarding the “where” and “why” of treeline occurrence. Of course it has been known for a long time that a complex web of interacting small-scale processes exists that, just like at any other forest site, modulate tree regeneration, growth and mortality (e.g., Tranquillini, 1979). However, this knowledge was of observational rather than empirical nature.

It is only in recent years that the increased awareness of the importance of this ecotone in terms of ecosystem goods and services, and the ongoing global climate change have created the demand for an improved understanding of regional- to local-scale patterns as well as potential climate change feedbacks (cf. Holtmeier and Broll, 2017; Malanson et al., 2011). This is exactly where I see the gap in knowledge that I tried to at least reduce with my thesis. In all three parts of the thesis, I revealed tree-internal, population-internal and -external effects that can, on a tree-by-tree basis, be of equal if not larger importance for growth than temperature variability alone. Taken together, these effects have a substantial influence on population-wide responses to climate variability, both in the reconstructed past and the simulated future. On the one hand, this knowledge is of particular relevance in terms of basic research about the functioning of the treeline ecotone. On the other hand, the knowledge on these smaller-scale drivers of treeline dynamics may also have benefits for more applied purposes, as the scope of interest of many stakeholders in mountain regions is at the rather small scale. I am thinking
in particular of more accurate and spatially highly-resolved predictions of potential carbon sequestration, the future development of protective functions and subalpine forest productivity, as well as research on the implications for the economically important touristic use of mountain landscapes. With regard to all these functions and interests, my thesis can help to better understand the underlying dynamics in the past as well as their development in the future.

Figure 5.1: Horizontal patterns and, most relevant for my PhD thesis, vertical distribution of plants of the world, based mainly on the studies by Alexander von Humboldt in the early 19th century. Already then, treeline was recognized as a phenomenon that varies in elevation according to latitude (cf. vertical profile). Note that the other elevational vegetation belts are referenced relative to the respective treeline, which thus serves as an “anchoring point” throughout the globe. Map from Bromme and Humboldt (1851).
5.4 Conclusions

Understanding the reactions of our environment in general and the treeline in particular to a changing climate is a complex venture, and the consequences are far from being clear. However, with my thesis I shed light on important aspects of the reactions of individual trees to climate variability and the consequences that these reactions have for treeline dynamics.

My thesis has underlined the large importance of considering processes on both the large scale and rather small spatial scales in explaining the response of the treeline ecotone and the subjacent subalpine forest to past and future climate variability. Of course, temperature as the global-scale determinant of tree growth at the cold edge of a species’ distribution has a major influence on forest dynamics at treeline. However, a full appreciation of the actual bioclimate that trees experience, the consideration of intra-species among-tree variability, competition-induced feedbacks or regional-to local scale precipitation patterns are of key importance if one wants to understand what shapes the treeline and subalpine forest today, and how it will develop under ongoing and future climate change.

My thesis has demonstrated that it is often inadequate to assume that increased air temperatures will simply improve growth conditions at treeline but that numerous factors modulate growth responses. At treeline, not only deciduous trees (in this case larch) but also conifers largely depend on the growth conditions at the end of the previous growing season. If their habitat is rich in snow, soil temperature rather than air temperature will drive the trees’ growth dynamics. The relationship between radial growth and key temperature variables is highly non-linear. Just as the temperature limitation is overcome, other growth-limiting factors are setting in, leading to a pronounced increase in growth variability. One of the reasons for this is the previously unquantified among-tree variability, indicating differing strategies both between and within tree species regarding the time when temperature actually affects ring-width formation, leading to more or fewer advantages due to increasing temperature. Furthermore, the declining growth trends that I found for some trees and some species with decreasing elevation are most likely due to neighborhood interactions and thus indicate negative feedback effects of climate change on tree growth slightly below treeline. In addition, I revealed an essential role of the site’s precipitation regime that significantly moderates growth conditions in two ways: (i) cloud cover and air humidity control the direct radiation available to trees, and (ii) the amount of snow restricting the period when trees can actually grow.

All in all, in my thesis I underlined the pronounced role of temperature
as the large-scale driver of both short-term variability of tree growth and long-term treeline dynamics. At the same time, I revealed pivotal biotic and abiotic influences that substantially modulate the trees’ responses to this large-scale driver. Without taking these modulators into account, it was impossible to explain regional- to local-scale characteristics of forest dynamics. It was only when I considered these drivers and modulators holistically and across scales that reconstructions of past treeline dynamics were congruent with real-life observations. Consequently, also the scenarios of a future development of treeline dynamics that I outlined are more realistic and robust in terms of the underlying ecological assumptions.
5.5 References


5.5. REFERENCES


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