Sensitivity and Response of Alpine Treelines to Climate Change - Insights from a Krummholz Treeline in Rolwaling Himal, Nepal

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Summary

Mountain forests cover large parts of mountainous regions on Earth and represent significant natural resources from both socio-economic and ecological perspectives. Mountains of the world, including the Himalaya, belong to the regions that have been most affected by climate change. Alpine treeline ecotones mark the transition from the uppermost occurrences of contiguous forests to a treeless area, i.e. the transition from upper subalpine forest via the treeline to alpine vegetation. At a global scale, insufficient temperatures during the growing season result in growth limitations that determine the elevation of natural alpine treelines. However, treeline positions, spatial patterns and dynamics depend on a multitude of environmental factors and ecological interactions at landscape and local scales. It is assumed that temperature increases due to climate change cause treelines to advance to higher elevations. However, empirical studies of diverse mountain ranges have yielded evidence of both advancing alpine treelines as well as rather insignificant responses. The reasons for this discrepancy are not well understood.

To address research deficits in global-change-related treeline dynamics, we applied a landscape approach that derives from the pattern-process paradigm in landscape ecology and hierarchy theory in ecology. The overall objective was to analyse the sensitivity and response of the investigated treeline ecotone to climate change. We collected extensive samples of vegetation and environmental variables in the near-natural treeline ecotone of the Rolwaling valley in east-central Nepal. Based on these data, we analysed population structures and regeneration patterns, investigated population density-environment relationships and correlated tree growth with climate in order to assess the treeline's sensitivity to climate warming.

The results demonstrate that growth and density variables indicate complex and heterogeneous stand structure patterns throughout the investigated treeline ecotone. The presence of an elevational zone dominated by a contorted and gnarled growth form of *Rhododendron campanulatum* physiognomically classifies the treeline as one with a krummholz belt. We identified various species-specific elevational limits for trees as well as variations in the abruptness of these limits. We found complex patterns of transitions of tree species compositions, growth parameters and site conditions along the elevational gradient. The most abrupt tree species composition change, i.e. that from closed forest to the krummholz belt, coincided with the most abrupt transition in soil temperature. The mapping of juvenile tree species individuals reflects prolific regeneration and stand densification. The species-specific variation in adult and juvenile stand density along the treeline ecotone depends not only on temperature but, as expected, also on edaphic, topographic, and other microclimatic conditions. *Rhododendron campanulatum* shows highest competitiveness in the krummholz belt under a

constellation of site conditions influenced by this species itself. By contrast, *Abies spectabilis* (Himalayan Silver Fir) and *Betula utilis* (Himalayan Birch) have gained predominance under warmer and more nutrient-rich habitat conditions in the closed forest below. The dense krummholz belt effectively controls the potential upslope migration of subalpine forest tree species. *Abies spectabilis* growth-climate correlations show changing growth limitations in the course of the 20th century, most likely due to intensified climate warming in recent decades, when insufficient moisture availability during the pre-monsoon season has affected *Abies spectabilis'* radial growth. Thus, amplified drought periods as a consequence of ongoing climate warming will most likely affect *Abies spectabilis* more adversely in the future and challenge its growth plasticity. It is evident from our results that to date the Rolwaling treeline position has responded to climate warming to a rather slight extent, and that a treeline shift is to be expected in the mid- to long-term only.

Based on detailed tree population data and tree-ring data as well as analysed interactions of vegetation and their environmental relationships, this thesis contributes novel findings on the sensitivity and response of Himalayan treelines to climate warming, enhancing the present understanding of treeline ecology in general and of the significance of climate-change-induced effects.

This cumulative thesis is based on three peer-reviewed studies that have been published in two journals and one edited volume (see Appendix I for the abstracts and author contributions, and Appendix II for full articles):

Study 1: 'Treeline responsiveness to climate warming: insights from a krummholz treeline in Rolwaling Himal, Nepal'
Authors: Niels Schwab, Udo Schickhoff, Michael Müller, Lars Gerlitz, Birgit Bürzle, Jürgen Böhner, Ram Prasad Chaudhary and Thomas Scholten
Published 2016 in Singh RB, Schickhoff U, Mal S (eds.) *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya*. Springer International Publishing, Cham, Switzerland, pp 307-345 doi: 10.1007/978-3-319-28977-9_16

Study 2: 'Implications of tree species - environment relationships for the responsiveness of Himalayan krummholz treelines to climate change'
Authors: Niels Schwab, Udo Schickhoff, Birgit Bürzle, Michael Müller, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten and Jens Oldeland
Published 2017 in *Journal of Mountain Science* 14:453–473 doi: 10.1007/s11629-016-4257-z

Study 3: 'Climate change-induced shift of tree growth sensitivity at a central Himalayan treeline ecotone'
Authors: Niels Schwab, Ryszard J. Kaczka, Karolina Janecka, Jürgen Böhner, Ram P. Chaudhary, Thomas Scholten and Udo Schickhoff
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I contributed to eight additional studies which are closely linked to the objective of this thesis and thereby added to the broader picture of the Rolwaling treeline ecology and its response to climate change. Appendix III includes abstracts of these studies.

Zusammenfassung

Bergwälder von hoher sozioökonomischer und ökologischer Bedeutung bedecken große Teile der Gebirgsregionen auf der Erde. Diese Regionen, einschließlich des Himalayas, sind neben den höheren Breiten am stärksten vom Klimawandel betroffen. Waldgrenzökotone stellen den Übergang von den obersten Vorkommen subalpiner Wälder über die Baumgrenze bis hin zur baumfreien alpinen Vegetation dar. Auf globaler Ebene führen unzureichende Temperaturen während der Vegetationsperiode zu Wachstumsbeschränkungen, die die Höhenlage der natürlichen alpinen Waldgrenze bestimmen. Jedoch sind Waldgrenzen, ihre räumlichen Muster und ihre Dynamik auf kleineren räumlichen Ebenen, zum Beispiel auf der Landschaftsebene und der lokalen Ebene, von einer Vielzahl weiterer Umweltfaktoren und von ökologischen Wechselwirkungen abhängig. Es wird generell angenommen, dass sich alpine Waldgrenzen infolge des Klimawandels in höhere Lagen verschieben. Empirische Untersuchungen in verschiedenen Gebirgszügen haben jedoch Hinweise sowohl auf einen Anstieg alpiner Waldgrenzen als auch auf die Persistenz dieser Höhengrenzen ergeben. Die Gründe für diese Diskrepanz sind bisher unzureichend erforscht.

Um entsprechende Forschungsdefizite abzubauen, haben wir einen landschaftsökologischen Ansatz angewendet, der aus dem Raummuster-Prozess-Paradigma der Landschaftsökologie und der Hierarchie-Theorie der Ökologie abgeleitet ist. Das übergeordnete Ziel bestand darin, die Sensitivität und Reaktion des untersuchten Waldgrenzökotons auf den Klimawandel zu analysieren. Wir haben umfangreiches Datenmaterial zu Vegetations- und Umweltvariablen im naturnahen Waldgrenzökoton des Rolwaling-Tales im östlichen Zentral-Nepal erstmalig erhoben. Auf dieser Grundlage konnten Populationsstrukturen und Verjüngungsmuster erfasst, Zusammenhänge zwischen Populationsdichten und Standortfaktoren untersucht und Korrelationen zwischen Baumwachstum und Klima ermittelt werden. Die Ergebnisse ermöglichten weitreichende Schlussfolgerungen hinsichtlich der Empfindlichkeit der Baumgrenze gegenüber der Klimaerwärmung.

Die Populationsstrukturen der Baumarten und ihre Wachstumsvariablen weisen auf komplexe und heterogene Bestandsstrukturmuster im gesamten untersuchten Waldgrenzökoton hin. Aufgrund der Ausbildung einer Höhenstufe, die von *Rhododendron campanulatum* mit einer krummholzartigen Wuchsform dominiert wird, lässt sich das Ökoton physiognomisch einer Waldgrenze mit einem vorgelagerten Krummholzgürtel zuordnen. Wir identifizierten verschiedene spezifische Höhengrenzen für einzelne Baumarten und zeigten hinsichtlich der Baumartenzusammensetzung und der Standortfaktoren Unterschiede in der Abruptheit der Übergänge zwischen verschiedenen Vegetationseinheiten entlang des Höhengradienten. Eine abrupte Änderung der Baumarten-Zusammensetzung beim Übergang vom geschlosse-

nen Wald zum Krummholzgürtel fällt mit einer abrupten räumlichen Änderung der Bodentemperatur zusammen. Die Kartierung des Jungwuchses aller Arten zeigt eine intensive Verjüngung und Verdichtung der Bestände. Die Variation der Bestandesdichte adulter und juveniler Populations-Kohorten entlang des Höhengradienten hängt in artspezifisch unterschiedlichem Ausmaß nicht nur von der Temperatur, sondern, wie zu erwarten war, auch von edaphischen, topographischen und anderen mikroklimatischen Bedingungen ab. *Rhododendron campanulatum* weist aufgrund von Standortbedingungen, die von dieser Art selbst stark beeinflusst werden, die höchste Konkurrenzfähigkeit im Krummholzgürtel auf. Auf wärmeren und nährstoffreicheren Standorten des geschlossenen Waldes dominieren dagegen *Abies spectabilis* (Himalaya-Tanne) und *Betula utilis* (Himalaya-Birke). Der dichte Krummholzgürtel kontrolliert die mögliche hangaufwärtsgerichtete Wanderung von subalpinen Baumarten sehr effektiv. Wachstums-Klima-Korrelationen von *Abies spectabilis* zeigen im 20. Jahrhundert einen Wechsel der das Wachstum limitierenden klimatischen Einflüsse, was höchstwahrscheinlich auf eine verstärkte Klimaerwärmung in den vergangenen Dekaden zurückzuführen ist. In diesem Zeitraum hat die zunehmende Trockenheit während der Vormonsunsaison das radiale Wachstum von *Abies spectabilis* begrenzt. Wahrscheinlich werden verstärkte Dürreperioden als Folge der fortschreitenden Klimaerwärmung die Vitalität von *Abies spectabilis* in Zukunft stärker beeinträchtigen und die Wachstumsplastizität herausfordern. Die Ergebnisse zeigen insgesamt, dass die Waldgrenze des Rolwaling auf die Klimaerwärmung in einem eher geringen Ausmaß reagiert und ein Vorrücken erst in mittel- bis langfristigen Zeiträumen zu erwarten ist.

Auf der Grundlage detaillierter Daten zu Baumpopulationen und Jahrringen und durch die Analyse von Vegetation-Standort-Interaktionen liefert diese Arbeit neue Erkenntnisse zu Sensitivität und Reaktion von Himalaya-Waldgrenzen im Zuge des Klimawandels und trägt zu einem besseren Verständnis der Ökologie von Waldgrenzen im Allgemeinen und der Signifikanz von Auswirkungen des Klimawandels bei.

Die Grundlage für diese kumulative Dissertation bilden drei durch Peer-Review geprüfte Studien, die in zwei Zeitschriften und einem Sammelband veröffentlicht wurden. Zusammenfassungen der Studien sind in Anhang I, die kompletten Artikel in Anhang II enthalten.

Studie 1: Treeline responsiveness to climate warming: insights from a krummholz treeline in Rolwaling Himal, Nepal
Autorinnen und Autoren: Niels Schwab, Udo Schickhoff, Michael Müller, Lars Gerlitz, Birgit Bürzle, Jürgen Böhner, Ram Prasad Chaudhary und Thomas Scholten
Veröffentlicht 2016 in Singh RB, Schickhoff U, Mal S (Hrsg.) *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya*. Springer International Publishing, Cham, Schweiz:307-345 doi: 10.1007/978-3-319-28977-9_16

Studie 2: Implications of tree species - environment relationships for the responsiveness of Himalayan krummholz treelines to climate change
Autorinnen und Autoren: Niels Schwab, Udo Schickhoff, Birgit Bürzle, Michael Müller, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten und Jens Oldeland
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Studie 3: Climate change-induced shift of tree growth sensitivity at a central Himalayan treeline ecotone
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Veröffentlicht 2018 in *Forests* 9:267 doi: 10.3390/f9050267

Ich habe zu weiteren acht Studien beigetragen, die in enger Verbindung zu den Zielen dieser Dissertation stehen. Sie tragen daher zum Gesamtbild der Waldgrenzökolgie des Rolwaling und der Reaktion der Waldgrenze auf den Klimawandel bei. Die Zusammenfassungen dieser Studien sind im Anhang III enthalten.

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List of Abbreviations

BI	Blue Intensity
BP	before present (before 1950)
CRU	University of East Anglia Climate Research Unit
dbh	diameter at breast height
kyr	kilo (thousand) years
MICE	multiple imputations by chained equations
p	probability (p-value, level of significance)
RDA	redundancy analyses
RI	regeneration index
SPEI	standardized precipitation-evapotranspiration index
TRW	tree-ring width
TS	time series

Synthesis of the Cumulative Thesis

1 Introduction

1.1 The significance of mountain forests

Mountain areas cover one-quarter of Earth's surface and accommodate one-eighth of the global population. Furthermore, they provide various goods and services to more than half of the world's people (Mc Morran and Price 2011). Mountain environments have increasingly attracted attention for their importance to scientific interest in global change research as well as sustainable development agendas in the past two to three decades, which has resulted in a higher level of integration in research initiatives (Messerli 2012; Schickhoff et al. 2016b). Mountain forests possess high global significance since many goods and services originate from these forests, which cover one-quarter of the world's mountain area. Such services can be categorised into the following groups: provisioning services, e.g., fuelwood and non-timber forest products; cultural services, e.g., spiritual values and recreational opportunities; and regulating and support services, e.g., protective functions, water storage, carbon sinks and biodiversity hotspots. The resilience and integrity of forests are under threat from population growth. Furthermore, demands for goods and services from within and outside mountain regions in addition to climate change impacts have created new challenges. As a consequence, the state of primary mountain forests is in decline. Climate change might increase tree growth rates, which could be beneficial for the use of wood and its protective function. Negative impacts seem predominant, e.g., facilitation of diseases and insect outbreaks, increased risk of wildfire and danger by climatic extreme events. Mountain forests can substantially contribute to both climate change mitigation and adaptation (Mc Morran and Price 2011). The study area of this thesis is located in Nepal. Forest covers more than 40% of the total area of Nepal, and about one-third of forests are high mountain forests which border on alpine vegetation at the treeline (DFRS 2015). The protection of mountain forest ecosystems and their biodiversity through for instance the development of sustainable land-use practices may require a full understanding of these systems' components and interactions. One part of mountain forests is the uppermost zone, i.e. the treeline ecotone, which presents as the transition from closed forest to treeless alpine vegetation. There is an urgent need to gain knowledge on this ecotone, as evidenced by the substantial research deficits regarding causes of mountain treelines, responses of such treelines to climate change (see below) and the scarcity of near-natural treeline ecotones.

1.2 Climate change in the Himalaya

Nearly all regions on Earth have been exposed to climate warming after the Little Ice Age. Globally averaged combined land and ocean temperature data revealed a warming trend of approximately 0.85 (0.65–1.06)°C over the period 1880–2012 (IPCC 2013). Subsequent impacts in recent decades have globally affected terrestrial and marine environments and their biota. In addition, temperature trends of mountain regions have exhibited a more pronounced increase in comparison to the global mean. These regions are particularly vulnerable as a consequence of their cryospheric systems, steep slopes, complex topography, associated steep ecological gradients and high variability of human-environmental subsystems. Distinct temperature trends in mountain ecosystems combined with narrow adaptation ranges of mountain plant and animal species could result in intense responses to climate warming, including changes in species richness, modified patterns and processes in alpine treeline ecotones and changes in elevational treeline position (IPCC 2014; Grover et al. 2015; Schickhoff et al. 2016a; Schickhoff et al. 2016b; Steinbauer et al. 2018).

In line with global warming trends in mountain regions, several studies have observed above-average current warming trends for the Himalayan region. Warming trends of the annual mean surface air temperature of up to 1.5 °C were detected over the Tibetan Plateau and the Himalaya during the period 1991–2012 (IPCC 2014; Mountain Research Initiative EDW Working Group 2015; Schickhoff et al. 2016b). Maximum values were found for the high elevations and during winter and pre-monsoon seasons (Shrestha et al. 1999; Liu and Chen 2000). For the Rolwaling valley, the target area of this thesis, monthly temperature trends in the order of 0.7 °C per decade were assessed in winter and pre-monsoon seasons (Gerlitz et al. 2014). During monsoon, no statistically significant trends were identified. Trend analyses of precipitation amounts in the Himalaya do not exhibit a consistent pattern. Some studies, however, have detected negative trends of winter and pre-monsoon precipitation over the western and central Himalaya (Duan et al. 2006; Bhutiyani et al. 2010; Jain et al. 2013). Wang et al. (2013) have reported an enhanced frequency of winter and pre-monsoon drought events for western Nepal. Additionally, Karki et al. (2017b) have found rising precipitation extremes across Nepal. Recent climatic changes will inevitably affect growth patterns and seedling performance in Himalayan treelines, albeit to a regionally differentiated extent (Schickhoff et al. 2015; Schickhoff et al. 2016a).

1.3 Holocene treeline dynamics in the Nepal Himalaya

During the Holocene, the temperature zone response pattern generally determined treeline dynamics in the Himalaya. These dynamics resulted in upslope expansion during warmer times and downward movement during colder periods. In detail, regional variations of treeline fluctuations throughout the Himalaya reflect that factors apart from temperature, e.g., moisture balance changing depending on monsoon intensity, have influenced the elevational position. Increased Asian monsoon precipitation after the Pleistocene-Holocene transition (approximately 11.7 kyr BP) resulted in uppermost treeline limits in the early Holocene that were several hundred metres higher than at the present time. Compared to the early and mid-Holocene, low temperatures after approximately 5 kyr BP caused a downward shift of treelines, which continued during the following millennia due to a weakening monsoonal influence and anthropogenic impacts. Treeline history deviated substantially from this general pattern at regional and local spatial scales and at different temporal scales (Schickhoff et al. 2016a).

Treeline advance was accompanied by an expansion of *Pinus* and *Quercus* trees in east Nepal under warmer climatic conditions after the Pleistocene-Holocene transition (Yonebayashi and Mutsuhiko 1997). *Quercus* sp. and temperate genera increased, whilst conifers and *Betula* sp. trees were on the decline in west Nepal during the further course of the Holocene (Yasuda and Tabata 1988). At this time, increased monsoon precipitation was associated with the establishment of *Pinus wallichiana* forests in central Nepal (Saijo and Tanaka 2002; Miehe et al. 2009). Climate conditions worsened in parallel with a decline in vegetation zones and treeline position during the Subboreal after approximately 5 kyr BP (Schlütz and Zech 2004). In addition to climatic causes, this downward shift of treelines in Nepal was most likely related to anthropogenic activities, e.g., the use of fire, grazing pressure or timber logging.

Treeline dynamics in recent centuries have been similarly due to a mix of human activity and climate changes (Beug and Miehe 1999; Schlütz and Zech 2004; Schickhoff et al. 2016a). Above-average warming rates have triggered multiple vegetation responses, such as changes in phenology, productivity, species composition of communities, structure and elevational ranges of species (Shrestha et al. 2012; Telwala et al. 2013; Zhang et al. 2013; Salick et al. 2014). Recent elevational shifts of alpine treelines and tree growth-climate relationships have received much attention (e.g., Dawadi et al. 2013; Liang et al. 2014; Gaire et al. 2017b; Kharal et al. 2017; Tiwari et al. 2017).

1.4 Trees, treelines and their functional ecology

The term 'tree' defines a life stage of a woody species that resembles an upright growth with a dominant stem of a certain height. This height exceeds the snow cover in regions with winter weather as well as the height reached by large browsers (Körner 2003; Miehe et al. 2007; Körner 2012a). Unlike smaller shrubs, grasses and herbs, the crowns of trees are aerodynamically coupled more closely to atmospheric conditions. Thus, they experience critically growth-limiting low temperatures at a lower elevation compared to smaller plants in mountain regions (Körner 2012b). In the transition from closed forests with trees to alpine vegetation with shrubs to represent the woody plants, there is almost no sharp boundary but rather a continuous change as determined by gradually changing environmental drivers. This transition zone is called the treeline ecotone. Terms such as treeline, timberline, forest line, outpost treeline or tree species line approximate specific limits of life stages or species occurrences to a linear boundary at a certain elevation. The scale of observation matters: a far distance, e.g., the view from a plane, eases the simplification of such transitions to a line, while close observations reveal their gradual character (Körner 2012a). Unless stated otherwise, this thesis employs the terms 'treeline' and 'treeline ecotone' as synonyms for the transition zone. Unlike so-called 'lower treelines', which are related to moisture deficits (e.g., in deserts), and latitudinal treelines, which are not necessarily related to high elevation, 'alpine' or 'upper' treelines are located in high mountain environments. Thus, it is no surprise that some of the side-by-side existing definitions of the term 'high mountains' refer to the formation of an upper treeline (Burga et al. 2004; Beierkuhnlein 2007).

Treeline species and their populations as well as their environments implicate specific taxonomic, spatial and temporal patterns. Such patterns also concern tree physiognomy, mountain climate and other environmental conditions, processes and drivers that govern reproduction, growth and development. Furthermore, they involve various forms of stress at diverse spatial scales. This thesis addresses some of these aspects. However, in view of the limited extent of this synthesis, I refer to Körner (2012a) for a comprehensive overview of basic knowledge on functional ecology of alpine treelines.

1.5 Assessment of the sensitivity and response of Himalayan treelines to climate change: state of the art and research deficits

In general, the upper limit of tree life depends on the heat balance. At a global scale, low air and soil temperatures during growing season determine the position of natural upper treelines (e.g., Troll 1973; Stevens and Fox 1991; Holtmeier 2009; Körner 2012a). Thus, climate warming is expected to cause treelines to advance to higher elevations. Treelines fluctuated repeatedly as a result of climate changes during the Holocene era (Reasoner and Tinner 2009; Schickhoff et al. 2016a). However, recent empirical studies in diverse mountain ranges have evidenced both currently advancing alpine treelines as well as rather insignificant responses (Baker and Moseley 2007; Hofgaard et al. 2009; Wieser et al. 2009; Grigor'ev et al. 2013; Chhetri and Cairns 2015; Shrestha et al. 2015), which suggests an evident research deficit. Harsch et al. (2009) have analysed data from 166 globally distributed treelines whose dynamics were monitored since AD 1900. Forty-seven per cent of the treelines did not reveal any elevational shift, while 52% advanced to higher altitudes, and only 1% evidenced recession. Apart from climate change, land-use changes have influenced high-altitude vegetation patterns and treeline positions (e.g., Dirnböck et al. 2003; Bolli et al. 2007; Gehrig-Fasel et al. 2007; Pauchard et al. 2009; Schickhoff 2011; Piermattei et al. 2014; Penniston and Lundberg 2014; Durak et al. 2015). Thus, there is a need to disentangle these effects in order to draw correct conclusions about the sensitivity of treelines to climate change. To this end, complex research approaches to natural treelines at local and landscape scales are needed (e.g., Malanson et al. 2011; Holtmeier and Broll 2017; see also section 2.1).

Despite a number of emerging studies which have analysed the sensitivity and response of Himalayan alpine treelines at a local scale, extensive research deficits persist in terms of the interactions of landscape-scale and local-scale abiotic and biotic factors and processes. Apart from temperature and moisture conditions, several notable factors influence treeline ecotone populations and treeline position; such factors include physical and chemical soil properties, disturbance regimes, individual tolerances and ecological demands of tree species, regeneration, migrational lags and competition from established vegetation (Holtmeier 2009; Schickhoff et al. 2016a). Thus, additional knowledge of local population structures and regeneration patterns, their relationships to abiotic and biotic site factors, and tree growth-climate relationships can enhance the present understanding of climate warming-induced non-linear treeline ecotone responses to local-scale modulators and their interactions.

Near-natural treeline ecotones can contain co-dominant tree species which respond differently to climate change (Trant and Hermanutz 2014). Most treeline studies in Nepal (e.g., Shrestha et al. 2007; Lv and Zhang 2012; Sujakhu et al. 2013; Gaire et al. 2014) have not entirely assessed the various treeline ecotone-forming tree species. In consequence, there is an urgent need for multispecies approaches to treeline dynamics, which survey all ecotone tree species and sufficiently capture the sensitivity of the ecotone to climate change.

Research can use treeline type, treeline form, seed-based regeneration and growth patterns as sensitivity indicators to assess current treeline dynamics (Schickhoff et al. 2015).

Treeline type and treeline form

Amongst treeline types, climatic treelines present a rather high sensitivity to climate change, although local-scale abiotic and biotic site factors and their interactions modify the direct influence of climate warming in complex ways. Orographic and edaphic treelines are considered to be less responsive. Anthropogenic treelines have evidenced distinct directional changes, which have often been attributed to climate warming; however, in the majority of cases, these most likely originated from reduced land-use impacts (Schickhoff et al. 2016a).

Recent studies based on a global treeline data set have suggested a close link between treeline form (spatial pattern) and dynamics. Harsch and Bader (2011) have identified treeline form (diffuse, abrupt, island, krummholz) as an indicator of controlling mechanisms (at the levels of direct tree performance, causative stresses and modifying neighbour interactions) and response to climate change. Thereby, they have confirmed the link between treeline form and dynamics as previously established (Lloyd 2005; Harsch et al. 2009) and supported the general suitability of treeline form to explain the variability of response to climate warming. According to a global meta-analysis, diffuse treelines, which are formed and maintained primarily by growth limitation, exhibit a strong response signal. Abrupt, island and krummholz treelines are controlled by seedling mortality and dieback, and they are comparatively unresponsive to climate changes (Harsch and Bader 2011). In the majority of Himalayan treelines, anthropogenic disturbances dominate the control of spatial patterns and thereby exacerbate the treeline form classification. Most near-natural treelines can be categorised as krummholz treelines. With regard to elevational shifts, krummholz treelines demonstrate rather low responsiveness to climate warming. However, short- to medium-term responses are expected in terms of tree growth and seedling recruitment (Schickhoff et al. 2016a).

Population structures and regeneration patterns

Apart from treeline form, tree species composition, tree density, diameter and height distributions can be indicators of treeline sensitivity to climate change. In addition, these parameters provide information about the establishment of recruits and their performance, which are among the most significant indicators of treeline sensitivity (Germino et al. 2002; Holtmeier 2009; Körner 2012a; Zurbriggen et al. 2013; Schickhoff et al. 2015; Schickhoff et al. 2016a).

To date, few studies have examined treeline seedlings in the Himalaya, and tree recruitment in treeline ecotones is not well understood (Schickhoff 2005; Shi and Wu 2013; Dutta et al. 2014; Schickhoff et al. 2015; Schickhoff et al. 2016a). The available studies have referred to treeline ecotones with deviating species compositions and population structures and have generally investigated ecotones which have been disturbed by land-use effects (Shrestha et al. 2007; Ghimire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Chhetri and Cairns 2015; Shrestha et al. 2015). Thus, they have offered only limited generalisability and informative value for near-natural treeline ecotones.

Population density-environment relationships

Detailed knowledge of tree species-environment relationships is among the basic requirements for a more thorough comprehension of treeline response patterns to region-wide climate warming inputs. However, the accumulated knowledge of treeline tree species ecology in the Himalaya remains immensely deficient (Schickhoff 2005; Miehe et al. 2015). For study 2, we analysed population-environment relationships in the treeline ecotone of the Rolwaling Valley in order to infer implications for the treeline sensitivity and response to climate change. Within the ecotone, we focused on the *Rhododendron campanulatum* krummholz belt since study 1 and other previous reports have highlighted the krummholz belt as a crucial ecotone element that largely prevents the upslope migration of tree species (Schickhoff et al. 2015; Müller et al. 2016a; Müller et al. 2016b; Schickhoff et al. 2016a). However, it is still unclear how the change in environmental conditions from closed forest stands to the krummholz belt is correlated along this gradient to modified adult and juvenile population densities of tree species.

Tree growth-climate relationships

Previous research has analysed various treeline tree species to explore tree growth-climate relationships in Himalayan sub-regions (e.g., Chaudhary et al. 1999; Cook et al. 2003; Ahmed et al. 2011; Yadav et al. 2011; Thapa et al. 2017). A frequently studied species is the widely distributed Himalayan Silver Fir, *Abies spectabilis*. Some *Abies spectabilis* studies have found a positive correlation between radial tree growth and the temperature of the current and previous growing seasons (e.g., Shrestha et al. 2015; Shrestha et al. 2017). Others have implied a limitation of tree growth by winter temperature (e.g., Chhetri and Cairns 2016; Rayback et al. 2017) or by available moisture in precipitation-deficient pre-monsoon seasons (e.g., Gaire et al. 2011; Kharal et al. 2017; Gaire et al. 2017a). In view of the generally sparse and partially inconsistent results, even in relatively nearby study areas (e.g., Gaire et al. 2017b), additional studies are needed and should preferably examine near-natural sites.

The majority of central Himalayan tree-ring studies have investigated growth-climate relationships over rather short periods because of a lack of long instrumental records of climate data. Some recent studies have employed gridded climate data that cover longer time periods. Most studies have analysed static correlations that represent the whole period without investigating the temporal pattern of correlations and referring to their temporal stability (e.g., Thapa et al. 2015). Two studies have recently mentioned unstable correlations of *Abies spectabilis* tree growth with climate variables (Shrestha et al. 2015; Sohar et al. 2016). Thus, an insufficient number of studies have investigated temporal stability and potential so-called ‘divergence phenomena’ in the Himalaya, which illustrates an immense need for further research.

2 Framework and Objectives

2.1 Conceptual background and institutional framework

The research for this thesis was conducted within the framework of the project ‘Sensitivity and Response of the Treeline Ecotone in Rolwaling Himal, Nepal, to Climate Warming’ (TREELINE), funded by the Deutsche Forschungsgemeinschaft (DFG) (DFG SCHI 436/14-1, SCHO 739/14-1, BO 1333/4-1). Three intensely co-operating groups focused on aspects related to soil (Prof. Dr. Thomas Scholten, University of Tübingen), climate (Prof. Dr. Jürgen Böhner, University of Hamburg), and vegetation (Prof. Dr. Udo Schickhoff, University of Hamburg, principal investigator), supported by the Nepalese counterpart Prof. Dr. Ram P. Chaudhary (Tribhuvan University, Kirtipur, Kathmandu). The interdisciplinary project aimed at contributing to a reduction of the aforementioned deficits in global-change-related treeline research in general and in treeline research in the Himalaya in particular. To fulfil this aim in compliance with the directions for treeline research proposed by Malanson et al. (2011), the present study investigates the sensitivity and response of a near-natural treeline ecotone to climate warming from the perspective of spatial patterns and processes through a landscape approach.

The spatial pattern influences multiple ecologically important processes (Turner and Gardner 2015), and can coincidentally indicate underlying processes and structures (Grimm et al. 2005). Turner (1989) has argued for its consideration in ecological studies. This claim has been termed the ‘pattern-process paradigm’ in landscape ecology (e.g., Malanson et al. 2011). Currently, the landscape approach, i.e. conducting research at the landscape level, is considered routinely in most types of ecological studies. It is based on hierarchy theory in ecology (Turner and Gardner 2015).

Hierarchy theory in ecology addresses the ecological consequences of levels of organisation in ecological systems. A hierarchy represents a system of relations. In such a system, the higher levels control the lower levels to varying degrees. These levels are differentiated by frequencies of characteristic processes of their elements. To identify levels of hierarchy, temporal scales serve as key criteria (Figure 1). Controls operate over various scales of time and space (Turner and Gardner 2015). For instance, as an element of the local scale, an individual tree within a treeline ecotone can interact with other trees as well as shrubs and the ground vegetation, as all operate at the same space-time scale. However, the tree cannot interact directly with the biome of the southern slopes of the Himalaya or the global orobiome in its entirety since their orders of scale differ in magnitudes. Nevertheless, the biome represents relatively constant background conditions for the individual tree. Ecological studies are recommended to consider the following three levels of hierarchy: the level of genuine interest, the level above and the level below. The level above provides the context and controls the lower level, whilst the level below contains details which are significant to explain occurrences at the focal level (Figure 2) (Turner and Gardner 2015). A change in scale might cause changes in the relative importance of variables and in directions of relationships between elements of the system (Turner and Gardner 2015; Holtmeier and Broll 2017). For instance, at a global scale, the position of upper treelines can be derived from broad-scale temperature conditions (Troll 1973; Körner 2012a). However, other fine-scale drivers have a substantial role in modulating treeline patterns at a local scale (Figure 2) (Holtmeier 2009; Malanson et al. 2011; Holtmeier and Broll 2017). As part of the temporal development of the forest stand structure, tree growth-climate relationships reveal varying patterns at different temporal scales. Weather conditions at a scale of days to weeks control cambial activity and development of single cells. The increment of the whole year depends on the mean temperature of larger parts of the whole growing season, whilst long-term, low-pass filtered fluctuations of tree growth correlate to corresponding changes of the macroclimate (Figure 1) (Fritts 1976). In hierarchy theory, multiple scales of patterns exist in landscapes since processes act at multiple scales. Thus, such theory has been influential in landscape ecology (Turner and Gardner 2015).

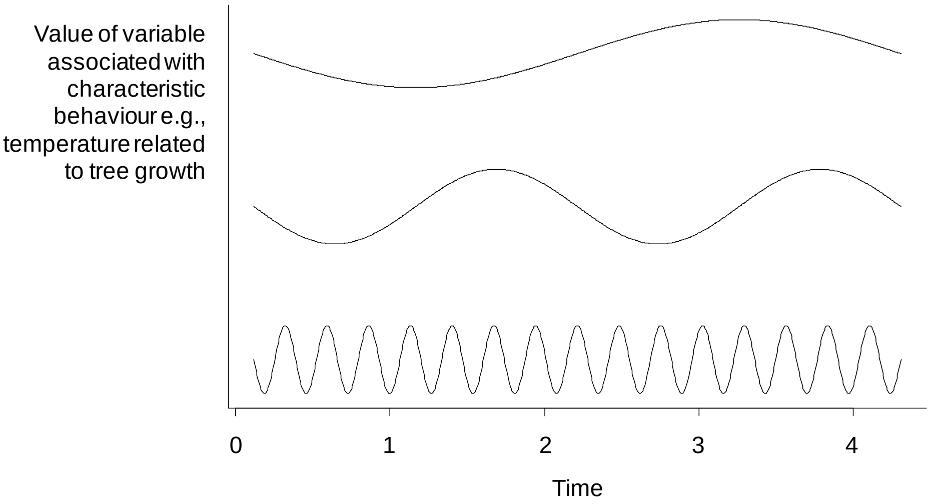

Figure 1. Different time scales associated with levels of ecological hierarchy. The top line is a slow variable, one that would serve as a constraint to the lower levels e.g., long-term changes of the atmospheric conditions. The middle line might be the scale of main interest e.g., the mean temperature of one growing season which influences tree-ring increment of that specific year. The lower line is a variable that changes quickly e.g., 6-h temperature measurements which capture differences between night and day which are not correlated directly with the yearly increment (redrawn from Turner and Gardner 2015).

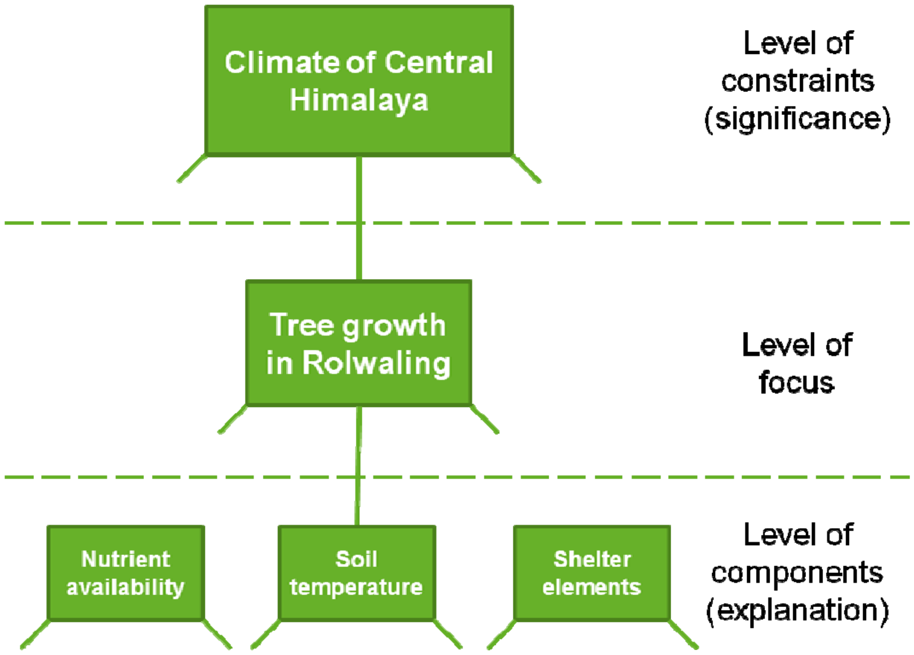

Figure 2. Greatly simplified examples for the three levels in hierarchy which are recommended to include in ecological studies: the upper level provides significance and constraints to the focal level, whilst the lower level contributes details to explain responses of the focal level (redrawn from Turner and Gardener 2015).

Based on the assumption that processes and patterns at treelines develop at multiple spatial and temporal scales, this study employs an appropriate landscape approach that is founded in the pattern-process paradigm and hierarchy ecology. From the TREELINE project's perspective, pattern-process feedback regulates complex patterns of treeline ecotones that change over time. Broad-scale, landscape-scale and local-scale controls interact to regulate these patterns. Previous research has considered regional- or landscape-scale climate to exert a top-down control on local treeline ecological patterns and processes (e.g., Batllori and Gutiérrez 2008; Elliott 2011). Thus, climate warming is assumed to be a factor that has a distinct influence on changes in processes and pattern at the investigated near-natural treeline ecotone. Local-scale site conditions presumably modify the broader-scale climate inputs. Accordingly, they might cause site-specific response patterns (Malanson et al. 2011; Holtmeier and Broll 2017).

The interactions of landscape- and local-scale abiotic and biotic factors and processes and their influences on the treeline and its response to climate change are not well understood. Thus, the interdisciplinary TREELINE approach includes analyses of local abiotic and biotic site factors and their spatial variation. These site factors comprise topographic and geomorphic controls, physical and chemical soil conditions, and plant interactions that include facilitation, competition and feedback mechanisms. The project aimed at quantifying the site factors' specific influences on treeline vegetation and on treeline response patterns. By addressing the research questions below, this thesis contributes to the objectives of the TREELINE project by considering the ′pattern-process paradigm′ and hierarchy theory in ecology.

2.2 Objectives

To reduce the aforementioned research deficits concerning the sensitivity and response of Himalayan treelines, this thesis pursues the following objectives:

1) Detecting altitudinal boundaries of tree species distributions in order to

    - analyse species-specific patterns and abruptness of transitions of trees as well as recruit densities and growth parameters along the elevational gradient (study 1)
    - assess the relation between abrupt changes of growth parameters and temperature gradients along the altitudinal zoning of the ecotone and relate the results to the sensitivity to climate warming (study 1)

2) Analysing the relationships of adult and juvenile population densities of tree species with environmental conditions which change along the gradient from closed forest stands to the krummholz belt in order to

    - identify crucial site factors for the high competitiveness of *Rhododendron campanulatum* in forming a dense krummholz belt above the treeline (study 2)
    - assess the susceptibility of these variables to climate change and derive implications for the responsiveness of Himalayan krummholz treelines (study 2)

3) Analysing the relations of *Abies spectabilis* radial growth to climate variables on the basis of over one century of gridded climate data in order to

    - evaluate the sensitivity of *Abies spectabilis* tree growth to climate change (study 3)
    - investigate the temporal stability of tree growth-climate relationships (study 3)

3 Material and Methods

3.1 Study area

We conducted the studies on the north-facing slope of the Rolwaling Valley (27°52' N; 86°25' E), located in Dolakha District, east-central Nepal, adjacent to the border of Tibet Autonomous Region (Figure 3). The Rolwaling Valley is part of the Gaurishankar Conservation Area, established in 2010 (Bhusal 2012).

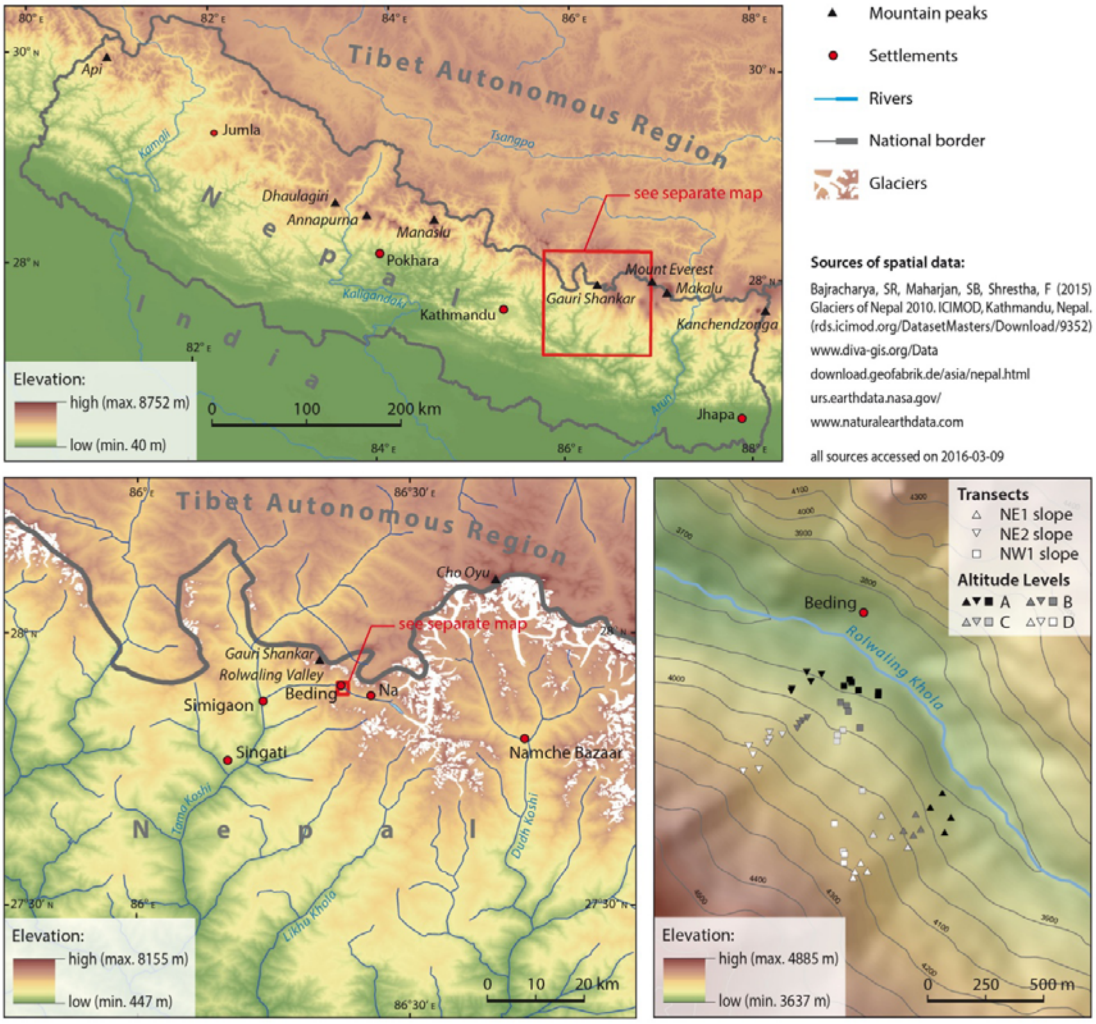

Figure 3. Location of the study area indicating investigated slopes and study sites (map preparation support by Kathryn Leve and Claus Carstens).

The climate of this area is continental, with dry and cold winter conditions. It is specifically characterised by the monsoon season, which spans from June to September (Böhner et al. 2015). The warming trend of the study area corresponds to general Himalayan trends (Gerlitz et al. 2014; cf. section 1.2). Soils in the treeline ecotone are classified as podzols (Müller et al. 2016a). The climate of the study site is considered temperate, with a dry winter and a warm summer (Köppen-Geiger Cwb) (Karki et al. 2016). The seasons are usually defined as winter (December to February), pre-monsoon/spring (March to May), monsoon (June to September) and post-monsoon (October to November) (Karki et al. 2017b). Precipitation during monsoon season accounts for approximately 80% of the total annual precipitation. The pre-monsoon season is a dry period with high solar insolation, maximum temperatures, little precipitation and low available soil water capacity (Figure 4) (Müller et al. 2016a; Karki et al. 2017a).

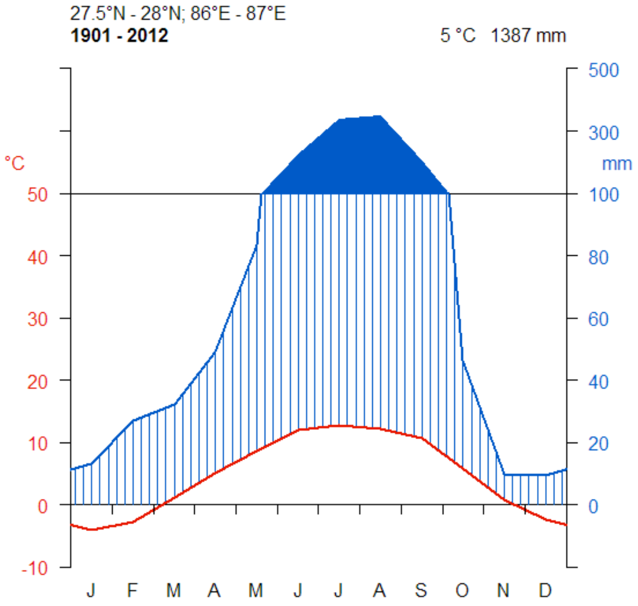

Figure 4. Climate chart of gridded climate data (CRU TS 4.0) (Harris et al. 2014) covering the study area, which were also used for tree growth-climate correlations (study 3) (diagram produced with R package climatol, Guijarro 2016).

The study area has a remote location which lacks a connection to the road network and entails a three-day walking distance. In addition, it contains a small human population, and the recurring Buddhist theme of a sacred hidden valley has protected plants and animals in Rolwaling to a certain extent (Baumgartner 2015). Consequently, the Rolwaling treeline at the north-facing slope exhibits a near-natural state and represents a climatic treeline. The study slopes evidence no signs of fire or grazing by cattle. Wood cutting has been negligible, as concluded from the mapping of stumps in the course of this thesis (study 1). The Rolwaling River separates the uninhabited north-facing study slope from the sparsely populated southern-facing slope, where human impact is likewise low. Thus, given that land-use effects have disturbed most Himalayan treeline sites (Schickhoff et al. 2015; Schickhoff et al. 2016a), the study slopes can provide a unique research opportunity to detect a climate change signal when assessing treeline dynamics.

The studied TREELINE site comprises three north-facing slopes, which are named NE1, NE2 (both northeast exposure) and NW (northwest exposure) according to their predominant exposition. The study site was subdivided into these three slope sectors. Each sampled slope sector covers the entire treeline ecotone from upper subalpine closed forests (upper limits of tall and upright *Acer caudatum*, *Abies spectabilis* and *Betula utilis*) via a dense *Rhododendron campanulatum* krummholz belt to alpine dwarf shrub heaths with small and stunted tree species individuals (Figures 5 and 6).

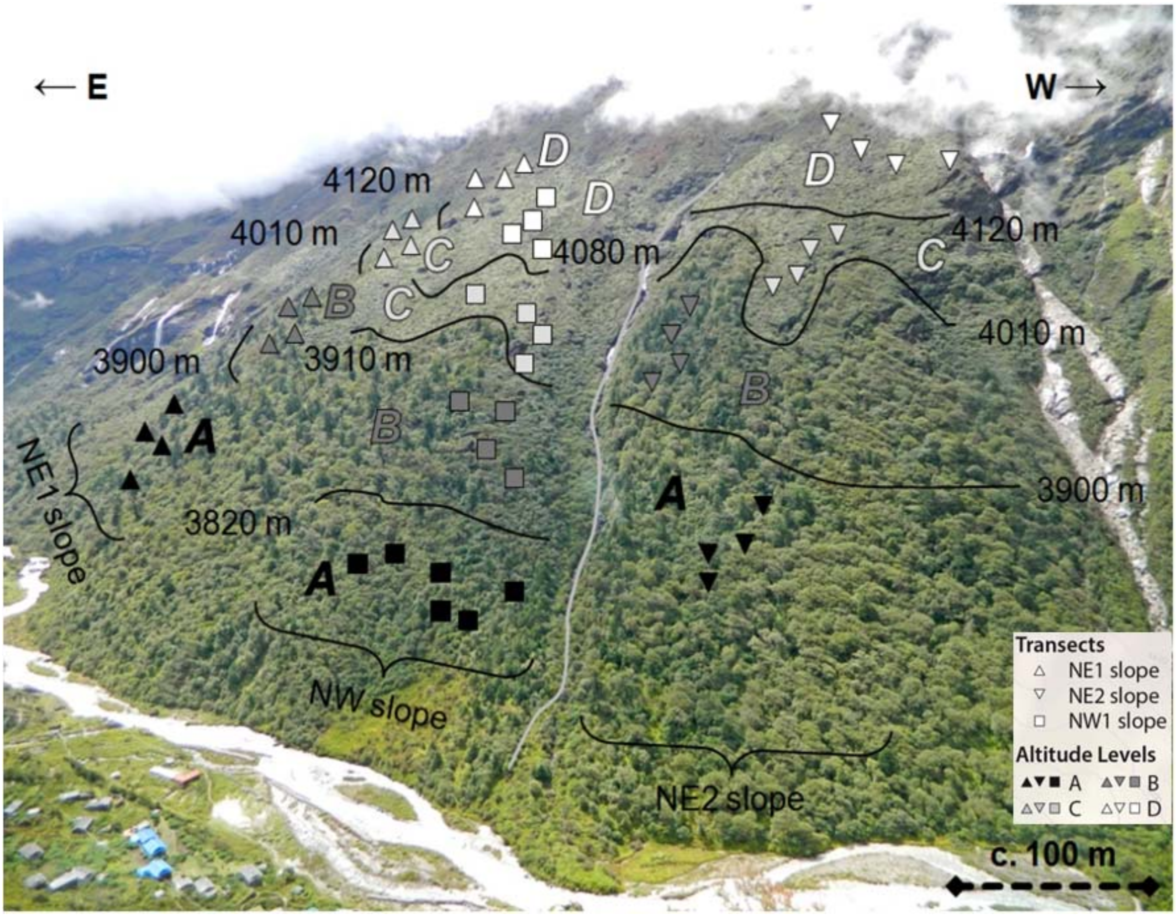

Figure 5. Stratification of the study area by elevation and aspect (NE, NW) and approximate location of plots; zones A and B represent the lower and upper sections of the upper subalpine forest, C labels the krummholz belt and D indicates the alpine dwarf shrub heath (18 September 2014).

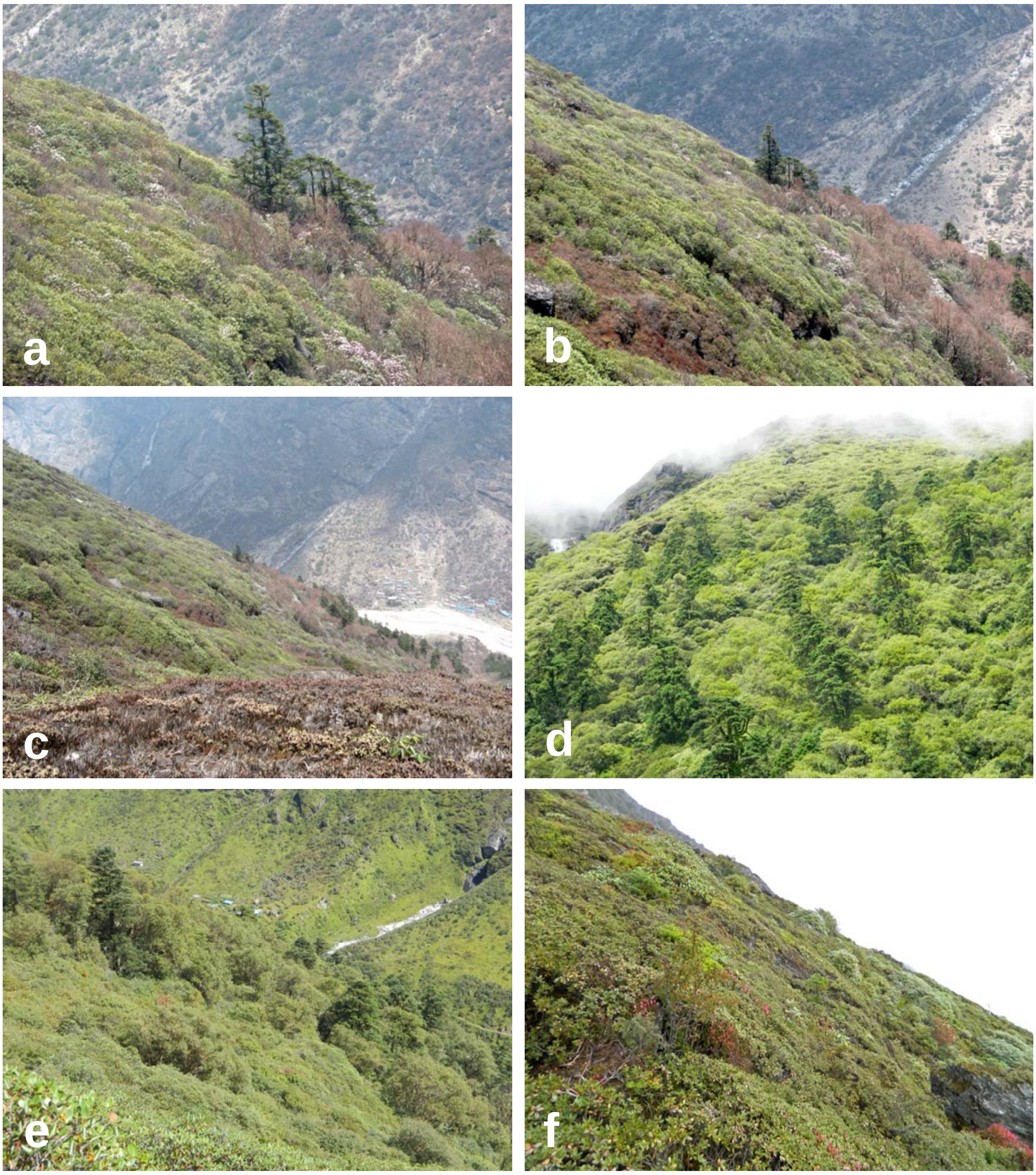

Figure 6. Transition from closed forest to alpine dwarf shrub heath: (a) uppermost stand of *Abies spectabilis* at NE slope (approximately 4000 m a.sl.); (b) *Rhododendron campanulatum* krummholz (in white-pink bloom) and transition to upper subalpine *Abies-Betula* forest; (c) elevational range from zones A to D with transition from upper subalpine forest to krummholz belt in focus; (d) mixed forest stand of upper subalpine forest and abrupt transition to *Rhododendron campanulatum* krummholz belt; (e) *Rhododendron campanulatum* krummholz (front) and abrupt transition to upper subalpine *Abies-Betula* forest; (f) alpine dwarf shrub heath with *Rhododendron campanulatum* and *Rhododendron* dwarf shrub species and single *Sorbus microphylla* individuals (a-c: 5 May 2013; d: 23 July 2013; e-f: 17 September 2014).

3.2 Data collection

Vegetation

We stratified the slopes according to the altitudinal zonation of tree species composition and stand structure in elevational zones A (lower section of upper subalpine closed forests) to D (alpine dwarf shrub heaths, cf. Figures 5 & 6). In total, 50 square plots of 20 m × 20 m were randomly selected and sampled. Sampling was conducted from April to September 2013 and in August 2014. We determined tree species based on Press et al. (2000) and Watson et al. (2011). We measured the diameter at breast height (dbh) at 130 cm above ground level as well as the height, crown height and crown width of all vital tree species individuals with dbh ≥ 7 cm in accordance with standard forest inventory procedures (Van Laar and Akça 2007). We identified and counted individuals of tree species with dbh <7 cm and assigned them to height classes. We termed individuals with dbh ≥ 7 cm '**adult trees**', whilst smaller ones were categorised as '**juvenile individuals**' or '**recruits**'. In order to analyse tree growth-climate relationships, we followed standard procedures for the collection, preparation and measurement of *Abies spectabilis* tree-ring samples. The cross-dating of the tree-ring width (TRW) chronology, removal of age-related growth trends and assessment of chronology quality followed standard methods and used inter alia the programs CDendro (Larsson 2016), Cofecha (Holmes 1983) and Arstan (Cook 1985).

Soil, topography and climate

All plots were sampled for Of, Ah and Ae soil horizons. Soil samples were analysed via standard methods at the laboratory of Soil Science and Geoecology of the University of Tübingen (see Müller et al. 2016b for details). To capture the variation in topography between and within plots, several topographic variables were determined. In addition to soil temperature and soil moisture (see Müller et al. 2016b), we recorded air temperatures from April 2013 to June 2014 through mobile climate stations which were installed in the lower and upper part of the ecotone (Gerlitz et al. 2016).

To assess tree growth-climate relationships, we consulted climate data from the Climatic Research Unit (CRU) TS4.00 dataset (Harris et al. 2014; University Of East Anglia Climatic Research Unit et al. 2017). Specifically, we used the mean, maximum, minimum temperature and precipitation for the period 1901–2012. In addition, we deployed the drought indices of the one-month and three-month Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010), which were based on CRU data.

3.3 Data analyses

Population structures, regeneration patterns and abruptness of transitions

Stem numbers and stand densities were calculated per hectare. To visualise population structures and species compositions, we created bar graphs and histograms. We also computed the regeneration index (RI) according to Schickhoff (2002) for all species and species specific to each elevational zone. In contrast to the mean height values of recruits, the RI includes information of abundance and combines it with the height of recruits. The RI provides information on growth performance and the success of establishment beyond the seedling stage.

To describe and analyse variation in stand structures and characterise abrupt or smooth and gradual transition patterns along the ecotone, we applied an approach based on Wiegand et al. (2006) and Batllori and Gutiérrez (2008) to calculate the abruptness of transitions between elevational subsequent zones. The abruptness of the transitions was calculated as the difference between the scaled values of successive zones (lower zone minus upper zone; scaled range [0,1]):

$$abruptness_{lh} = \frac{\bar{x}_{arith(l)} - min_l}{max_l - min_l} - \frac{\bar{x}_{arith(h)} - min_h}{max_h - min_h}$$

where l and h are the altitudinal zones (A,B,C,D). A lower zone (e.g., A) is denoted as l, and a successive higher zone (e.g., B) is denoted as h. A positive abruptness indicates a transition of decreasing values of a stand parameter with elevation as it is generally expected in a treeline ecotone, whilst a negative abruptness conveys an increasing value with elevation. The abruptness was calculated for the height and density of trees and recruits and the dbh of trees. Total abruptness was gained as the arithmetic mean abruptness of all parameters under consideration at a specific transition. We computed both the abruptness values for all individuals of the stands and the species-wise values. In order to compare to abruptness patterns of tree species, we calculated the abruptness of annual and seasonal soil temperatures.

Population density-environment relationships

We analysed population density-environment relationships through redundancy analyses (RDA) with backward elimination of explanatory variables as well as through variation partitioning (Legendre and Legendre 2012). To preselect important variables and apply variation partitioning, the explanatory dataset was split into three groups: soil, topography and climate variables. To avoid high multicollinearity, we removed within-group correlations of

$|r| > 0.7$ (Spearman, $p<0.05$, adjusted according to Benjamini and Hochberg 1995) by excluding variables.

Missing values in variables (mostly soil temperature and soil moisture) would have restricted the multivariate analyses to a minor part of the entire dataset. Hence, we applied multivariate imputation by chained equations (MICE; Van Buuren 2012) based on a random forest classification (Doove et al. 2014) to estimate the missing values based on the relationships between the variables.

Tree growth-climate relationships

To analyse the relationships between the standardised TRW chronologies and the climate variables, we calculated Pearson's correlation coefficients and confidence intervals through a stationary bootstrapped correlation function with optimal block-length selection (Politis and Romano 1994; Politis and White 2004) at a level of significance of $p < 0.05$. The correlations were calculated for the period of climate data availability, namely 1902–2012.

We computed static correlations of TRW with mean, mean minimum and mean maximum temperatures as well as precipitation sums and SPEI for single months and seasons. To examine the stability of correlations for the analysed period, we calculated 31-year moving window correlations (Biondi and Waikul 2004) with a one-year offset between consecutive windows. Whilst moving windows are suitable for detecting the presence of stable periods over a range of time, evolutionary interval correlations reveal the lengths of specific periods (Biondi and Waikul 2004). Thus, we used backward evolving window correlations to determine the lengths of most recent periods with stable correlations.

Unless stated otherwise, all computations and figure plotting were carried out through the functions of several packages (see studies 1-3 for package names) in the most recent versions of the program R (R Core Team 2018).

4 Main Results and Discussion

4.1 Altitudinal boundaries of tree species distributions and regeneration (study 1)

Results (study 1)

In general, the upper subalpine forests under investigation were primarily composed of *Betula utilis* and *Abies spectabilis*, with *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer. *Acer caudatum* and *Prunus rufa* occasionally occurred as companions. The tree species composition differed between the lower (zone A) and upper (zone B) elevational sections of the upper subalpine forest. Specifically, the density of *Abies spectabilis* trees in zone B was smaller than in zone A, whilst the density of *Betula utilis* increased with elevation. The most distinct difference between the subalpine forest zones was the distinctly higher proportion of *Rhododendron campanulatum* individuals in zone B compared to zone A (Figure 7). Closed forests gave way to a dense and nearly impenetrable *Rhododendron campanulatum* krummholz belt at approximately 3910 m a.s.l. (NW slope) and 4010 m a.s.l. (NE slopes). There, *Rhododendron campanulatum* dominated the tree species composition and was accompanied by few *Sorbus microphylla* individuals. The *Rhododendron* belt turned into alpine *Rhododendron* sp. dwarf shrub heaths at approximately 4080 m a.s.l. (NW slope) and 4120 m a.s.l (NE slopes). These heaths were mainly composed of *Rhododendron anthopogon*, *Rhododendron lepidotum*, and *Rhododendron setosum* (Figure 6f).

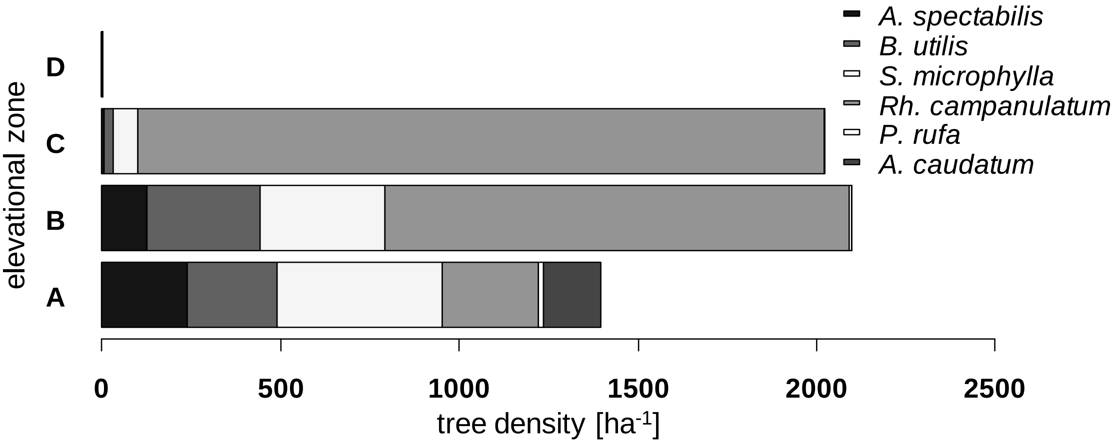

Figure 7. Tree species population density of adult individuals (≥ 7 cm dbh) across the elevational gradient.

The recruit density pattern (Figure 8) mostly resembles that of individuals with dbh ≥7 cm. The occurrence of *Juniperus recurva*, a species that can grow to tree size, remarkably differed between recruits and adults. We found no individual with dbh ≥ 7 cm (adults) whilst *Junipe-*

rus recurva recruits were existent in the subalpine forest and the krummholz belt. *Rhododendron campanulatum* and *Sorbus microphylla* seedlings occurred in rather high abundance in the alpine dwarf shrub heath; however, no tree-sized individual of these species was detected there.

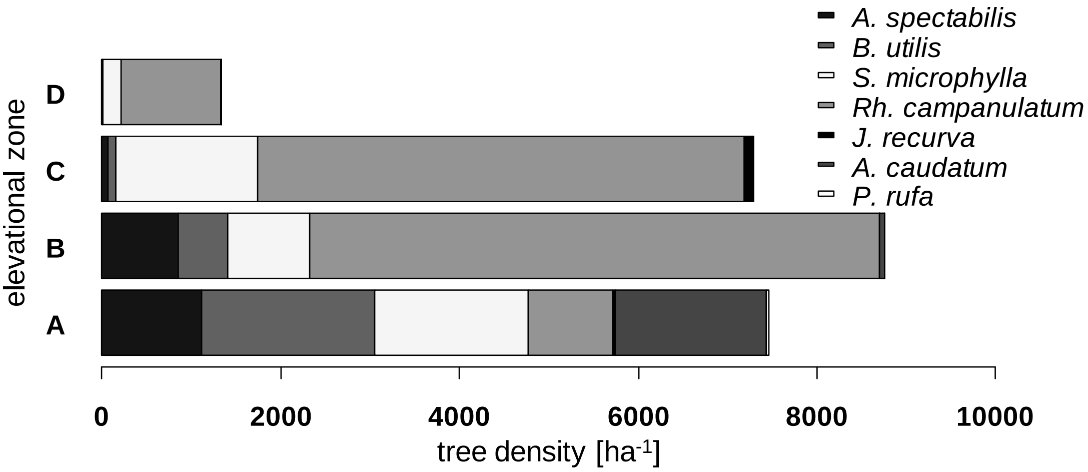

Figure 8. Tree species population density of juvenile individuals (< 7 cm dbh, 'recruits') across the elevational gradient.

Different species seemed to perform better at different altitudinal positions depending on the regeneration indicator of focus. While the mean height reflected whether the population of a species could reach a specific mean sprout height, the RI provided information on the actual performance of the recruits of a species by incorporating their abundance. A comparison of values of both indicators clearly revealed that the height-abundance patterns of the various species were complex and non-uniform in nature.

The krummholz belt contained the uppermost stunted individuals of *Abies spectabilis* and *Betula utilis* with dbh ≥ 7 cm (adults). The uppermost trees with true tree habitus (upright stem with crown) grew in the upper section of the upper subalpine forest (zone B). Thus, the treeline coincided with the transition from subalpine forest to krummholz belt, as only a few outpost-treeline trees occurred in the krummholz belt (in this instance, the term 'treeline' does not refer to the entire transition zone). In addition, we identified several tree species lines inside the ecotone.

In general, certain values of stand parameters, such as dbh, tree height and tree density, decreased with elevation. Along this gradient, the all-species degree of abruptness of these parameters increased at the transitions between single zones. The abruptness of all-species recruit density exhibited the same trend, whilst the abruptness in terms of recruit height classes was sharpest at the transition A to B within the upper subalpine forest, lowest at the transition from subalpine forest to krummholz belt and intermediate at the transition from the krummholz belt to the alpine vegetation. This pattern differed between single species. The density of *Betula utilis*, *Sorbus microphylla* and, to a certain extent, *Abies spectabilis* trees decreased abruptly at the transition from forest to krummholz belt (B-C), whilst the density of *Rhododendron campanulatum* increased intermediately from forest to krummholz belt (B-C) and dropped abruptly from the maximum to the smallest density at the transition from krummholz to alpine dwarf shrub heath (C-D) (Figure 9). The abruptness of the transitions with regard to dbh and tree height did not resemble density abruptness for all species or per species. Annual mean soil temperature dropped most abruptly at the transition from closed forest to krummholz belt (Figure 9). The most abrupt decrease of winter and spring soil temperature occurred at the same transition while the decrease was most abrupt at the transition AB in summer and autumn.

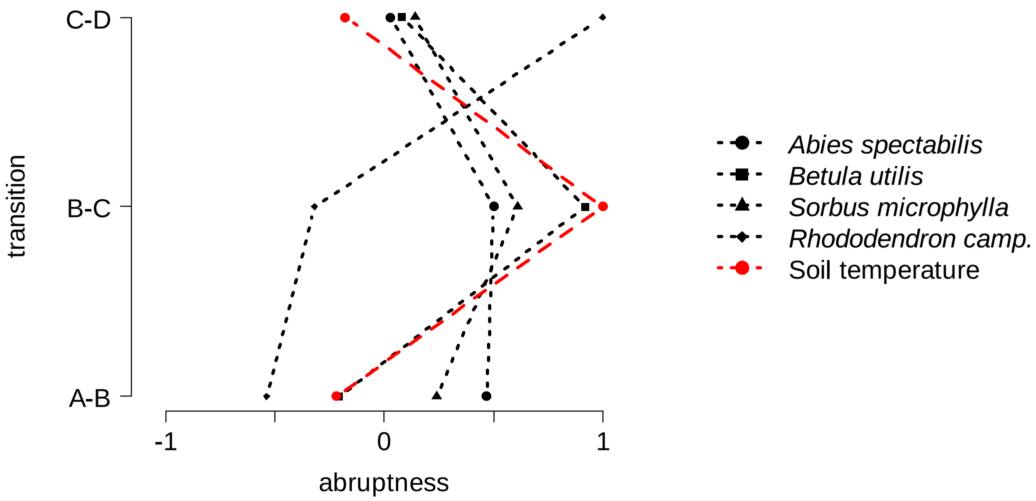

Figure 9. Tree species density and annual mean soil temperature: abruptness of transitions from lower to upper part of subalpine forest (A-B), from upper part of subalpine forest to krummholz belt (B-C) and from krummholz belt to alpine dwarf shrub heath (C-D). Population densities and soil temperature were generalized across all investigated slopes.

Discussion (study 1)

In general, the tree species composition and altitudinal position of the Rolwaling treeline ecotone coincides with previous findings for north-facing slopes in central and east Nepal (Schickhoff 2005; Miehe et al. 2015). Changes in tree species composition along the elevational gradient are apparent also in the phytosociological communities which comprise all vegetation layers as a whole. Whilst the forest stands were classified into two communities, the species-poor *Boschniakia himalaica-Rhododendron campanulatum* community represents the krummholz belt. The alpine dwarf shrub heaths were assigned to two communities of the class *Dasiphora arbuscula-Rhododendron anthopogon* (Bürzle et al. 2017). From the wide and dense *Rhododendron campanulatum* thicket in particular, it is evident that the Rolwaling treeline must be physiognomically assigned to treelines with a krummholz belt (Holtmeier 2009).

Species-specific transition patterns (in terms of diameter at breast height, height, tree and recruit densities) and varying degrees of abruptness of these transitions occurred across the treeline ecotone, which resulted in a complex stand structure. High standard deviations from mean values of the growth and density variables indicated heterogeneous patterns that differed according to slope, species and altitudinal zone. The transiton from the uppermost part of the subalpine forest (zone B) to the krummholz belt (zone C) presented the most abrupt change in *Abies spectabilis*, *Betula utilis* and *Sorbus microphylla* tree densities along the altitudinal gradient (Figure 9). This abrupt change in species composition coincided with the most abrupt changes in annual, winter and spring seasonal mean soil temperature at that transition. Abrupt microenvironmental changes have been associated with abrupt treelines (Harsch and Bader 2011; Cieraad and McGlone 2014). Although krummholz treelines represent a definite treeline form, they can still feature abrupt treeline characteristics.

Sorbus microphylla occurred with high continuity, and its density-diameter distribution implied an established population in the krummholz belt (zone C), which co-exists alongside the *Rhododendron campanulatum* population. Physiognomic transitions, treeline position and spatial regeneration patterns are associated with soil temperatures rather than lapse-rate air temperatures. Thus, the Rolwaling treeline is potentially susceptible to climate change, and treeline tree species might migrate upslope in the future, with *Sorbus microphylla* presenting particularly high dynamics. Established recruit populations in the alpine dwarf shrub heath convey the potential of *Rhododendron campanulatum* and *Sorbus microphylla* to sprout and survive at this high altitude in at least their early life stages. The results of our regeneration studies have yielded reverse J-shaped density-diameter distributions and indicate intense, sustainable regeneration and, thus, a potential for upward migrations. Such findings are in line with other studies of treelines in Nepal (Ghimire and Lekhak 2007; Shrestha et al. 2007; Gaire et al. 2010; Ghimire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Gaire et al. 2014). A comparative discussion of the findings is complicated by the deficiency of research on treeline ecotones which comprise a krummholz belt with a similar dominance and spatial extent to our study area. Moreover, human impact has already disturbed most treeline ecotones in Nepal and consequently altered population structures. The dense krummholz belt effectively controls the upslope migration of subalpine forest tree species *Abies spectabilis* and *Betula utilis*. Even above the krummholz belt, the dense alpine dwarf shrub heath vegetation might hinder tree species because the competitive abilities of the shrub community could affect tree establishment (Körner 2012a; Chhetri and Cairns 2015; Schickhoff et al. 2016a). The treeline is currently rather stable and is thus in line with the conclusions of Harsch and Bader (2011) regarding krummholz treelines.

4.2 Population density-environment relationships (study 2)

Results (study 2)

Both ordinations for adult and juvenile trees support *Rhododendron campanulatum* to be the dominant tree species at topographically finely structured and colder habitats with reduced nitrogen availability. This combination of site properties in the krummholz belt and alpine dwarf shrub heath has resulted in a high competitiveness of *Rhododendron campanulatum* that diminished in more nutrient-rich and warmer sites of the upper subalpine forest where other tree species have gained predominance.

Adult trees

Seventeen selected environmental variables explained a total of 77% of the variation in adult tree species density. The first RDA axis accounted for 58% of the variance, and the first and second axes together explained 68% of the variance. The ordination reflects a clear separation between plots of the *Rhododendron campanulatum* krummholz belt (zone C), a mixed zone of A and B groups (sections of upper subalpine forest) and a pure zone of the A group (Figure 10). These three groups were arranged mainly along the first RDA axis. In general, the plots spread only slightly along the second RDA axis. Plots of the krummholz belt especially formed a tight cluster due to the strong dominance of *Rhododendron campanulatum*. In contrast, the group that contained plots of the lower section of the upper subalpine forest (zone A) with a higher number of tree species exhibited variation along the second axis.

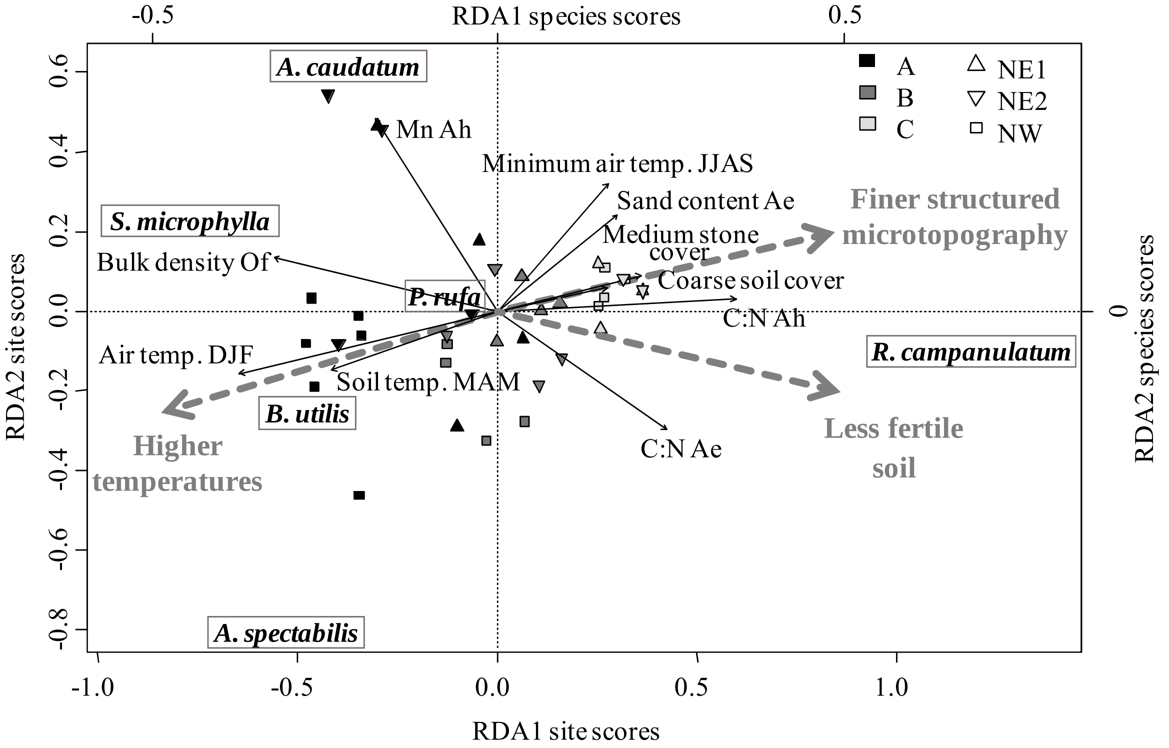

Figure 10. Ordination diagram of RDA analysis for adult tree density: Vector directions show relation to environmental variables, vector lengths show their importance. Only the most important environmental variables with a biplot score (axis one, axis two or both) ≥ 0.3 are depicted. The first two constrained RDA axes here explain 68% of the variation in adult tree species density. Dashed arrows signify the appropriate direction of the summarised main gradients, with the length not true to scale.

Most environmental variables were correlated with RDA axis one rather than with axis two (Figure 10). Thereby, they formed a complex gradient along the first axis which can be divided roughly into three non-hierarchical groups. The first group refers to differences in microtopographic groundcover, namely the size and shape of rocks. *Rhododendron campanulatum* was associated with plots that contain coarse soil cover and large stones, i.e. with a more finely structured microtopography, compared to sites dominated by other tree species. The second group concerns a temperature gradient that was expressed in lower soil and air temperatures in plots with a high density of *Rhododendron campanulatum* and higher temperatures at other plots. The third group regards differences in soil texture and soil fertility as indicated by manganese content and carbon-to-nitrogen (C:N) ratios of Ah and Ae horizons. The C:N ratios of elevational zones A (closed forest) and C (krummholz belt) were significantly different. Despite the strong gradient in the ordination, there were no significant disparities in manganese content between the elevational zones. Sites of the krummholz belt and *Rhododendron campanulatum* were associated with less nitrogen mineralisation and increased nitrogen immobilisation relative to other sites and species. Furthermore, they contained fewer nutrient-fixing clay and silt particles. This trend generally indicated less fertile soil conditions at krummholz belt plots that were dominated by adult *Rhododendron campanulatum* trees as well as more fertile conditions at plots of the upper subalpine forest in which other tree species were more abundant.

Recruits

Fourteen selected environmental variables explained a total of 66% of the variation in juvenile tree species density. The first RDA axis accounted for 51% of the variation, and the first and second axes explained a total of 60% of the variance. The ordination of juvenile individuals revealed a clear separation into a group of plots from elevational zone A (lower section of upper subalpine forest), a group from zone B (upper section of upper subalpine forest) and a mixed group of plots from the krummholz belt and alpine dwarf shrub heath (zones C and D) (Figure 11). The groups were separated from each other along the first RDA axis. Compared to the adult tree ordination (Figure 11), the sites were distributed along the second RDA axis to a higher degree. Plots from slope NE1 tended to separate from the plots of other slopes, especially in case of those from the krummholz belt and alpine dwarf shrub heath, because of differences in juvenile tree species composition between the slopes.

The differentiations in groups of krummholz belt and alpine heath sites versus other sites and of *Rhododendron campanulatum* versus other species relate to differences in nitrogen availability (C:N ratios of the Ah and Ae horizons), the manganese content of the Ah horizon, the calcium content of the Ae horizon, the dissimilarity of surface structure within and between plots, and differences in mean and minimum air temperatures. *Rhododendron campanulatum* and *Sorbus microphylla* had comparable conditions in terms of temperature, manganese content and microrelief dissimilarity within plots.

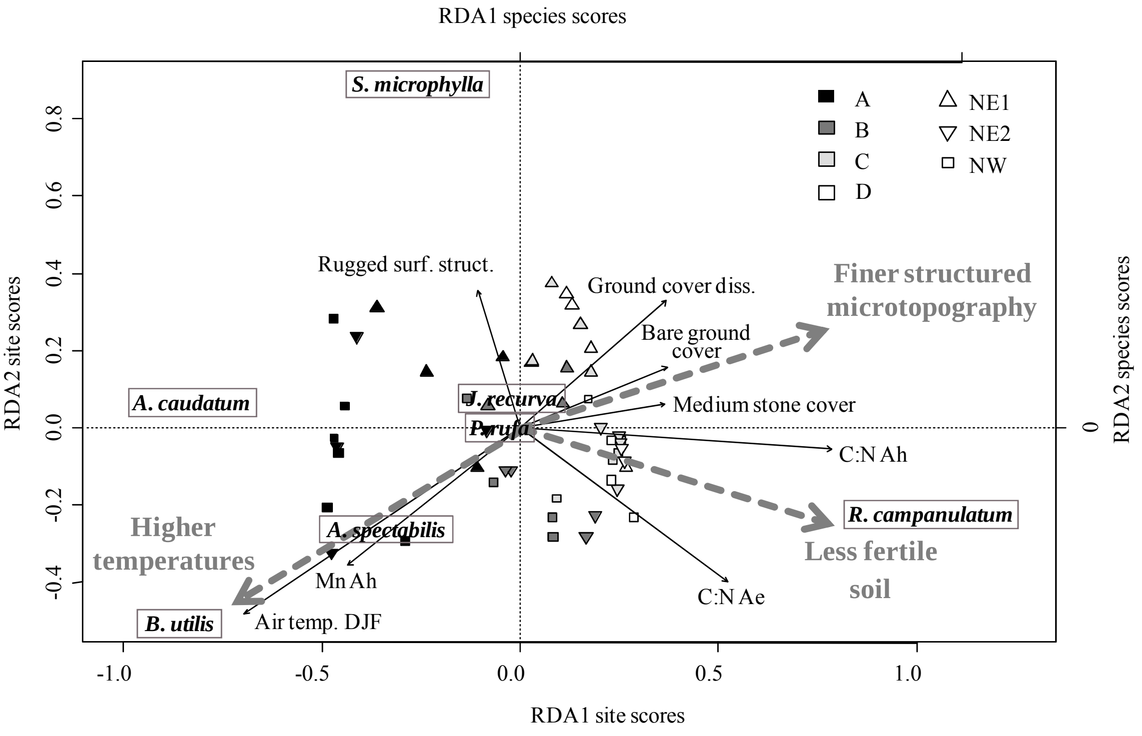

Figure 11. Ordination diagram of RDA analysis for juvenile tree species density: Vector directions show relation to environmental variables, vector lengths show their importance. Only the most important environmental variables with a biplot score (axis one, axis two or both) ≥ 0.3 are depicted. The first two constrained RDA axes included here explain 55% of the variation in juvenile tree species density. Dashed arrows signify the appropriate direction of the summarised main gradients, with the length not true to scale. (rugged surf. struct. = surface structure category 'rugged'; ground cover diss. = ground cover dissimilarity).

In contrast to the adult tree ordination, sites and species were scattered to a higher degree in the ordination of juvenile individuals. Compared to adult tree ordination, the juvenile ordination was influenced by more complex combinations of variables to gradients. However, the main factors were likewise related to nutrient availability, temperature and microtopography.

Variance partitioning results

By means of variation partitioning, the explained variability was separated into amounts which were accounted for exclusively by edaphic, topographic or climatic explanatory data sets as well as into amounts that were explained jointly by two or three of these explanatory data sets. In the case of adult trees, the edaphic group of variables was the most important independent predictor of species distribution (28% explained variability), whilst climatic and topographic variation were of secondary (7%) and tertiary importance (6%; Figure 12a), respectively. The analyses revealed that 25% of the shared variation of adult tree density was explained by soil variables, climate variables or both (Figure 12a).

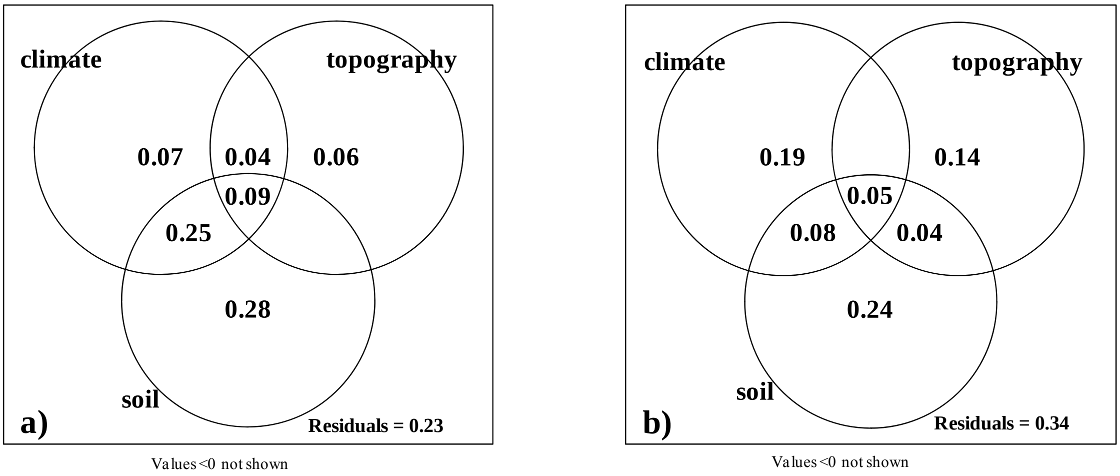

Figure 12. Variation partitioning of **(a)** adult tree density using the matrices of soil variables, climate variables and topographic variables and **(b)** juvenile density using the matrices of soil variables, climate variables and topographic variables. The numbers indicate the percentage of total explained variability, explained exclusively or jointly by the variable matrices.

As in adult tree density, the edaphic group of variables in the case of juvenile tree density was the key independent predictor of species distribution (24% explained variability), whilst climatic and topographic variation were of secondary (19%) and tertiary importance (14%; Figure 12b), respectively. The analyses highlighted that soil, climate or topographic variables, or any combination of these, accounted for small amounts of the shared variation of juvenile tree density. In comparison to the partitioning of variation of the adult tree density, the partitioning of juvenile stand density variation revealed a more balanced distribution of explained variance per variable group (cf. Figures 12). Although topography was of minor importance for adult trees, its share in accounting for the total variation of juvenile density is substantial.

Discussion (study 2)

The results support that species-specific variation in adult and juvenile stand density along the treeline ecotone depends, to varying extents, on edaphic, climatic and topographic variables. Variables with a strong influence on the ordinations reflect significant differences in mean values between zones with differing densities of *Rhododendron campanulatum*. Low temperature and poor nutrient availability characterise the ecological niche that *Rhododendron campanulatum* occupies. Juvenile population density evidences a stronger dependence on the climatic variable of temperature. Microtopographic variables have a more significant role compared to adult tree density. Variation partitioning indicated that soil variables, and nutrient variables in particular, significantly contributed to the total explained variation of adult tree density. Likewise, soil temperature, nitrogen supply and availability, and soil moisture differentiated the species composition of phytosociological communities throughout the Rolwaling treeline ecotone (Bürzle et al. 2017). In addition, Bürzle et al. (2018) have found species-specific microhabitat preferences for the establishment of seedlings and reported that *Abies spectabilis* seedlings grew on ground that was covered mainly by litter, whilst *Betula utilis* and *Rhododendron campanulatum* were established on bryophyte mats. Thus, the role of temperature for treeline tree population density and species distributions has to be relativised in accordance with the results of Weiss et al. (2015), Müller et al. (2016a; 2016b) and others. Differences in temperature, surface structure and within-plot ground cover influence the occurrence of juvenile individuals to a larger extent compared to adult tree density, which supports previous assumptions of differences between juvenile and adult tree growth (e.g., Smith et al. 2003; Wieser et al. 2014).

Interaction of edaphic, climatic and topographic variable components and response to climate warming

Positive feedback processes (Scheffer et al. 2001; Kim and Lee 2015) most likely maintained the *Rhododendron* krummholz belt. Such processes result from slowly decomposing *Rhododendron* litter, which causes low nitrogen mineralisation rates and nitrogen availability (Maithani et al. 1998), as well as from high amounts of polyphenol contents of *Rhododendron* leaves, which enhances nitrate and ammonium immobilisation (Figure 13) (Northup et al. 1995; DeLuca et al. 2002) that reduces nitrogen availability. In addition, the Ah horizon in the krummholz belt contains a small amount of manganese. Most likely, reduced availability of both nitrogen and manganese at the elevated sites leads to lowered competitive strength of tree species. As an exception, the *Rhododendron* species and ericaceous perennials in general are low-nutrient users that grow in soils that are poor in most essential elements and consequently unsuitable to other species; in fact, they are even favoured by poor soil conditions (Cox 1990; Ristvey et al. 2007). The high root-to-shoot ratio of *Rhododendron campanulatum* and its evergreen nature enhance these competitive advantages by resulting in nutrient storage and sources, increased photosynthetic capacity in spring and some supposed allelopathic effects of polyphenol-rich *Rhododendron* litter. In consequence of such positive feedback processes, the treeline is not necessarily in equlibrium with climate change. The modification of the krummholz belt by the *Rhododendron campanulatum* dominated vegetation constrains the potential climate-driven establishment of *Abies spectabilis* and *Betula utilis* seedlings and the subsequent migration of the treeline. The gradual changes in climate do not entail gradual linear changes in vegetation. Such non-linearity leads to delays in response to climate change and potential abrupt switches once a certain threshold e.g., of soil temperature is crossed (Figure 13). The lagged response limits the usefulness of the Rolwaling treeline as indicator for climate change. The positive feedback processes control the spatial pattern and temporal dynamics of the treeline ecotone which is in consequence an alternative stable state ecosystem (Scheffer et al. 2001; Kim and Lee 2015).

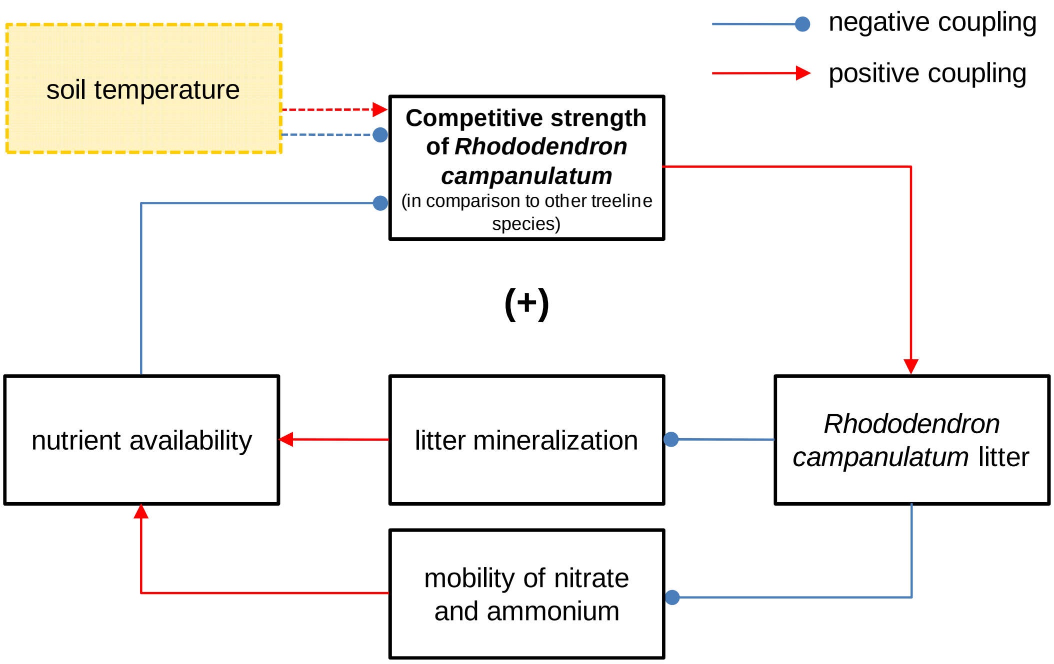

Figure 13. Potential positive feedback process that maintains the *Rhododendron campanulatum* krummholz belt. Positive feedback loops have an even number of negative couplings. They tend to have unstable equilibrium states (Kump et al. 2004). Thus, a forcing such as a soil temperature increase above a certain threshold might carry the system to a different equilibrium state. The temperature increase might take growth conditions in the alpine zone closer to *Rhododendron campanulatum*'s optimum and amplify its competitive strength (positive temperature coupling). In consequence, *Rhododendron campanulatum* might grow better and to tree size at what is currently the alpine dwarf shrub heath. Another, in near future rather unlikely option for an equilibrium state might be characterised by enhanced recruitment and growth of subalpine tree species to tree size in the krummholz belt leading to an upward shift of the treeline (negative temperature coupling).

Even if climate warming will change the competitive patterns in the treeline ecotone and create new niches the general constraints of low temperatures and low nutrient availability most likely remain. In view of their generally intense regeneration and comparatively high mean annual temperatures (Müller et al. 2016a; Müller et al. 2016b), *Abies spectabilis* and *Betula utilis* could potentially establish populations above the krummholz belt. However, cold, nutrient-poor conditions will probably continue to be more beneficial for *Rhododendron campanulatum* and *Rhododendron* dwarf shrub species in the krummholz belt and alpine dwarf shrub zone, regardless of slight increases in mean temperatures. In opposite to the subalpine forest species, the *Rhododendron campanulatum* belt might migrate upwards, into the alpine dwarf shrub zone. We did not investigate migration potentials and species-specific seed-dispersal strategies in depth. The results of our analyses of tree population spatial patterns and our empirical as well as general model-based findings (Müterthies 2002; Dullinger et al. 2004; Holtmeier and Broll 2010; Nathan et al. 2011; Martínez et al. 2012; Johnson et al. 2017) indicate a potential contribution to yet-unexplained variance.

Since the *Rhododendron campanulatum* population of the krummholz belt is firmly established and feedback mechanisms maintain its predominance, this thicket likely constitutes an insurmountable barrier for seedlings and saplings of *Betula utilis* and *Abies spectabilis* even under warmer conditions. It can be assumed that the small numbers of *Abies spectabilis* and *Betula utilis* individuals that were found in the krummholz belt and the alpine dwarf shrub heath are related to microtopographic features similarly to observed establishment patterns in Taiwanese *Abies* treelines (Greenwood et al. 2015). The few individuals of other tree species might consolidate towards established populations at locations above the contemporary krummholz belt position only in the long term. Persistent low nutrient availability and allelopathic effects will most likely prevent juvenile tree individuals from growing into mature, fruiting trees within or above the current krummholz belt. The *Rhododendron campanulatum* krummholz belt constitutes a bottleneck for the establishment of *Betula utilis* and *Abies spectabilis* individuals above the contemporary treeline. A substantial establishment in the dwarf shrub heaths above the krummholz belt is similarly unlikely, as comparable soil and environmental conditions prevail. However, the few *Abies spectabilis* and *Betula utilis* individuals in and above the krummholz belt illustrate a potential to survive in that area and reach tree dimensions.

The results suggest that the Rolwaling treeline will most likely remain at its present position during the coming decades. Additionally, the responsiveness of the Rolwaling treeline to climate warming will probably be rather low, as assumed for near-natural Himalayan treelines and krummholz treelines in general (Harsch and Bader 2011; Chhetri and Cairns 2015; Schickhoff et al. 2016a). However, the krummholz belt and the alpine dwarf shrub heath might change in terms of population structures and species composition in the mid- to long-term future if certain thresholds of e.g., temperature or nutrient availability are crossed.

4.3 Tree growth-climate relationships (study 3)

Results (study 3)

The collection and subsequent processing of TRW measurements yielded a chronology that represents the radial growth of *Abies spectablilis* back to 1748 (Figure 14). The results of the analyses of *Abies spectabilis* tree growth-climate relationships evidence a significantly unstable dendroclimatic signal over time. Climate-warming-induced moisture deficits during pre-monsoon seasons have become a major limiting factor for radial tree growth in recent decades. Previously, the dendroclimatic signal was weaker, which predominantly reflected a positive relationship between tree growth and summer temperature.

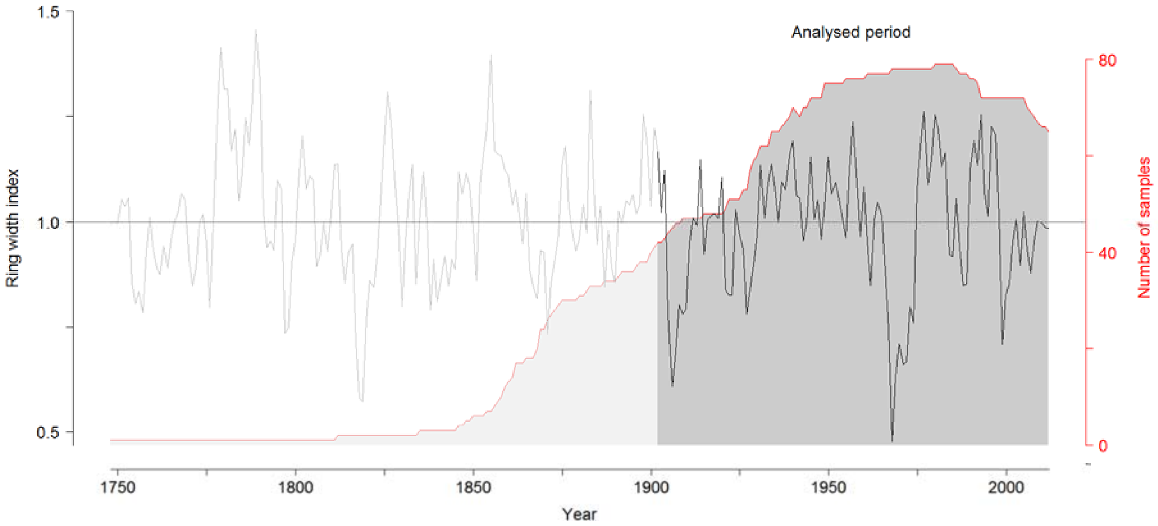

Figure 14. Tree-ring width standard chronology (black curve) and sample depth (red curve); darker section represents the part of the chronology that was used for tree growth-climate analyses.

For recent decades, the correlation analyses identified a significantly negative relationship between the radial growth and the mean, minimum and maximum temperatures for the current year's pre-monsoon season (March-May). Moreover, they detected significant negative correlations of mean and maximum temperatures during winter prior to the current growing season (December-February) (Figure 15). Precipitation sums and TRW reflected a significantly positive correlation during the current January and April. The current monsoon season (June-August) exhibited a significant negative correlation between radial growth and precipitation sum (Figure 15). Significantly positive correlations of TRW to one-month SPEI variables (Figure 15) emphasise pre-monsoon moisture sensitivity, which is in line with the relations of TRW to temperature and precipitation.

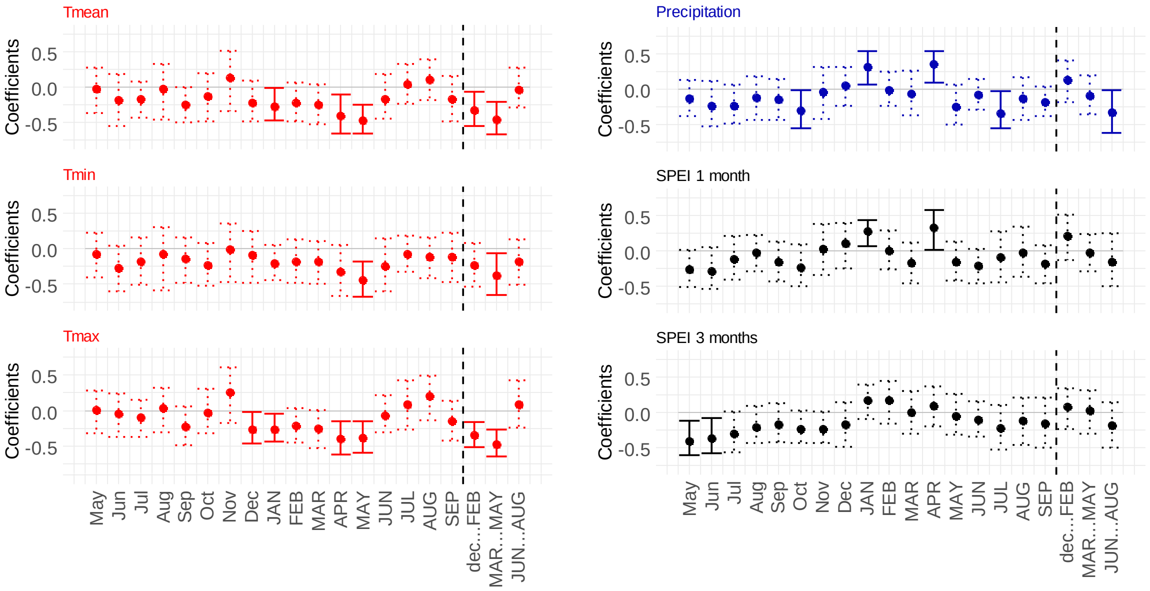

Figure 15. Static correlations (1972–2012) of the TRW chronology with temperature, precipitation and drought indices (SPEI) for current and previous year's months and current year seasons; solid bars indicate significant correlations ($p < 0.05$).

During the investigated period, i.e. the entire 20th century, the interdependence of TRW and climate variables alternated at least once from a positive to a negative correlation, or vice versa. Phases with significant correlations without these alternations did not exceed approximately 50 years, and most of the periods were distinctly shorter (cf. Figure 16). In summary, both TRW-temperature and TRW-precipitation moving windows exhibit a fragmented pattern of significant tree growth-climate relationships with long insignificant phases.

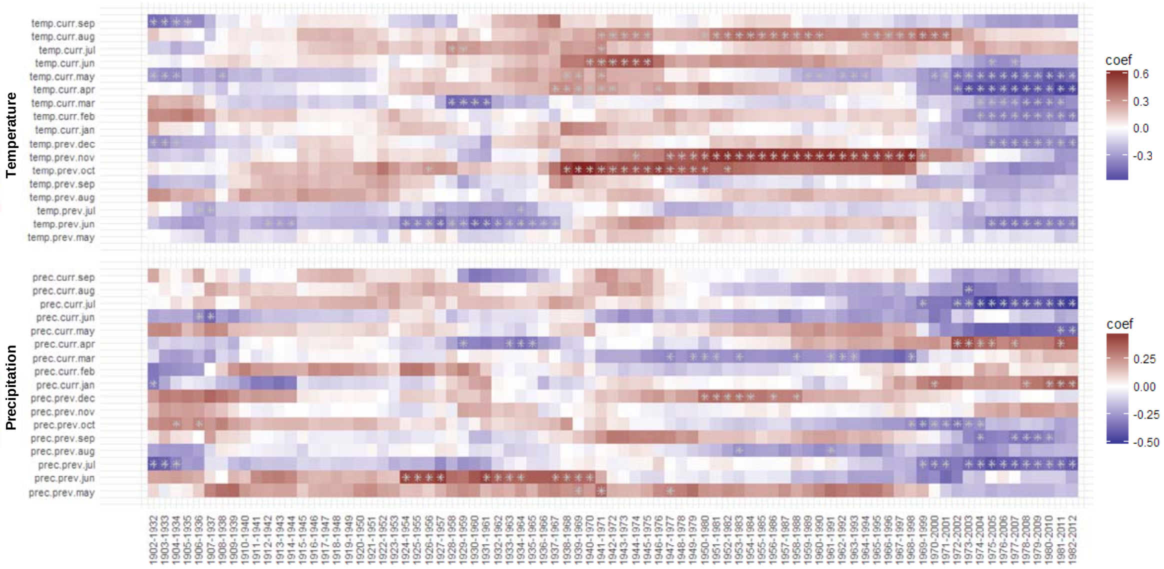

Figure 16. Moving window correlations of the TRW chronology with mean temperatures and precipitation sums: 31-year windows were shifted in one-year steps throughout the entire period of climate data availability (1901 – 2012); periods with asterisks indicate significant ($p < 0.05$) correlations.

Discussion (study 3)

Results for the period with most stable correlations, namely 1972–2012, suggest that *Abies spectabilis* tree growth was sensitive to temperature-induced moisture deficits during the pre-monsoon season. A negative relationship between radial tree growth and spring temperature was apparent and indicates a negative relation of growth to evapotranspiration, which temperature enhances. In addition, the positive correlation between TRW and April precipitation implies moisture sensitivity during the springtime (Fritts 1976).

These results are consistent with several previous studies on *Abies spectabilis* growth patterns (Cook et al. 2003; Sano et al. 2005; Gaire et al. 2011; Lv and Zhang 2012; Kharal et al. 2014; Sohar et al. 2016; Kharal et al. 2017; Tiwari et al. 2017; Gaire et al. 2017a) and other coniferous species from sites in the Himalaya and the Tibetan Plateau (Bräuning and Grießinger 2006; Fan et al. 2008; Borgaonkar et al. 2011; Thapa et al. 2015; Li et al. 2017; Panthi et al. 2017). Compared to the results of the present study, the correlation coefficient values of the aforementioned studies were mostly in a similar, rather low range. In summary, a relatively wide spectrum of various radial growth-climate relationships exists at regional and local scales within the Himalayan region of Nepal.

With regard to spring moisture sensitivity, the results of the present thesis largely match the results of earlier studies on sites in Nepal and other Himalayan regions. However, certain published results, including those from study sites near the TREELINE site, have evidenced disparate relations of tree growth to temperatures and precipitation in the winter prior to the growing season. The general east-west precipitation gradient in the Himalaya (Zurick and Pacheco 2006) explains variations in tree growth-climate relations to only a limited extent. From several previous studies (Shrestha et al. 2015; Thapa et al. 2015; Elliott and Cowell 2015; Sohar et al. 2016; Chhetri and Cairns 2016; Kharal et al. 2017; Rayback et al. 2017; Shrestha et al. 2017), it can be assumed that deviations in results were due to local variations in the heterogeneous environment which were not captured by sparse (and rather short) records of climate data from high elevation sites or derived gridded data. Moreover, spatially differing characteristics of climate factors at local and regional scales require consideration in order to develop generalised conclusions. For instance, the date of monsoon onset affects the radial increment in varying intensities at dry and wet sites (Shrestha et al. 2015). Finally, soil conditions, micro-topography, light conditions, land use and other site factors might account for differences in tree growth-climate relationships.

Changing long-term tree growth-climate relationships (the entire 20th century)

The static correlation of the whole CRU data period evidences rather low correlation coefficients. This finding is in line with previous studies on the Himalaya (e.g., Gaire et al. 2017b; Kharal et al. 2017; Tiwari et al. 2017) and other regions (St. George 2014; Kaczka et al. 2016). A closer examination of tree growth-climate relationships through moving windows correlations revealed unstable correlations throughout the entire period under analysis.

According to the results of the moving correlations, *Abies* trees presumably became more sensitive to climate during the reinforced climate-warming period that began in the 1970s. In a similar fashion to the alterations of radial tree growth-climate correlations and signal strengths, the climate changed non-linearly, with a temperature increase in the early-20th century, a stable phase during the mid-20th century and a pronounced warming during the late-20th century and early-21st century. The period of stable climate conditions coincided with a positive relationship of TRW to summer temperature and a negative relationship of TRW to March precipitation, which implies sufficient moisture availability in spring and growth limitation mostly due to low summer temperatures. During the climate-warming phase that occurred earlier in the century, the negative relation of tree growth and the May temperature indicated moisture sensitivity. This signal was less significant than it was during the last 40 years of the investigated period but already apparent. The climate-warming-induced increase in evapotranspiration and the consequently intensified moisture stress might have triggered a shift from the summer temperature-limited to the spring moisture-limited growth response and the stabilisation of the correlations towards the end of the investigated period. This assumption is consistent with the change in temperature and SPEI trends of the study area as well as the intensified spring droughts in the central Himalaya in recent decades (Panthi et al. 2017). Thus, increased drought might have led to divergence in growth-climate relationships, as other studies have observed (Rita et al. 2014; Galván et al. 2015; Jiao et al. 2015), with *Abies spectabilis* trees exhibiting growth plasticity towards the changing environment similarly to other coniferous species (e.g., Zhang and Wilmking 2010; Zhang et al. 2011; Natalini et al. 2016; Martin-Benito et al. 2017). This potential adaptation clearly contributed to the rather low responsiveness of the Rolwaling treeline to climate warming and may be crucial for its future sensitivity to climate change.

Until the end of the period of relatively stable climate conditions in the mid-20th century, tree growth was limited by previous winter temperatures and current spring and summer temperatures and was related inversely to winter precipitation and snow height. Other studies on the period after the mid-20th century have noted these linkages as well (Shrestha et al. 2015; Kharal et al. 2017; Rayback et al. 2017). Moreover, there are stable correlations for the whole 20th century that signify a negative relation of tree growth to spring drought (Thapa et al. 2015) as well as a positive relation to summer temperature (Gaire et al. 2017b). Some studies have clearly neglected information for specific periods or individual trees due to the methodology used in the static analysis (Zhang and Wilmking 2010), or there may have been sites where climate warming has or has not reached the potential threshold (D'Arrigo et al. 2008) for temperature-induced moisture deficits during the pre-monsoon season.

4.4 Additional results

The three main studies of this cumulative thesis have yielded additional results. However, since they are not related closely to the main objectives of this synthesis, it does not discuss them in depth. In brief, these results comprise the following:

- The thorough mapping of tree stumps revealed that wood cutting and its influence on stand structures were negligible in the upper part of the closed forest and above. Other factors under consideration, such as density-diameter distributions, field observations of herbivores and domestic animals, soil bulk densities, and atmospheric nitrogen and ammonia deposition (refer to Müller et al. 2017 for the latter), indicated a near-natural state of the Rolwaling treeline ecotone.
- Spatial pattern analyses of population densities evidenced that environmental variables could not account for some of the variance of spatial patterns. This finding suggests that dispersal and ecological drift might contribute to this yet-unexplained variance, and future studies should accordingly consider them.

- The tree-ring parameter blue intensity (BI) of *Abies spectabilis* was demonstrated to be a climate proxy for the first time. The BI signal was more stable and expressed higher correlation coefficients compared to the radial increment. Thus, *Abies spectabilis* BI proved to be a promising proxy for climate reconstruction.

5 Conclusions

Together, the key findings of this thesis reveal that the elevational position of the Rolwaling treeline has responded only slightly to climate warming as supposed for krummholz treelines in general. The tree growth-climate relations have changed most likely due to intensified climate warming in recent decades. The intense regeneration indicates a potential for upward migration of species. However, the treeline will most likely remain stable at its present position in the coming decades due to the constancy of the *Rhododendron campanulatum* krummholz belt. The feedback mechanisms of the krummholz belt constrain the treeline's response to climate warming by retarding or inhibiting the upward migration of other tree species. High levels of recruitment within the near-natural treeline ecotone indicate climate-warming-induced stand densification. Recruits of *Betula utilis* and *Abies spectabilis* illustrate that the aforementioned feedback mechanisms do not completely restrict seed-based regeneration beyond the krummholz belt. However, low temperatures and low nutrient availability will continue to offer competitive advantages for *Rhododendron campanulatum* and, to some extent, *Sorbus microphylla*. Thus, an upward extension of the krummholz belt into the alpine dwarf shrub heath as an alternative stable state seems to be more likely than a migration of subalpine forest into and beyond the krummholz belt. Moreover, spring drought will likely continue to limit the tree growth of *Abies spectabilis* and restrict its potential for upward migration to the relatively dry, wind- and solar radiation-exposed alpine zone. The identification of potential positive feedbacks within the treeline ecotone shows that the treeline position is not necessarily in equilibrium with current climatic conditions. Thus, the treeline might respond with delay to climate change, putting the treeline's usefulness as indicator for climate change into perspective. Although not directly transferable to other mountain regions (see below), the results of this thesis contribute to an understanding of the impact of climate change on treeline ecotones and its consequences for alpine environments, mountain forests and ecosystems.

We assume that the results of this study are transferable to a large extent to other near-natural treeline ecotones in the Himalaya. Intact krummholz belts of *Rhododendron campanulatum* will constrain the upslope migration of other tree species at other treeline sites as well. Findings of the tree growth-climate correlations are restricted to *Abies spectabilis* as the target species. The results of a few *Betula utilis* studies from Nepal and the Tibetan plateau likewise imply moisture sensitivity. However, the small number of available studies prohibits generalisations, and studies of other tree species in the ecotone do not exist. In general, the reliability of statements on past and future development of Himalayan treeline ecotones in relation to changing climate conditions depends on the quality and length of employed climate records. For instance, gridded climate datasets such as those used in this thesis for tree growth-climate correlations might be a source of inaccuracy. Nevertheless, we consider the results in their entirety based on an effective methodology as robust. The applied abruptness index proved to be a suitable measure to characterise transitions of population density, height and dbh along the elevational gradient of the treeline ecotone. Moreover, we demonstrated that multivariate imputation by chained equations is an appropriate approach to close data gaps in the variables involved in multivariate ordination analyses such as RDA. The broad approach to sample all occurring tree species and the incorporation of a multitude of environmental variables proved to be especially beneficial to obtain detailed insight into treeline ecology. We produced the first comprehensive adult and juvenile tree population data from the Rolwaling valley. The data have a much higher degree of detail than previous studies on Himalayan treeline ecotones. Thus, this thesis derives a novel characteristic from its analyses, which relate tree populations of all occurring species of a Himalayan treeline ecotone to a comprehensive set of environmental factors for the first time.

Given the spatial heterogeneity of Himalayan treeline ecotones, further studies are needed to fully understand the relations between tree population densities and environmental conditions as well as the complex conditions for the establishment and development of tree seedlings. Establishing permanent sample plots combined with experimental treatments is strongly recommended in this respect. In general, standardised sampling and analytical protocols could improve the comparability of ecological treeline studies at regional and global scales. Acquiring information about tree growth-climate relationships for more tree species would necessitate additional dendroclimatic studies, especially of *Rhododendron campanulatum*. A determination of the age structures of all tree populations could provide additional insight into the sensitivity of the ecotone to climate change. Future dendrochronological studies should analyse individual growth responses to environmental factors in order to quantify strategies of single trees or groups of trees. Furthermore, future studies could gain meaningful results by modelling forest and ecotone dynamics from an ecological perspective through the application of succession models (i.e. gap models, transition models or both) and species distribution models at different spatial scales that also consider dispersal.

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Appendix I: Abstracts and Author Contributions to Original Publications

1 'Treeline responsiveness to climate warming: insights from a krummholz treeline in Rolwaling Himal, Nepal' (study 1)

Authors: Niels Schwab, Udo Schickhoff, Michael Müller, Lars Gerlitz, Birgit Bürzle, Jürgen Böhner, Ram Prasad Chaudhary, and Thomas Scholten

Published 2016 in: Singh RB, Schickhoff U, Mal S (eds.) *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya*. Springer International Publishing, Cham, Switzerland, pp 307-345. doi: 10.1007/978-3-319-28977-9_16

At a global scale, the elevational position of natural upper treelines is determined by low temperatures during growing season. Thus, climate warming is expected to induce treelines to advance to higher elevations. Empirical studies in diverse mountain ranges, however, give evidence of both advancing alpine treelines as well as rather insignificant responses. Himalayan treeline ecotones show considerable differences in altitudinal position as well as in physiognomy and species composition. To assess the sensitivity of a near-natural treeline to climate warming at local scale, we analysed the relations between changes of growth parameters and temperature gradients along the elevational gradient in the treeline ecotone in Rolwaling valley, Nepal, by a multispecies approach. We observed species-specific transition patterns (diameter at breast height, height, tree and recruit densities) and varying degrees of abruptness of these transitions across the treeline ecotone resulting in a complex stand structure. Soil temperatures are associated with physiognomic transitions, treeline position and spatial regeneration patterns. In conclusion, treeline tree species have the potential to migrate upslope in future. Upslope migration, however, is controlled by a dense krummholz belt of *Rhododendron campanulatum*. Currently, the treeline is rather stable; however we found a prolific regeneration as well as signs of stand densification. Given the spatial heterogeneity of Himalayan treeline ecotones, further studies are needed to fully understand the complex conditions for the establishment and development of tree seedlings and the responsiveness of Himalayan treeline ecotones to climate change.

Author contributions

Niels Schwab conducted the mapping and measurement of trees and recruits with the support of student assistants Helge Heyken, Nina Kiese, Hanna Wanli and Ronja Wedegärtner as well as local guide Ram Bahadur. Michael Müller contributed soil temperature data, and Lars Gerlitz provided air temperature data. Niels Schwab performed the data analyses, including the further development of the abruptness index, and prepared the figures and tables, interpreted the results and wrote the first draft of the manuscript. Udo Schickhoff revised the first draft. All co-authors copyedited the final version of the manuscript, and Niels Schwab acted as the corresponding author.

2 'Implications of tree species - environment relationships for the responsiveness of Himalayan krummholz treelines to climate change' (study 2)

Authors: Niels Schwab, Udo Schickhoff, Birgit Bürzle, Michael Müller, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten, and Jens Oldeland

Published 2017 in: *Journal of Mountain Science* 14:453–473. doi: 10.1007/s11629-016-4257-z

Climate warming is expected to advance treelines to higher elevations. However, empirical studies in diverse mountain ranges give evidence of both advancing alpine treelines as well as rather insignificant responses. In this context, we aim at investigating the sensitivity and responsiveness of the near-natural treeline ecotone in Rolwaling Himal, Nepal, to climate warming. We analysed population densities of tree species along the treeline ecotone from closed forest stands via the krummholz belt to alpine dwarf shrub heaths (3700-4200 m) at 50 plots in 2013 and 2014. We quantified species - environment relationships, i.e. the change of environmental conditions (e.g., nutrient and thermal deficits, plant interactions) across the ecotone by means of redundancy analyses, variation partitioning and distance-based Moran's eigenvector maps. In particular, we focus on explaining the high competitiveness of *Rhododendron campanulatum* forming a dense krummholz belt and on the implications for the responsiveness of Himalayan krummholz treelines to climate change. Results indicate that treeline trees in the ecotone show species-specific responses to the influence of environmental parameters, and that juvenile and adult tree responses are modulated by environmental constraints in differing intensity. Moreover, the species - environment relationships suggest that the investigated krummholz belt will largely prevent the upward migration of other tree species and thus constrain the future response of Himalayan krummholz treelines to climate warming.

Author contributions

Niels Schwab conducted the counting and measurement of trees and recruits and the mapping of topographic data with the support of student assistants Helge Heyken, Nina Kiese, Hanna Wanli and Ronja Wedegärtner as well as local guide Ram Bahadur. Michael Müller contributed soil data. Niels Schwab conceived of the data analysis together with Birgit Bürzle and Jens Oldeland. Niels Schwab performed the data analyses, including the application of MICE in combination with RDA, and also prepared the corresponding figures and tables and interpreted the results. Niels Schwab wrote the first draft of the manuscript, which Birgit Bürzle, Jens Oldeland and Udo Schickhoff revised. All co-authors copyedited the final version of the manuscript, and Niels Schwab acted as the corresponding author.

3 'Climate change-induced shift of tree growth sensitivity at a central Himalayan treeline ecotone' (study 3)

Authors: Niels Schwab, Ryszard J. Kaczka, Karolina Janecka, Jürgen Böhner, Ram P. Chaudhary, Thomas Scholten, and Udo Schickhoff

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Himalayan treelines are exposed to above average climate change impact, resulting in complex tree growth–climate relationships for Himalayan Silver Fir (*Abies spectabilis* (D. Don) Spach) at central Himalayan treelines. The majority of recent studies detected current tree growth sensitivity to dry conditions during pre-monsoon seasons. The aim of this study was to analyze growth–climate relationships for more than a century for a treeline ecotone in east-central Nepal and to test for Blue Intensity (BI; used as a surrogate of maximum late wood density) as climate proxy. We determined the relationships of *Abies spectabilis* radial tree growth and BI to climate by correlating both to temperature, precipitation and drought index data. The results showed a significantly unstable dendroclimatic signal over time. Climate warming-induced moisture deficits during pre-monsoon seasons became a major factor limiting radial tree growth during recent decades. Earlier in time, the dendroclimatic signal was weaker, predominantly reflecting a positive relationship of tree growth and summer temperature. Compared to radial tree growth, BI showed a different but strong climate signal. Temporally unstable correlations may be attributed to increasing effects of above-average rates of climate warming. An extended network of Himalayan tree-ring sites is needed to further analyze cause–effect relationships and to solve this attribution problem.

Author contributions

Niels Schwab collected the tree-ring cores with the support of student assistants Helge Heyken, Nina Kiese, Hanna Wanli and Ronja Wedegärtner as well as local guide Ram Bahadur. Niels Schwab prepared the samples with the assistance of Julika Hellmold, MSc, Aleksandra Lewandowska-Duzy, cand, MSc, Hendrik Maaß, MSc and Ravel Malanda, BSc, whose related theses he co-supervised. Niels Schwab measured TRW, whilst Karolina Janecka contributed BI measurements. Niels Schwab conceived of the data analysis together with Karolina Janecka and Ryszard J. Kaczka. Niels Schwab also performed the data analyses and interpretation together with Karolina Janecka and Ryszard J. Kaczka, and he prepared the corresponding figures and tables and wrote the first draft of the manuscript. Karolina Janecka, Ryszard J. Kaczka and Udo Schickhoff revised the first draft. All co-authors copyedited the final version of the manuscript, and Niels Schwab acted as the corresponding author.

Appendix II: Original Publications

1 'Treeline responsiveness to climate warming: insights from a krummholz treeline in Rolwaling Himal, Nepal' (study 1)

Authors: Niels Schwab, Udo Schickhoff, Michael Müller, Lars Gerlitz, Birgit Bürzle, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten

Published 2016 in Singh RB, Schickhoff U, Mal S (eds.) *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya*. Springer International Publishing, Cham, Switzerland, pp 307-345. doi: 10.1007/978-3-319-28977-9_16

Chapter 16

Treeline Responsiveness to Climate Warming: Insights from a Krummholz Treeline in Rolwaling Himal, Nepal

Niels Schwab, Udo Schickhoff, Michael Müller, Lars Gerlitz, Birgit Bürzle, Jürgen Böhner, Ram Prasad Chaudhary, and Thomas Scholten

Abstract At a global scale, the elevational position of natural upper treelines is determined by low temperatures during growing season. Thus, climate warming is expected to induce treelines to advance to higher elevations. Empirical studies in diverse mountain ranges, however, give evidence of both advancing alpine treelines as well as rather insignificant responses. Himalayan treeline ecotones show considerable differences in altitudinal position as well as in physiognomy and species composition. To assess the sensitivity of a near-natural treeline to climate warming at local scale, we analysed the relations between changes of growth parameters and temperature gradients along the elevational gradient in the treeline ecotone in Rolwaling valley, Nepal, by a multispecies approach. We observed species-specific transition patterns (diameter at breast height, height, tree and recruit densities) and varying degrees of abruptness of these transitions across the treeline ecotone resulting in a complex stand structure. Soil temperatures are associated with physiognomic transitions, treeline position and spatial regeneration patterns. In conclusion, treeline tree species have the potential to migrate upslope in future. Upslope migration, however, is controlled by a dense krummholz belt of *Rhododendron campanulatum*. Currently, the treeline is rather stable; however we found a prolific regeneration as well as signs of stand densification. Given the spatial heterogeneity

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of Himalayan treeline ecotones, further studies are needed to fully understand the complex conditions for the establishment and development of tree seedlings and the responsiveness of Himalayan treeline ecotones to climate change.

Keywords Density–diameter curve • Regeneration • Soil temperature • Species composition • Treeline dynamics • *Abies spectabilis* • *Betula utilis* • *Rhododendron campanulatum* • *Sorbus microphylla*

16.1 Introduction

At a global scale, the position of natural upper treelines is determined by low air and soil temperatures during growing season (e.g. Troll 1973; Stevens and Fox 1991; Holtmeier 2009; Körner 2012). Climate warming is expected to induce treelines to advance to higher elevations. Empirical studies in diverse mountain ranges, however, give evidence of both advancing alpine treelines as well as rather insignificant responses (Baker and Moseley 2007; Hofgaard et al. 2009; Wieser et al. 2009; Grigor'ev et al. 2013; Shrestha et al. 2014; Chhetri and Cairns 2015), pointing to an evident research deficit. Harsch et al. (2009) analysed data from 166 globally distributed treelines which dynamics were monitored since AD 1900. 47 % of the treelines did not show any elevational shift, while 52 % of the treelines advanced to higher altitudes and only 1 % showed recession. Apart from climate change, land use changes influence high-altitude vegetation patterns and treeline positions (e.g. Dirnböck et al. 2003; Bolli et al. 2007; Gehrig-Fasel et al. 2007; Pauchard et al. 2009; Schickhoff 2011; Penniston and Lundberg 2014; Piermattei et al. 2014; Durak et al. 2015). Thus there is the need to disentangle these effects to draw correct conclusions concerning the sensitivity of treelines to climate change.

Many studies detected above-average current warming trends between 0.6 and 1 °C per decade for the Himalayan region. Maximum values were found for the high elevations and during winter and pre-monsoon seasons (Shrestha et al. 1999; Liu and Chen 2000). For the Rolwaling valley, the target area of the present study, monthly temperature trends in the order of 0.7 °C per decade were assessed in winter and pre-monsoon seasons (Gerlitz et al. 2014). During monsoon, no statistically significant trends were identified. Trend analyses of precipitation amounts in the Himalayas do not show a consistent pattern. Some studies, however, detected negative trends of winter and pre-monsoon precipitation over the western and central Himalaya (Duan et al. 2006; Bhutiyani et al. 2010; Jain et al. 2013). An enhanced frequency of winter and pre-monsoon drought events was reported for western Nepal by Wang et al. (2013). Recent climatic changes will inevitably affect growth patterns and seedling performance at Himalayan treelines, albeit to a regionally differentiated extent (Schickhoff et al. 2015, 2016).

It is widely accepted that climate exerts a top-down control on local ecological processes at the treeline (e.g. Batllori and Gutiérrez 2008; Elliott 2011). However, it is not well understood how landscape-scale and local-scale abiotic and biotic factors and processes interact and influence the treeline and its response to climate change. Moreover, effects of climate warming often mix up with impacts of land use (Malanson et al. 2007; Batllori et al. 2009). In consequence, complex research approaches at local and landscape scales at natural treelines are needed (e.g. Malanson et al. 2011). Recent studies based on a global treeline data set suggest a close link between treeline form (spatial pattern) and dynamics. Harsch and Bader (2011) consider treeline form (diffuse, abrupt, island, krummholz) to be an indicator of controlling mechanisms (at the levels of direct tree performance, causative stresses and modifying neighbour interactions) and response to climate change. They confirmed the link between treeline form and dynamics established earlier (Lloyd 2005; Harsch et al. 2009) and supported the general suitability of treeline form for explaining the variability of response to climate warming. Apart from treeline form, tree species composition, tree density, diameter and height distributions can be indicators for treeline sensitivity to climate change. In addition, these parameters provide information on the establishment of recruits and their performance which are among the most significant indicators of treeline sensitivity (Germino et al. 2002; Holtmeier 2009; Körner 2012; Zurbriggen et al. 2013; Schickhoff et al. 2015, 2016).

In the Himalaya, only very few studies on treeline seedlings have been conducted so far, and tree recruitment in treeline ecotones is not well understood (Schickhoff 2005; Shi and Wu 2013; Dutta et al. 2014; Schickhoff et al. 2015, 2016). Hitherto available studies refer to treeline ecotones with deviating species compositions and population structures and generally to ecotones which have been disturbed by land use effects (e.g. Shrestha et al. 2007, 2014; Ghimire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Chhetri and Cairns 2015). Thus, their generalisability and informative value for near-natural treeline ecotones are limited. The present study was conducted in the framework of the research scheme TREELINE which focuses on spatially differentiated patterns and processes by correlating varied treeline responses to landscape- and local-scale site conditions and mechanisms (geomorphic controls, soil physical and chemical conditions, plant interactions associated with facilitation, competition and feedback systems). We present population structures from a near-natural treeline ecotone in Rolwaling Himal, Nepal, focussing on species compositions and growth parameters with an emphasis on the ratio of recruits to adult trees. Unlike most other treeline studies in Nepal (e.g. Shrestha et al. 2007; Lv and Zhang 2012; Sujakhu et al. 2013; Gaire et al. 2014), we assessed the treeline-forming tree species of our study area in its entirety. Near-natural treeline ecotones can contain codominant tree species which respond differently to climate change (Trant and Hermanutz 2014). In consequence, multispecies approaches to treeline dynamics, which survey all ecotone tree species, can capture the sensitivity of the ecotone to climate change sufficiently. We aim at (1) analysing species-specific patterns and abruptness of transitions of tree and recruit densities and growth parameters along the elevational gradient, (2) detecting altitudinal boundaries of tree species distributions and (3) assessing the relation between abrupt changes of growth parameters and temperature gradients along the altitudinal zoning of the ecotone and relating the results to the sensitivity to climate warming. We hypothesise that changes in tree physiognomy (diameter at breast height (dbh), tree height, growth forms) and density occur species specific with varying abruptness intensities along the treeline ecotone, indicating complex spatial structures and resulting in several tree species limits inside the ecotone, each potentially susceptible to climate change. Air and soil temperatures are supposed to be crucial variables explaining species-specific responses.

16.2 Materials and Methods

16.2.1 The Study Area

The Rolwaling valley (27°52′ N; 86°25′ E) is located in Dolakha District, east-central Nepal, adjacent to the border of Tibet Autonomous Region. It is embedded in the Gaurishankar Conservation Area (2035 km^2), which has been a protected area since 2010 (Shrestha et al. 2010; Bhusal 2012). Our study site is located at a north-facing slope ranging from the closed subalpine forest via timberline and treeline to

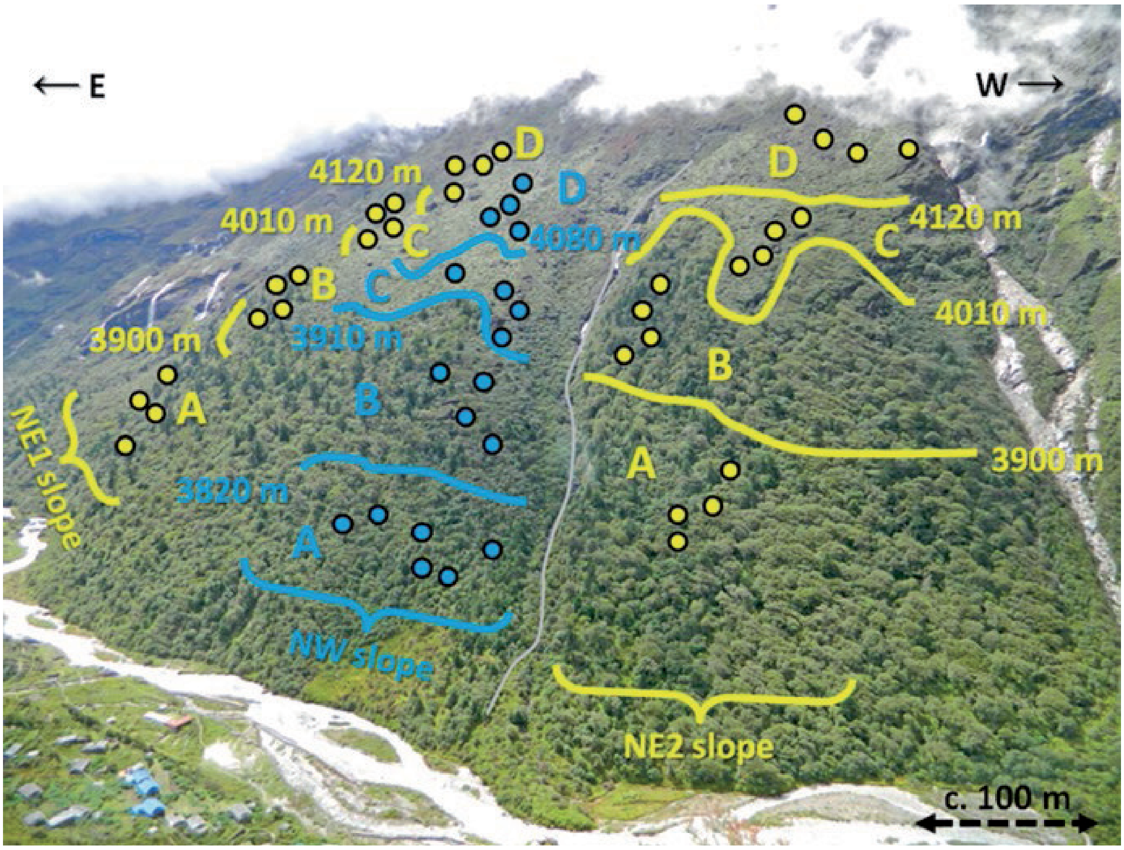

Fig. 16.1 Stratification of the study area by altitude (zones *A*, *B*, *C*, *D*) and aspect (NE, NW) and approximate location of plots (*blue* and *yellow points*) (Schwab, 18 September 2014) (Source: Niels Schwab)

the lower alpine vegetation zone (3740 m to 4250 m a.s.l.). We subdivided the study site into three slope sectors according to their deviating exposure (Fig. 16.1).

Due to the remote location without connection to the road network (3-day walking distance), the small human population and the fact that plants and animals in Rolwaling are protected to a certain extent by the recurring Buddhist theme of a sacred hidden valley (Sacherer 1979; Baumgartner 2015), the Rolwaling treeline exhibits a near-natural state (cf. Sect. 16.3.6) and represents a climatic treeline. The study slopes show no signs of fire or of grazing by cattle; wood cutting is negligible. The Rolwaling River separates the uninhabited north-facing study slope from the very sparsely populated south-facing slope where human impact is likewise low. Thus, in view of the fact that most Himalayan treeline sites are disturbed by land use effects (Schickhoff et al. 2015, 2016), the study slopes provide a unique research opportunity for detecting a climate change signal when assessing treeline dynamics.

The study sites cover the entire treeline ecotone. The lower reaches contain mixed forest stands with the upper limits of tall, upright-growing individuals of *Acer caudatum*, *Abies spectabilis* and *Betula utilis*. A krummholz belt with dense and largely impenetrable *Rhododendron campanulatum* thickets represents the transition to alpine dwarf scrub heaths with only small (dbh <7 cm) and stunted tree species individuals (Fig. 16.2).

16.2.2 Data Collection

We stratified the treeline ecotone according to the altitudinal zoning of tree species composition and stand structure into four altitudinal zones, reaching from closed forests (zone A) to alpine dwarf scrub heaths (zone D; Table 16.1). We established a total of 50 plots, each with a size of 20 × 20 m^2 (projected on a horizontal plain), comprising four randomly selected plots in each of the zones A–D at three slopes (two slopes NE-exposed, one slope NW-exposed; Table 16.1). Nomenclature of identified tree species follows Press et al. (2000). We measured dbh with a diameter measuring tape at 1.3 m above ground level (Van Laar and Akça 2007) and height of all trees with dbh ≥7 cm with a laser dendrometer (Laser Technology Criterion RD 1000, distance measurement: MDL LaserAce 300). Individuals of tree species with dbh <7 cm (recruits) were identified, counted and assigned to height classes (Table 16.2). We counted all stumps ≥7 cm diameter and measured diameters 10 cm above ground or, if stump height was less than 10 cm, at highest point above ground. We identified the species and cause of death (natural, anthropogenic, unidentified) in each plot. We classified the degree of decomposition of tree stumps into four classes (undecomposed, slight, medium, intense decomposition) to roughly estimate the dieback period (Schickhoff 2002). We assumed the intensely decomposed stumps to not influence the current stand structure. Vegetation surveys took place in April, May, July and August 2013 and September 2014.

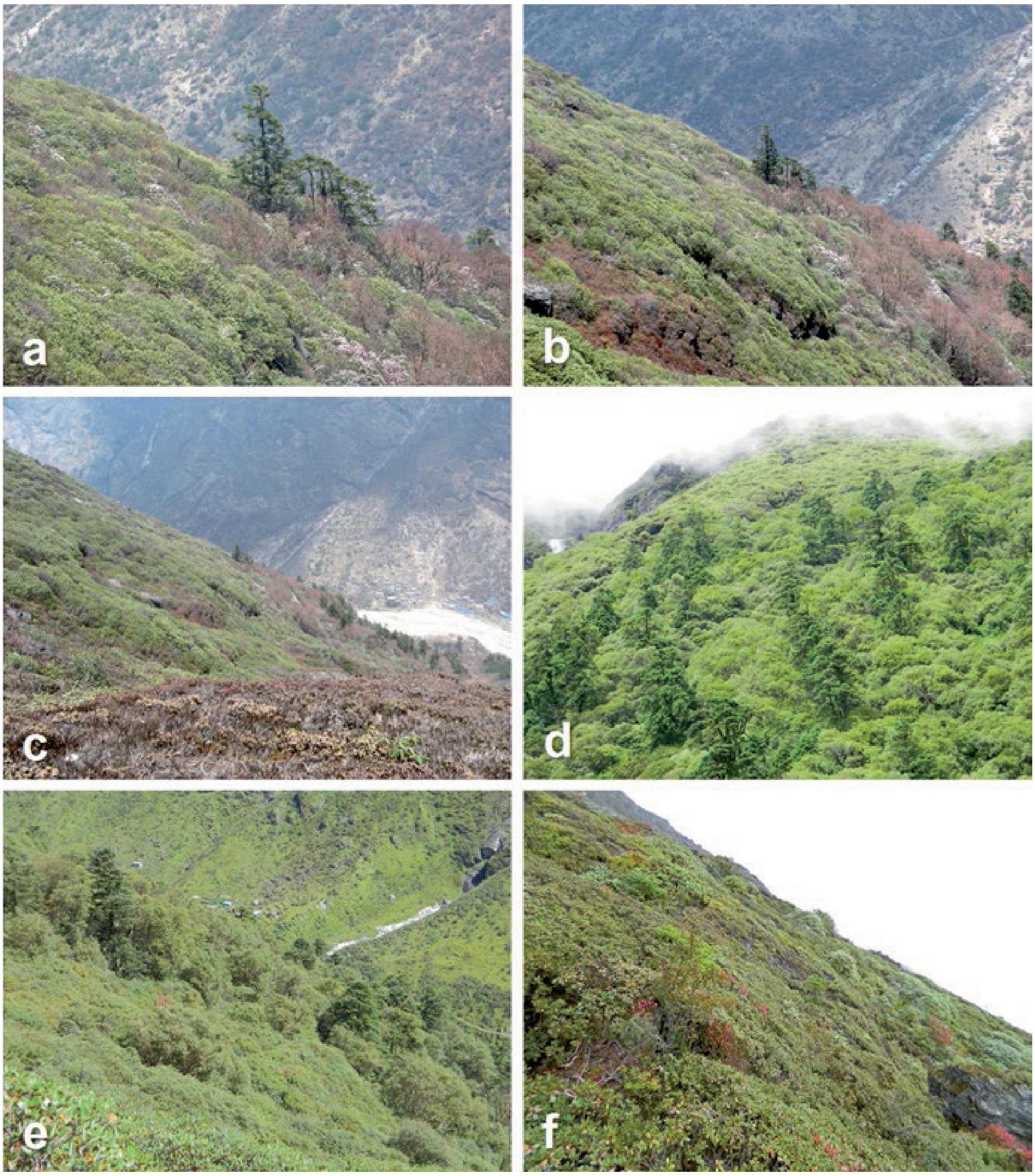

Fig. 16.2 Transition from closed forest to alpine dwarf scrub heath. (**a**) Uppermost stand of *A. spectabilis* at NE-slope (c. 4000 m a.sl.); (**b**) *Rh. campanulatum* krummholz (in *white-pink* bloom) and transition to *Abies-Betula* forest (zone B); (**c**) Elevational range from zone A to D with transition from B to C in focus; (**d**) Mixed forest stand of zone B and abrupt transition to *Rh. campanulatum* krummholz belt; (**e**) *Rh. campanulatum* krummholz (front) and abrupt transition to mixed *Abies-Betula* forest of zone B; (**f**) Alpine dwarf scrub heath with *Rh. campanulatum* and *Rhododendron* dwarf shrub species and single *S. microphylla* individuals (**a**–**c**: 5 May 2013; **d**: 23 July 2013; **e**–**f**: 17 September 2014; Schwab) (Source: Niels Schwab)

To relate soil temperature to growth parameters, we installed 34 modified Wi-Fi Plant sensors (Koubachi AG), which have monitored soil temperature in 10 cm depth in a 1 h interval since May 2013. For this paper we use data from June 2013 to May 2014. Thirty-two sensors were placed on the NW-exposed and on one of the NE-exposed slopes (2 transects × 4 altitudinal zones × 4 plots). Mobile climate sta-

Table 16.1 Study site properties

		Zones			
	Aspect	A	B	C	D
Slope 1	NE				
Altitude [m a.s.l.]		3830–3895	3920–3990	4015–4080	4180–4245
No. of plots		4	4	4	4
Slope 2	NE				
Altitude [m a.s.l.]		3795–3875	3925–3990	4040–4090	4130–4225
No. of plots		4	4	4	4
Slope 3	NW				
Altitude [m a.s.l.]		3770–3795	3845–3890	3925–4020	4140–4200
No. of plots		6	4	4	4
Total no. of plots		14	12	12	12
NE transition altitudes [m a.s.l.]		3900 (AB)	4010 (BC, TL)	4120 (CD)	
NW transition altitudes [m a.s.l.]		3820 (AB)	3910 (BC, TL)	4080 (CD)	
Vegetation		Mixed forest	Mixed forest	Krummholz	Alpine scrubs

Aspects: *NE* north-east, *NW* north-west, *TL* treeline

Table 16.2 Size classifications of tree species individuals and abruptness parameters

dbh [cm]	Height [cm]	Recruit class	Terms		Indication of abruptness for
<7	0–10	1	Seedlings	Recruits	Height, density
<7	11–50	2			
<7	51–130	3	Saplings		
<7	131–200	4			
<7	201–∞	5			
≥7	ns	–		Trees	dbh, height, density

dbh diameter at breast height, *ns* not specified

tions installed in the lower and upper part of the ecotone have recorded air temperatures since April 2013 (data evaluated until June 2014). Soil bulk density of field-moist soils was sampled using soil core cutters (100 cm^3) and analysed following DIN EN ISO 11272:2014. Additionally, atmospheric nitrogen deposition (NO$_2$, NH$_3$) was measured using passive devices (Passam AG) requiring no power for their operation. The samplers were placed in a special shelter 2 m above ground to protect them from rain and minimise wind influence. Exposition time was 2 weeks.

16.2.3 Data Analyses

We computed stem numbers and stand densities per hectare (ha) and visualised population structures and species compositions by plotting barplots and histograms of all samples and subsamples. Comparisons of our density–diameter distributions

Table 16.3 Definitions and interpretation of abruptness values

Abruptness	Definition/interpretation
−1,…,1	Maximum range
Positive	Decreasing parameter with elevation
Negative	Increasing parameter with elevation
−1	Transition from maximum to zero
−1	Transition from zero to maximum
0	No change
1/3 resp. −1/3	Linear transition in case of 4 zones
−0.33 ≤ abruptness ≤0.33	Gradual/smooth transition
−0.5 ≥ abruptness ≥0.5	Abrupt transition, change by half or more of the parameters range
0.33,…,0.5 resp. −0.33,…,−0.5	Intermediate transition

to other studies should be understood as only rough estimates due to the differing study-specific definitions of size classes and classification intervals. In order to analyse regeneration patterns, we calculated values for the mean height of recruits as mean of the class configurations. We calculated a regeneration index (*RI*) according to Schickhoff (2002):

$$RI = \sum_{i=1}^{5} \bar{x}_{\text{med}(i)} n_i$$

where n_i is the number of recruits in the 5 recruit height classes (Table 16.2) and $\bar{x}_{\text{med}(i)}$ is the median of the height class limits. In contrast to mean height values of recruits, the *RI* includes information of abundance and combines it with the recruits' height. Thus the *RI* provides information on growth performance and success of establishment beyond the seedling stage.

In order to describe and analyse variation in stand structures and to characterise abrupt or smooth/gradual transition patterns along the ecotone, we calculated the abruptness of transitions between subsequent zones ($\text{abruptness}_{\text{AB}}$, $\text{abruptness}_{\text{BC}}$, $\text{abruptness}_{\text{CD}}$). We computed the abruptness for various parameters (Table 16.2) using a modified approach by Wiegand et al. (2006) and Batllori and Gutiérrez (2008). The abruptness of the transitions was the difference of the scaled values of successive zones (lower zone minus upper zone; scaled range [0,1]):

$$\text{abruptness}_{lh} = \frac{\bar{x}_{\text{arith}(l)} - \min_l}{\max_l - \min_l} - \frac{\bar{x}_{\text{arith}(h)} - \min_h}{\max_h - \min_h}$$

where l and h are the altitudinal zones (A, B, C, D). The lower zone (e.g. A) is denoted l and the successive higher zone (e.g. B) is denoted [h]. A positive abruptness indicates a transition of decreasing values with elevation as it is generally expected in a treeline ecotone while a negative abruptness points to an increasing value of a stand parameter with elevation (see Table 16.3 for further differentiation of abruptness values). Total abruptness was gained as the arithmetic mean abruptness of all parameters under consideration at a specific transition. We calculated both the abruptness for all individuals of the stands and the species-wise abruptness.

Seasonal means for discrete time steps (0, 6, 12, 18 h local time) were calculated for air temperature for each climate station. Topographically induced 6 hourly temperature lapse rates ($\Delta T/\Delta Z*100$) were derived for the NW and NE transects to assign site-specific air temperatures (Gerlitz et al. 2016). We calculated growing season mean soil temperature at treeline and number of growing degree days according to Körner and Paulsen (2004). For soil temperatures we calculated abruptness values according to the above described procedure for mean annual and mean seasons' temperatures (MAM, JJAS, ON, DJF). All computations and figure plottings were carried out using 'base' and 'graphic' R functions (version 3.1.2; R Core Team 2014) and the packages 'plyr' (Wickham 2011) and 'vegan' (Oksanen et al. 2014).

16.3 Results

16.3.1 General Vegetation Patterns and Species Limits

In general, upper subalpine forests are primarily composed of *Betula utilis* and *Abies spectabilis*, with *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer. Closed forests give way to an extensive krummholz belt of *Rh. campanulatum* at c. 3910 m a.s.l. (NW)/4010 m a.s.l. (NE), which turns into alpine *Rhododendron* sp. dwarf scrub heaths at c. 4080/4120 m a.s.l (Fig. 16.2). Total plant species richness decreases from the closed forests in the subalpine zone across the treeline ecotone and increases again in the uppermost dwarf scrub heath plots of zone D at the transition to alpine grassland. Minimum species numbers are found in the krummholz belt zone C with a mean species number of 12 and in the lower dwarf scrub heath plots with 11 species. Zone A contains the maximum of 25 plant species (unpublished data by B. Bürzle).

We identified different tree species-specific altitudinal limits (i.e. 'the uppermost occurrence regardless of size', Körner 2012) throughout an altitudinal gradient from zone A to zone D (Fig. 16.3): We found the uppermost individuals of *Prunus rufa* at 3925 m a.s.l. (NE) resp. 3890 m a.s.l. (NW) in zone B, of *Acer caudatum* at 3950 m a.s.l. (NE) resp. 3890 m a.s.l. (NW) in zone B and of *Juniperus recurva* at 4080 m a.s.l. (NE, no *J. recurva* at NW) in zone C. All other species still occurred in zone D. We found *B. utilis* recruits at 4140 m a.s.l. in the lowest plot in zone D at the NW slope but in none of the higher plots. Thus the species limit of *B. utilis* appears to be at the lower part of zone D. In contrast, we found *A. spectabilis* individuals even at 4185 m a.s.l. Similarly, *S. microphylla* and *Rh. campanulatum* occur at nearly all plots in zone D (both maximum altitude 4245 m a.s.l.). Vegetation analyses above zone D point to a position of their tree species lines at the upper border of zone D (c. 4260 m, unpublished data by B. Bürzle, Fig. 16.3).

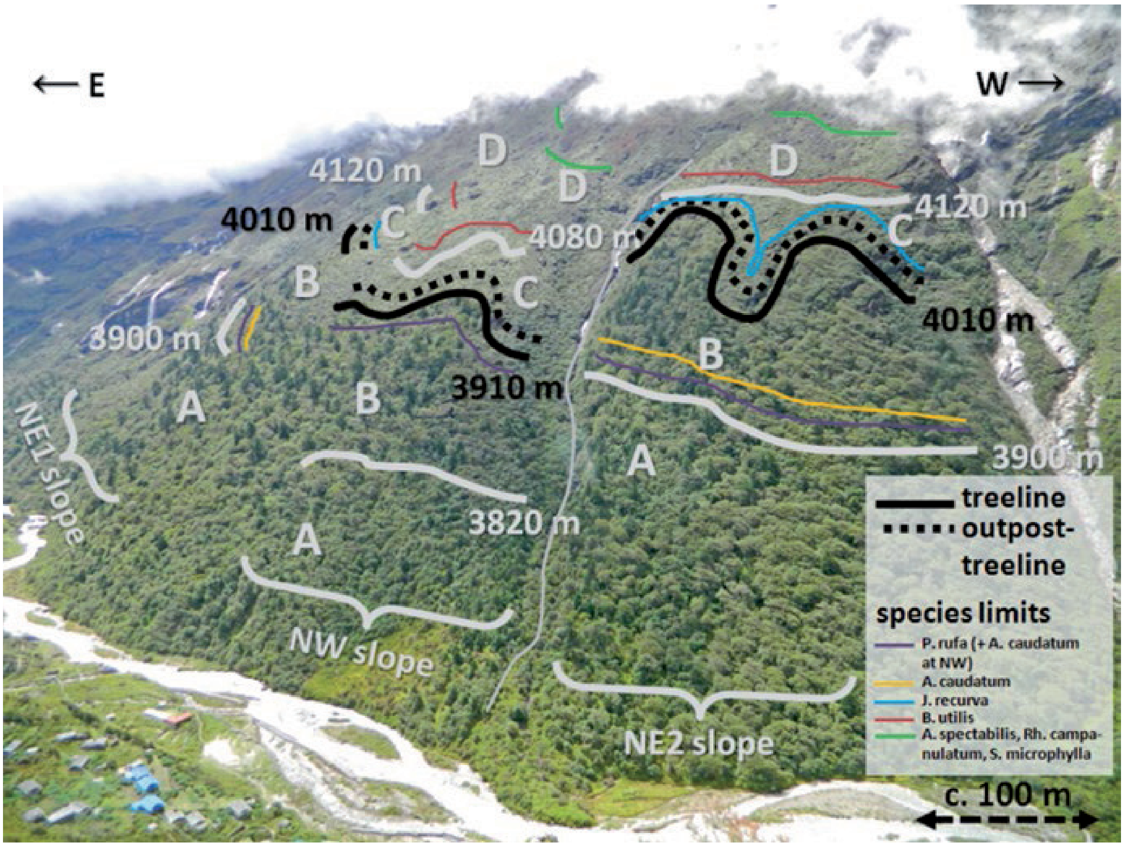

Fig. 16.3 Approximate locations of treeline, outpost-treeline and species limits (Schwab, 18 September 2014) (Source: Niels Schwab)

16.3.2 Tree Species Composition

The lowest zones A and B contain mixed forest stands where tall, upright-growing, adult individuals of most tree species reach their upper limits (*Acer caudatum* in A; *Abies spectabilis*, *Betula utilis* and *Prunus rufa* in B). Zone C represent the krummholz belt with dense and largely impenetrable *Rhododendron campanulatum* thickets and upper limits of stunted *A. spectabilis* and *B. utilis* tree individuals with dbh ≥7 cm. Zone D is occupied by alpine vegetation (mainly dwarf scrub heaths), interspersed with only low-growing individuals or young growth (dbh <7 cm) of *A. spectabilis*, *B. utilis* and *Rh. campanulatum* (Fig. 16.2). We found very few *Sorbus microphylla* individuals with dbh ≥7 cm in zone D (Figs. 16.4 and 16.5). The recruit density pattern (Fig. 16.6) mostly resembled the one of individuals with dbh ≥7 cm. The occurrence of *Juniperus recurva*, a species that can grow to tree size, remarkably differed between recruits and adults. We found no individual with dbh ≥ 7 cm; *J. recurva* recruits were existent in zones A, B and C. *Rh. campanulatum* and *S. microphylla* seedlings occurred in rather high abundance in zone D; however no tree-sized individual of these species was detected. We found the highest number of individuals of both trees and recruits in zone B. Zone C exhibited nearly the same

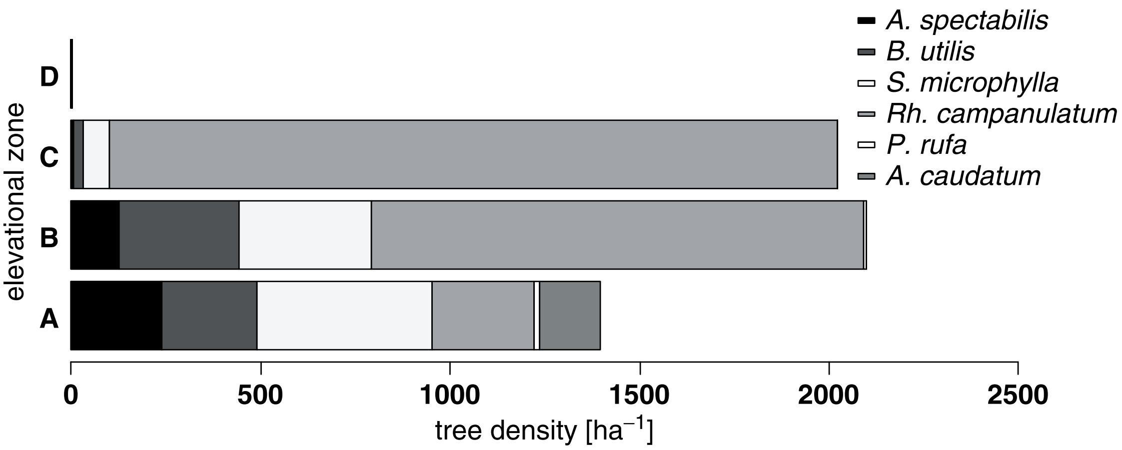

Fig. 16.4 Tree species density of individuals ≥7 cm dbh (trees) (Source: Niels Schwab)

number of trees per ha as zone B. Zones A and C resembled each other in terms of recruit numbers, whereas recruit density indicated distinct differences between both zones and zone B. However, altitudinal zones differed in the percentages of the individual species. *P. rufa* and *J. recurva* individuals occurred in very low abundance and are thus not analysed in detail.

All tree species occurring in zone A except the rare *P. rufa* exhibited evenly distributed numbers of individuals. *Rh. campanulatum* becomes more frequent with elevation. In zone C, *Rh. campanulatum* dominates the tree species composition and is accompanied by few *Sorbus* individuals. Although *Rh. campanulatum* accounts for more than 50 % of tree individuals and more than 75 % of recruits in zone B, the transition from zone B to C shows the most abrupt change in tree species composition along the altitudinal gradient. This abrupt change in species composition coincides with the most abrupt changes in annual and seasonal mean soil temperature at transition BC (cf. Sect. 16.3.7). *S. microphylla* occurred with high constancy and its density–diameter distribution points to an established population in zone C, which coexists aside the *Rh. campanulatum* population. Established recruit populations in zone D indicate the potential of *Rh. campanulatum* and *S. microphylla* to sprout and survive at least the early life stages at this high altitude (see discussion Sect. 16.4.3).

16.3.3 Stand Densities

Stand densities showed similar patterns in zones A, B and C: We found 7473 (zone A, standard deviation SD = 4432), 8748 (zone B, SD = 6718) and 7280 (zone C, SD = 3948) individuals per ha belonging to the recruit class (dbh <7 cm) (Figs. 16.6

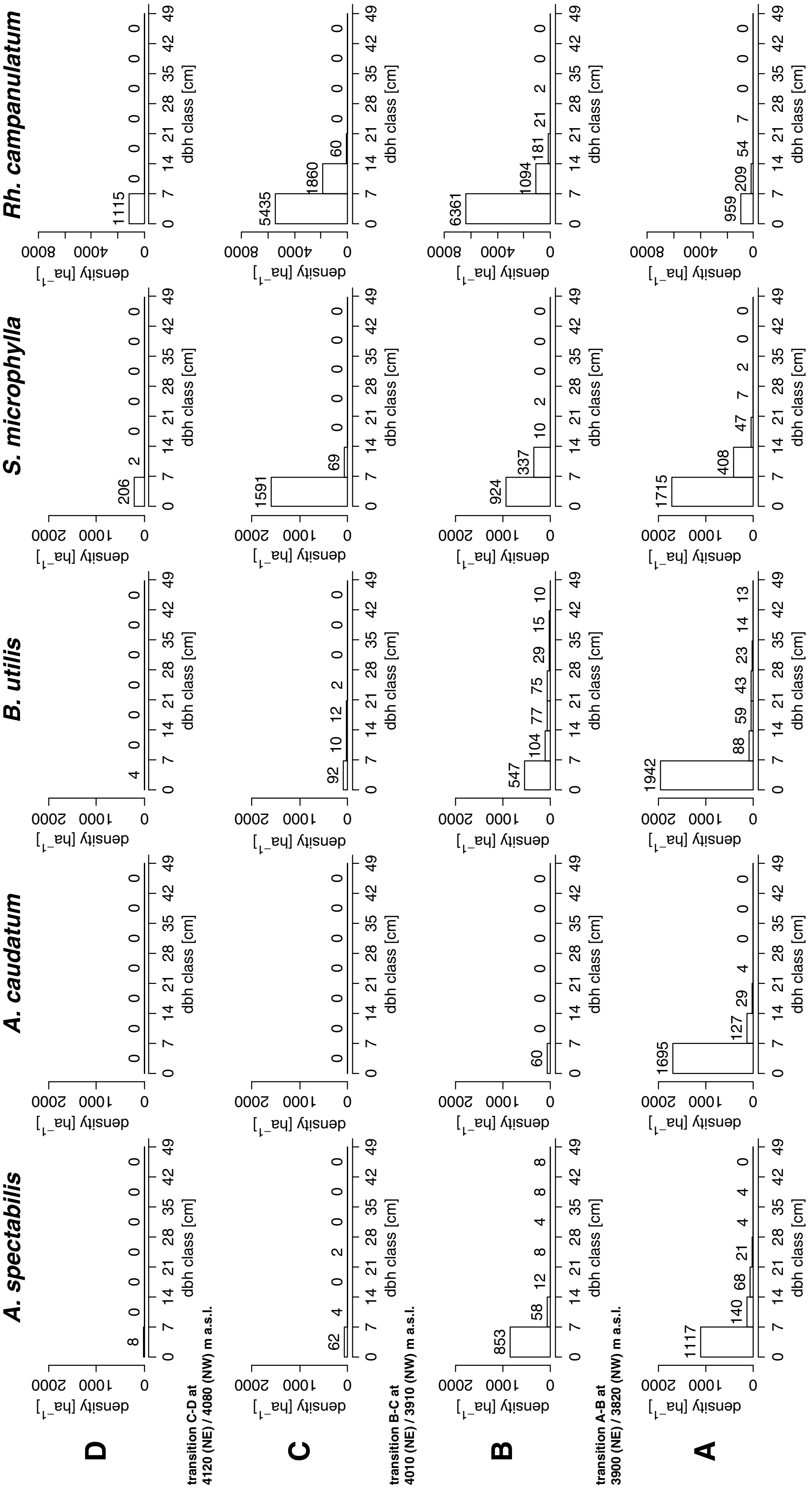

Fig. 16.5 Species-wise density–diameter distribution of the most abundant tree species in the altitudinal zones *A*, *B*, *C* and *D*. Only classes <49 cm dbh are printed. Note difference in scaling of *Rhododendron campanulatum* y-axis (Source: Niels Schwab)

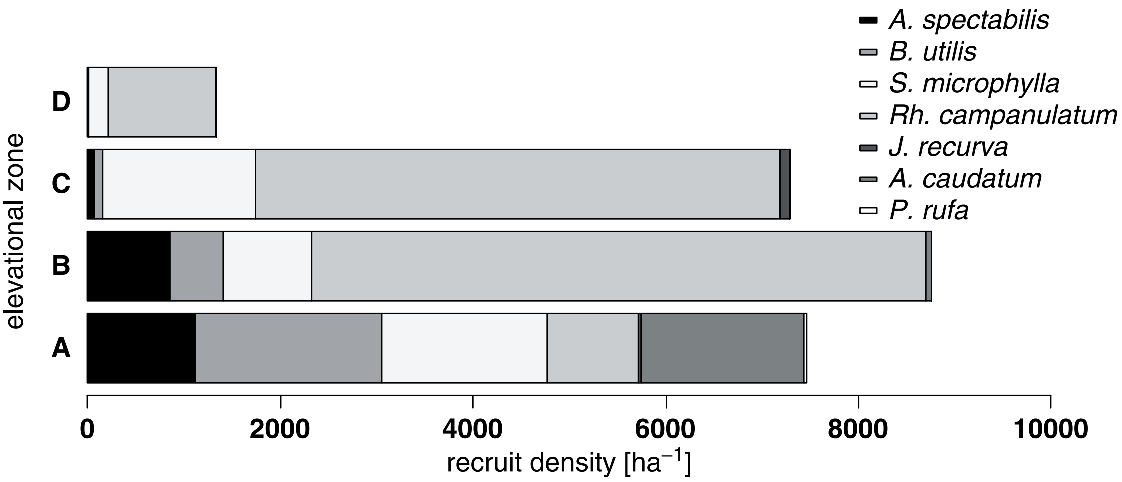

Fig. 16.6 Tree species density of individuals <7 cm dbh (recruits) (Source: Niels Schwab)

and 16.7). The number was significantly smaller in zone D. Here, 1333 individuals per ha (SD = 1197) represent more than one tree species recruit individual per 10 m^2 in the alpine dwarf scrub heath. However, zone D exhibited only two tree individuals per ha in the 7–14 cm dbh class and not a single individual of higher dbh classes. The number of trees in the dbh class 7–14 cm increased continuously with elevation from 984 trees per ha (SD = 386) in zone A to 1597 (SD = 869) in zone B and to 1943 (SD = 1246) in zone C. The following class (14–21 cm dbh) showed most individuals in zone A and B (258 resp. 283 trees per ha, SD = 157 resp. SD = 177) and only 73 trees per ha (SD = 104) in zone C. In the latter we sampled four trees per ha (SD = 9) in the 21–28 cm class; trees did not exceed 28 cm dbh. The number of individuals per class decreased with increasing dbh in zones A and B. All dbh classes in zone B revealed higher numbers of trees and recruits compared to zone A. Old trees exceeding 49 cm dbh doubled in number in zone B (31) compared to zone A (14, not shown in Fig. 16.7). The largest dbh were 114 cm in zone A and 113 cm in zone B.

16.3.4 Tree Species Population Structures and Regeneration

16.3.4.1 Density–Diameter Distributions

The different tree species *Abies spectabilis*, *Acer caudatum*, *Betula utilis*, *Sorbus microphylla* and *Rhododendron campanulatum* showed species-specific deviations from a basically similar density–diameter distribution (Fig. 16.5). A common characteristic is the reverse J-shape of the density–diameter distributions with significantly higher numbers of recruits in comparison to numbers of all other dbh classes. We found recruits only but no trees in nearly all uppermost reaches of each species' occurrences.

A. spectabilis: *A. spectabilis* exhibited high numbers of recruits <7 cm dbh in relation to the larger dbh classes in zones A and B. In general, this holds also for

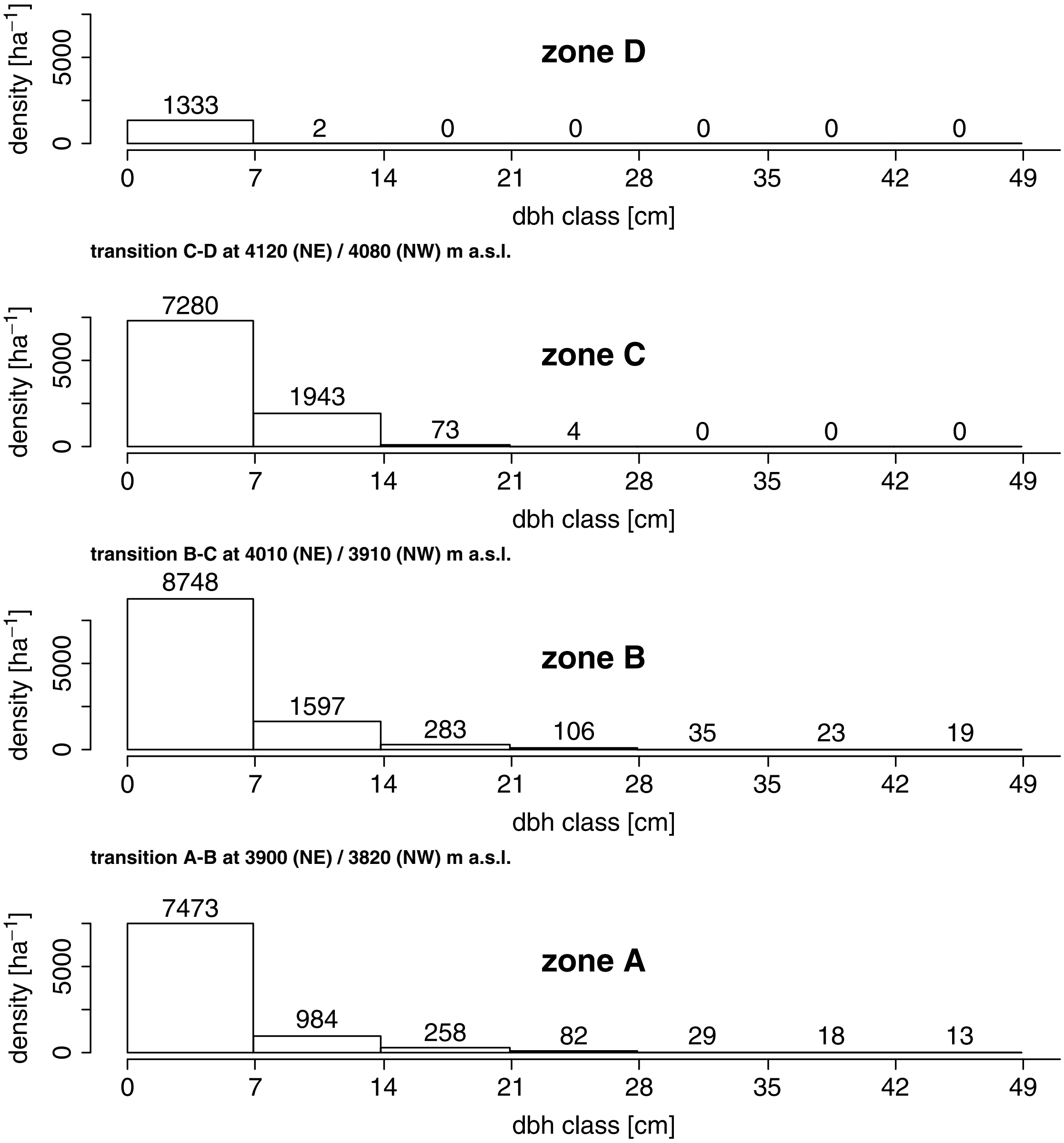

Fig. 16.7 Density–diameter distribution of all tree species in the altitudinal zones *A*, *B*, *C* and *D*. Only classes <49 cm dbh are printed (Source: Niels Schwab)

zone C; however recruit (62 per ha, SD = 120) and tree (6 per ha, SD = 12) abundances were very low and we did not find trees exceeding 22.8 cm dbh. In zone D only eight *A. spectabilis* recruits per ha (SD = 22) occurred and no individuals with dbh >7 cm. The number of trees exceeding 49 cm dbh differed in zones A and B: We found only four trees per ha in A and 27 per ha in B.

A. caudatum: *A. caudatum* occurred in zones A and B only and showed a high abundance of recruits (1695 per ha, SD = 1641) and tree individuals up to the dbh class 21–28 cm. No *A. caudatum* trees >7 cm dbh were detected in zone B, but 60 recruit individuals per ha (SD = 85).

B. utilis: Similar to *A. spectabilis*, the population structure of *B. utilis* differed with altitude. We found a high number of recruits in zone A (1942 per ha, SD = 1627) and decreasing abundances in larger dbh classes. In contrast to *A. spectabilis*, *B. utilis* exhibits a higher number of trees in all classes from 7 to 42 cm dbh in zone B. Further, the number of *B. utilis* exceeding 42 cm dbh is higher in zone A (24 per ha) compared to B (14 per ha). The absolute number of *B. utilis* recruits in zone B (547 per ha, SD = 611) is smaller compared to *A. spectabilis* recruits, and the ratio of recruits to trees is smaller due to the higher number of individuals in the tree classes > 7 cm dbh. In zone C, *B. utilis* showed 92 recruits per ha (SD = 219) and tree individuals in higher number and larger dbh's than *A. spectabilis*. We found merely four *B. utilis* recruits per ha (SD = 14) in zone D.

S. microphylla: *S. microphylla* recruits are of high abundance in zones A (1715 per ha, SD = 1248), B (924 per ha, SD = 798) and C (1591 per ha, SD = 2064). In zone A, *S. microphylla* tree individuals occurred only up to the dbh class 28–35 cm. *S. microphylla* is the only species with a substantial number of individuals in zone C, apart from *Rh. campanulatum* (see below). Even 206 recruits per ha (SD = 297) were present in zone D.

Rh. campanulatum: The population structure of *Rh. campanulatum* differed significantly from other species. In zone A, the number of recruits (959 per ha, SD = 1180) and trees per ha were in the same range as other species. *Rh. campanulatum* recruits exhibited significantly higher abundances of recruits in zones B (6361 per ha, SD = 5893), C (5435 per ha, SD = 2395) and D (1115 per ha, SD = 963). This prolific regeneration was followed by correspondingly high abundances in the subsequent dbh classes. However, *Rh. campanulatum* populations were poor concerning maximum dbh, which was 22.5 cm in zone A, 29.8 cm in zone B and 18.7 cm in zone C. In zone D, we found only recruits <7 cm dbh. Zone C exhibited a much more homogeneous all-species configuration of the 7–14 cm dbh class due to the high percentage of *Rh. campanulatum* individuals and less recruits per ha compared to zone B. Altitudinal transitions in *Rh. campanulatum* populations did not follow the trend of other species in terms of decreasing dbh and abundance with elevation (cf. Fig. 16.5). The smaller SD values of *Rh. campanulatum* recruit densities in zones B, C and D indicate that *Rh. campanulatum* population is spatially more homogenous intra-zone than recruit populations of other species. In contrast to zone A, *Rh. campanulatum* accounts for the significantly higher all-species tree densities in zones B and C (Fig. 16.4).

Total all-species recruit densities of zones A, B and C did not differ as much as the tree densities. All species show L-shaped or reverse J-shaped density–diameter distributions (Fig. 16.5). At some altitudinal zones, several species exhibit a very pronounced L-shape indicating an overproportional number of recruits compared to the classes above 7 cm dbh, e.g. *A. caudatum* and *B. utilis* in zone A and *S. microphylla* in C. Zone A contains more recruits of *A. spectabilis*, *B. utilis* and *S. microphylla* compared to zone B, where their recruit numbers are distinctly lower compared to tree densities (Figs. 16.4, 16.5 and 16.6).

In summary, we assessed largely prolific regeneration of all tree species. Seedling establishment of *B. utilis*, *A. spectabilis* and *S. microphylla* occurred to some extent far above the upper limit of adult trees. Some individuals of more than 2 m height even grew vigorously above the krummholz belt, where a small birch tree of 1.7 m in height was found in 4140 m a.s.l. Maximum recruit density occurred between 3920 and 3990 m a.s.l. (NE) resp. 3845–3890 m a.s.l. (NW) in zone B (more than 8700 N ha^{-1}), where *Rh. campanulatum* showed most intense recruitment (more than 6300 N ha^{-1}). Seedling/sapling density sharply decreased towards the alpine tundra (zone D), where only *Rh. campanulatum* and to some extent *S. microphylla* recruits occurred with considerable numbers of individuals.

16.3.4.2 Recruit Heights

The height class distributions of recruits showed clear variations between species and between altitudinal zones (Fig. 16.8). *Abies spectabilis* exhibited reverse J-shaped distributions in zones A and B, whereas the small numbers of recruits in zones C and D were rather homogenously distributed among classes. For *Acer caudatum*, we found a high percentage of tall recruits exceeding 2 m height and a slight increase in individual numbers from the 10 to 200 cm height classes in zone A. An evenly distributed small number of *A. caudatum* recruits occurred in zone B but was absent in zones C and D. *Betula utilis* recruits showed a heterogeneous distribution between height classes with a relative small number of seedlings smaller than 10 cm in height in zone A. In zone B, the taller height classes exceeding 50 cm had higher recruit densities. The same holds for zone C, however with distinctly smaller recruit numbers. In zone D, we found four *B. utilis* recruits per ha exclusively in the height class of 131–200 cm. *Sorbus microphylla* showed increasing class sizes with increasing recruit heights in zones A, B and C, except for the 10 cm class in zone B which contained c. three times more recruits than the subsequent 50 cm class. The distribution of *S. microphylla* recruits in zone D corresponds to a bell shape with no individuals smaller than 10 cm. *Rhododendron campanulatum* exhibited a reverse J-shape in zone A and a reverse L-shape with the overall highest number of recruits in any class in zone B with c. 4400 per ha in the ≤10 cm class. The height class distribution in zone C was rather homogenous, while it resembled the bell shape in zone D.

The average recruit height of all tree species was tallest in zone C followed closely by mean height in zone A (Fig. 16.9, black dotted line). Likewise, the recruits of most single species reached their maximum height in zone C. In general, recruits of *Prunus rufa*, *B. utilis*, *S. microphylla* and *A. caudatum* showed a mean height of more than 130 cm, which is taller than the recruit mean height of *Juniperus recurva*, *Rh. campanulatum* and *A. spectabilis* in all altitudinal zones. Recruits of all species in zone D showed a lower height growth compared to zone C, except for *B. utilis*, whose recruit height increased slightly. *B. utilis* was the only species with a continuous, however gentle, increase in mean recruit height with elevation. The average height of *B. utilis* and *S. microphylla* recruits were distinctly taller than *A. spectabilis* and *Rh. campanulatum* recruits in zone D (cf. Fig. 16.9). *S. microphylla* recruits' height did not change distinctly along the altitudinal gradient. The height of *Rh. campanulatum* recruits exhibited highest values in zone C and smallest in

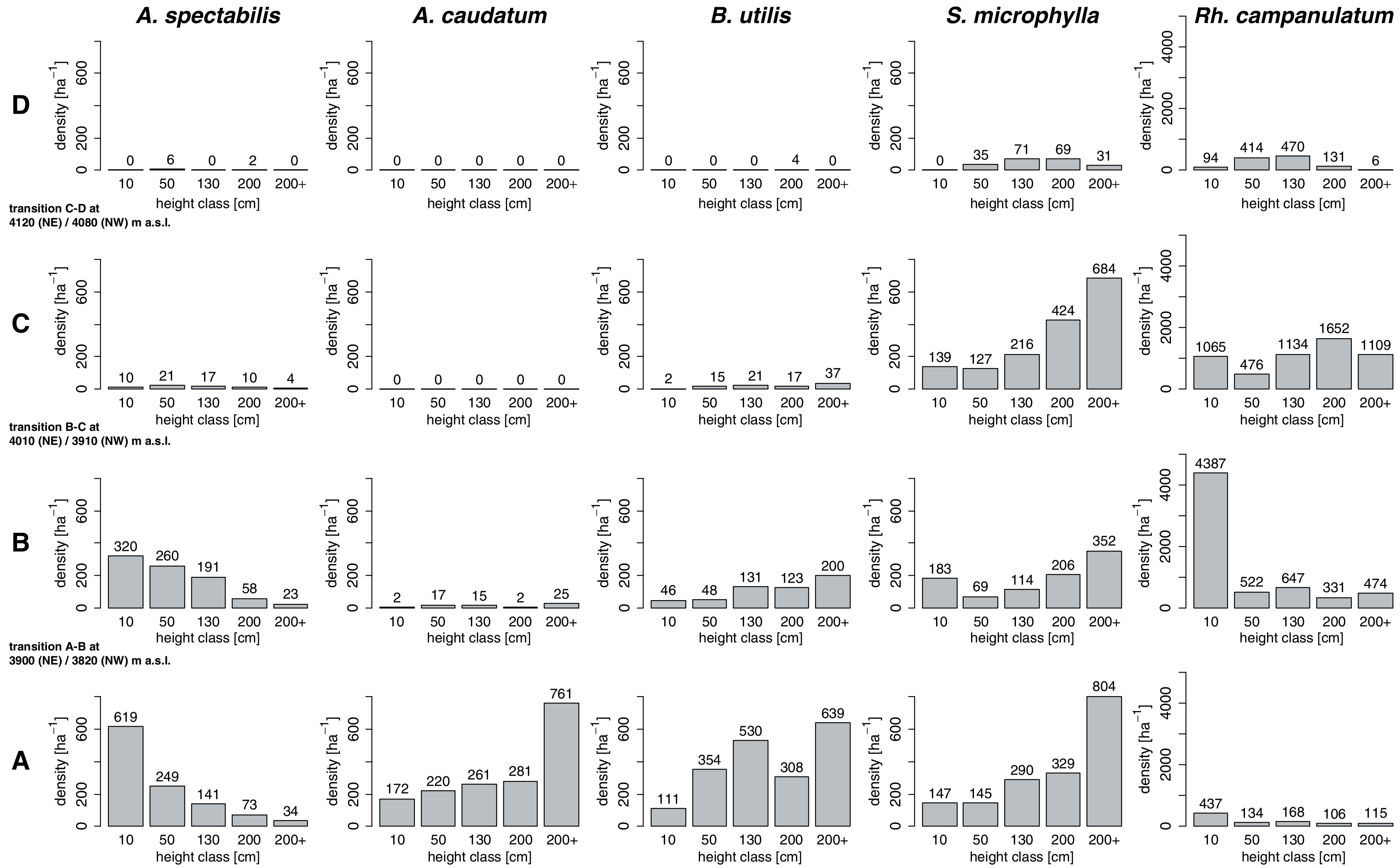

Fig. 16.8 Species-wise recruit (<7 cm dbh) height class distribution of the most abundant tree species in the altitudinal zones *A*, *B*, *C* and *D*. Height class intervals: 10: ≤10 cm, 50: ≤50 cm, 130: ≤130 cm, 200: ≤200 cm, 200+: >200 cm. Note difference in scaling of *Rhododendron campanulatum* y-axis (Source: Niels Schwab)

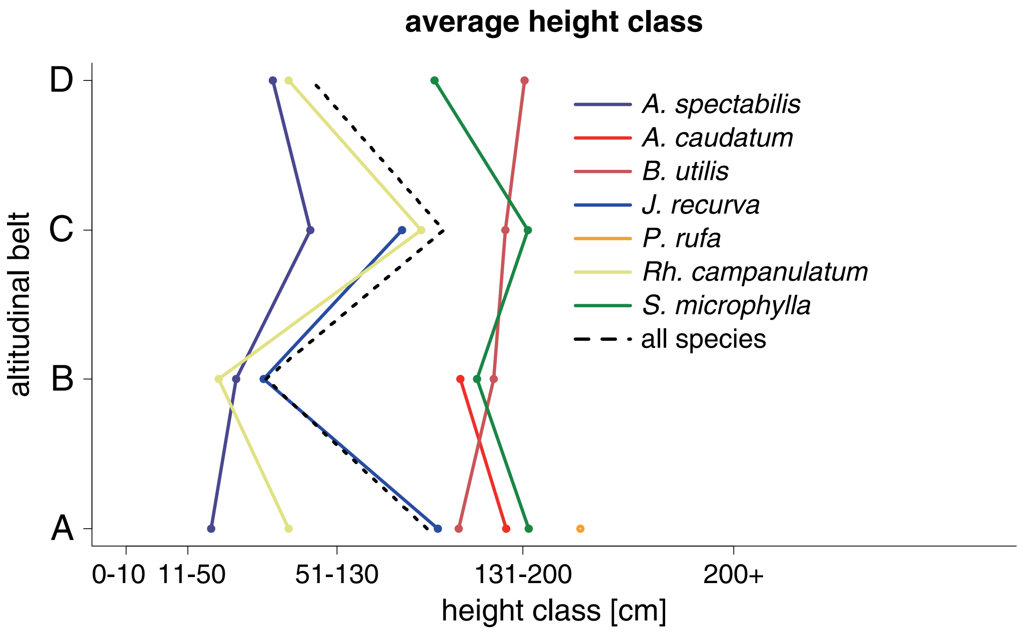

Fig. 16.9 Recruit height class distribution along the altitudinal gradient for all species and species wise (Source: Niels Schwab)

zone B (in average < 50 cm). *A. spectabilis* recruits showed compared to other species smallest heights in all zones except in zone B where *Rh. campanulatum* recruits did not reach the height level of *A. spectabilis*. Nevertheless, the mean height of *A. spectabilis* recruits increased constantly with elevation up to zone C (cf. Fig. 16.9).

16.3.4.3 Regeneration Index (*RI*)

The regeneration index (*RI*) of the recruits of all species showed the highest value in zone A, followed by C, B and D (Fig. 16.10, black dotted line). The single species showed different *RI* patterns: *Rhododendron campanulatum* exhibited the most conspicuous values along the altitudinal gradient with a rather low *RI* in zone A and an *RI* higher than any of the other species in zones B, C and D (Fig. 16.10). Like *Rh. campanulatum Sorbus microphylla* shows a non-uniform *RI* trend along the gradient with the second highest *RI* level of all species in zones B, C and D (Fig. 16.10). The *RI* reached nearly 130,000 in zone C, while the maximum of all other species except *Rhododendron* was only 7000 (*Betula utilis*). In contrast to *S. microphylla*, the *RI* value of *Acer caudatum* was very low in zone B. The *RI*s of *B. utilis* and *Abies spectabilis* constantly decreased towards zone D (Fig. 16.10). For instance, *A. spectabilis* showed a value of 25,000 in zone A, 20,000 in B and only 2400 and 260 in zones C and D. *Juniperus recurva* and *Prunus rufa* showed the overall smallest *RI* values in zones A and B (Fig. 16.10).

Depending on the regeneration indicator in focus, different species seem to perform better at different altitudinal positions. While the mean height (Fig. 16.9) shows whether the population of a species is able to reach a specific mean sprout height, the *RI* (Fig. 16.10) provides information on the actual performance of the recruits of a species by incorporating their abundance. Comparing values of both

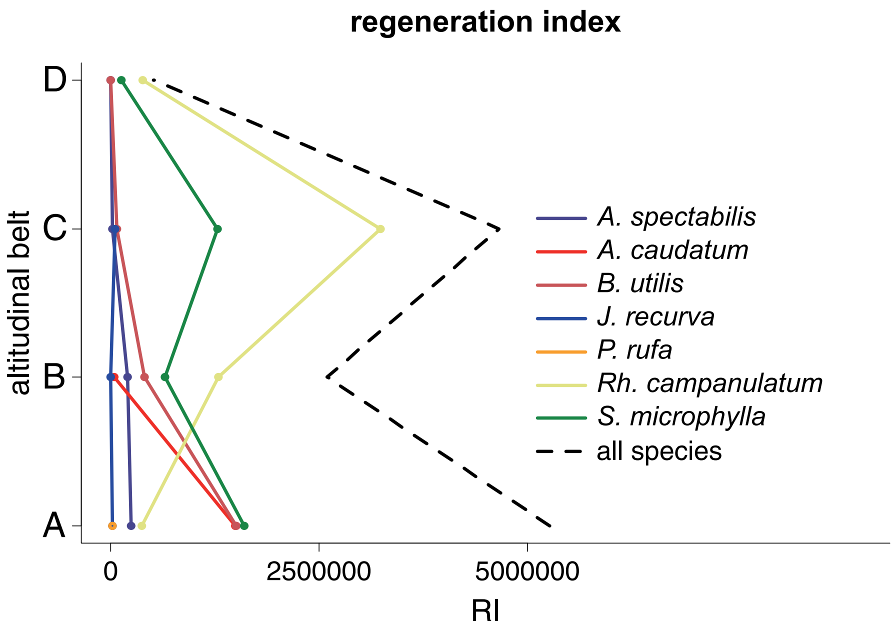

Fig. 16.10 Regeneration index *RI* species wise and sum of all species (Source: Niels Schwab)

indicators, it becomes obvious that the height–abundance patterns of the different species are complex and non-uniform. The small *RI* values of *B. utilis* in zones C and D contrast with their high mean heights. Obviously *B. utilis* recruits are able to grow at these altitudes but they do not grow in considerable abundance. On the other hand, *A. spectabilis* recruits with similarly low *RI* values in C and D grow up to a considerably lower height only, the lowest of all species in zones C and D. These relations indicate a comparatively better performance of *B. utilis* at these high-elevation environments. Both height and *RI* of *S. microphylla* exhibited high and even highest values and we even found rare tree individuals ≥7 cm dbh in zone D. The dbh classes above 14 cm dbh include only small numbers of *S. microphylla* in the lower zones (Fig. 16.5). *Rh. campanulatum* exhibited an enormously high *RI* and highest *Rhododendron*-specific mean height together with the absolute dominance in zone C (Figs. 16.4 and 16.6). In zone D, *Rh. campanulatum*'s heights are lower, and we did not find any individuals ≥7 cm dbh among the number of 1115 recruits per ha, which is more than five times the abundance of *S. microphylla* recruits.

16.3.5 Abruptness Patterns of Trees and Recruits at Elevational Transitions

In general, values of stand parameters such as dbh, tree height and tree density decreased with elevation. Along this gradient, the degree of abruptness of these parameters increased at the transitions between single zones (Fig. 16.11 and Tables 16.4 and 16.5). The abruptness of recruit density exhibited the same trend, while the abruptness in terms of recruit height classes was highest at the transition A to B, lowest at B to C and intermediate at the transition from zone C to D (Fig. 16.11 and Tables 16.4 and 16.5).

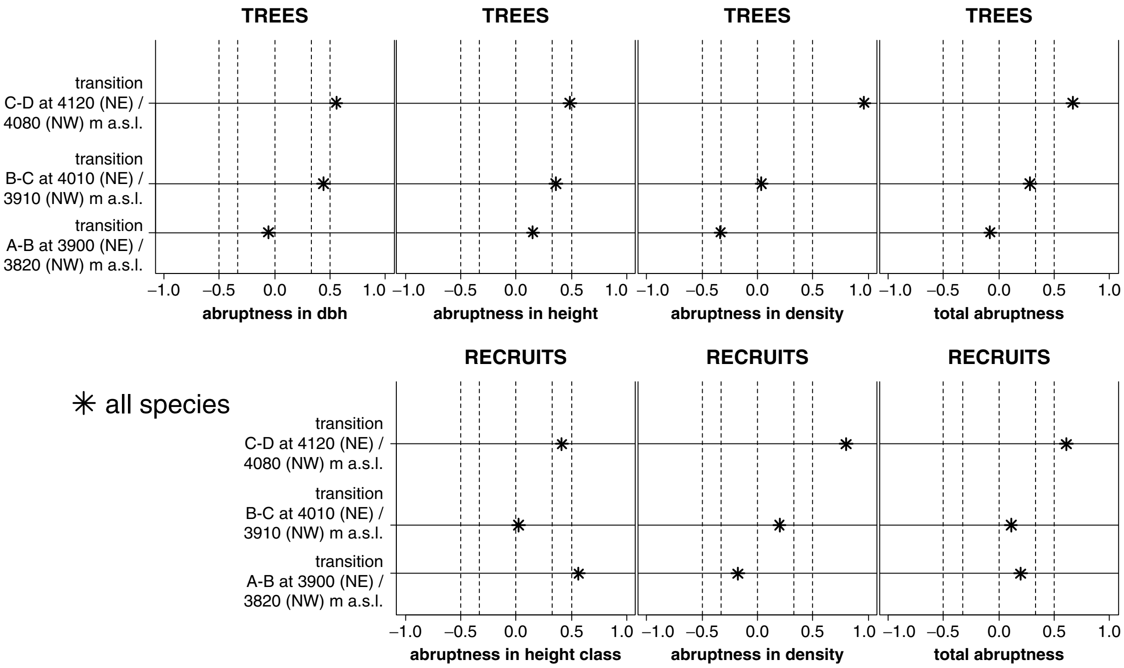

Fig. 16.11 Abruptness in dbh, height, density and sum of abruptness values for trees and recruits from zone *A* to *B*, *B* to *C* and *C* to *D* (Source: Niels Schwab)

The total all-species tree density (Table 16.4, Fig. 16.11) decreased most abruptly (abruptness = 0.96) at the transition CD, while the decrease was less but nearly equally abrupt for dbh and tree height at BC and CD (dbh: abruptness = 0.48 resp. 0.52; height: abruptness = 0.39 resp. 0.45). This pattern differed between single species: Density of *Betula utilis*, *Sorbus microphylla* and to a certain extent *Abies spectabilis* trees decreased abruptly at the transition from B to C (abruptness = 0.92 resp. 0.62 resp. 0.5), while *Rhododendron campanulatum*'s density increased intermediately from B to C (abruptness= –0.32) and dropped abruptly from maximum to the smallest density at the transition from C to D (abruptness = 1). Abruptness of the transitions with regard to dbh and tree height did not resemble density abruptness, neither for all species nor species-wise (Table 16.4).

For instance, *B. utilis*, *Rh. campanulatum* and *A. spectabilis* showed the most abrupt transitions in tree height at CD and this applied also for dbh of *B. utilis* and *Rh. campanulatum*. The majority of transitions of all species' trees showed positive abruptness values, indicating the decrease of dbh, height and stand density with elevation. Negative values mainly occurred at the transition from zone A to B, e.g. for all species density (intermediate, abruptness = –0.34), densities of *B. utilis* (smooth, abruptness = –0.21) and *Rh. campanulatum* (abrupt, abruptness = –0.54) and dbh of *A. spectabilis* (abrupt, abruptness = –0.53). While we found uniform numbers of abrupt and smooth transitions for trees of *A. spectabilis*, *B. utilis* and *Rh. campanulatum*, the smooth transitions nearly doubled the number of abrupt ones in case of *S. microphylla*.

The total all-species recruit density (Table 16.5 and Fig. 16.11) decreased most abruptly (abruptness = 0.8) at the transition from zone C to D, while there were distinct decreases in terms of recruit height at the transitions from zone A to B (abrupt, abruptness = 0.57) and from C to D (intermediate, abruptness = 0.41). As

Table 16.4 Abruptness of transitions of tree (dbh ≥7 cm) densities, dbh and height for all species and species–wise

	All species			*Abies spectabilis*			*Acer caudatum*			*Betula utilis*			*Prunus rufa*			*Rhododendron campanulatum*			*Sorbus microphylla*		
	Density	dbh	Height	Density	dbh	Height	Density	dbh	Height	Density	dbh	Height	Density	dbh	Height	Density	dbh	Height	Density	dbh	Height
CD	0.96	0.52	0.45	0.03	0.44	0.65	0.00	0.00	0.00	0.08	0.70	0.76	0.00	0.00	0.00	1.00	0.78	0.60	0.14	0.38	0.18
BC	0.04	0.48	0.39	0.50	0.56	0.35	0.00	0.00	0.00	0.92	0.26	0.22	0.44	1.00	0.90	−0.32	0.18	0.33	0.61	0.30	0.65
AB	−0.34	−0.06	0.16	0.47	−0.53	−0.28	1.00	1.00	1.00	−0.21	0.04	0.02	0.56	−0.14	0.10	−0.54	0.05	0.07	0.24	0.32	0.17

Table 16.5 Abruptness of transitions of recruit (dbh <7 cm) density and height for all species and species–wise

	All species		*Abies spectabilis*		*Acer caudatum*		*Betula utilis*		*Juniperus recurva*		*Prunus rufa*		*Rhododendron campanulatum*		*Sorbus microphylla*	
	Density	Height cl.	Density	Height cl.	Density	Height cl.	Density	Height cl.	Density	Height cl.	Density	Height cl.	Density	Height cl.	Density	Height cl.
CD	0.80	0.41	0.05	0.16	0.00	0.00	0.05	–0.43	1.00	0.96	0.00	0.00	0.80	0.43	0.92	1.00
BC	0.20	0.02	0.72	–0.68	0.04	0.94	0.24	–0.20	–0.96	–0.23	0.00	0.00	0.17	–1.00	–0.44	–0.88
AB	–0.18	0.57	0.24	–0.32	0.96	0.06	0.72	–0.37	0.17	0.27	1.00	1.00	–1.00	0.37	0.52	0.88

for trees this all-species pattern was not resembled by every single species: Density of *Rh. campanulatum* and *S. microphylla* recruits decreased abruptly at the transition from zone C to D (abruptness = 0.8 resp. abruptness = 0.92), while the most abrupt decreases of *A. spectabilis* and *B. utilis* recruits occurred at the transition BC (abruptness = 0.72) and AB (abruptness = 0.72), respectively. Again, abruptness of the transitions with regard to recruits' height did not resemble density abruptness neither for all species nor species-wise (Table 16.5). In general, we found many negative values, indicating increasing recruit heights with elevation. *Rh. campanulatum*, *S. microphylla* and *A. spectabilis* recruits' mean height increased abruptly at the transition from zone B to C (abruptness = −1.0 resp. abruptness = −0.88 resp. abruptness = −0.68). Except *B. utilis*, which showed increasing recruit height at all transitions, decreasing recruit heights at the transition from zone C to D were found. These were smooth for *A. spectabilis* (abruptness = 0.16), intermediate for *Rh. campanulatum* (abruptness = 0.43) and abrupt for *S. microphylla* (abruptness = 1.0).

16.3.6 Near-Natural State of Treeline Ecotone

All assessed density–diameter distributions resembled a reverse J- or L-shape, thus indicating a near-natural state of the Rolwaling treeline. The total number of tree stumps decreased considerably with elevation (Table 16.6). In zone B, the basal area of stumps (medium and less decomposition) amounted only to 3 % of the total basal area (living trees and stumps), while it was less than 0.5 % in zone C. Thus, wood cutting and its influence on stand structures is negligible. In zone A, the stump basal area was higher (21 %), but potential modifications of stand structure here do not affect timberline and treeline transitions at higher altitudes. The species composition of stumps of all decomposition classes exhibited *Sorbus microphylla* (c. 17 stumps per plot in average), *Acer caudatum* (c. 11) and *Betula utilis* (c. 9) as most affected in zone A. *S. microphylla* (c. 7), *Rhododendron campanulatum* (c. 7) and *B. utilis* (c. 6) accounted for most stumps in zone B (Table 16.6).

According to our field observations, influences of herbivores and domesticated animals can be ruled out. We found minimal evidence for deer, like faeces and bark stripping. We observed pika (*Ochotona* sp.), weasel (*Mustela* sp.) and snowcock (*Tetraogallus* sp.) more often, but no influence on treeline stand structures could be identified. Since the study slopes are separated by the river from settlements and thus very difficult to access, we did not observe any grazing impact. Further evidence for a negligible anthropogenic impact in the Rolwaling treeline ecotone is given by soil and atmospheric data. Investigations of bulk densities in the prevailing podzol soils revealed low mean values from 0.01 g cm^{-3} (decomposition layer) to a maximum of 1.14 g cm^{-3} (Ae horizons), indicating obviously undisturbed soils. Monitoring of atmospheric nitrogen deposition (nitrogen dioxide (NO_2), ammonia (NH_3)) below detection limit indicate no effect in the study area.

Table 16.6 Mean basal area of tree stumps (≥7 cm diameter) in proportion to stump + living trees (≥7 cm dbh) mean basal area in altitudinal zones *A, B, C* and *D* (in total and differentiated in causes of death) and species composition of stumps

Condition		*A*	*B*	*C*	*D*
Living trees	Basal area trees [m^2/ha]	28.77	47.93	13.29	0.01
Undecomposed + slight decomposition	**Stumps basal area (total basal area of living trees + stumps = 100 %) [%]**	**7.1**	**0.04**	**0.08**	**0.00**
	Natural cause [%]	0.00	43.36	0.00	–
	Anthropogenic cause [%]	93.71	56.64	0.00	–
	Unidentified cause [%]	6.29	0.00	100.00	–
Undecomposed + slight + medium decomposition	**Stumps basal area (total basal area of living trees + stumps = 100 %) [%]**	**19.04**	**2.89**	**0.49**	**0.00**
	Natural cause [%]	0.00	0.56	0.00	–
	Anthropogenic cause [%]	96.13	90.94	20.20	–
	Unidentified cause [%]	3.87	8.50	79.80	–
Undecomposed + slight + medium + intense decomposition	**Stumps basal area (total basal area of living trees + stumps = 100 %) [%]**	**64.65**	**20.81**	**5.15**	**0.00**
	Natural cause [%]	0.17	28.56	35.63	–
	Anthropogenic cause [%]	51.29	31.57	32.68	–
	Unidentified cause [%]	48.54	39.87	31.69	–
Species composition of stumps					
	Mean number of stumps per plot	*A*	*B*	*C*	*D*
All decomposition classes	*Abies spectabilis*	6.00	1.86	0.00	0.00
	Acer caudatum	11.00	0.00	0.00	0.00
	Betula utilis	9.00	5.67	2.50	0.00
	Prunus rufa	1.67	0.00	0.00	0.00
	Rhododendron campanulatum	3.00	6.67	4.00	0.00
	Sorbus microphylla	16.62	6.60	3.00	0.00
	Unidentified	9.00	5.00	0.00	0.00
	Sum	**56.28**	**25.79**	**9.50**	**0.00**

16.3.7 Soil and Air Temperatures

In general, mean soil and mean air temperatures show similarly decreasing trends with elevation (Fig. 16.12). In winter (DJF) and autumn (ON) seasons of 2013, the mean soil temperatures of zones B and D exceeded soil temperatures of the respective subjacent zones, most likely due to cold air drainage (A) and less irradiation and/or less snow cover insulation (evergreen *Rhododendron campanulatum* cover in zone C). We measured a growing season mean soil temperature of 7.5 ± 0.5 °C at the transition from zone B to C. Growing degree days differed between the two lower

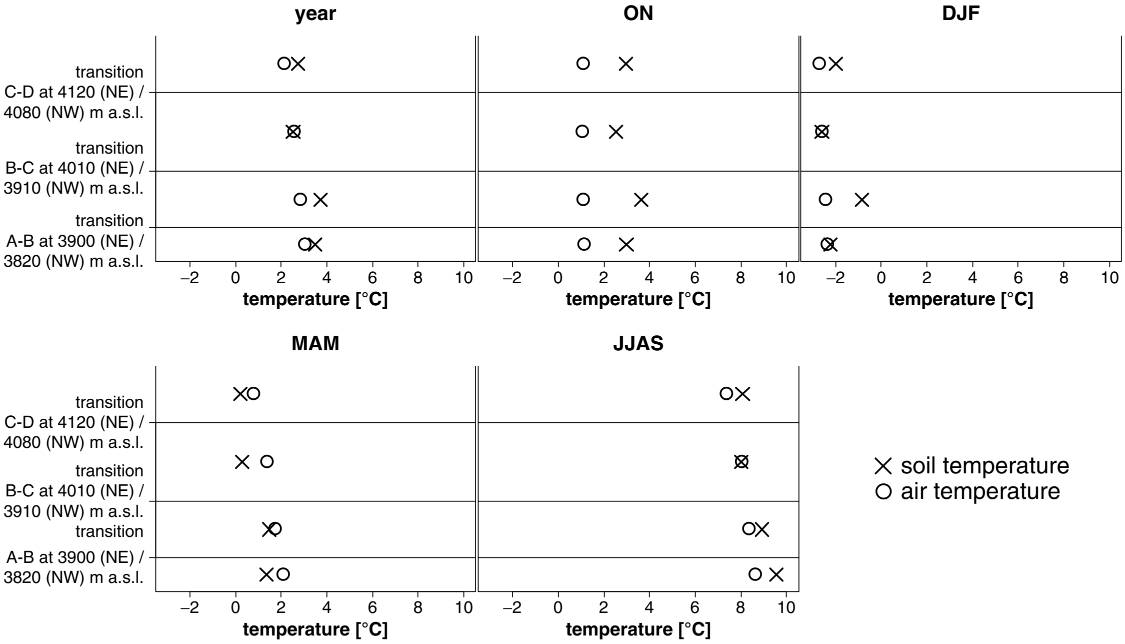

Fig. 16.12 Yearly and seasons' mean soil and air temperatures of the four altitudinal zones *A*, *B*, *C*, *D*. *ON* October/November, *DJF* December–February, *MAM* March–May, *JJAS* June–September (Source: Niels Schwab)

zones (A: 175 days, B: 177 days) and the upper zones (C: 158 days, D: 154 days) showing a shortening of the growing season in the uppermost zones by c. 3 weeks.

Yearly mean soil and air temperatures differed most in altitudinal zone B (soil: 3.7 °C; air: 2.8 °C) and nearly equalled in zone C (soil: 2.5 °C; air: 2.6 °C). At BC, the transitions of soil temperature (zone B → zone C; year: −1.2 °C; ON: −1.1 °C; DJF: −1.8 °C; MAM: −1.2 °C; JJAS: −0.9 °C) exceeded the differences of air temperatures (zone B → zone C; year: −0.3 °C; ON: −0.1 °C; DJF: −0.1 °C; MAM: −0.4 °C; JJAS: −0.3 °C). Soil temperatures exhibited abrupt transitions along the elevational gradient (Fig. 16.13). The annual mean soil temperature and mean soil temperatures of autumn, winter (all abruptness = 1) and spring (abruptness = 0.94) dropped very abruptly at the transition BC. This decrease was less pronounced in summer (abruptness = 0.59). We found rather unexpected increases of soil temperatures with increasing elevation at the AB and CD transitions in autumn (abruptness = −0.59 resp. abruptness = −0.39), winter (abruptness = −0.78 resp. abruptness = −0.34) and for the annual mean soil temperatures (abruptness = −0.22 resp. abruptness = −0.18). In spring, the soil temperatures of the transitions AB (abruptness = −0.08) and CD (abruptness = 0.06) were similar to each other. In summer, soil temperatures decreased nearly abruptly from zone A to B (abruptness = 0.41), while they differed only slightly at the transition from zone C to D (abruptness = −0.03).

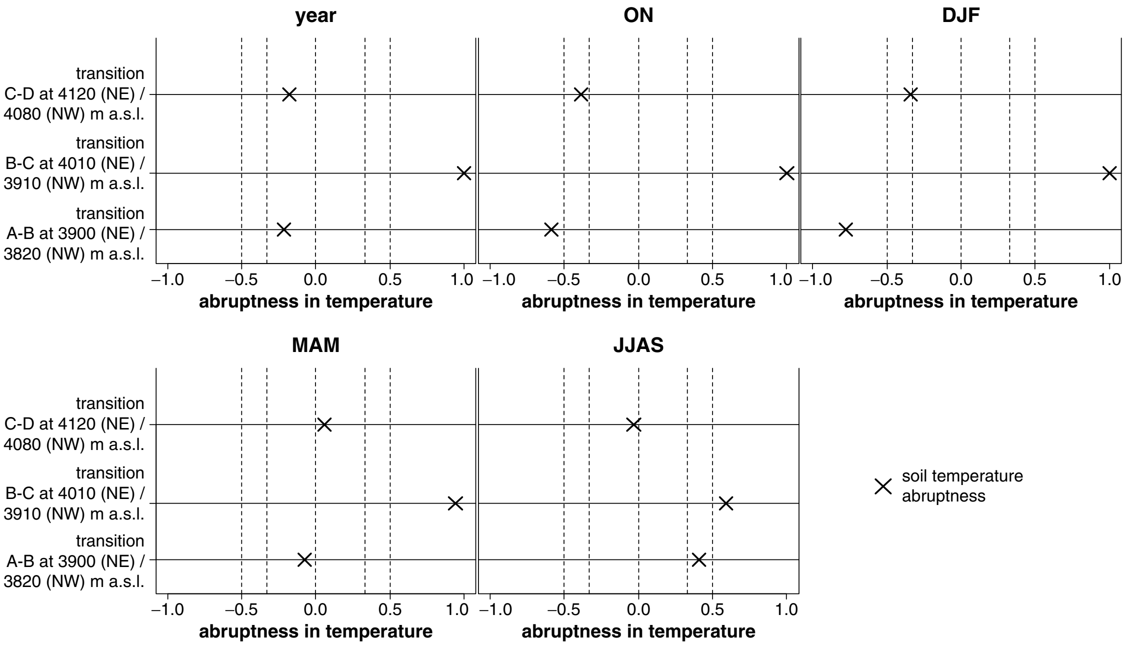

Fig. 16.13 Yearly and seasons' mean soil temperature abruptness along the altitudinal gradient at transitions from zone *A* to *B*, *B* to *C* and *C* to *D*. *ON* October/November, *DJF* December–February, *MAM* March–May, *JJAS* June–September (Source: Niels Schwab)

16.4 Discussion

16.4.1 Treeline Structure and Treeline Responsiveness to Climate Warming

In general, the tree species composition and altitudinal position of the Rolwaling treeline ecotone coincides with previous findings for north-facing slopes in central and E Nepal, where *Abies spectabilis*, *Betula utilis*, *Sorbus microphylla* and *Rhododendron campanulatum* dominate the ecotones between 3900 and 4400 m (Schickhoff 2005; Miehe et al. 2015). Considering the altitudinal zonation of vegetation within the treeline ecotone, in particular the dense *Rh. campanulatum* thicket in zone C, it is evident that the Rolwaling treeline has to be assigned physiognomically to treelines with a krummholz belt (cf. Holtmeier 2009). The contorted and gnarled growth form of *Rh. campanulatum* is, however, not necessarily genetically predetermined (cf. Miehe 1990), since there are some upright-growing individuals at lower altitudes in zones A and B (Fig. 16.14). *Rh. campanulatum* thickets in the lower C zone reach a considerable height of more than 3–4 m and stems may attain large diameters. Thus, these thickets can also be termed dwarf forests (cf. Masuzawa 1985). Towards their upper altitudinal limit at the transition CD, these thickets or dwarf forests are gradually reduced in height and become climatically stunted. Within the krummholz thicket in lower zone C, the uppermost tree individuals (>3 m height) of *A. spectabilis* and *B. utilis* mark the outpost-treeline sensu Körner (2012, Fig. 16.3), which is located slightly upslope (30–50 m altitude difference) from the treeline. The latter connects the uppermost patches of forest composed of

Fig. 16.14 *Rhododendron campanulatum* growing upright in zones *A* and *B* (**a** Schwab, 30 July 2013) and as krummholz in zone *C* (**b** Schwab, 29 September 2014) (Source: Niels Schwab)

trees with true tree habitus and coincides with the transition BC (4010 m NE; 3910 m NW) in our slope stratification scheme (cf. Figs. 16.1 and 16.2). Within the subalpine forest, *Abies* and *Betula* trees reach timber size up to the treeline, thus the difference in altitude between timberline and treeline is negligible (terminology sensu Körner 2012).

Variations in uppermost distribution limits of treeline species basically reflect species-specific physiological capacities to survive environmental stresses. Limits on upslope expansion can be imposed by potentially limiting resources (carbon, water, nutrients) and by physical factors, e.g. growing season length, frost intensity, wind exposure, abrasion, etc. (Crawford 2008). Obviously, physiological tolerances of treeline species in Rolwaling are sufficient to establish recruits far above the uppermost adult trees. The wide krummholz belt (up to 200 m altitude difference) with absolute dominance of *Rh. campanulatum* does not constitute an insurmountable barrier for other treeline species. Uppermost individuals of *A. spectabilis* (4185 m), *B. utilis* (4140 m) and *S. microphylla* (4245 m) occur above the krummholz belt in zone D. The tree species lines give evidence of successful regeneration even under the harsh climatic conditions of treeless terrain, at least to a sapling stage of 1–2 m height. Although these recruits are few in number, mostly stunted, mostly growing in the ‘chamaephyte environment’ (Wieser et al. 2014), and far away from reaching any tree size definition, they partially project above the snow cover and indicate the potential for treeline advance under more favourable environmental conditions. Even above the krummholz belt, tree species might be hindered by the dense alpine dwarf scrub heath vegetation (mainly composed of *Rhododendron anthopogon*, *Rhododendron lepidotum*, *Rhododendron setosum*) because shrub community competitive abilities might affect tree establishment (Körner 2012; Schickhoff et al. 2016; Chhetri and Cairns 2015). The recruit density of *A. spectabilis* decreases abruptly from B to C. The abrupt decrease indicates a lower potential for upward migration in comparison to *B. utilis* recruits which showed a smooth transition in density and height from B to C. *S. microphylla* has the best premise to advance to higher elevations given the negative abruptness values of *Sorbus* recruits at the transition from zone B to C and absolute density and mean height values.

How is the structure of the Rolwaling treeline related to the responsiveness to climate warming? Our data suggests that the extensive *Rh. campanulatum* krummholz belt plays a crucial role for any treeline shift to higher altitudes. High competitiveness and absolute dominance of *Rh. campanulatum* prohibits to a large extent upslope migration of other treeline tree species from the closed forests in zones A and B. Supposed allelopathic effects of *Rh. campanulatum* might contribute to the low establishment rates of other tree species in the krummholz thickets (Schickhoff et al. 2015, 2016). Thus, the treeline position is rather stable, and a considerable treeline advance is not to be expected in the medium term (several years to a few decades). Our results are in line with Harsch and Bader (2011), who concluded from a global treeline dataset a comparatively low responsiveness of krummholz treelines compared to diffuse treelines. They found the majority of diffuse treelines and only one third of krummholz treelines to be advancing, while abrupt and island treelines were found to be rather stable. The disjunction of mechanisms and environmental conditions primarily associated with these different treeline forms seem to explain this pattern (cf. Harsch and Bader 2011). Krummholz treelines in the Himalaya (cf. Miehe 1990, 1991; Schmidt-Vogt 1990; Miehe and Miehe 2000) have not been analysed so far with regard to their responsiveness to climate warming. Schickhoff et al. (2015) provide a first overview of the sensitivity of krummholz treelines in Rolwaling and Langtang. In the latter, seedling establishment beyond the actual upper limit of contiguous forests was detected which is a sign for a potential treeline shift. Chhetri and Cairns (2015) found a slight upward shift of an undisturbed diffuse treeline in Nepal’s Makalu Barun National Park. However, they state that the treeline has advanced only until the early twentieth century. Other studies on treelines in Nepal Himalaya report tree and/or recruit densities of all occurring or selected species (Ghimire and Lekhak 2007; Shrestha et al. 2007, 2014; Gaire et al. 2010, 2011, 2014; Ghimire et al. 2010; Lv and Zhang 2012; Sujakhu et al. 2013). None of the cited studies refers to a treeline ecotone which is regarding dominance and spatial extent similar to zone C of our study area. In general, most treeline ecotones in Nepal are disturbed by human impact which has changed population structures since long.

Our data suggest that high abruptness values along the altitudinal gradient are associated with major changes in site factors. At the transition BC, i.e. the transition from upright-growing tree individuals to krummholz, we found the most abrupt change in soil temperatures. The distinct decrease in soil temperatures is obviously related to the dense foliage and canopy of the evergreen *Rh. campanulatum* thickets which provide a more efficient isolation of the soil surface from solar radiation and subsequent heat transformation compared to the upper subalpine *Abies*-*Betula* forest. Abrupt microenvironmental changes are commonly associated with abrupt treelines (cf. Harsch and Bader 2011; Cieraad and McGlone 2014), corresponding in the Rolwaling case to an abrupt transition from forest to krummholz. Although krummholz treelines represent a definite treeline form, they can obviously feature abrupt treeline characteristics (cf. Fig. 16.2).

In contrast to diffuse treelines, advances of both abrupt and krummholz treelines are connected rather to winter warming and reduced winter stress factors than to growing season temperature (Harsch et al. 2009). Tree growth is assumed being rather limited by dieback (short-term stressors) than by limited biomass gain (long-term mild stress, Harsch and Bader 2011). In consequence, it is likely that the Rolwaling treeline is rather influenced by winter condition stress factors. These lead to plant damage and limit survival. Vertical growth in krummholz depends on the degree of structural microsite facilitation, e.g. reduced wind and sun exposure, and beyond treeline tall seedling growth is likely limited by the same factors (Smith et al. 2003). Thus, recruitment beyond treeline is restricted as long as vertical growth-limiting conditions prevail (Harsch et al. 2009). In Rolwaling, growing season temperature and length is likely to increase while duration of winter conditions (frost days) decreases (Gerlitz et al. 2014). Nevertheless, we assume that the consequences of winter conditions for plant growth will not change substantially because processes like wind abrasion, snow and ice damage occur regardless of the length of the frost period. Most likely heavy snowpack provokes mechanical stress and dieback in the krummholz belt. A short-term treeline shift in response to climate warming is not to be expected.

Obviously, *Rh. campanulatum* wood has mechanical properties which enable the described growth form, similar to the flexibility of, for example, *Alnus* sp., *Betula* sp., *Salix* sp. and *Nothofagus* sp. at various treelines on earth (Jalkanen and Konocpka 1998; Gallenmüller et al. 1999; Körner 2012). Most likely, this property facilitates the establishment of *Rh. campanulatum* under harsh climatic conditions.

B. utilis, and to a lesser extent *A. spectabilis* and *S. microphylla*, shows maximum abruptness values over different transitions (Tables 16.4 and 16.5). This distribution indicates that these species still perform well in growth parameters like dbh and tree height in zone C, while density decreases abruptly at lower altitude. Single individuals of *A. spectabilis*, *B. utilis* and *S. microphylla* appear to profit from variations in *Rh. campanulatum* density (canopy openings) and/or variations in environmental factors like exposition and soil parameters (microsite facilitation). The abruptness values of the Rolwaling treeline ecotone show a heterogeneous pattern across slopes and development stages (Tables 16.4 and 16.5 and Fig. 16.15) confirming the need for a differentiated categorization and species-specific analyses of treelines at local and landscape scales (Trant and Hermanutz 2014; Schickhoff et al. 2015, 2016).

16.4.2 Soil Temperature and Regeneration

In general, tree and recruit species compositions of altitudinal zones correspond to each other with distinct higher number of recruits than trees (Figs. 16.4, 16.5 and 16.6), indicating sustainable regeneration and stable populations. However, no tree individual of any species occurred in zone D (except *Sorbus microphylla*), while recruits of *Abies spectabilis*, *Betula utilis*, *S. microphylla* and *Rhododendron campanulatum* exist. These recruits are potential indicators for an upward shift of tree species distributions triggered by recent climate warming (see above), and a recent

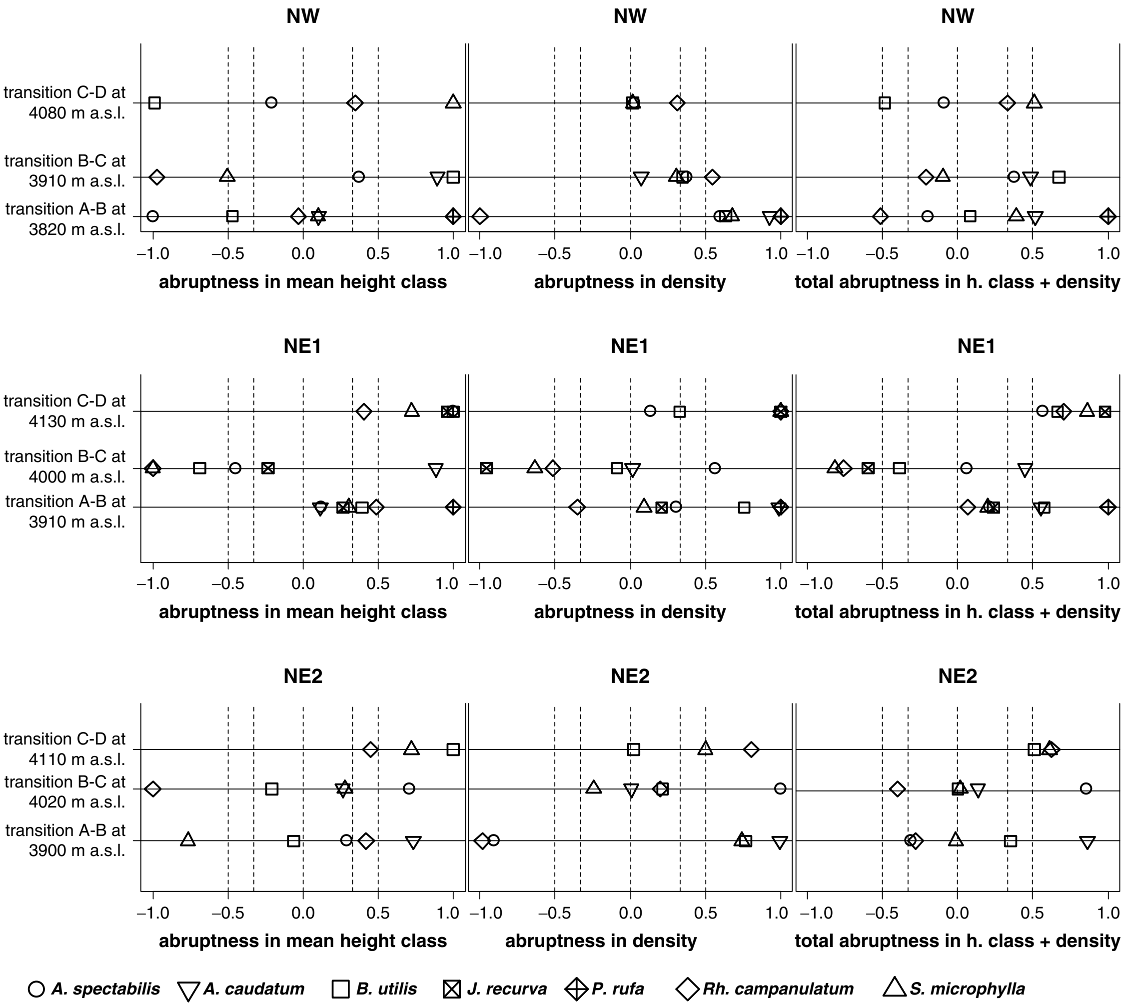

Fig. 16.15 Species- and slope-wise height, density and total recruit abruptness of transitions from zone *A* to *B*, *B* to *C* and *C* to *D* (Source: Niels Schwab)

increase in recruit density could increase the numbers of trees in the near future. The occurrence of recruits in zone D indicates the potential of tree species to become established above the krummholz belt.

Recruit densities of *A. spectabilis*, *B. utilis* and *S. microphylla* correlate positively in nearly all height classes with soil temperature. *Rh. campanulatum* densities correlate both, positively (height classes <3 cm and >200 cm) and negatively (height ≥3 cm and ≤200 cm; cf. Schickhoff et al. 2015). Thus, increasing soil temperatures potentially support the process of tree species establishment above the current treeline. Interestingly, soil temperatures at the Rolwaling treeline are higher compared to the global mean at treeline elevations. We measured a growing season mean soil temperature of 7.5 ± 0.5 °C under uppermost forest stands of *A. spectabilis* and *B. utilis* at the transition BC (Müller et al. 2015), a similar value as the warm temperate bioclimatic region seasonal mean temperature of 7.4 ± 0.4 °C, but distinctly higher than the global growing season mean soil temperature of 6.4 ± 0.7 °C (Körner 2012). This significant deviation from the global mean adds to the rather broad range of soil temperatures (5–9 °C) measured at treeline elevations (e.g.

Walter and Medina 1969; Winiger 1981; Bernoulli and Körner 1999; Körner and Paulsen 2004; Gehrig-Fasel et al. 2008; Shi et al. 2008; Hoch and Körner 2009; Kessler et al. 2014) and suggests a broadening rather than a narrowing of the error term of ±0.7 °C postulated by Körner (2012). In terms of soil temperatures, the Rolwaling treeline appears to be decoupled from rapid climate warming, i.e. the above-average soil temperatures might imply a retarded tracking of climate warming and a decelerated shift of treeline position (cf. Müller et al. 2015).

The more linear trend of air temperatures and in comparison to soil temperatures less pronounced differences between zone B and C can be attributed to the statistical method used to obtain these values (Gerlitz et al. 2016), while the soil temperatures were measured directly on site. However, heat deficiency above the subalpine forests is caused by a combination of low soil and air temperatures.

Above-average soil temperatures as well as an increasing number of growing degree days (representative for the Himalayan south slope; cf. Shrestha et al. 2012; Gerlitz et al. 2014) set the stage for an upward migration of tree species. We assume the current treeline to be located below its potential climatic limit. Since the ecotone is not affected by land use, the treeline is obviously suppressed by the given constellation of environmental factors (e.g. soil nutrient availability, krummholz barrier, allelopathic effects) and of facilitative (positive) resp. competitive (negative) interactions of recruits with neighbouring vegetation. The high numbers of *S. microphylla* recruits above the treeline (= in zones C and D) might result from a recent upward migration resp. stand densification and, if so, support the view of a species-specific response to climate change. Rather *S. microphylla* recruits than those of other tree species are capable to overcome the permanently densely foliated and potentially allelopathic krummholz belt.

16.4.3 Species-Specific Regeneration

In general, the results of our regeneration studies which show reverse J-shaped density–diameter distributions, and indicate intense and sustainable regeneration and thus the potential for upward migrations, are in line with other studies from treelines in Nepal (e.g. Ghimire and Lekhak 2007; Shrestha et al. 2007; Gaire et al. 2010, 2011, 2014; Ghimire et al. 2010; Sujakhu et al. 2013). In some of the J-shapes of these studies, the smallest dbh class is not included (Ghimire and Lekhak 2007; Shrestha et al. 2007) or shows smaller numbers than the subsequent class (Gaire et al. 2010, 2011, 2014; Sujakhu et al. 2013) putting their statements regarding intense and sustainable regeneration into a different perspective. Low numbers in the small dbh class indicate grazing impact by domesticated or wild animals which exacerbate the interpretation of the results regarding migration potentials. The species-specific low numbers in the tallest diameter classes or absence of classes above 50 cm dbh in some studies (Ghimire and Lekhak 2007, Gaire et al. 2010, 2011, 2014; Sujakhu et al. 2013) are signs indicating anthropogenic impacts. Some studies (Lv and Zhang 2012; Gaire et al. 2014) detected rather bell-shaped density–diameter distributions or reverse J-shaped distributions (Gaire et al. 2010, 2011, 2014; Sujakhu et al. 2013) that do not correspond to the reverse J- or L-shaped ones we found in Rolwaling being to a much higher degree dominated by recruits. However, Gaire et al. (2014) assessed a significant upward shift, densification and high recruitment intensity of *Abies spectabilis* at their study site in Manaslu Conservation Area. Even in this study, the low dbh classes show only small numbers of recruits, especially in case of *Betula utilis*. In our study area, zone A provides a much better basis for regeneration of *A. spectabilis*, *B. utilis* and *Sorbus microphylla* compared to zone B, where their recruit numbers are distinctly lower compared to tree densities (Figs. 16.4, 16.5 and 16.6). The reason might be competitive advantages of *Rhododendron campanulatum* in zone B. However, the competitive strength of *Rh. campanulatum* seems to be strongest in zone C. This applies especially for the taller individuals (≥7 cm dbh).

Few studies from Nepal provide data on recruit densities. In Langtang valley, Gaire et al. (2010, 2011) found significantly less *B. utilis* recruits per ha, about the same number of *A. spectabilis* and significantly less *Rh. campanulatum* and *S. microphylla* recruits compared to the ecotone in Rolwaling. In comparison to our results, Schickhoff et al. (2015) found a comparable distribution of seedling and sapling species and slightly higher total numbers of recruits in Langtang. *Pinus wallichiana* recruit density was very high (c. 4500 N/ha at lower altitude; c. 1000 N/ha at higher altitude) in Manang (Ghimire et al. 2010); however the investigated forest was obviously dominated by this single species and thus showed a different species composition than the Rolwaling ecotone. In another study from Manang, *A. spectabilis* exhibited very high recruit numbers (c. 3200 N/ha). In the Manang study of Shrestha et al. (2007), *B. utilis* recruit numbers were comparable to the present study. In contrast, they found a very high number of *A. spectabilis* recruits at lower altitude (3500–3900 m a.s.l.; c. 5600 N/ha), while the number was distinctly smaller than ours at higher altitude (3900–4200 m a.s.l.; c. 160 N/ha). *Pinus wallichiana* showed a similar pattern with high numbers at lower and smaller numbers at higher altitude. Recruit densities of *A. spectabilis* and *B. utilis* in Manaslu Conservation Area resembled roughly the corresponding densities in Rolwaling. In contrast, *Rh. campanulatum* recruits occurred only rarely (c. 200 N/ha, Sujakhu et al. 2013). *A. spectabilis* recruit numbers were smaller in Barun valley (c. 200 N/ha; Chhetri and Cairns 2015) compared to Rolwaling. In summary, several studies from Nepal report continuous regeneration and potentials for treeline shifts, consistent with our findings.

In our study, the recruit height class distribution of *A. spectabilis* differs from *B. utilis*, *Acer caudatum* and *S. microphylla*. Obviously, the latter species grow faster and aggregate more individuals in taller height classes. The height class patterns reflect inter alia varying reproduction strategies: We found vegetative propagation (coppices) for *B. utilis* and *S. microphylla*, while *A. spectabilis* recruits grow separately from other individuals and sprout from seeds. As low temperatures restrict rather germination than layering (Holtmeier 2009; Wieser et al. 2014), temperatures obviously do not restrict seed-based regeneration of *A. spectabilis* given the recruit height class and dbh distributions. The results of recruit mean height and *RI* show that *A. spectabilis* and *B. utilis* have the potential to develop above the transition BC beyond the seedling stage. The rare occurrence of trees indicates the potential to develop even further and become established. There are less *A. spectabilis* and *B. utilis* recruits in upper altitudinal zones, but the percentage of survivors that grow successfully to taller height classes is distinctly higher compared to lower elevation. Asynchronous shortages in seedling establishment in each zone at different time periods might be one reason for differing species- and altitudinal-specific patterns. Another reason could be that competitive stress is higher in the lower zones and thus a smaller percentage of recruits survive. More favourable light conditions appear to favour the growth of *B. utilis* in zone D and in openings in zone C. *S. microphylla* can be considered established in zones C and D given height class distribution and *RI*. Some species show no distinct signs of treeline shift but more obvious an intensified regeneration, indicating ongoing stand densification below treeline. This applies species specific especially for *A. spectabilis* in zones A and B, *B. utilis* in zone A, *S. microphylla* in zone A and C and *Rh. campanulatum* in zones B to D where we found evidences for stand densification. Climate warming impact may influence regeneration below treeline and treeline shift in different intensities (e.g. Camarero and Gutiérrez 2004; Wang et al. 2006; Kirdyanov et al. 2012; Gaire et al. 2014; Shrestha et al. 2014) which seems to apply for our study area.

Rh. campanulatum's population structure in zones C and D is a sign for its potential to spread out further (cf. Figs. 16.4, 16.5, 16.6 and 16.8). In comparison to zones C and D, *Rh. campanulatum* seems to grow under more intense competitive stress in zone B. While the high *RI* and the very high number of recruits smaller than 10 cm height point to a viable regeneration, the very low mean height and relative small numbers of recruits in classes above 10 cm height imply competitive pressure by other species and a distinct self-thinning process. Obviously, *Rh. campanulatum* keeps its regeneration capacity in the zones above, while the competitive strength of other species except *S. microphylla* seems to be reduced. As especially the *RI* of *S. microphylla* and also its average recruit height are relatively low in zone B, this species becomes more competitive in zones C and D. The shift in the ratio of recruits to trees at the specific tree species lines, recruit height and *RI* distributions indicate the potential for sustainable recruitment and tree growth. Positive correlations of recruit density with soil temperatures and soil moisture give evidence of the relevance of these site factors (cf. Schickhoff et al. 2015). However, other site factors, e.g. nutrient availability, microclimatic variations and germination conditions like surface structure and light conditions, might in addition hinder or facilitate intensified recruitment (e.g. Holtmeier and Broll 2005, 2010; Malanson et al. 2007; Hofgaard et al. 2009; Batllori et al. 2010; Renaud et al. 2011; Elliott 2012; Wang et al. 2012; Durak et al. 2015; Treml and Chuman 2015).

The high standard deviations of the mean densities which we present in the results reveal the heterogeneous patterns of the populations even within same altitudinal zones. Analyses of subsets of our sample, e.g. single slopes, confirm this finding. This applies also for general and species-specific abruptness patterns (e.g. recruits, species and slope-wise, Fig. 16.15 and Tables 16.4 and 16.5). This variability suggests differences in site conditions apart from altitude and thus a varied potential for recruitment at local scales. No distinct differences in soil temperatures between zone C and D were detected during growing season (Figs. 16.12 and 16.13). If dissemination depended on temperature, only species which once was established in zone C could migrate easily to zone D as there is no temperature threshold to pass.

In summary we assessed a prolific regeneration in the Rolwaling treeline ecotone which indicates a considerable potential to respond to climate warming with a treeline shift. Any treeline advance, however, will be controlled to a large extent by the dense krummholz belt which acts as an effective barrier for upslope migration of treeline-forming tree species. Most likely the treeline in Rolwaling confirms the low responsiveness of near-natural Himalayan treelines and upward shifts only in the long term, despite the currently existing potential (Shrestha et al. 2014; Schickhoff et al. 2015, 2016; Chhetri and Cairns 2015).

16.5 Conclusions

Changes in tree dbh and tree and recruit height and density are species specific and occur with varying degrees of abruptness along the treeline ecotone. We identified several tree species lines inside the ecotone. The stand structure is complex; high standard deviations from mean values indicate heterogeneous patterns, differing between different slopes, species and altitudinal zones. Soil temperatures rather than lapse rate air temperatures are associated with physiognomic transitions, treeline position and spatial regeneration patterns. Thus, the Rolwaling treeline is potentially susceptible to climate change, and treeline tree species have the potential to migrate upslope in future with *Sorbus microphylla* showing particularly high dynamics. Upslope migration, however, is effectively controlled by the dense krummholz belt. Currently, the treeline is rather stable; however we found a prolific regeneration as well as signs of stand densification. Further investigations including dendroecological analyses will clarify the complex conditions for establishment and development from recruits to trees. Moreover, investigations at additional Rolwaling study sites and in other valleys are needed to better understand the spatial heterogeneity of Himalayan treeline ecotones and their responsiveness to climate change.

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2 'Implications of tree species - environment relationships for the responsiveness of Himalayan krummholz treelines to climate change' (study 2)

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‘Implications of tree species - environment relationships for the responsiveness of Himalayan krummholz treelines to climate change’

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Abstract: Climate warming is expected to advance treelines to higher elevations. However, empirical studies in diverse mountain ranges give evidence of both advancing alpine treelines as well as rather insignificant responses. In this context, we aim at investigating the sensitivity and responsiveness of the near-natural treeline ecotone in Rolwaling Himal, Nepal, to climate warming. We analysed population densities of tree species along the treeline ecotone from closed forest stands via the krummholz belt to alpine dwarf shrub heaths (3700-4200 m) at 50 plots in 2013 and 2014. We quantified species-environment relationships, i.e. the change of environmental conditions (e.g., nutrient and thermal deficits, plant interactions) across the ecotone by means of redundancy analyses, variation partitioning and distance-based Moran's eigenvector maps. In particular, we focus on explaining the high competitiveness of *Rhododendron campanulatum* forming a dense krummholz belt and on the implications for the responsiveness of Himalayan krummholz treelines to climate change. Results indicate that treeline trees in the ecotone show species-specific responses to the influence of environmental parameters, and that juvenile and adult tree responses are modulated by environmental constraints in differing intensity. Moreover, the species - environment relationships suggest that the investigated krummholz belt will largely prevent the upward migration of other tree species and thus constrain the future response of Himalayan krummholz treelines to climate warming.

Keywords: Himalaya; Nepal; Population structure; *Rhododendron campanulatum*; Spatial patterns; Species-environment relationships; Stand density; Variation partitioning

1 Introduction

Thermal deficits control the elevational position of natural treeline ecotones at mountain ranges worldwide which is expected to advance to higher elevations in the long term (e.g., Troll 1973; Holtmeier 2009; Körner 2012). At local scales, various abiotic factors and biotic interactions govern the elevational treeline position and the response to climatic controls (Case and Duncan 2014; Wieser et al. 2014; Weiss et al. 2015; Müller et al. 2016a). Inconsistent and sometimes contradictory responses to climate warming, observed in empirical studies, must be attributed to the local-scale complexity of interacting site factors (Schickhoff et al. 2015). The response gradient ranging from static treelines with insignificant responses to dynamic treelines with fairly rapid upslope migration is reflected in the results of a global meta-analysis with 52% of treelines showing advance, 47% inertia and 1% recession (Harsch et al. 2009). Land abandonment is often the dominant driver of treeline advance (Gehrig-Fasel et al. 2007), making it very difficult to disentangle effects of human land use and climate change (Schickhoff 2011).

Treeline ecotones in the Himalaya are subjected to above average warming rates. Warming trends are in the order of up to 1.2°C per decade (c. 0.9°C on average) over the past 40 years, leading to an average growing season extension of 4.7 days (Shrestha and Aryal 2011; Shrestha et al. 2012; Hasson et al. 2016). Precipitation trends are spatially and temporally variable, however, negative trends of monsoonal precipitation over the western and central Himalaya and a higher frequency of drought events in winter and premonsoon seasons in western Nepal were documented (Schickhoff et al. 2016a). Himalayan ecosystems are highly sensitive and vulnerable to climate change effects, with multi-faceted interactions and diverse response patterns (Shrestha et al. 2012; Telwala et al. 2013; Ferrarini et al. 2014; Salick et al. 2014; KC and Ghimire 2015; Padma Alekhya et al. 2015; Schickhoff et al. 2016b). Recent reviews of the sensitivity and response of Himalayan treeline ecotones emphasize the low responsiveness of krummholz treelines, but also highlight intense recruitment of treeline trees within the treeline ecotone and beyond and the respective potential for future treeline advance (Schickhoff et al. 2015; Schickhoff et al. 2016b). Treeline shifts are reported in studies which consider uppermost seedling positions as synonymous with treeline advance (e.g., Gaire et al. 2014). However, occurrence of seedlings does not necessarily mean effective regeneration and treeline advance given the generally low survival rate of seedlings after germination and during critical later life stages (Graumlich et al. 2005; Schickhoff et al. 2016b).

Detailed knowledge of tree species - environment relationships is among the basic requirements for a better understanding of treeline response patterns to region-wide climate warming inputs. However, accumulated knowledge of treeline tree species ecology in the Himalaya is still very deficient (Schickhoff 2005; Miehe et al. 2015). Here, we analyse population-environment relationships in the treeline ecotone of the Rolwaling Valley in order to infer implications for the treeline sensitivity and response to climate change. We focus on the *Rhododendron campanulatum* krummholz belt within the ecotone since previous studies indicated the krummholz belt to be a crucial ecotone element largely preventing the upslope migration of tree species (Schickhoff et al. 2015; Müller et al. 2016a; Müller et al. 2016b; Schickhoff et al. 2016b; Schwab et al. 2016). It is still not understood how the change of environmental conditions from closed forest stands to the krummholz belt (e.g., nutrient and thermal deficits, plant interactions) is correlated to modified population densities of tree species. We aim at analyzing this correlation in order to derive insights into response variabilities of tree species populations to changing constellations of site factors and to climate change. We hypothesize that populations of different life stages show modified environmental relationships. Thus, we differentiate between juvenile individuals and adult trees and further hypothesize that species-specific variation in adult and juvenile population density along the treeline ecotone and especially the krummholz belt depends on nutrient and moisture supply as well as thermal conditions.

In particular, we aim at answering the following research questions: What are crucial site factors for the high competitiveness of *Rhododendron campanulatum* forming a dense krummholz belt above treeline? Can the population decline of tree species along the treeline ecotone be attributed to specific environmental variables? Are these variables related to climate change and if so, what are the implications for the responsiveness of Himalayan krummholz treelines?

2 Materials and Methods

2.1 Study site

The study was conducted on the north-facing slope of the Rolwaling Valley (27°52' N; 86°25' E), located in Dolakha District, east-central Nepal (Figure 1). The Rolwaling Valley is part of the Gaurishankar Conservation Area, established in

2010 (Bhusal 2012). The climate is continental with dry and cold winter conditions and specifically characterized by the monsoon season which lasts from June to September (Böhner et al. 2015; for detailed Rolwaling climate data see Gerlitz et al. 2016). The warming trend of the study area corresponds to general Himalayan trends; Gerlitz et al. (2014) assessed monthly temperature trends of c. 0.7°C per decade in winter and pre-monsoon seasons. The Rolwaling treeline at the north-facing slopes represents near-natural conditions (Schwab et al. 2016), having been preserved due to the valley's remote location, its sparse population and the status as a sacred abode (Baumgartner 2015). We studied three north-facing slopes, named according to their predominant exposition NE1, NE2 (both north-east exposed) and NW (northwest exposed). Each sampled slope covers the entire treeline ecotone from upper subalpine closed forests (upper limits of tall and upright *Acer caudatum*, *Abies spectabilis* and *Betula utilis*) via a dense *Rhododendron campanulatum* krummholz belt to alpine dwarf scrub heaths with small and stunted tree species individuals (Figure 1 & 2).

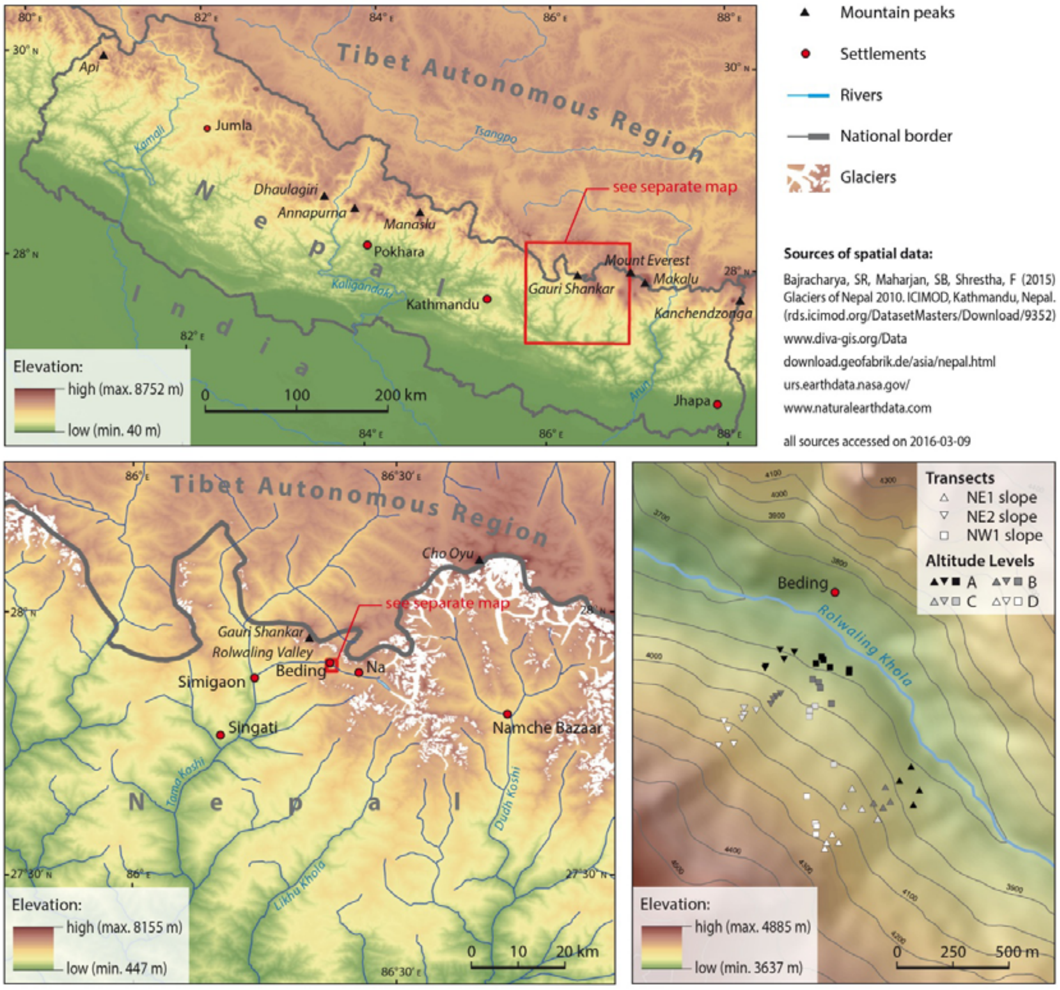

Figure 1. Location of the study area with studied slopes and sites

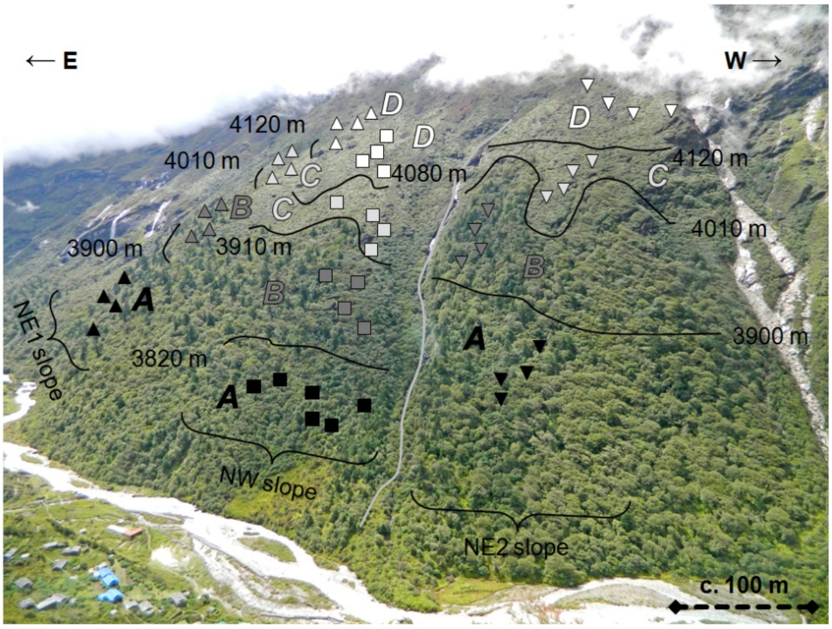

Figure 2. Stratification of the study area by elevation (zones A, B, C, D) and aspect (NE, NW), and approximate location of plots (Schwab, 18 September 2014)

2.2 Tree species composition and population densities

Upper subalpine forests (corresponding to elevational zones A and B in Figure 2) are mixed forest stands consisting of tall upright growing individuals of *Betula utilis* and *Abies spectabilis* as well as *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer (Figure 3). *Acer caudatum* and *Prunus rufa* occasionally occur as companions. Dense and nearly impenetrable *Rhododendron campanulatum* thickets form the krummholz belt in zone C which contains the uppermost stunted individuals of *Abies spectabilis* and *Betula utilis* with dbh ≥ 7 cm. The uppermost trees with true tree habitus (upright stem with crown) grow in elevational zone B. Thus the treeline coincides with the transition from zone B to C as in zone C only few outpost-treeline trees occur (Schwab et al. 2016). Zone D in Figure 2 represents the alpine vegetation belt composed of dwarf scrub heaths interspersed with few low growing individuals of *Sorbus microphylla*. In general, the density pattern of the juvenile individuals (dbh < 7 cm) resembles the pattern of adult trees. However, we found prolific regeneration (dbh < 7 cm) of *Abies spectabilis*, *Betula utilis*, *Rhododendron campanulatum*, and *Sorbus microphylla* in zone D (Figure 3 & Appendix 1) (Schwab et al. 2016). Especially seedlings of *Betula utilis*, *Abies spectabilis*, and *Sorbus microphylla* are established above the upper limit of adult trees.

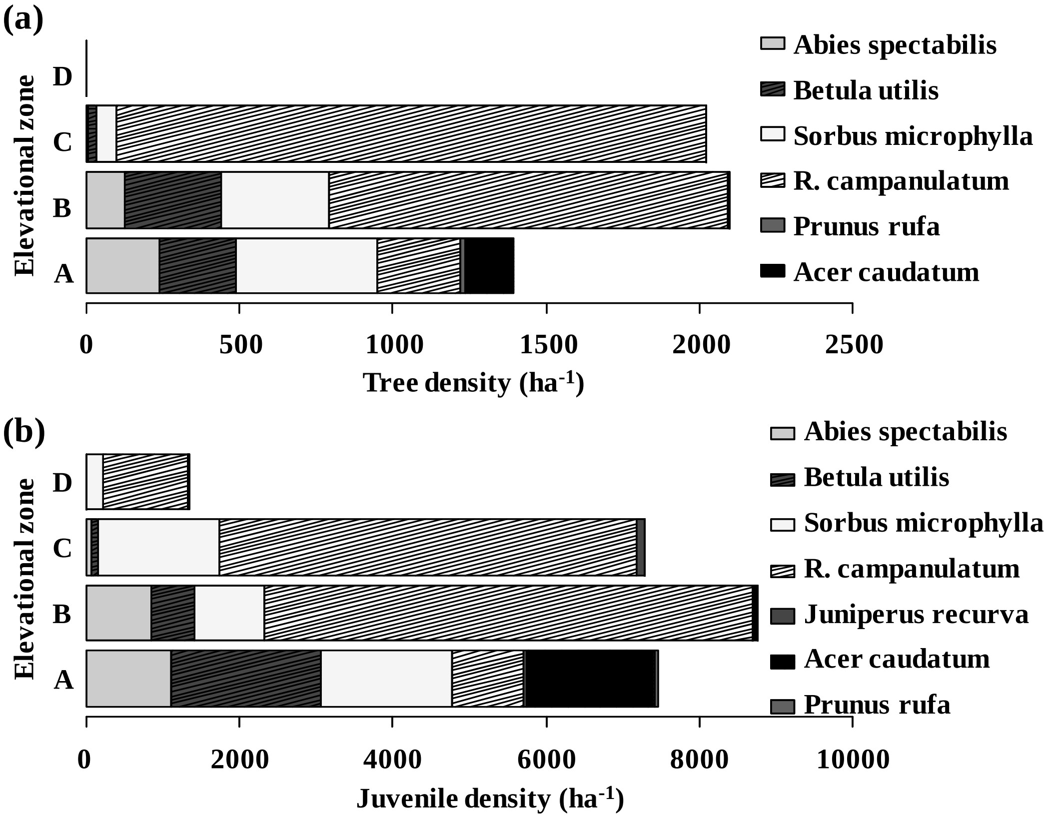

Figure 3. (a) Tree species density of individuals ≥ 7 cm dbh (adult trees); (b) tree species density of individuals < 7 cm dbh (juvenile individuals)

2.3 Sampling

2.3.1 Species

We stratified the slopes according to the altitudinal zonation of tree species composition and stand structure in elevational zones A (closed forests) to D (alpine dwarf shrub heaths, cf. Figure 2) (Schwab et al. 2016). We selected plots randomly by Microsoft Excel function RANDBETWEEN. In total, 50 square plots of 20 m × 20 m were sampled. Sampling was conducted from April to September 2013 and in August 2014. We determined tree species after Press et al. (2000) and Watson et al. (2011). We measured dbh at 130 cm above ground level, height, crown height and crown width of all vital tree species individuals with dbh ≥ 7 cm following standard forest inventory procedures (Van Laar and Akça 2007). We counted all tree species individuals of any size in each plot. All individuals with dbh ≥ 7 cm are termed "adult trees" while smaller ones are categorized as "juvenile individuals".

2.3.2 Soil, topography and climate

All plots were sampled for Of, Ah and Ae horizons. Soil samples were analysed using standard methods at the laboratory of the University of Tübingen (see Müller et al. 2016b for details).

We determined the following topographic variables per plot: elevation, aspect, centre coordinates, slope, curvature, and ground cover variables. Ground cover variables captured the percentage of ground surface covered with rock fragments of eight size classes (fine soil, coarse soil, small stone, medium stone, large stone, small rock, medium rock, large rock; see Appendix 2 for size class definitions). In presence of large rocks we distinguished between outcrop rocks (protruding from slope) or plane rocks (bare, little or no vegetation). Other ground cover variables were bare ground cover (percentage of bare soil and rock cover) and vegetation cover (percentage of ground vegetation and litter cover). Furthermore, we divided each plot into four quadrants and collected topographic data in each quadrant to gather information about microtopography (see Appendix 2 for details).

In addition to soil temperature and soil moisture (see Müller et al. 2016b), we used air temperatures recorded from April 2013 to June 2014 by mobile climate stations which were installed in the lower and upper part of the ecotone (Gerlitz et al. 2016).

2.4 Statistical analyses

2.4.1 Data preparation

All data preparation and consequent statistical analyses were performed using the statistical software environment R (version 3.2.2; R Core Team 2015) with functions of packages "plyr" (Wickham 2011), "xlsx" (Dragulescu 2014) and others referred to in the following sections.

To obtain nutrient stocks per plot (kg 400 m^{-2}), the concentrations were multiplied by the bulk density of the soil (g cm^{-3}) multiplied by the product of plot size (400 m^{-2}) and soil horizon thickness (cm), all divided by 1000. Nutrient stocks in t ha^{-1} were calculated by multiplication of nutrient stocks per plot with 25, all divided by 1000. Descriptive statistics of soil variables used in statistical analyses are presented in Appendix 3.

We computed Jaccard dissimilarity indices of quadrant-specific ground cover and other topographical variables of each plot as measures of within-plot microtopographic homogeneity. We derived the following dissimilarity variables, using different subsets and combinations of topographic variables: microrelief, ground cover, microrelief and ground cover combined, curvature, aspect, surface structure (see Appendix 2 for details).

We derived annual as well as seasonal (winter December - February: DJF, premonsoon March - May: MAM, monsoon June - September: JJAS, post-monsoon October - November: ON) mean and minimum air and soil temperatures from site specific temperature lapse rates (Gerlitz et al. 2016). Moreover, we determined the number of frost days (< 0°C air temperature for a minimum of 6 hours) and soil frost days. We counted days with soil temperature ≥ 3.2°C to derive the number of growing degree days (GDD) as a measure for the length of the growing season (cf. Körner and Paulsen 2004). We calculated annual as well as seasonal mean and seasonal maximum pF values, i.e. minimum soil moisture.

2.4.2 Correlation analyses of independent variables

We split the environmental dataset into three groups: soil, topography and climate variables. The latter comprise “true” climate variables, e.g. air temperatures and derived minimum values, as well as soil temperature, soil moisture and thereof derived variables. In order to avoid high multicollinearity in the following analytical steps we removed within-group correlations of $|r| > 0.7$ (Spearman, $p<0.05$, adjusted according to Benjamini and Hochberg 1995) by exclusion of variables. We used the function "*corr.test*" of the R "psych" package (Revelle 2015). By this procedure, selected variables as well as all uncorrelated variables were included in the final matrices (Table 1).

Table 1. Uncorrelated variables contained in final edaphic, topographic and climatic data matrices

Topography	**Soil: Ah-horizon**	**Climate**
Eastness	Total nitrogen	Mean air temperature of DJF season
Slope	Carbon concentration / nitrogen concentration ratio (C:N)	
Surface structure		Minimum air temperatures of MAM season
Fine soil cover	Carbon stock / nitrogen stock ratio (C:N)	
Coarse soil cover		Minimum air temperature of JJAS season
Medium stone cover	Aluminium concentration	
Large stone cover	Aluminium stock	Soil temperature of MAM season
Small rock cover	Manganese concentration	
Medium rock cover	Manganese stock	Soil temperature of DJF season
Large rock cover	Potassium concentration	Soil moisture of ON season
Presence of plane rocks	Calcium concentration	Soil moisture of DJF season
Bare ground cover	Sodium concentration	Soil moisture of MAM season
Litter cover	Bulk density	Soil moisture of JJAS season
Microrelief and ground cover dissimilarity	**Soil: Ae-horizon**	
	Total nitrogen concentration	
Ground cover dissimilarity	Mineralised nitrogen concentration	
Microrelief dissimilarity	Carbon concentration / nitrogen concentration ratio (C:N)	
Curvature dissimilarity		
Aspect dissimilarity	Aluminium concentration	
Surface structure dissimilarity	Calcium concentration	
Soil: Of-horizon	Hydrogen concentration	
Manganese stock	Sodium concentration	
Total nitrogen stock	Manganese concentration	
Potassium stock	pH (H_2O)	
Aluminium stock	pH (KCl)	
Sodium stock	Sand content	
Bulk density	Layer thickness	

Missing values in several parameters could lead to problems in the multivariate analysis. Hence, we used multivariate imputation by chained equations (MICE; Van Buuren 2012) based on a random forest classification (Doove et al. 2014) to estimate the missing values based on the multivariate relationships between the variables (see Appendix 4 for predictors of imputed variables, determined following Van Buuren et al. (1999)). We followed recommendations of Van Buuren (2012) to specify the imputation model and used the MICE implementation "*mice*" in the R package "mice" (Van Buuren and Groothuis-Oudshoorn 2011) (for details on this procedure see Appendix 5). From here on, the data analysis will be based on imputed environmental datasets, with missing values replaced by imputed values.

2.4.3 Species-environment relationships

We analyzed Hellinger transformed population densities with redundancy analyses (RDA) and backward elimination (Legendre and Legendre 2012). Prior and after elimination, we tested each variable group for global significance ($p<0.05$). We applied a two-step selection procedure (hereafter: two-step backward elimination; $p<0.1$ for dropping a term from the model): First, in order to preselect important variables, we selected variables separated by groups (soil, topography, climate) with significant contribution to species distribution. Secondly, we included within-groups selected variables in a second backward elimination procedure, containing soil, topography and climate variables selected in the first step.

Variables included in at least half of the imputed data models of the second step were included in the final models. Their RDA parameters were averaged to obtain the final RDA result. We calculated the explained variance for the first and second RDA axes by multiplication of R^2_{adj} with the proportion of variance explained by the first two canonical axes with respect to the total explained variance (Borcard et al. 2011). Tree species densities and the variables which were included in the final models were tested by H-test for significant differences of mean values of elevational zones. Multiple comparisons led to the determination of significant differences between elevational zones. We used the function "*kruskal.test*" and the function "*kruskalmc*" of the package "pgirmess" for computations (Giraudoux 2015).

In order to assess the contribution of each of the three independent environmental variable groups (soil, topography, climate indicators) we performed variation partitioning based on the adjusted canonical R^2. In addition, the procedure revealed the proportion of variation that remained unexplained by sampled environmental variables (Legendre and Legendre 2012). Variation partitioning was calculated by the "*varpart*" function of the "vegan" package (Oksanen et al. 2015) and was followed by significance tests of the fractions using Monte Carlo permutation tests (Legendre and Legendre 2012).

2.4.4 Spatial patterns: Distance-based Moran's eigenvector maps and linear trend

Notwithstanding the random selection of plots, the spatial dependence of the species data is most likely not only related to functional correlation with the environmental variables but may be the result of neutral processes of various population and community dynamics leading to spatial autocorrelation. In order to assess the spatial structure of the population data, we first assessed a broad scale spatial pattern by fitting a linear trend to the species data. Then we used spatial eigenfunctions to examine fine scale spatial patterns (Legendre and Legendre 2012). We found and analyzed a significant spatial linear trend in the adult and juvenile tree species density data. In order to assess the contribution of the linear trend to adult and juvenile tree species densities we analyzed the spatial linear trend by RDA using the x-y coordinates of the plots as constraining variables for the Hellinger transformed vegetation matrix (Andersen et al. 2011; Borcard et al. 2011).

We selected significant RDA axes by backward elimination using the functions "*rda*" and "*ordistep*" of the R "vegan" package. The permutation p-value was 0.1 for dropping a term from the model (Borcard et al. 2011; Oksanen et al. 2015). In order to assess spatial structures which are on a finer scale than the linear trend we used a set of spatial variables, i.e. distance-based Moran's eigenvector maps (dbMEM). First, we removed the linear trend by detrending of the species data and applying regression on the x-y coordinates of the plots. By using information of spatial autocorrelation, dBMEMs define multiscale spatial correlations to define the spatial patterns. For transformation of geographical UTM x-y coordinates to a geographical distance matrix of the plots we used functions of the R "rgdal" and "sp" libraries (Bivand et al. 2013; Bivand et al. 2015). Afterwards, the dbMEMs were calculated by the function "*PCNM*" of the package "PCNM" (Legendre et al. 2013) with 9999 permutations. We selected significant dbMEMs out of all positively correlated dbMEMs by backward elimination. As there was not much difference in the scales of the finer scaled spatial patterns (dbMEMs) we refrained from differentiating patterns arbitrarily into dbMEMs of different scales (Legendre and Legendre 2012), and stick to the distinction of broad (first RDA axes of linear trend and dbMEM) and finer than broad spatial scales (remaining RDA axes).

We assessed the contribution of the dbMEM model to adult and juvenile density data by RDAs. To detect associations of single tree species to spatial patterns, we tested site scores of the significant axes of linear trend and dbMEM RDAs and species data for correlations (Spearman,

$p<0.05$, adjusted according to Benjamini and Hochberg 1995). In order to determine the extent to which spatial structures are related to environmental variables, we analyzed site scores of the significant constrained RDA axes of both linear trend RDAs and spatial variables (dbMEM) by RDAs and backward elimination (adapted from Andersen et al. 2011). We applied the two-step backward elimination procedure. In order to visually inspect spatial patterns, site scores of the significant axes of linear trend and dbMEM RDAs were plotted in maps.

3 Results

3.1 Species-environment relationships

3.1.1 Constrained ordination - adult trees

A total of 77% of variation in adult tree species density was explained by 17 selected environmental variables (Appendix 6). The first RDA axis explained 58 % variance and the first and second axis in total 68 % variance (Table 2). The ordination shows a clear separation between plots of zone C, a mixed zone A and B group, and a pure zone A group (Figure 4). These three groups were arranged mainly along the first RDA axis. In general, the plots spread only slightly along RDA axis 2. Especially plots of zone C formed a tight cluster, due to the strong dominance of *Rhododendron campanulatum*. In contrast, the group containing A-plots with higher number of tree species exhibited variation along axis 2.

Table 2. Explained variance of adult tree density by first and second RDA axes. R^2_{adj} of ordination was 0.77.

RDA axis	Proportion explained by accumulated constrained eigenvalues	Explained variance by axes
Axis 1	0.75	0.58
Axes 1+2	0.88	0.68

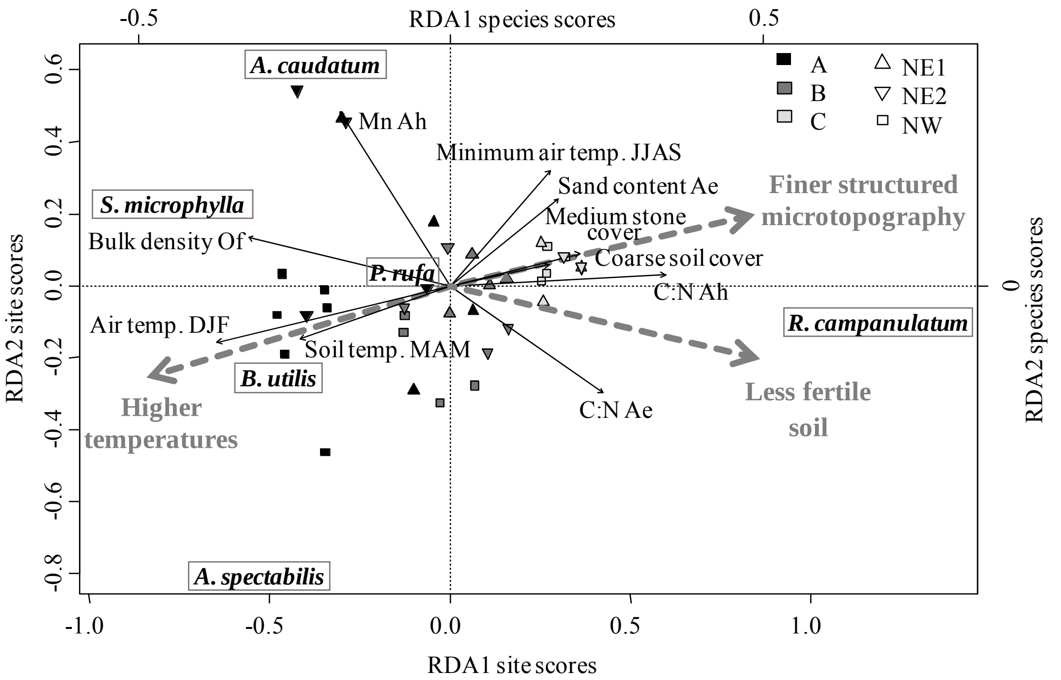

Figure 4. Ordination diagram of redundancy analysis (RDA) for adult tree density. Vector directions show relation to and vector lengths importance of environmental variables. Only the most important environmental variables with biplot score (axis 1 and/or axis 2) ≥ 0.3 are shown. Appendix 6 contains all 17 variables and their biplot scores. The first two constrained RDA axes shown here explain 68% variation in adult tree species density. Dashed arrows show appropriate direction of summarized main gradients, length not true to scale. **Notes:** Of, Of horizon; Ah, Ah horizon; Ae, Ae horizon; temp., temperature; MAM, pre-monsoon season; JJAS, monsoon season; Mn, manganese; C:N, carbon-to-nitrogen ratio

Most environmental variables were correlated rather with RDA axis 1 than with axis 2 (Figure 4), forming a complex gradient along axis 1 which can be divided roughly in three non-hierarchical groups: The first group referred to differences in microtopographic groundcover, namely size and shape of rocks. *Rhododendron campanulatum* was associated to plots with coarse soil cover and large stones, i.e., to a finer structured microtopography compared to the sites dominated by other tree species. Those sites were structured by medium sized and large rock fragments and exhibited dissimilarities in exposition and curvature within plots (relatively weak gradients, not shown in Figure 4). Cover of medium-sized and large stones differed significantly between elevational zones A and C (Appendix 7). The second group referred to a temperature gradient, expressed in lower soil and air temperature at plots with high density of *Rhododendron campanulatum* and higher temperatures at other plots. Soil temperature differed significantly between the two lower zones and zone C while the difference in air temperature was significant between elevational zones A and C (Figure 5 and Appendix 7). The third group referred to differences in soil texture and soil fertility, indicated by manganese content and C:N ratios of Ah and Ae horizons. The C:N ratios of elevational zones A and C were significantly different. In spite of the strong gradient in the ordination, there were no significant differences in manganese content between the elevational zones (Figure 5 and Appendix 7). Sites of zone C and *Rhododendron campanulatum* were associated to less nitrogen mineralization and increased nitrogen immobilization compared to other sites and species. Furthermore, there were less nutrient fixing clay and silt particles. In consequence, the trend indicated in general less fertile soil conditions at zone C plots dominated by adult *Rhododendron campanulatum* trees as well as more fertile conditions at A and B plots where other tree species showed higher abundances. In addition, we found a strong gradient of increasing bulk density of the Of horizon towards less elevated plots and towards all tree species except *Rhododendron campanulatum*. The difference in bulk density between zone A and zones B and C was significant (Figure 5 and Appendix 7). Environmental gradients along the second axis exhibited less pronounced differences regarding soil fertility and nutrient availability, temperature and microtopography. Related variables did not show significant differences between elevational zones (Figure 5 and Appendix 7).

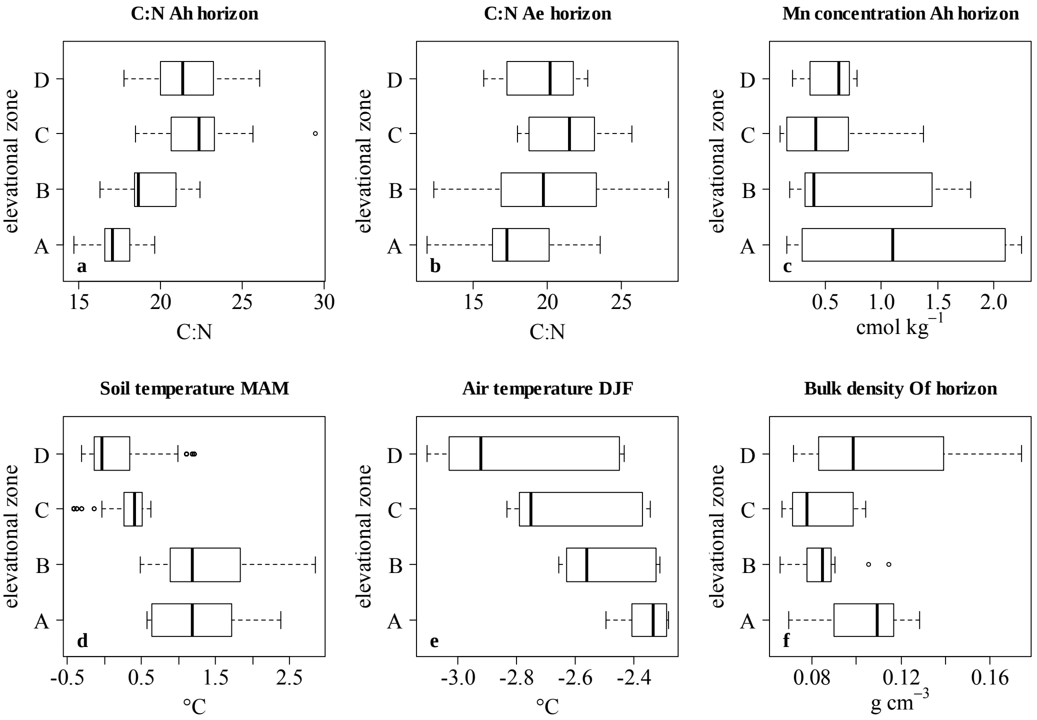

Figure 5. Variation of most important environmental variables with elevation. Outliers are excluded in Figure 5c. All imputed datasets are included in Figure 5d. Other Figures show variables with complete, not imputed data sets

For adult trees, the complex microtopography-soil fertility-temperature gradient along axis 1 had major influence on tree species distribution in the ordination, in particular on the separation of *Rhododendron campanulatum* from all other tree species. We found a species-specific response of adult *Rhododendron campanulatum* density to environmental variables. The partial overlaps of zones A and B (especially adult trees) and C and D (juvenile individuals) showed that the separated zones had features of population density in common. We found similar proportions of juvenile *Rhododendron campanulatum* and *Sorbus microphylla* trees in zones C and D, but lower densities of both species in zone D (cf. Figure 3 and Schwab et al. 2016).

3.1.2 Constrained ordination – juvenile individuals

A total of 66% of variation in juvenile tree species density was explained by 14 selected environmental variables (Appendix 6). The first RDA axis explained 51% variation and the first and second axis in total 60% variance (Table 3). The ordination of juvenile individuals showed a clear separation into a group of plots from elevational zone A, a group from zone B and a mixed group of plots from zones C and D (Figure 6). The groups were separated from each other along RDA axis 1. Compared to the adult tree ordination (Figure

4), the sites were to a higher degree distributed along RDA axis 2. Plots from slope NE1 tended to separate from the other slopes' plots, especially in case of C and D plots, due to differences in juvenile tree species composition between the slopes.

Table 3. Explained variance of juvenile stand density by first and second RDA axes. R^2_{adj} of ordination was 0.66.

RDA axis	Proportion explained by accumulated constrained eigenvalues	Explained variance by axes
Axis 1	0.77	0.51
Axes 1+2	0.91	0.60

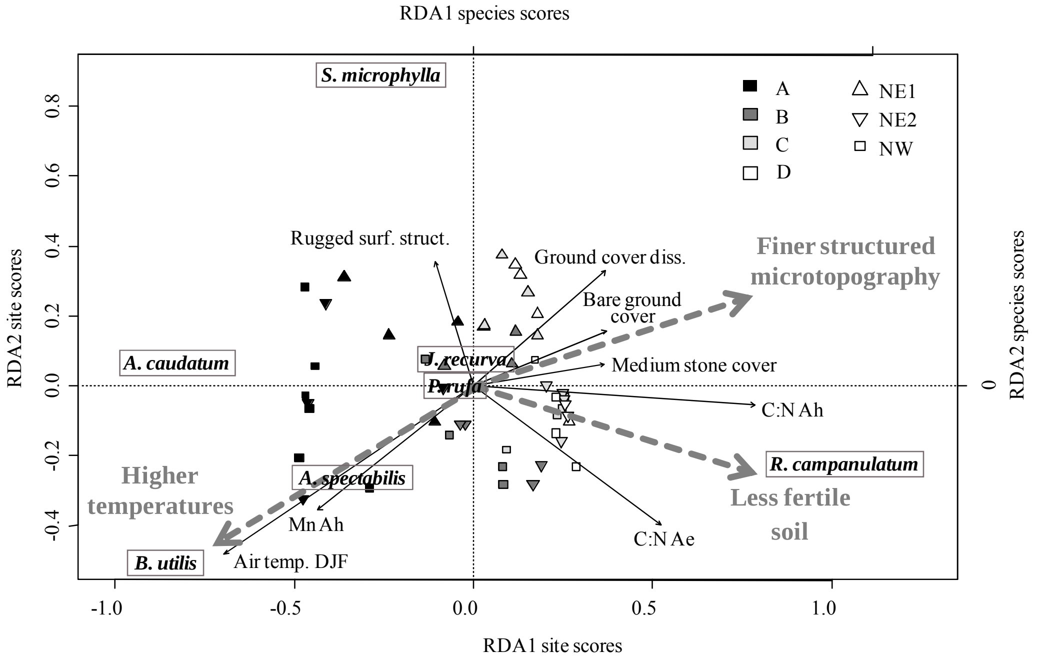

Figure 6. Ordination diagram of RDA analysis for juvenile tree species density. Vectors show direction and importance of environmental variables. Only the most important environmental variables with biplot score (axis 1 and/or axis 2) ≥ 0.3 are shown. Appendix 7 contains biplot scores of all 14 variables. The first two constrained RDA axes shown here explain 55% variation in juvenile tree species density. Dashed arrows show appropriate direction of summarized main gradients, length not true to scale. **Notes:** Ah, Ah horizon; Ae, Ae horizon; temp., temperature; DJF, winter season; diss., dissimilarity; Mn, manganese; C:N, carbon-to-nitrogen ratio; surf. struct., surface structure

Most environmental variables were related to both axes and all tree species. From all variables with strong correlation to ordination (Figure 6), the C:N ratio of the Ah horizon correlated only with RDA axis 1. Likewise, other variables which were correlated to both axes contribute to plot and species differentiation, e.g., C:N ratio of Ae horizon, air temperature, manganese content, surface structure and microrelief dissimilarity. These variables formed complex gradients, together with variables showing weaker correlation to the ordination. The variables could be classified into nutrient, microtopography and climate related groups. The differentiation in groups of C and D sites versus other sites and of *Rhododendron campanulatum* versus other species was related to differences in nitrogen availability (C:N ratios of Ah and Ae horizons), manganese content of Ah horizon, calcium content of Ae horizon, dissimilarity of surface structure within and between plots, and differences in mean and minimum air temperatures. *Rhododendron campanulatum* and *Sorbus microphylla* shared comparable conditions regarding temperature, manganese content and microrelief dissimilarity within plots. Differentiation within elevational zones and between tree species was related mainly to differences in nitrogen availability, surface structure, bulk density of Ah horizon and pH. Similar to the adult tree ordination, some but not all variables which were included in the ordination exhibited significant differences between elevational zones (Figure 5, Appendix 7).

In contrast to the adult tree ordination, sites and species were scattered to a higher degree in the ordination of juvenile individuals. The ordination was influenced by more complex combinations of variables to gradients in comparison to adult tree ordination. However, the main factors were likewise related to nutrient availability, temperature and microtopography.

3.1.3 Variation partitioning - adult trees

Results from RDA showed that the selected variables explained 77% of variability in adult tree density distribution of the treeline ecotone. By means of variation partitioning we separated explained variability into amounts which were explained exclusively by edaphic or topographic or climatic explanatory data sets and into amounts that were explained jointly by two or three of these explanatory data sets. The edaphic group of variables was the most important, independent predictor of species distribution (28% explained variability), while climatic and topographic variation was of secondary (7%) and tertiary importance (6%; Figure 7a). We found 25% shared variation of adult tree density explained by soil and/or climate variables (Figure 7a).

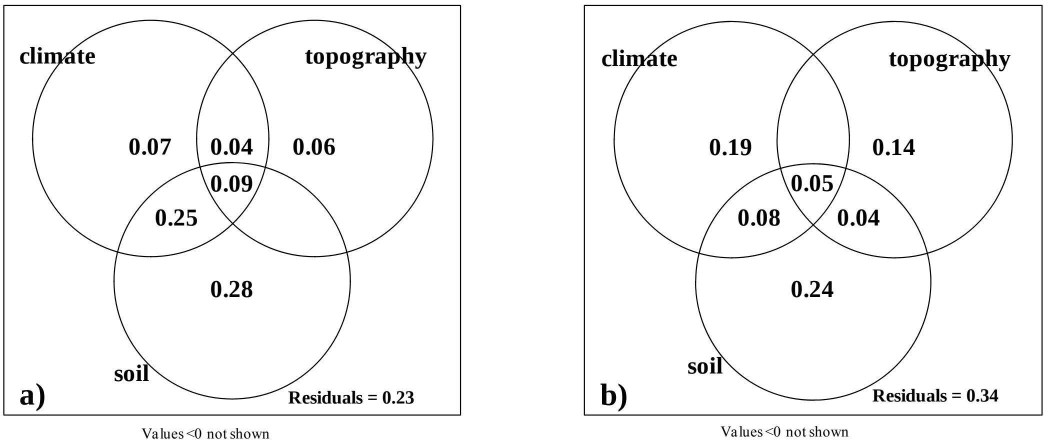

Figure 7. Variation partitioning of a) adult tree density using the matrices of soil variables (5), climate variables (3) and topographic variables (9) and b) juvenile density using the matrices of soil variables (6), climate variables (2) and topographic variables (6). **Note:** Numbers in brackets are numbers of variables in each matrix

3.1.4 Variation partitioning – juvenile individuals

Results from RDA showed that variables could explain 66% of variability in juvenile tree species density distribution of the treeline ecotone. As in adult tree density, the edaphic group of variables was the most important, independent predictor of species distribution (24% explained variability), while climatic and topographic variation was of secondary (19%) and tertiary importance (14%; Figure 7b). We found small amounts of shared variation of juvenile tree density explained by soil and/or climate and/or topographic variables. In comparison to partitioning of variation of adult tree density, the juvenile stand density variation partitioning revealed a more balanced distribution of explained variance per variable group (cf. Figure 7 a, b). While topography was of minor importance in case of adult trees, its share in total explained variation of juvenile density was substantial.

3.2 Spatial patterns: Distance-based Moran's eigenvector maps and linear trend

Each spatial model produced varying numbers of significant RDA axes (Figure 8). Their contributions to explained variance of adult and juvenile stand densities are displayed in Table 4. The models constructed with site scores of all significant RDA axes of the linear trend RDAs and of the positive dbMEMs RDAs explained proportions of variation in species distribution in the treeline ecotone, without considering other sources of variation (Figure 8). We found a strong spatial linear trend for all species variables: Redundancy analyses revealed an R^2_{adj} of 0.52 (p= 0.001) for adult tree density and of 0.47 (p=

0.001) for juvenile stand density. Moreover, RDAs on dbMEMs revealed an R^2_{adj} of 0.57 (p=0.001) for tree density and of 0.25 (p=0.001) for juvenile stand density.

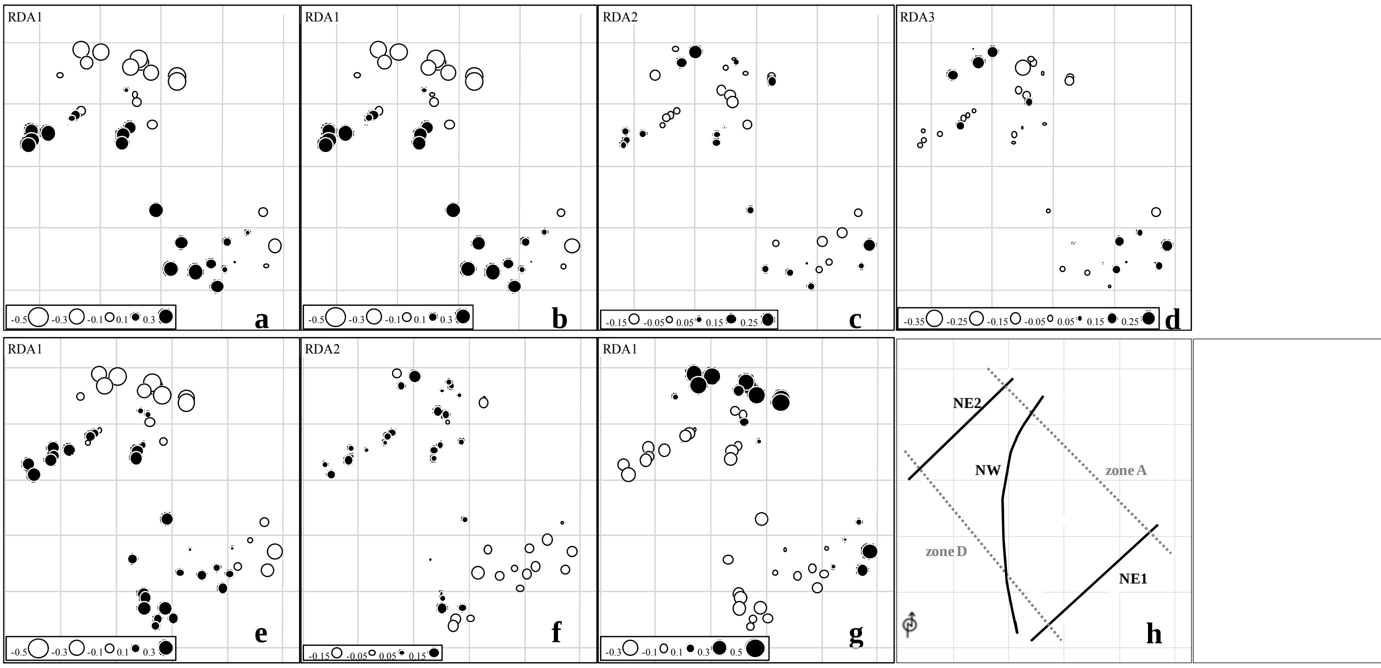

Figure 8. Maps of the site scores of significant canonical RDA axes of the linear trends (a, e, f) and the spatial models (b, c, d, g) of adult tree (a-d) and juvenile stand (e-g) density. Map (h) shows for orientation the approximate position of slopes, elevational zones A and D and north arrow (see also Figure 1). Size of the circles are proportional to the absolute site score values, black circles symbolize positive, white circles negative correlations. Spatial patterns are featured by groups of circles of similar size and colour (grid distance: 200 m).

Table 4. Variation of tree species density explained by significant dbMEM and linear spatial trend RDA axes

Cumulative % explained	Adult density	Juvenile den-
Lin. trend RDA axis 1	0.52	0.41
Lin. trend RDA axis 1+2	n.s.	0.47
dbMEM RDA axis 1	0.47	0.25
dbMEM RDA axis 1+2	0.54	n.s.
dbMEM RDA axis 1+2+3	0.57	n.s.

Note: n.s.: no significant contribution to tree species density spatial patterns

The axes of the RDAs on linear trend and on dbMEMs were significantly correlated to the distributions of single tree species (Table 5). For both, adult and juvenile individuals, first axes of linear trend RDAs and dbMEM RDAs yielded nearly the same results: *Rhododendron campanulatum* correlated very strongly with the axes (|r|≥ 0.95). All other tree species showed opposing direction of correlations. These correlations were weaker ($0.42 \le |r| \le 0.89$), however significant, and showed distinct relation to RDA axes and thus to spatial patterns for the most frequent species *Sorbus microphylla*, *Abies spectabilis*, *Betula utilis*, as well as for juvenile *Acer caudatum* individuals (Table 5).

RDAs on spatial linear trends and on dbMEMs with environmental variables as constraining factors explained up to 95% (axis 1, adult trees) of stand density spatial patterns. Up to 32% (finer scale spatial pattern of adult trees) of spatial variation could not be explained by environmental variables (see Table 6 for details).

Table 5. Significant ($p<0.05$) correlations of plant species with spatial patterns (Figure 8)

Spatial variable	Positive correlation		Negative correlation	
	Species	**Strength of correlation (r)**	**Species**	**Strength of correlation (r)**
Adult trees				
Axis 1 linear trend RDA	*Rhododendron campanulatum*	0.99	*Sorbus microphylla*	-0.88
			Abies spectabilis	-0.72
			Betula utilis	-0.67
			Acer caudatum	-0.63
			Prunus rufa	-0.44
Axis 1 dbMEM RDA	*Rhododendron campanulatum*	0.99	*Sorbus microphylla*	-0.89
			Abies spectabilis	-0.71
			Betula utilis	-0.65
			Acer caudatum	-0.64
			Prunus rufa	-0.44
Axis 2 dbMEM RDA	*Acer caudatum*	0.37	*Betula utilis*	-0.72
			Abies spectabilis	-0.51
Axis 3 dbMEM RDA			*Abies spectabilis*	-0.84
Juvenile individuals				
Axis 1 linear trend RDA	*Rhododendron campanulatum*	0.95	*Betula utilis*	-0.88
			Acer caudatum	-0.81
			Abies spectabilis	-0.58
			Sorbus microphylla	-0.42
Axis 2 linear trend RDA	*Rhododendron campanulatum*	0.48	*Sorbus microphylla*	-0.94
			Juniperus recurva	-0.35
Axis 1 dbMEM RDA	*Betula utilis*	0.83	*Rhododendron campanulatum*	-0.97
	Acer caudatum	0.80		
	Sorbus microphylla	0.54		
	Abies spectabilis	0.45		
	Prunus rufa	0.32		

Note: axis 2 of linear trend RDA, axis 2 of dbMEM RDA and axis 3 of dbMEM RDA showed no significant correlations.

Table 6. Proportion of variation of significant dbMEM and linear spatial trend RDA axes, explained by environmental variables

	Adult density	Juvenile density
Lin. trend RDA axis 1	0.95	0.75
Lin trend RDA axis 2	n.s.	0.74
dbMEM RDA axis 1	0.90	0.84
dbMEM RDA axis 2	n.s.	n.s.
dbMEM RDA axis 3	0.68	n.s.

Note: There is only one axis to explain. In consequence, the proportion explained by accumulated constrained eigenvalues is always = 1. Thus the R^2_{adj} of the models equals variance explained by the single axis which is indicated in the table.

The maps of RDA axes' site scores exhibited spatial patterns at broad and finer spatial scales (Figure 8). The first axes of both linear trend and dbMEM spatial patterns reflected the contrast in tree species composition between lower and upper elevational zones (Figure 8 a, b, e, g). In addition, the second and third axes showed spatial structures resembling differences in tree species composition between slopes (Figure 8 f) and within elevational zones (Figure 8c, d, f). In general, patterns of adult and juvenile individuals resembled each other. However, the distinct contrast between slope NE1 and the two other slopes NE2 and NW existed for juvenile individuals only (Figure 8 f). Similarly, the compartmentalized, rather small scale pattern of adult trees lacked a counterpart in the spatial pattern of juvenile individuals (Figure 8 d).

4 Discussion

Our results are consistent with the hypothesis that species-specific variation in adult and juvenile stand density along the treeline ecotone depends to a varying extent on edaphic, climatic and topographic variables. Variables with strong influence on the ordinations show significant differences of mean values between zones with differing densities of *Rhododendron campanulatum*. The ecological niche occupied by *Rhododendron campanulatum* is characterized by low temperature and poor nutrient availability. Juvenile population density shows a stronger dependence on climatic variables, i.e. temperature. Microtopographic variables play a greater role compared to adult tree density. Variation partitioning indicates that soil variables, in particular nutrient variables, significantly contribute to total explained variation of adult tree density. Thus, the role of temperature for treeline tree population density has to be relativized, in accordance to results of Weiss et al. (2015), Müller et al. (2016 a, b) and others. Differences in temperature, surface structure and within-plot ground cover influence the occurrence of juvenile individuals to a larger extent compared to adult tree density, supporting previous assumptions regarding differences between juvenile and adult tree growth, e.g. Smith et al. (2003); Wieser et al. (2014).

4.1 Species-environment relationships

Both ordinations show *Rhododendron campanulatum* to be the dominant tree species at topographically finer structured and colder habitats with reduced nitrogen availability. This combination of site properties in elevational zones C and D results in a high competitiveness of *Rhododendron campanulatum* that is reduced at more nutrient-rich and warmer sites of zones A and B where other tree species gain predominance

4.1.1 Topography

Differences in species-environment relationships between adult and juvenile population densities originate mainly from variables associated to the topographic variable group: For adult tree density, topographic variables such as size of rock fragments covering the plot were sorted out by backward selection. In contrast, for juvenile population density microrelief dissimilarity was selected as significant. Similarly, exposition of the sites was relevant for juvenile population density but not for adult trees. These findings are in line with previous assumptions: Rich microtopography is an important factor for seedling and sapling establishment, in terms of shelter elements and creation of safe sites and expected to influence juvenile individuals rather than adults (Li and Yang 2004; Batllori et al. 2009; Holtmeier and Broll 2012).

Heterogeneous, compartmentalized microreliefs with many small rocks covering the ground surface favors juvenile *Sorbus microphylla* and *Rhododendron campanulatum* individuals. By contrast, *Abies spectabilis*, *Acer caudatum* and *Betula utilis* recruits suppress *Rhododendron campanulatum* at microreliefs with more homogeneous surface structure containing large boulders at some sites, but not structured by many small rock fragments. Physiognomically, *Rhododendron campanulatum* can better adapt to the rugged terrain and poor rooting conditions between many small rocks. *Rhododendron campanulatum* shows the capability to "creep" in horizontal direction. We frequently observed vital *Rhododendron campanulatum* individuals having their flexible branches covered by litter, soil and debris. Features of heterogeneous microrelief favor establishment of juvenile individuals, as concave topographies can serve as nutrient and moisture sinks and provide shelter elements, mitigating abiotic constraints (Holtmeier 2009; Scherrer and Körner 2010; Llambí et al. 2013). Furthermore, microtopography (e.g. curvature) is related to soil temperature, for example the ground is warmer at convex topography than in micro-gullies in summer (Kajimoto et al. 2003; Körner 2012). Such a curvature-effect might be included in the temperature gradient of our ordinations. Moreover, microrelief can influence for instance snow cover and precipitation distribution. Effects of radiation and temperature are influenced by slope and aspect, with consequences for water availability (Li and Yang 2004) and rich microtopography can provide more shelter elements (Smith et al. 2009).

At a smaller scale of c. 1m^2 a direct relation between shelter elements, seedbeds and juvenile tree individuals might be even more significant as the effect of thermal habitat differentiation by microtopographic elements becomes more effective (Scherrer and Körner 2011). Further small-scale studies are necessary to deepen our understanding of the relations between microtopography and juvenile tree species individuals.

4.1.2 Nutrients

According to the ordination results, the main physiological stressor of the Rolwaling treeline is limited nutrient (nitrogen) availability (see also Müller et al. 2016 a, b). Sites of elevational zones C and D, where *Rhododendron campanulatum* dominates the tree species composition, show much wider C:N ratios. In addition, reduced manganese contents of the soils seem to play an important role as environmental variable. Sites of zone A, where other tree species such as *Betula utilis* and *Abies spectabilis* are predominant, differ in C:N ratios significantly from zone C with a maximum density of *Rhododendron campanulatum*.

Soil nitrogen content and availability can make the difference in soil fertility of alpine regions (Körner 2003) and is one of the most important macro nutrients for plant growth; after carbon it is required in largest amounts (Hawkesford et al. 2012). Nutrient poor podzols with a thick layer of litter are widespread at our study site (Müller et al. 2016b), and are the characteristic soil type of Himalayan treeline ecotone *Rhododendron* thickets (Miehe et al. 2015). Nutrient availability to plants is primarily limited by soil temperature and moisture and is largest at snowmelt (Larcher 2003; Baptist and Aranjuelo 2012). The C:N ratio is mainly influenced by increasing C contents, corresponding to sites with higher density of *Rhododendron campanulatum* (Appendix 3). This finding coincides with results from nutrient cycling models with and without *Rhododendron* understory (Chastain Jr. et al. 2006). Slowly decomposing *Rhododendron* litter causes low nitrogen mineralization rates and nitrogen availability (Maithani et al. 1998). Moreover, the leaves contain high amounts of polyphenols which might cause increasing nitrate and ammonium immobilization (Northup et al. 1995; DeLuca et al. 2002), leading to a decrease of nitrogen availability (Bürzle et al. 2017). The trace element manganese has various functions in basal metabolism, chloroplast structure stabilization, nucleic-acid synthesis, and lignin synthesis. Manganese-deficient plants show reduced dry matter production, reduced net photosynthesis and they are more susceptible to damage by freezing temperatures and root-rotting fungal diseases. Manganese deficiency causes inhibition of growth especially at young growth stages, chloroses and necroses of young leaves and drying of conifer shoot tips and tree tops (Larcher 2003; Broadley et al. 2012).

We assume that both reduced nitrogen and manganese availability at the elevated sites lead to lowered competitive strength of tree species. As an exception, *Rhododendron* species and ericaceous perennials in general are low nutrient users and grow on soils poor in most essential elements which are unsuitable to other species, and are even favoured by poor soil conditions (Cox 1990; Ristvey et al. 2007). Shrestha (2007) found *Betula utilis* associated with higher soil nitrogen than mixed forest. Compared to *Acer* and *Betula* species, *Rhododendron campanulatum* seems to use nutrients more efficiently. At the elevated sites of zones C and D where nutrient availability is low the tradeoff between nutrient acquisition and carbon cost for root production is unfavourable for deciduous species with nutrient rich leaves. Therefore, evergreen *Rhododendron* species with lower leaf tissue nutrient status may compete successfully with the deciduous species and are better adapted to poor nutrient conditions (Garkoti and Singh 1994; Garkoti and Singh 1995a; Eckstein et al. 1999).

Another competitive advantage of *Rhododendron campanulatum* at sites of zone C and D is its high root/shoot ratio. More investment in root biomass supports the species in capturing more nutrients at the high elevated, nutrient poor sites (Garkoti and Singh 1995b), a typical feature of stunted woody plants at the treeline and of ericaceous dwarf shrubs (Larcher 2003). Moreover, *Rhododendron campanulatum* leaves may serve as a nutrient storage in winter and source in spring and, as they are present when the growing season starts, increase photosynthetic capacity at the beginning of the growing season (Pornon and Lamaze 2007). Area based leaf nitrogen content of *Rhododendron campanulatum* was distinctly higher than those of *Abies spectabilis* and *Betula utilis* (De Lillis et al. 2004). In the European Alps, *Rhododendron ferrugineum* stores nitrogen in leaves especially at young growth stages (later mainly in woody tissues) and is able to decouple from competition for nitrogen from the soil. This might be beneficial at sites with low nitrogen resources at the beginning of the growing season (Pasche et al. 2002; Lamaze et al. 2003). We assume that other Rolwaling treeline tree species lack these competitive advantages and are thus suppressed by *Rhododendron campanulatum* in zone C and by *Rhododendron campanulatum* and *Rhododendron* dwarf shrub species in zone D.

In addition, *Rhododendron* litter is associated with high concentrations of polyphenols, and is assumed to have allelopathic effects, both exerting an unfavorable influence on the competitiveness of *Betula utilis* and *Abies spectabilis* in *Rhododendron*-dominated habitats (Schickhoff et al. 2016b; Schwab et al. 2016; Bürzle et al. 2017). Slowly decomposing *Rhododendron campanulatum* litter and allelopathic effects might be part of a positive feedback controlling low nutrient availability from the soil to which the species is better adapted than its competitors (Hobbie 1992; Berendse 1994; Aerts 1995).

Bulk density of Of horizon showed a strong gradient along RDA axis 1. However, the maximum difference between medians of elevational zones was 0.03 g cm^{-3} only (maximum range of zones 0.1 g cm^{-3} in zone D) which is a negligible low variation despite the significance of the difference between zone A and zones B and C. For instance, histosols typically range from 0.1 to 0.7 g cm^{-3} (Brady and Weil 2014). In consequence, we consider the bulk density not causing substantial different conditions for plant growth. For instance, bulk density related soil moisture was not selected to contribute significantly to explain variation in tree species density. Thus the influence of Of horizon bulk density on adult tree distribution is not further discussed.

In our case study, in addition to limited nutrient availability which favors *Rhododendron campanulatum*, climatic and topographic factors limit tree species distribution.

4.1.3 Climate

Ordinations of juvenile and of adult tree density indicate a strong influence of temperature gradients. Similar to nutrient availability, this trend separates *Rhododendron campanulatum* density from all other tree species. In case of juvenile individuals, the ordination differentiates *Sorbus microphylla* from the other tree species in addition to *Rhododendron campanulatum*. *Rhododendron campanulatum* and juvenile *Sorbus microphylla* occur in high density at sites of elevational zones C and D characterized by lower temperatures. Variation partitioning revealed that the climate variables are important constraints for juvenile population density compared to soil and topography variables. In case of adult trees, the variation that is explained by a pure component of climate variables is rather small. However, there is a combined soil-climate component that explains roughly the same proportion of variance as the pure soil variable component. To our knowledge, there are no studies from other Himalayan *Rhododendron* krummholz belts which focus on the relationships of species and population densities with temperature. Previous studies in Rolwaling found a significant decline of mean soil temperatures (annual and growing season) along the elevational gradient towards the krummholz zone and the dwarf shrub thickets, albeit with differences between NW- and NE-facing slopes (see Müller et al. 2016b; Bürzle et al. 2017 for details). In particular, the dense evergreen canopy of the krummholz belt prevents soil heat flux and radiative warming. The Rolwaling data are in accordance with the general description of the *Rhododendron* krummholz belt environment as cold habitat with prolonged snow cover and longlasting frozen ground (cf. Miehe et al. 2015).

Many other studies found soil and air temperatures being the main constraining factors for tree growth at treeline. The positive correlation between soil and air temperature and tree species population density is well documented (Körner 2012; Greenwood et al. 2015; Müller et al. 2016a). The close link of differences in temperature with the dominance of *Rhododendron campanulatum* and with the low density of other tree species at elevational zones C and D (cf. Figure 4 & 6) point to a low temperature ecological niche occupied by *Rhododendron* as described by Miehe et al. (2015). Low temperatures obviously provide a competitive advantage for *Rhododendron campanulatum*, probably due to evergreeness, capability of early blooming (before *Betula utilis* leaves fully develop) and slowed soil development processes at cold sites (see above). In consequence, temperature does not only limit tree species distribution in general but it contributes to species-specific elevational limits of established stands (Vitasse et al. 2012; Trant and Hermanutz 2014). In our case, the very few juvenile individuals of *Abies spectabilis* and *Betula utilis* in zone D are restricted most likely to favorable microsite conditions. Nevertheless, it remains unclear whether the upper range limits of *Abies spectabilis* and *Betula utilis* originate from restricted growth by low temperature itself or from suppression by *Rhododendron campanulatum* competing better at colder sites.

Due to the high degree of correlation of air and soil temperatures with each other and with respective seasonal temperatures and length of growing season, we cannot differentiate which temperature components are directly related to tree species distribution and density. In a review of global and local scale treeline studies, Müller et al. (2016a) found air temperature to be considered the most important tree growth controlling factor at upper limits, while soil temperature was of secondary importance. Minimum temperature was not identified as significant for tree species distribution in the present study, except the minimum air temperature in JJAS season. Most likely, the minimum summer temperature does not restrict plant growth but is just indicating colder conditions at higher elevation, as part of the general temperature gradient. *Rhododendron campanulatum* is roughly as frost resistant as *Abies spectabilis* (c. -25°C), while *Betula utilis* survives at distinctly lower temperatures (c. -40°C) (Sakai and Malla 1981). These are autecological physiological limits, however, which might be modified under competitive stress in real field situations. Nevertheless, single extreme minimum temperature values play obviously a minor role for the distribution of *Rhododendron campanulatum* within the ecotone. We assume mean minimum to maximum temperatures, especially during growing season, and growing season length to be more important, in accordance with Vetaas (2002) who identified niches of several *Rhododendron* species, including *Rhododendron campanulatum*, to be defined by mean annual temperature, not by minimum or maximum temperatures.

Despite positive correlations of natural regeneration of tree species with soil moisture and temperature at Himalayan treeline ecotones (cf. Schickhoff et al. 2015), soil moisture was not selected as significantly influencing tree species densities, i.e. population densities were not constrained by any moisture variable in the RDAs of the present study. However, we detected seasons with soil water scarcity (Müller et al. 2016a) and a declining soil moisture trend along the investigated elevational gradient (Bürzle et al. 2017). In addition to temperature several studies found soil moisture and/or precipitation to be a relevant site factor at treelines, however for tree growth performance, e.g. tree ring increment (e.g., Gaire et al. 2014; Gaire et al. 2016; Tiwari et al. 2016) while soil moisture was not related to population density. *Rhododendron campanulatum* shows higher water use efficiency compared to other species at same elevations, and the most distinct increase in water use efficiency with increasing elevation (De Lillis et al. 2004). Accordingly, *Rhododendron campanulatum* is obviously better adapted to drier conditions which might occur under high irradiance in zones C and D and in drier seasons than competing tree species.

In summary, the temperature gradient contributes to elevational differentiation of juvenile and adult tree populations and controls, together with nutrient availability, the growth of tree species at their upper limits. Especially in case of juvenile individuals topography is an important constraint as well.

4.2 Spatial patterns and neutral effects

The tree density spatial pattern is defined by the contrast of *Rhododendron campanulatum* vs. all other tree species. The dominance of *Rhododendron campanulatum* controls the broad scale spatial pattern, even after removal of the linear trend, indicating the huge contrast in tree species composition between the lower and upper elevational zones.

The massive influence of *Rhododendron campanulatum* on the general spatial pattern results in a coarser pattern of distinguishable spatial scales compared to other studies using the same analytical approach (e.g. Andersen et al. 2011), i.e., the contrast between upper and lower elevational zones along the entire gradient dominates while the smaller scale patterns within elevational zones are of minor importance to capture spatial variation in tree species density. This finding applies for both, adult and juvenile population densities. However, the amount of variation explained by dbMEM RDA axis 1 is distinctly smaller compared to adult tree density, showing that juvenile population density is to a lesser extent defined by the spatial position of sites.

Environmental variables explain considerable amounts of variation in spatial patterns, with higher amounts explained for adult compared to juvenile population density spatial patterns. Neutral processes of community and population dynamics could explain remaining spatial variation. These include variation in species demography due to competition (ecological drift) and propagule dispersion (random dispersal) creating spatial autocorrelation in response variables (Legendre and Legendre 2012). Especially finer scaled spatial patterns and the juvenile population density pattern contain proportions of variation assigned to neutral processes. This finding reveals that in addition to microtopographic features, nutrient availability, and temperature, competition and dispersal need to be considered to explain variation of tree species density. The sampled tree species propagate in different ways: For instance, *Betula utilis* and *Rhododendron campanulatum* use anemochorous dispersal paths. In addition, we observed frequent clonal propagation of *Betula utilis*, while *Abies spectabilis* relies rather on zoochorous paths. These different dispersal strategies might result in species-specific responses to climate change. In addition to dispersal, seed quality and quantity might play a role (Cuevas 2000; Dullinger et al. 2004; Holtmeier 2009; Batllori et al. 2010; Kroiss and HilleRisLambers 2015). Future studies are needed to analyse these species-specific properties in order to determine their influence on tree species density and interaction with upslope migration potential.

4.3 Interaction of edaphic, climatic and topographic variable components and response to climate warming

We suppose that the response to climate warming will change the competitive patterns in the treeline ecotone and create new niches while the general constraints of low temperatures and low nutrient availability remain. Given the generally intense regeneration (Schickhoff et al. 2015; Schickhoff et al. 2016b) and comparatively high mean annual temperatures (Müller et al. 2016a, b), *Abies spectabilis* and *Betula utilis* could potentially establish populations above the krummholz belt. However, cold, nutrient-poor conditions will most likely continue to be more beneficial for *Rhododendron campanulatum* and *Rhododendron* dwarf shrub species in zones C and D and above, regardless of slightly increasing mean temperatures. In consequence the *Rhododendron campanulatum* belt might migrate upwards as well.

As the *Rhododendron campanulatum* population of the krummholz belt is firmly established and its predominance is maintained by feedback mechanisms, this thicket likely constitutes an insurmountable barrier for seedlings and saplings of *Betula utilis* and *Abies spectabilis*, even under warmer conditions. We assume that the small numbers of *Abies spectabilis* and *Betula utilis* individuals found at elevational zones C and D are related to microtopographic features, similar to observed establishment patterns at Taiwanese *Abies* treelines (Greenwood et al. 2015). However, small-scale safe sites were not sufficiently captured by our sampling. Currently, the few individuals of other tree species might consolidate towards established populations at locations above the contemporary krummholz belt's position only in the long term. Persistent low nutrient availability and allelopathic effects will most likely prevent juvenile tree individuals from growing to mature, fruiting trees within the current krummholz belt or above it. The *Rhododendron campanulatum* krummholz belt constitutes a bottleneck for the establishment of *Betula utilis* and *Abies spectabilis* individuals above the contemporary treeline. Similarly, a substantial establishment in the dwarf shrub heaths above the krummholz belt is unlikely since comparable soil and environmental conditions prevail. However, the few *Abies spectabilis* and *Betula utilis* individuals in elevational zones C and D indicate that they potentially survive there and can reach tree dimensions.

Our results suggest that the Rolwaling treeline will most likely remain at its present position during the coming decades, and that the responsiveness of the Rolwaling treeline to climate warming will be rather low as assumed for near-natural Himalayan treelines and krummholz treelines in general (Harsch and Bader 2011; Chhetri and Cairns 2015; Schickhoff et al. 2016b).

5 Conclusion

Our findings corroborate assumptions that local treeline elevation, species composition and tree density are not defined by thermal deficits alone. If treeline elevation relied on temperature alone, a detectable treeline advance to higher elevation would have been observed at the Rolwaling treeline during recent decades. The feedback mechanisms of the *Rhododendron campanulatum* krummholz belt constrain the treeline response to climate warming through retarding or inhibiting upward migration of other tree species. The sensitivity of treeline ecotones to climate change should be further assessed by analysing species-specific responses not only to climatic variables but also to other environmental site factors, despite site factors' partial dependence on thermal conditions.

Results might be site- and community-specific. Differences in variables explaining adult and juvenile population densities point to the need to investigate different life stages and their relation to abiotic and biotic conditions. Spatial pattern analyses reveal that dispersal mechanisms and biotic interactions should be considered in future studies on treelines.

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Appendices

Appendix 1. Variation of density of tree species in the treeline ecotone

Variation of adult tree density [ha^{-1}]

Eleva-tional zone	*Abies spectabilis*			*Acer caudatum*			*Betula utilis*			*Juniperus recurva*			*Prunus rufa*			*Rhododendron campanulatum*			*Sorbus microphylla*			All species		
	M	SD		M	SD		M	SD		M	SD		M	SD		M	SD		M	SD		M	SD	
A	239	347	a	159	280	a	250	236	a	0	-	a	14	25	a	270	408	a	463	230	a	232	304	a
B	127	118	a	0	-	b	315	227	a	0	-	a	6	16	a	1300	936	b	350	232	a	350	597	a
C	6	11	b	0	-	b	25	67	b	0	-	a	0	-	a	1923	1225	b	69	100	b	337	863	a
All zones	130	237		59	184		199	227		0	-		7	18		1117	1122		303	257		-	-	

Variation of juvenile stand density [ha^{-1}]

Eleva-tional zone	*Abies spectabilis*			*Acer caudatum*			*Betula utilis*			*Juniperus recurva*			*Prunus rufa*			*Rhododendron campanulatum*			*Sorbus microphylla*			All species		
	M	SD		M	SD		M	SD		M	SD		M	SD		M	SD		M	SD		M	SD	
A	1114	2509	a	1691	1636	a	1938	1623	a	21	73	a	23	54	a	957	1178	a	1711	1245	a	1065	1579	a
B	854	890	a	60	86	b	548	612	ab	4	14	a	0	-	a	6371	5903	bc	925	800	ab	1252	3068	a
C	63	120	b	0	-	b	92	219	bc	100	324	a	0	-	a	5444	2399	b	1594	2068	ab	1042	2216	a
D	8	22	b	0	-	b	4	14	c	0	-	a	0	-	a	1117	965	ac	206	298	b	191	534	b
All zones	534	1447		488	1135		697	1203		31	163		7	29		3372	3982		1133	1380		-	-	

Notes: Mean values of species subsamples with different letters are significantly different at $p < 0.05$ between elevational zones. M: mean, SD: standard deviation.

Appendix 2. Descriptive statistics of soil variables

Soil horizon	Zone	C [mg g^{-1}]			N [mg g^{-1}]			Nmin [mg g^{-1}]			P [mg g^{-1}]			K [cmol kg^{-1}]		
		Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min
Ah	**A**	204.20 ± 84.82	344.89	73.05	12.11 ± 5.49	20.96	3.94	0.04 ± 0.04	0.14	0.01	0.04 ± 0.03	0.11	0.00	0.49 ± 0.27	0.99	0.15
	B	235.01 ± 67.79	395.37	166.54	12.98 ± 3.37	20.01	8.78	0.05 ± 0.04	0.15	0.01	0.04 ± 0.03	0.08	0.00	0.47 ± 0.32	1.39	0.18
	C	245.10 ± 73.91	366.47	98.13	11.41 ± 3.25	16.21	4.54	0.02 ± 0.01	0.05	0.00	0.05 ± 0.03	0.12	0.00	0.55 ± 0.31	1.35	0.11
	D	171.02 ± 70.10	230.62	54.17	7.39 ± 3.58	9.56	2.70	0.01 ± 0.01	0.03	0.00	0.04 ± 0.03	0.08	0.00	0.55 ± 0.32	0.98	0.17
Ae	**A**	27.84 ± 15.13	72.16	13.53	1.47 ± 0.64	3.10	0.83	0.00 ± 0.00	0.00	0.00	0.00 ± 0.00	0.00	0.00	0.07 ± 0.02	0.11	0.02
	B	30.83 ± 20.80	88.11	15.07	1.45 ± 0.76	3.37	0.81	0.01 ± 0.01	0.03	0.00	0.00 ± 0.00	0.01	0.00	0.06 ± 0.03	0.12	0.03
	C	33.47 ± 17.86	78.39	15.76	1.58 ± 0.87	4.02	0.78	0.01 ± 0.01	0.02	0.00	0.00 ± 0.00	0.01	0.00	0.09 ± 0.07	0.26	0.03
	D	45.43 ± 14.43	70.58	26.69	2.26 ± 0.56	3.32	1.45	0.00 ± 0.00	0.01	0.00	0.01 ± 0.00	0.02	0.00	0.14 ± 0.05	0.22	0.08

Soil horizon	Zone	Mg [cmol kg^{-1}]			Na [cmol kg^{-1}]			Ca [cmol kg^{-1}]			Mn [cmol kg^{-1}]			Al [cmol kg^{-1}]		
		Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min
Ah	**A**	1.68 ± 1.07	4.20	0.37	0.02 ± 0.02	0.07	0.00	6.35 ± 6.17	21.45	1.46	0.73 ± 2.48	9.36	0.01	5.07 ± 4.06	15.85	0.59
	B	1.78 ± 1.21	4.91	0.63	0.03 ± 0.03	0.11	0.00	5.92 ± 4.20	13.32	0.10	0.09 ± 0.14	0.52	0.01	4.21 ± 3.21	12.64	1.05
	C	2.11 ± 1.53	5.94	0.58	0.01 ± 0.02	0.05	0.00	9.12 ± 6.64	23.85	0.02	0.06 ± 0.08	0.26	0.01	2.87 ± 2.12	7.99	0.39
	D	1.11 ± 1.01	2.35	0.25	0.02 ± 0.02	0.05	0.00	2.90 ± 4.85	7.03	0.34	0.10 ± 0.15	0.49	0.01	2.80 ± 1.55	5.48	0.63
Ae	**A**	0.23 ± 0.15	0.64	0.05	0.01 ± 0.01	0.02	0.00	0.59 ± 0.41	1.32	0.08	0.01 ± 0.00	0.01	0.00	1.86 ± 2.42	10.00	0.22
	B	0.13 ± 0.09	0.32	0.03	0.01 ± 0.01	0.02	0.00	0.44 ± 0.44	1.43	0.02	0.00 ± 0.01	0.03	0.00	2.08 ± 3.05	11.78	0.40
	C	0.19 ± 0.13	0.54	0.05	0.01 ± 0.01	0.03	0.00	0.38 ± 0.45	1.47	0.02	0.00 ± 0.01	0.03	0.00	0.77 ± 0.12	1.01	0.62
	D	0.22 ± 0.07	0.33	0.12	0.01 ± 0.01	0.02	0.00	0.37 ± 0.20	0.78	0.08	0.02 ± 0.03	0.09	0.00	1.94 ± 0.81	4.06	1.08

Soil horizon	Zone	Fe [cmol kg^{-1}]			pH [KCl]			Bulk density [g cm^{-3}]			Sand [%]			Silt [%]		
		Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min	Mean (± s.e.)	Max	Min
Ah	**A**	0.54 ± 0.39	1.40	0.11	3.17 ± 0.24	3.56	2.84	0.41 ± 0.27	0.92	0.16	na	na	na	na	na	na
	B	0.44 ± 0.56	2.23	0.06	2.96 ± 0.27	3.41	2.64	0.32 ± 0.10	0.49	0.21	na	na	na	na	na	na
	C	0.37 ± 0.61	2.28	0.13	2.89 ± 0.25	3.49	2.67	0.28 ± 0.19	0.79	0.15	na	na	na	na	na	na
	D	0.52 ± 0.33	1.10	0.13	3.27 ± 0.33	4.11	2.97	0.53 ± 0.23	0.95	0.30	na	na	na	na	na	na
Ae	**A**	0.17 ± 0.32	1.27	0.03	3.40 ± 0.25	3.84	3.07	1.25 ± 0.14	1.42	0.95	66 ± 5	77.6	59.2	26 ± 3	29.8	16.5
	B	0.16 ± 0.24	0.93	0.02	3.27 ± 0.28	4.02	3.04	1.23 ± 0.50	1.48	1.06	64 ± 4	69.9	58.9	28 ± 2	31.1	23.3
	C	0.12 ± 0.07	0.23	0.01	3.11 ± 0.14	3.27	2.86	1.18 ± 0.61	1.41	1.09	70 ± 6	79.1	60.7	23 ± 4	29.7	16.1
	D	0.21 ± 0.10	0.36	0.06	3.35 ± 0.18	3.60	3.06	1.08 ± 0.54	1.52	0.58	71 ± 5	78.7	62.9	21 ± 4	28.6	15.7

Soil horizon	Zone	Clay [%]		
		Mean (± s.e.)	Max	Min
Ah	A	na	na	na
	B	na	na	na
	C	na	na	na
	D	na	na	na
Ae	A	8 ± 2	11.2	4.8
	B	8 ± 2	10.6	6.4
	C	7 ± 2	9.4	4.4
	D	8 ± 2	11.8	5.6

Appendix 3. (Micro-) topographic variables and derived Jaccard dissimilarity indices as measures of inside-plot microtopographic homogeneity. Four quadrants resulted in six dissimilarity values that we averaged for each plot

Variable	Description	Variable used to derive...					
		Microrelief and ground cover dissimilarity	Ground cover dissimilarity	Microrelief dissimilarity	Curvature dissimilarity	Aspect dissimilarity	Surface structure dissimilarity
Northness, eastness	Converted aspect; eastness: sin(aspect), northness: cos(aspect), where 1 = E or N, and -1 = W or S	X	-	X	-	X	-
Slope	Inclination of the slope	X	-	X	-	-	-
Surface structure	Structure of ground surface: plane, terraced or rugged	X	-	X	-	-	X
Curvature	Vertical and horizontal curvature of ground surface	X	-	X	X	-	-
Fine soil cover	Percentage of ground surface covered with particles< 0.2 cm	X	X	-	-	-	-
Coarse soil cover	Percentage of ground surface covered with coarse fragments 0.2 to < 2 cm	X	X	-	-	-	-
Small stone cover	Percentage of ground surface covered with coarse fragments 2 cm to < 20 cm	X	X	-	-	-	-
Medium stone cover	Percentage of ground surface covered with coarse fragments 20 cm to < 60 cm	X	X	-	-	-	-
Large stone cover	Percentage of ground surface covered with coarse fragments 60 cm to < 200 cm	X	X	-	-	-	-
Small rock cover	Percentage of ground surface covered with coarse fragments 2 m to < 5 m	X	X	-	-	-	-
Medium rock cover	Percentage of ground surface covered with coarse fragments 5 m to < 10 m	X	X	-	-	-	-
Large rock cover	Percentage of ground surface covered with coarse fragments 10 m and larger	X	X	-	-	-	-
Large rock attribute	In case of large rock presence: outcrop rock (protruding from slope) or plane rock (bare, little or no vegetation)	X	-	X	-	-	X
Bare ground cover	Percentage of bare soil and rock cover (mineral objects)	X	-	X	-	-	-
Vegetation cover	Percentage of ground vegetation and litter cover (organic objects)	X	-	X	-	-	-

Notes: X: variable used to derive dissimilarity measure; -: variable not used to derive dissimilarity measure

Appendix 4. Predictors for imputed variables

Imputed variables	Predictors
Soil temperature and moisture variables	Eastness, latitude, longitude, slope, percentage of rock and of litter cover, presence/absence of plane bare rocks, canopy closure, LAI, ISF, DSF, VisSky, GSF, sand content of Ae-horizon, bulk densities of Of- and Ah-horizons, mean air temperature of DJF-season, minimum air temperature of MAM- and JJAS-season, soil temperature and moisture variables
LAI, ISF, DSF, VisSky, GSF	Percentage of bare ground cover, elevational zone, elevation, position of plot (combined slope name and elevational zone), species specific number and basal area of stumps, species specific and total number of adult and juvenile individuals per plot, species specific descriptive statistics of dbh, tree height, crown width, crown height, crown development, crown area, LAI, ISF, DSF, VisSky, GSF
Crown width and derived variables of *Rhododendron campanulatum*	Nearly equal to predictors for HemiView variables. For crown area descriptive statistics some species specific stump basal area variables and number of *Abies spectabilis* juvenile individuals were excluded.

Appendix 5 Imputation of missing data

Multiple imputation and especially multivariate imputation by chained equations ("MICE", Van Buuren 2012) is an approved and widely used technique to deal with missing values in various sciences (García et al. 2015) including ecology (Conradi et al. 2015; Laughlin et al. 2015). We used MICE based on a random forest classification (Doove et al. 2014) to estimate the missing values based on the relationships between the variables. We followed recommendations of Van Buuren (2012) to specify the imputation model and used the MICE implementation "*mice*" in the "mice" R package (Van Buuren and Groothuis- Oudshoorn 2011).

In order to use stand characteristics as imputation predictors, we sampled vegetative crown development by a straightforward index ranging from a very good, dense and round crown to a less than half side developed crown with dead branches (Schickhoff 2002). We approximated crown projection area (hereafter: crown area) from crown width measurements (Röhle 1986). We identified the species and cause of death (natural, anthropogenic, unidentified) and counted all stumps ≥ 7 cm diameter. We measured diameters 10 cm above ground, stumps with a height less than 10 cm were measured at highest point above ground. Total canopy closure was estimated by visual assessment according to Jennings et al. (1999) for each plot in the following classes: sparse, gappy, closed and very dense (Grabherr et al. 1998). Light conditions were measured by hemispherical photography pictures at five points of a cross pattern in every plot (Rich et al. 1999; Wood and Webb 2006). The following indices i.e. leaf area index (LAI), indirect site factor (ISF), direct site factor (DSF), visible sky (VisSky) and global site factor (GSF) were derived from hemispherical photography pictures using HemiView software (Delta-T Devices Ltd; Rich et al. 1999). In order to provide a sufficient basis for imputation we derived plot and species specific descriptive statistics of tree species growth and HemiView data (mean, median, minimum, maximum, 1st and 3rd quartiles).

Missing data occurred in the following environmental variables: crown width of *Rhododendron campanulatum* individuals in krummholz zone C (due to very dense and entangled growth allocation of branches to individuals was not reliable; 26% missing values), from hemispherical photography pictures derived variables (due to rainy weather conditions during growing season; 38% missing values) and soil temperature and soil moisture (38% missing values). We used 38 imputations following the rule of thumb recommendation to use the percentage of missing data as number of imputations (Van Buuren 2012).

In order to yield multiple imputations with minimal bias and maximal certainty we applied the "quickpred"-function of "mice" for the selection of predictors for the imputations of soil temperature and soil moisture, LAI, ISF, DSF, VisSky, GSF, crown width of *Rhododendron campanulatum* and derived variables. The function creates a predictor matrix by selecting variables for which the patterns of missing data differ and variables that explain a considerable amount of variance of the variables with missing values (Van Buuren et al. 1999). See appendix 4 for predictors for the imputed variables.

The imputation algorithm imputes the incomplete columns of the variable matrix (the target columns) by generating plausible synthetic values given the other variables columns (predictors) in the data. The random forest method is a recursive partitioning technique that creates and averages numerous classification/regression trees. The whole dataset is split into more homogenous subsets ('leaves' of the classification tree) by the random forest method. Imputed values are iterative and randomly chosen from observed values in the same leaf (Doove et al. 2014). Several imputed datasets are generated and analyzed separately. Final results are produced by an averaging method ("pooling", Barnard and Rubin 1999; Van Buuren and Groothuis-Oudshoorn 2011). Recursive partitioning imputation outperforms other imputation methods as non-linear relationships like interaction effects among variables are incorporated (Doove et al. 2014). We preferred random forest to predictive mean matching, the robust and "good overall imputation method" (Van Buuren and Groothuis-Oudshoorn 2011) for numerical data. Random forest is more effective for small samples with higher percentage of missing data (Van Buuren 2012) and random forest imputations showed most reliable results compared to other methods for our data (Van Buuren 2012). To prevent imputations with meaningless outliers we restricted the range of imputed values to the range of observed values +/- 10% of the respective elevational zone (Van Buuren 2012). The pooling method of "mice" is not implemented for RDA results. Thus we calculated means of estimates and applied the procrustean randomization test (PROTEST) with rescaled to unit sum of squares configurations of the ordinations (Legendre and Legendre 2012). We used the test results as measures for between - imputation variance. PROTEST is designed to compare two models against each other, therefore we analyzed the 38 imputed models each against all and averaged results (Table Appendix 5). Climate variable models exhibited maximum mean sum of squared differences of 0.333 (Table Appendix 5). As they did not include any imputed variables, soil and topography models showed full congruence (sum of squares = 0, Table Appendix 5). Mean sum of squares of the final models was max. 0.001 (Table Appendix 5), indicating minor difference between final models. Imputed values had means and ranges comparable to the observed values for all variables with missing data. In consequence, our imputation approach did not introduce any directional bias in the environmental data matrix.

Table Appendix 5. Soil, climate, topography and final models for adult and juvenile tree species density: between-imputation variance

Model	Mean sum of squared differences		Significance	
	Sites	Species	Sites	Species
Adult tree density: soil	0	0	0.001	0.001
Adult tree density: climate	0.207	0.070	0.001	0.004
Adult tree density: topography	0	0	0.001	0.001
Adult tree density: soil + climate + topography	0.001	0.001	0.001	0.001
Juvenile density: soil	0	0	0.001	0.001
Juvenile density: climate	0.333	0.041	0.002	0.001
Juvenile density: topography	0	0	0.001	0.001
Juvenile density: soil + climate + topography	0	0	0.001	0.001

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Appendix 6. RDAs of adult and juvenile tree density: Biplot scores of respective axes 1 and 2 indicating importance of environmental variables

	Adult tree density RDA	
	RDA axis 1	**RDA axis 2**
Air temperature DJF	-0.746	-0.181
C:N Ah-horizon	0.688	0.036
Bulk density Of-horizon	-0.645	0.154
C:N Ae-horizon	0.489	-0.343
Soil temperature MAM	-0.477	-0.170
Medium stone cover	0.414	0.103
Large stone cover	0.361	0.219
Mn concentration Ah-horizon	-0.354	0.555
Sand content	0.348	0.279
Min. air temperature JJAS	0.320	0.368
Coarse soil cover	0.316	0.067
Large rock cover	-0.296	0.067
Surface structure dissimilarity	-0.212	-0.142
Fine soil cover	-0.154	-0.230
Small rock cover	-0.148	0.155
Medium rock cover	-0.017	-0.002
Litter cover	0.009	-0.138
	Juvenile density RDA	
	RDA axis 1	**RDA axis 2**
C:N Ah-horizon	0.707	-0.049
Air temperature DJF	-0.625	-0.433
C:N Ae-horizon	0.468	-0.358
Mn concentration Ah-horizon	-0.391	-0.319
Bare ground cover	0.334	0.142
Microrelief dissimilarity	0.333	0.295
Medium stone cover	0.328	0.056
Ca concentration Ae-horizon	0.186	0.024
Terraced surface structure	0.169	-0.074
Bulk density Ah	-0.152	0.185
Rugged surface structure	-0.095	0.320
Eastness	-0.050	0.157
Min. air temperature JJAS	-0.040	-0.102
pH$_{H_2O}$	0.038	-0.145

Note: variables sorted by absolute values of RDA axes 1.

Appendix 7. Differences of constraining variables, for adult and juvenile tree species ordinations

	Growth stage	Elevational zone			
		A	B	C	D
Air temperature DJF	adult	a	ab	b	-
	juvenile	a	ab	bc	bc
C:N Ah-horizon	adult	a	ab	b	-
	juvenile	a	ab	bc	bc
Bulk density Of-horizon	adult	a	b	b	-
C:N Ae-horizon	adult	a	ab	b	-
	juvenile	a	ab	b	ab
Soil temperature MAM	adult	a	a	b	-
Medium stone cover	adult	a	ab	b	-
	juvenile	a	a	a	a
Bare ground cover	juvenile	a	a	a	b
Microrelief dissimilarity	juvenile	a	a	a	b
Ca concentration Ae-horizon	juvenile	a	a	a	a
Large stone cover	adult	a	ab	b	-
Mn concentration Ah-horizon	adult	a	a	a	-
	juvenile	a	a	a	a
Sand content	adult	ab	a	b	-
Bulk density Ah-horizon	juvenile	ab	ab	b	a
Rugged surface structure	juvenile	a	a	a	a
Eastness	juvenile	a	a	a	a
Min. air temperature JJAS	adult	a	a	a	-
	juvenile	a	a	a	b
pH$_{H2O}$	juvenile	a	a	a	b
Coarse soil cover	adult	a	a	a	-
Large rock cover	adult	a	a	a	-
Surface structure dissimilarity	adult	a	a	a	-
Fine soil cover	adult	a	a	a	-
Small rock cover	adult	a	a	a	-
Medium rock cover	adult	a	a	a	-
Litter cover	adult	a	a	a	-

Notes: mean values of subsamples with different letters are significantly different at $p < 0.05$ between elevational zones. All 38 imputed data sets were tested in case of soil temperature MAM. Variables sorted by absolute values of RDA axes 1 (cf. Appendix 7).

3 'Climate change-induced shift of tree growth sensitivity at a central Himalayan treeline ecotone' (study 3)

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Climate Change-Induced Shift of Tree Growth Sensitivity at a Central Himalayan Treeline Ecotone

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Abstract: Himalayan treelines are exposed to above average climate change impact, resulting in complex tree growth–climate relationships for Himalayan Silver Fir (*Abies spectabilis* (D. Don) Spach) at central Himalayan treelines. The majority of recent studies detected current tree growth sensitivity to dry conditions during pre-monsoon seasons. The aim of this study was to analyze growth–climate relationships for more than a century for a treeline ecotone in east-central Nepal and to test for Blue Intensity (BI; used as a surrogate of maximum late wood density) as climate proxy. We determined the relationships of *Abies spectabilis* radial tree growth and BI to climate by correlating both to temperature, precipitation and drought index data. The results showed a significantly unstable dendroclimatic signal over time. Climate warming-induced moisture deficits during pre-monsoon seasons became a major factor limiting radial tree growth during recent decades. Earlier in time, the dendroclimatic signal was weaker, predominantly reflecting a positive relationship of tree growth and summer temperature. Compared to radial tree growth, BI showed a different but strong climate signal. Temporally unstable correlations may be attributed to increasing effects of above-average rates of climate warming. An extended network of Himalayan tree-ring sites is needed to further analyze cause–effect relationships and to solve this attribution problem.

Keywords: Blue Intensity; climate warming; Himalayan Silver Fir (*Abies spectabilis*), Nepal Himalaya; temporal dynamics; tree growth–climate correlation; treeline ecotone; tree-ring width

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1. Introduction

Mountains of the world, including the Himalaya, belong to the regions most affected by climate change. Warming trends of the annual mean surface air temperature of up to 1.5 °C were detected over the Tibetan Plateau and the Himalaya during the period 1991–2012 [1–3]. Above-average warming rates trigger multiple vegetation responses such as changes in phenology, productivity, species composition of communities, structure, and elevational ranges of species [4–7]. In this regard, elevational shifts of alpine treelines and tree growth–climate relationships have received much attention (e.g., [8–12]). However, the knowledge concerning tree growth sensitivity and response to climate change is still rather limited [13–15]. Growth–climate relationships are influenced, inter alia, by length and temperature of the growing season [16–18]. Other influencing factors include moisture availability, nitrogen deposition, winter snowpack, snow melt and frost intensity [14–16,19]. Tree growth and various climate variables do not show consistent relations. In the Himalaya, climate–growth relations vary across different regions even for the same species [20–22]. Thus, more tree-ring based studies on different treeline tree species, tree-ring proxies and various mountain regions are needed to close this knowledge gap.

Various treeline tree species have been analyzed for tree growth–climate relationships in the Himalayan subregions (e.g., [23–27]). One of the frequently studied species is the widely distributed Himalayan Silver Fir, *Abies spectabilis* (D. Don) Spach. Some *Abies spectabilis* studies found a positive correlation of radial tree growth and the temperature of the current and previous growing season (e.g., [28,29]). Others pointed to a limitation of tree growth by winter temperature (e.g., [30,31]) or by available moisture in precipitation-deficient pre-monsoon seasons (e.g., [11,32,33]). With regard to generally sparse and partially inconsistent results, in some cases, even from study areas relatively near to each other (e.g., [10]), additional studies are needed, preferably from near natural sites.

Tree-ring width–climate relations are generally recognized to be stable over time [34–36]. However, climatic factors formerly limiting tree growth can alter and/or lose their limiting character while other factors become main drivers [37–39]. For instance, previously temperature-sensitive tree-ring widths showed less or no sensitivity to temperature in recent decades, sometimes even resulting in inverted tree growth-temperature relations [38,40–44]. Such inversions of the tree growth–climate relationships during an analyzed period are termed “divergence problem” [43] while “divergence phenomenon” [43,45] and “divergence effect” [43,46] are related to declines in temperature sensitivity. Divergence effects matter especially in the context of tree-ring based climate reconstruction [43,46,47]. A climate warming-induced increase in evapotranspiration and consequent moisture stress was often mentioned as the potential main cause for divergence effects [43,48], possibly linked to temperature thresholds [49]. Other climate-related causes include direct limitation by precipitation [38], differential responses to maximum and minimum temperatures [43], and changes in seasonality, e.g., of winter precipitation and snowmelt [19]. Decreasing stratospheric ozone concentrations as well as global dimming caused by cloud cover changes and atmospheric contamination, both influencing photosynthesis efficiency and tree productivity, are further potentially relevant factors [43]. In summary, anthropogenic impacts are most likely causing the divergence phenomenon [43,50]. From a methodological point of view, divergence problems might result from “detrending end effects”, caused by the detrending procedure of tree-ring series [43,46]. The majority of chronologies in which the divergence phenomenon was detected originated from high latitudes (e.g., [38,51,52]), however, there is also evidence from other regions, including high mountains [46,53,54]. Variations of environmental factors within the area of origin of a chronology might also cause diverging tree growth–climate interactions (e.g., [48,55]), often termed individualistic tree growth responses [47,55,56] rather than divergence phenomena. As long as trees growing within the same stand are not genetically and physiologically identical, some degree of individual response to environmental factors can be expected in the frame of natural adaptation. The knowledge of divergence effects and the stability of explicitly moisture-related relationships is still deficient [57].

The majority of central Himalayan tree-ring studies investigated growth–climate relationships for rather short periods due to the lack of long instrumental records of climate data. Some recent studies used gridded climate data that cover longer time periods without referring to divergence of correlations or without finding unstable ones (e.g., [58]). Unstable correlations of *Abies spectabilis* tree growth with climate variables were recently mentioned by a couple of studies [28,59]. However, the number of studies that investigate temporal stability and potential divergence phenomena in the Himalaya is insufficient, pointing to a great need for further research.

Maximum latewood density (MXD), a function of latewood cell size and cell wall thickness [34], provides a strong climate signal, especially of growing season temperature in high latitudes and elevations [60,61]. The integration of wood density and its relation to climate can increase the precision of biomass and carbon sequestration estimations based on tree-ring width or CO_2 fluxes measured by eddy covariance [62–64]. The only study on the relationship between climate and MXD of *Abies spectabilis* from Nepal [65] showed a significantly positive influence of pre-monsoon and monsoon temperatures and a negative impact of monsoon precipitation on minimum wood density, while mean and maximum densities correlated positively with late-monsoon and the entire growing season temperatures, respectively. Another study from the western Indian Himalaya showed a negative relationship of June temperature and *Abies spectabilis* MXD, pointing to late spring moisture sensitivity [59].

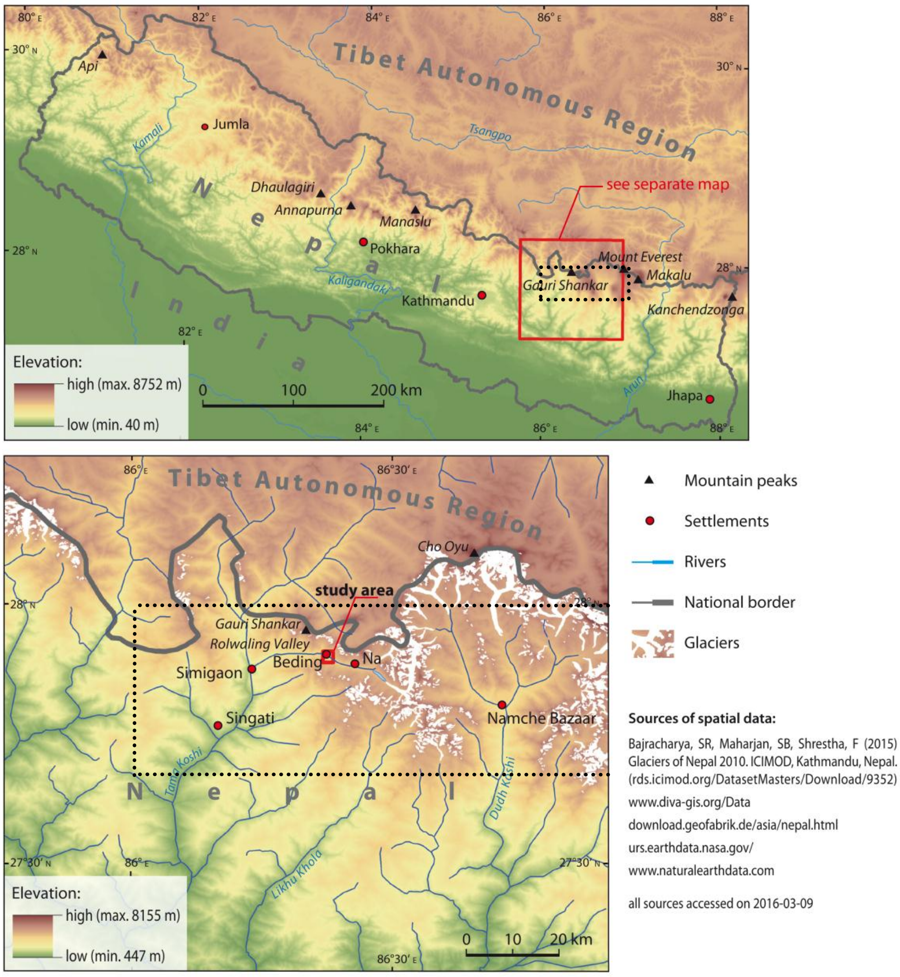
Blue Intensity (BI) has increasingly been applied in recent years as a reliable surrogate for MXD [66–70]. The BI parameter is measured as value of the blue light absorbed by wood surface recorded directly from the RGB (red, green, and blue light components) digital image [70,71]. The close relationship of MXD and BI might be attributed to the effective absorption of short wavelength energy by lignin and potentially co-varying structural wood components [67,70]. BI studies which could provide an additional climate proxy and improve carbon allocation estimates were not conducted in the Himalaya so far.

This paper analyzes long-term growth–climate relationships for a treeline ecotone in east-central Nepal, and the applicability of BI as a climate proxy. We hypothesize that the occasionally detected instability of *Abies spectabilis* tree growth–climate relationships over long timeframes is a general pattern which is also emergent in the Rolwaling treeline ecotone. We further hypothesize that BI as a wood density proxy should be less affected by climatic changes due to the previously assessed stability of wood density signals. To contribute to a better understanding of the dependence of tree growth on (changing) climate in the central Himalaya, this paper aims at: (i) analyzing the relationships of *Abies spectabilis* radial growth, measured by tree-ring width, to climate variables on the basis of more than one century-long gridded climate data; (ii) investigating the temporal stability of tree ring width (TRW)–climate relationships to check whether diverging growth trends occur in the course of distinctly changing climate conditions; and (iii) analyzing the relationships of *Abies spectabilis* BI (as a surrogate for MXD) and their temporal stability to the aforementioned climate data in order to compare the temporal stabilities of the BI and TRW signals.

2. Materials and Methods

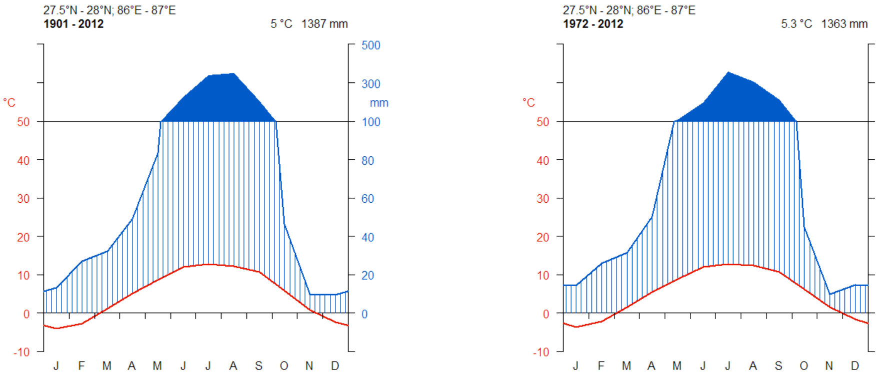
2.1. Study Area and Sampling Site

We collected tree-ring samples at a north-facing slope in the Rolwaling valley, Gaurishankar Conservation Area, Dolakha District, East Central Nepal (Figure 1). The samples originate from the upper subalpine forest between ca. 3700 and 4000 m a.s.l., i.e., from the lower section of the treeline ecotone. The cored individuals grow in a mixed forest composed of *Abies spectabilis* and *Betula utilis* D. Don with *Rhododendron campanulatum* D. Don and *Sorbus microphylla* (Wallich ex J. D. Hooker) Wenzig as a second tree layer. *Abies spectabilis* and *Betula utilis* are co-dominant constituents in the lower part of the subalpine forest with an increasing percentage of *Betula* towards higher elevation. Above the sampling area, at the treeline, the subalpine forest gives way to a dense *Rhododendron campanulatum* krummholz belt which is replaced upslope by alpine vegetation dominated by *Rhododendron* dwarf thickets (cf. [72–74]). Soils in the treeline ecotone are classified as podzols [18]. Due to the valley's remote location, inaccessibility, low population density, and relevance for the Buddhist mythology [75], the entire treeline ecotone is in near-natural condition [72]. The study site's climate is classified as temperate with dry winter and warm summer (Köppen-Geiger Cwb) [76]. The seasons are usually defined as winter (December to February), pre-monsoon/spring (March to May), monsoon (June to September), and post-monsoon (October to November) [77]. Precipitation during monsoon season accounts for ca. 80% of the total annual precipitation. The pre-monsoon season is a dry period with high solar insolation, maximum temperatures, small amounts of precipitation and low available soil water capacity (cf. Figure 2) [18,78].



Sources of spatial data:
Bajracharya, SR, Maharjan, SB, Shrestha, F (2015) Glaciers of Nepal 2010. ICIMOD, Kathmandu, Nepal. (rds.icimod.org/DatasetMasters/Download/9352)
www.diva-gis.org/Data
download.geofabrik.de/asia/nepal.html
urs.earthdata.nasa.gov/
www.naturalearthdata.com
all sources accessed on 2016-03-09

Figure 1. Study area in east-central Nepal. The dashed rectangle shows the approximate position of University of East Anglia Climatic Research Unit (CRU) grid cells.



(**a**) (**b**)

Figure 2. Climate charts of used CRU data. See Figure 1 for the location of the grid cells. The entire period of CRU data availability (**a**) shows higher amounts of precipitation in November and June and lower annual mean temperatures compared to last decades (**b**). Diagrams were produced with R package climatol [79].

2.2. Tree-Ring Data

The target species, *Abies spectabilis*, occurs as a common coniferous species in the central Himalayan arc between 3000 and 4200 m a.s.l. [80]. We applied standard sampling and core preparation methods [36,81]. We sampled all individuals growing within randomly selected 20 × 20 m^2 plots in homogenous stands at the upper subalpine forest which were established for intensive treeline ecological studies (e.g., [73]). For further details on site-ecological conditions, see [72–74,82]. In addition, we cored old trees around these plots to increase the pool of data for dendroecological and dendroclimatological analyses. We collected at least two cores per tree during two sampling campaigns in 2013 and 2014. In total, 359 radii of 114 trees were prepared and scanned in darkroom conditions at 2400 dpi, in RGB mode using an Epson Perfection V850 optical flatbed scanner. To measure BI, the scanner was calibrated according to the International Colour Consortium (ICC) standard with the use of a standard calibration target (IT 8.7/2) printed on Kodak Professional Endure paper and the SilverFast 8.0 scanning software (LaserSoft Imaging, Kiel, Germany). Both TRW and BI were measured in CooRecorder 8.1.1 software (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Samples with rot and compression wood were excluded from measuring since the occurrence of compression wood in tree ring biases the climatic signal [83,84]. The settings in CooRecorder were adjusted to measure only BI of the latewood, therefore one collector was applied. The fir wood was characterized by a clear pattern of annual ring boundaries and lack of resin ducts, therefore a rather wide area of BI probing was selected (the dimensions of the so-called "frame": 100/3/50 pixels, width/front/late wood overlap respectively with the relative margin between frames maximum 50%); for details see [71,85]. All TRW and BI series were cross-dated visually in CDendro 8.1.1 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden) and statistically in Cofecha 6.06P software (Laboratory of Tree-Ring Research, University of Arizona, Tucson, and Instituto Argentino de Nivologia y Glaciologia (IANIGLA), Mendoza, Argentina) [86].

We started building the TRW chronology with 359 radii of 114 trees initially. Due to poor quality (mold, decay, and distorted growth patterns due to compression wood and branches) and short length (distorting juvenile effects), cross-dating was not reliable for all series (low inter-series correlation). Thus, some series were not included in TRW and/or BI chronologies. In total, we included 81 radii of 51 trees and 87 radii of 52 trees in the final TRW and BI chronologies, respectively. However, the two chronologies do not represent exactly the same bunch of cores (but they originate from the collection of 359 radii), i.e., samples fitted partially only to TRW and/or only to BI chronologies. For instance, BI could not be measured on samples which were partly rotten or affected by compression wood due to significant changes of color, including reflectance of blue light. As a result of visual and statistical cross-dating we added five missing rings in single series of both chronologies (1877, 1887, 1892, 1906 and 1963). The raw TRW and BI chronologies exhibited significance ($p < 0.001$) for the long term declining growth trends, interrupted by several breakpoints that were also visible for individual trees. Therefore, standardization was applied to remove the age trends in series of both proxies.

The standard TRW and BI chronologies were calculated by applying a 100-year cubic smoothing splines with fixed 50% variance cutoff in the software ARSTAN 44h3 (Tree-Ring Laboratory, Lamont-Doherty Earth Observatory, Palisades, New York, USA) to remove age-related growth trends [87]. To assess unbiased temporal stability of the tree growth–climate relations, we applied a spline that preserves low frequency variability following [88]. To reduce heteroscedastic behavior of the tree-ring series, we applied a data-adaptive power transformation prior to the detrending process [89].

To assess chronology quality and properties, we calculated the following statistics for the entire chronology and for the analyzed period 1902–2012: mean sensitivity, mean inter-series correlation, running and mean *R*-bar, running and mean expressed population signal (EPS), signal-to-noise ratio, and first-order autocorrelation. Mean sensitivity shows the interannual variability of tree growth. Mean inter-series correlation is the average of all individual series' master chronology correlations coefficients and indicates the common stand-level signal. The signal strength throughout the chronology is represented by the running and the mean R-bar which represent correlations between all series in 30-year windows with 15-year overlap. EPS was calculated for the same periods revealing the common variability in a chronology. It depends on sample depth and shows how much a chronology is dominated by individual tree signals rather than by a coherent stand level signal. EPS threshold values are subjective. Similar to EPS, although even more dependent on the sample size, signal-to-noise ratio quantifies the strength of an observed common high-frequency signal among trees in the chronology. First-order autocorrelation shows the influence of previous year's growth on current year's growth [34,36,90–93].

2.3. Climate Data

We used the University of East Anglia Climatic Research Unit (CRU) Time-Series (TS) 4.00 climate dataset [94,95]: mean temperature, maximum (actually mean maximum) temperature, minimum (actually mean minimum) temperature, and precipitation (monthly sums) for the period 1901–2012. In addition, we made use of the drought indices one- and three-month SPEI (Standardized Precipitation-Evapotranspiration Index) [96] based on CRU data which are commonly applied to monitor drought conditions. SPEIs, calculated over periods of different time scales, support the identification of cumulative periods that cause water deficits. We used the CRU TS google earth interface [97] to examine which instrumental records contribute to the grid cell data. All gridded datasets at 0.5° spatial resolution were accessed by Koninklijk Nederlands Meteorologisch Instituut (KNMI) Climate Explorer [98], and the means of two grid cells closest to the site (extending from 27.5° to 28° N and 86° to 87° E; Figure 1) were calculated. These cells cover roughly the extent of the Rolwaling valley. The inclusion of further neighboring cells decreased the tree growth–climate correlation coefficients, most likely due to less elevated terrain in the southern grid row and Trans-Himalayan position of the northern grid row.

To investigate temporal changes of local climate, we fitted nonparametric local polynomial regressions (LOESS) to monthly precipitation sums and monthly mean temperatures to visualize potential non-linearity of the trends during the entire period analyzed (1901–2012). The fitting and plotting was done with the *scatterplot()* function of the car 2.1–5 package [99] in R 3.4.1 [100]. We calculated monthly and yearly differences of mean temperature and precipitation sums between the means of the first and last 30 years of the investigated period (1901–1930 vs. 1984–2012) to gain information on the intensity of climate change represented by the CRU data.

2.4. Tree Growth–Climate and BI–Climate Correlations

To analyze the relationships between the standardized TRW and BI chronologies and the climate variables, we calculated Pearson's correlation coefficients and confidence intervals by using a stationary bootstrapped correlation function with optimal block length selection [101,102]. We calculated correlations for all months and seasons from previous year's May (first month of the previous growing season) to current year's September (last month of the current growing season) at a level of significance of $p < 0.05$. Climate conditions of the previous year can pre-condition trees physiologically and may affect biochemical processes and tree growth of the current season [34]. Since climate data were available from 1901 onwards, and to refer to previous growing seasons, the correlations were calculated for the 1902–2012 period. In the first year of correlations (1902), chronologies contained 42 TRW and 18 BI series originating from 27 and 14 trees, respectively, which in both cases constitute the lowest replications for the studied period.

We calculated static correlations of TRW and BI with mean, mean minimum and mean maximum temperatures, precipitation sums, and SPEI for single months and seasons. To examine the stability of correlations for the analyzed period, we calculated 31-year moving window correlations [103] with one year offset between consecutive windows of TRW and BI.

Moving window correlations were computed for monthly mean temperatures and precipitation sums. While moving windows are suitable to detect the presence of stable periods over a range of time, evolutionary interval correlations reveal the lengths of specific periods [103]. To find the lengths of most recent periods with stable correlations, we used backward evolving window correlations with an initial window size of 31 years that increases in one-year steps starting from 2012 backwards. All correlation analyses were computed with the *dcc()* function of the treeclim 2.0.0 package [104] in R 3.4.1 [100].

3. Results

3.1. CRU Climate Data Trends

Temperature trends were positive in all months of the period 1901–2012 (Table 1), however, the intensity of the increase changed over time (Figures 3 and A1). The annual mean temperature of the last 30 years of our TRW chronology (1982–2012) was 0.87 °C warmer than the first 30 years of the investigated period (1901–1931, $p < 0.05$). The temperature was significantly stable in June and July (+0.44 °C and +0.05 °C, respectively; $p < 0.05$), while the increase was significant and most pronounced in November and December (both +1.56 °C, $p < 0.05$). Additionally, winter season (DJF, +1.31 °C, $p < 0.05$) and pre-monsoon season (MAM, +0.89 °C, $p < 0.05$) temperatures increased significantly. The changes did not proceed linearly (Figures 3 and A1): after an increase until the mid-20th century, temperatures stagnated or decreased slightly, followed by an increase beginning from ca. the 1970s until the end of the investigated period in 2012. This pattern was obvious in all months except February and July. February temperatures increased linearly. By contrast, July temperatures showed a slight decrease during the first part of the period, followed by a more pronounced increase towards the 21st century.

Table 1. Differences between means of precipitation sums and mean temperature of the periods 1901–1931 and 1982–2012 for single months and the entire year.

	Mean Temperature (°C)	Precipitation (mm)
January	1.07 *	4.68
February	1.32 *	−4.74
March	1.36 *	−9.88
April	0.79 *	6.40
May	0.53 *	44.73 *
June	0.44	−78.10 *
July	0.05	42.82
August	0.41 *	−103.49 *
September	0.37 *	−2.17
October	0.97 *	3.83
November	1.56 *	−3.44
December	1.56 *	8.01
Year	0.87 *	−7.25

Note: Asterisk indicates significant differences at $p < 0.05$; data source: CRU, see Section 2.

Precipitation values of all months have fluctuated over the investigated period without any clear trend (Figures 3 and A2). Comparing the first and last 30 years of the investigated period, annual precipitation did not change significantly ($p < 0.05$). However, monthly precipitation sums showed trends in different directions: they increased significantly ($p < 0.05$) in May (+45 mm) and decreased in June (−78 mm) and August (−104 mm). Changes in other months were not significant (cf. Table 1). Due to the high interannual variability of monthly precipitation sums, periods of different trends are less distinctly visible in comparison to temperature. However, the non-parametric regressions showed two or three trend segments for most months (cf. Figures 3 and A2). The last directional change of the trends occurred during the second half of the 20th century, at ca. 1970. The changes in temperature and precipitation trends are also reflected by SPEI trends.

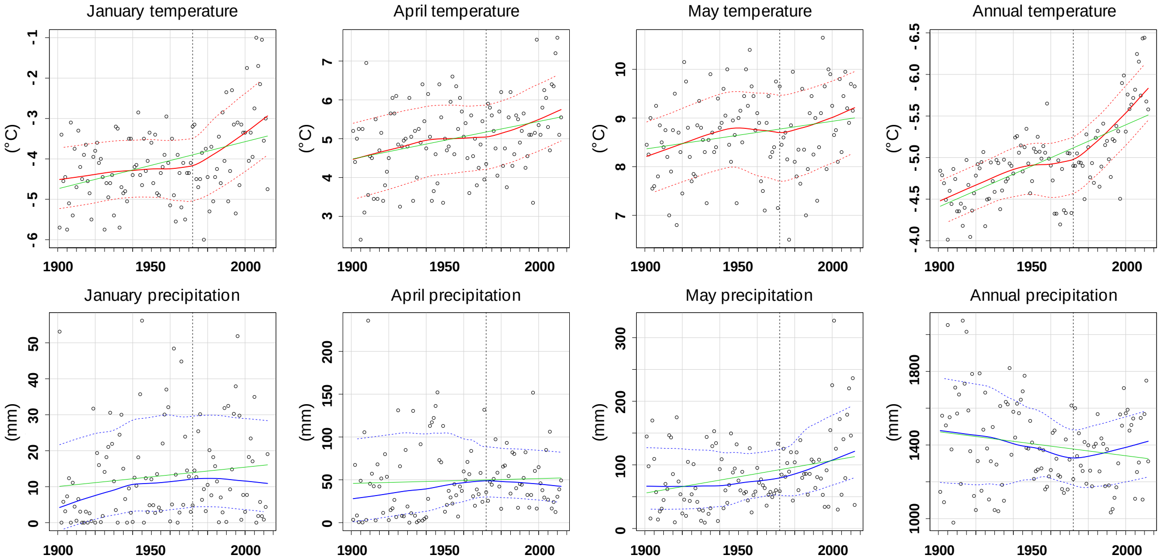


Figure 3. Monthly (January, April, and May; see Figures A1 and A2 for all months) and annual CRU TS 4.0 mean temperature and precipitation sums: non-parametric trends 1901–2012 of the study area. The solid and dashed red lines show locally weighted scatterplot smoothing (LOESS) and corresponding spread smooths, respectively. For comparison, the green line illustrates a linear regression. The dashed black line indicates 1972, i.e., the first year of the period that was analyzed by static tree growth–climate correlations.

3.2. TRW and BI Chronologies

The span of the TRW and BI chronologies (Figures 4 and 5) ranged from 1748 to 2012 and 1819 to 2012, respectively. Distinct growth reductions occurred in TRW in 1818, 1891, 1906, 1968, and 1999 (Figure 4), and in BI in 1820, 1838–1841, 1850, 1862, and 1962 (Figure 5). Running EPS of TRW chronology was greater than the arbitrary [93] threshold of 0.85 in all periods except the first one centered upon 1840 with EPS of 0.61 (Figure 4). In case of BI chronology EPS was <0.85 in the periods centered upon 1865, 1880, 1925, and 1940 (Figure 5). Running R-bar changed in course of the TRW chronology and ranged from 0.19 in the period centered upon 1930 to 0.58 in the period centered upon 1870 (Figure 4). In the case of BI, R-bar ranged from 0.08 in the period centered upon 1940 to 0.35 in the 1865 period (Figure 5). The static descriptive statistics of TRW and BI chronologies are presented in Table 2.

Table 2. Descriptive chronology statistics.

	TRW Chronology Interval 1748–2012	TRW Correlation Analyses Interval 1902–2012	BI Chronology Interval 1819–2012	BI Correlation Analyses Interval 1902–2012
Mean sensitivity	0.099	0.082	0.024	0.019
Mean R-bar	0.324	0.337	0.217	0.176
First-order autocorrelation	0.696	0.671	0.522	0.436
Mean expressed population signal (EPS)	0.910	0.947	0.853	0.903
Signal-to-noise ratio	NA	18.031	NA	4.358

NA: not available.

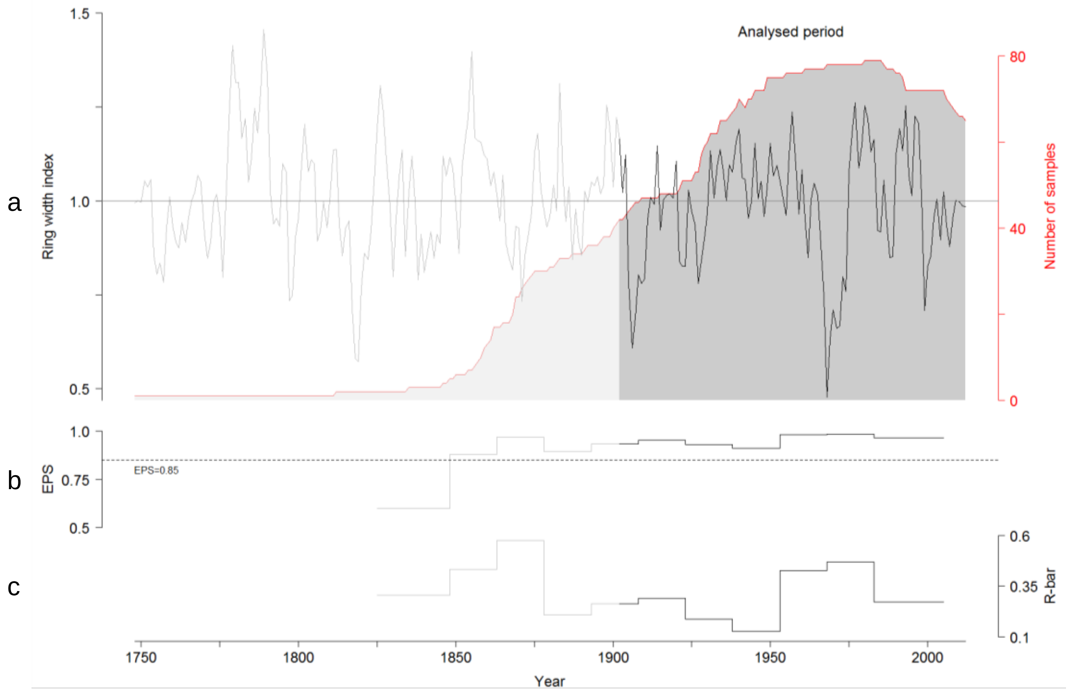


Figure 4. Tree-ring width standard chronology (black curve) and sample depth (red curve) (**a**); and corresponding EPS (**b**) and *R*-bar values (**c**). The lighter sections of the graphs show the part of the chronology that was not used for tree growth–climate analyses.

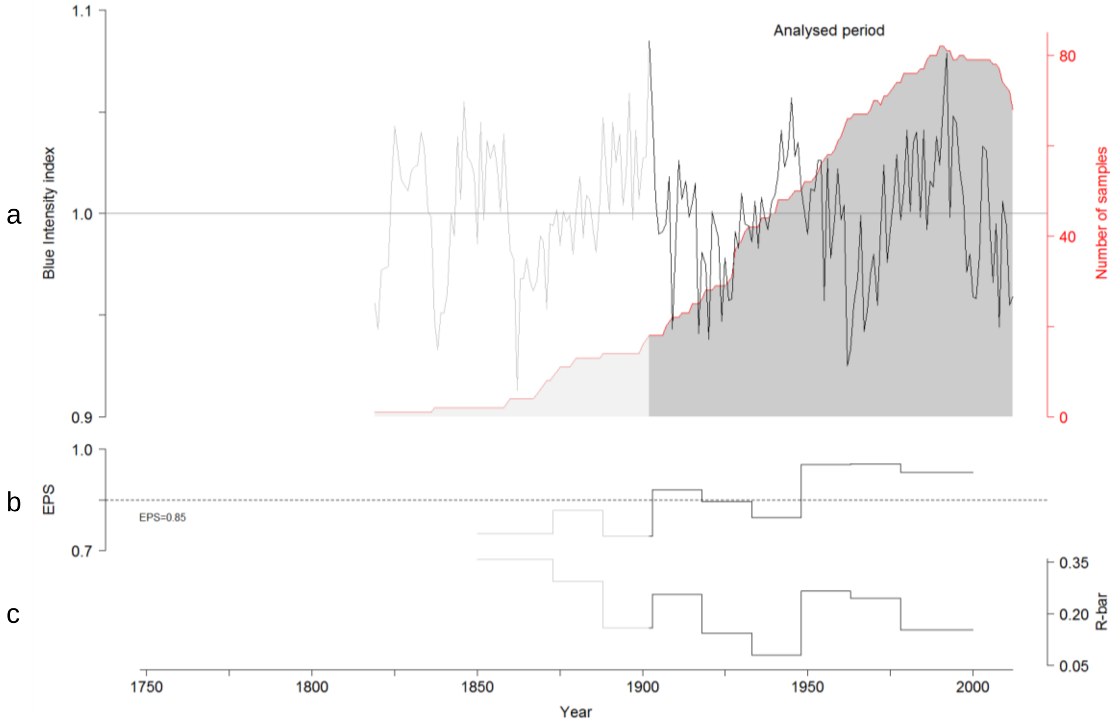


Figure 5. Blue Intensity standard chronology (black curve) and sample depth (red curve) (**a**); and corresponding EPS (**b**) and R-bar values (**c**). The lighter sections of the graphs show the part of the chronology that was not used for BI–climate analyses.

3.3. Moving and Evolving Window Correlations of TRW and BI Chronologies with Climate in the Period 1902–2012

Since we found rather weak static TRW–climate and BI–climate correlations for the entire investigated period (Figure A3), we tested the temporal stability of correlations by applying 31-year moving windows with a one year offset to compare both proxies. Both TRW and BI showed distinct changes in correlations with mean temperature and precipitation over time for the 1902–2012 period.

3.3.1. Moving TRW–Climate Correlations

The interdependence of TRW and climate variables alternated during the investigated period at least once from positive to negative correlation or vice versa. Phases with significant correlations without these alternations did not exceed ca. 50 years, and most of the periods were distinctly shorter. To characterize the changes, we consider periods of at least four consecutive significant 31-year windows.

There was a period of positive correlations of TRW and summer temperature (August: 1941–2001; June: 1940–1976). Negative correlations of TRW and temperature occurred in spring (February to May) from the beginning of the 1970s until the end of the investigated period (2012, cf. Figure 6).

TRW and March precipitation correlated negatively during the mid-20th century. This relation inverted and shifted by one month, resulting in a positive correlation of TRW and April precipitation from 1972 until the end of the investigated period. TRW and July precipitation correlated negatively at about the same time. In addition, there were several significant correlations of TRW and previous year's climate variables (cf. Figure 6). In summary, both TRW–temperature and TRW–precipitation moving windows showed a fragmented pattern of significant tree growth–climate relationships with long insignificant phases.

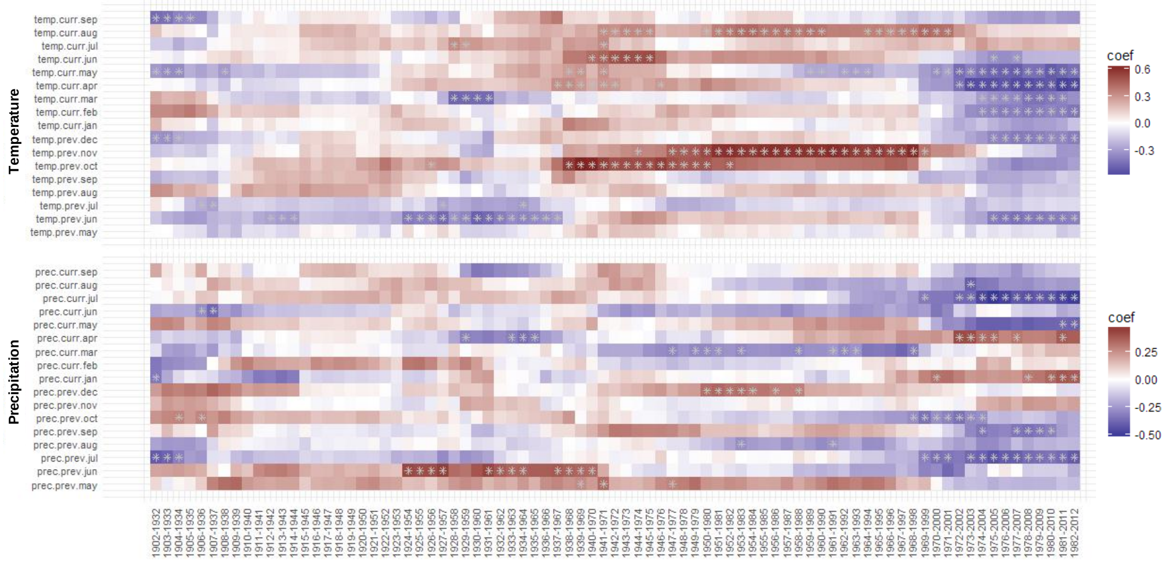


Figure 6. Tree-ring width chronology–mean temperatures and tree-ring width chronology–precipitation sums moving window correlations. Periods with asterisk indicate significant ($p < 0.05$) correlations.

3.3.2. Moving BI–Climate Correlations

The BI–temperature correlations showed a more stable, less fragmented pattern in comparison to TRW–temperature relations (Figure 7): there were long periods of rather strong positive BI–temperature correlations in all months of the current growth year except January and July. This pattern lost strength and significance from the ca. 1970s onwards, and current January and February showed windows with negative BI–temperature correlations from 1976 until the end of the investigated period.

The correlations of BI with precipitation showed a smaller number of significant periods (Figure 7): from 1927 to 1976 BI and September precipitation correlated positively. This relation was replaced by a negative BI–August precipitation correlation lasting from 1946 to 1990. Negative correlations of BI and precipitation occurred in late spring and summer (May, June: 1978–2012, July: 1969–2003). In addition, there were several significant positive correlations of BI and previous year's climate, especially temperature, with the longest and most significant ones in November and December (cf. Figure 7). In summary, a similar change in BI–climate correlations as in the case of TRW in the second half of the 20th century is obvious, however, without reaching comparable significant correlation coefficients during the period after 1970s.

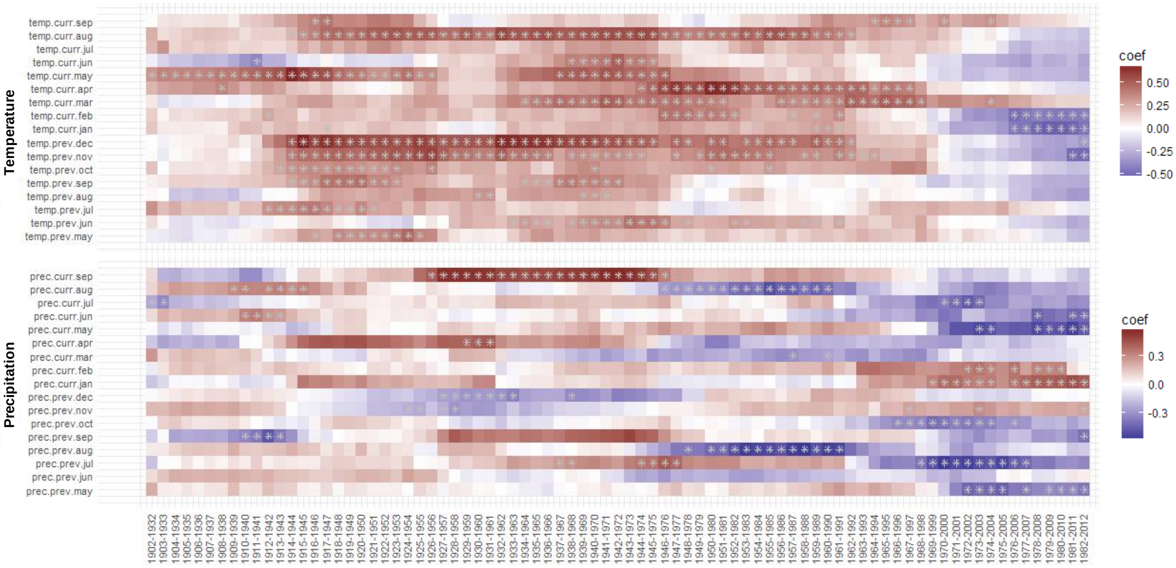


Figure 7. Blue Intensity chronology–mean temperatures and blue Intensity chronology–precipitation sums moving window correlations. Periods with asterisk indicate significant ($p < 0.05$) correlations.

3.4. Static Correlations of TRW and BI Chronologies with Climate in the Period 1972–2012

3.4.1. Static TRW–Climate Correlations

Radial growth, measured by TRW, and climate variables showed continuously strongest correlations towards the end of the investigated period. Evolving windows of TRW–climate and BI–climate relations (Figures A4 and A5) showed that the stable periods from 2012 backwards differ in length, depending on the considered combination of climate variable and month. On average, 1972 was identified as the onset of the phase of stable correlations. Thus, it can be considered to represent the beginning of the most recent era of *Abies spectabilis* TRW and BI (see Section 3.4.2) in our study area.

We found significant static correlations of TRW with climate variables mainly during winter and spring for both single months and seasons of recent decades (Figure 8). The correlation analyses showed a significantly negative relationship between radial growth and mean ($r = -0.46$), minimum ($r = -0.38$) and maximum temperature ($r = -0.47$) for the current year's pre-monsoon season (March–May). Moreover, we detected significant negative correlations of mean ($r = -0.32$) and maximum ($r = -0.35$) temperature during winter prior to the current growing season (December–February) (Figure 8).

Precipitation sums and TRW correlated significantly positively during current January ($r = 0.31$) and April ($r = 0.35$). The current monsoon season (June–August) exhibited a significant negative correlation of radial growth and precipitation sum ($r = -0.33$) (Figure 8). We found significantly positive correlations of TRW to one-month SPEI variables (January: $r = 0.27$, April $r = 0.33$) (Figure 8) pointing to pre-monsoon moisture sensitivity, in line with the relations of TRW to temperature and precipitation.

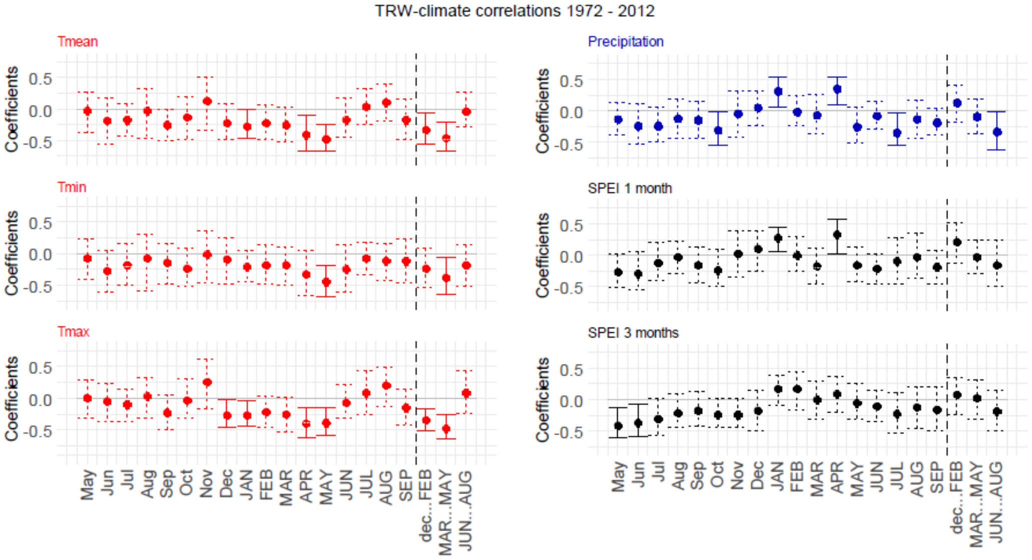


Figure 8. The 1972–2012 static correlations of the tree-ring width chronology with temperature, precipitation and drought indices for current and previous year's months and current year seasons. Solid bars indicate significant correlations ($p < 0.05$).

3.4.2. Static BI–Climate Correlations

Compared to TRW, BI exhibited similar correlations to temperature (Figure 9). Winter season prior to growing season (December–February) showed negative correlations of BI with mean temperature ($r = -0.43$, $p < 0.05$), also reflected in minimum and maximum temperature correlations of single months. In addition, we found negative correlations of BI with mean and minimum temperatures of the single months of the pre-monsoon period and the whole monsoon season of the current year (e.g., May mean temperature $r = -0.28$, June to August minimum temperature: $r = -0.43$).

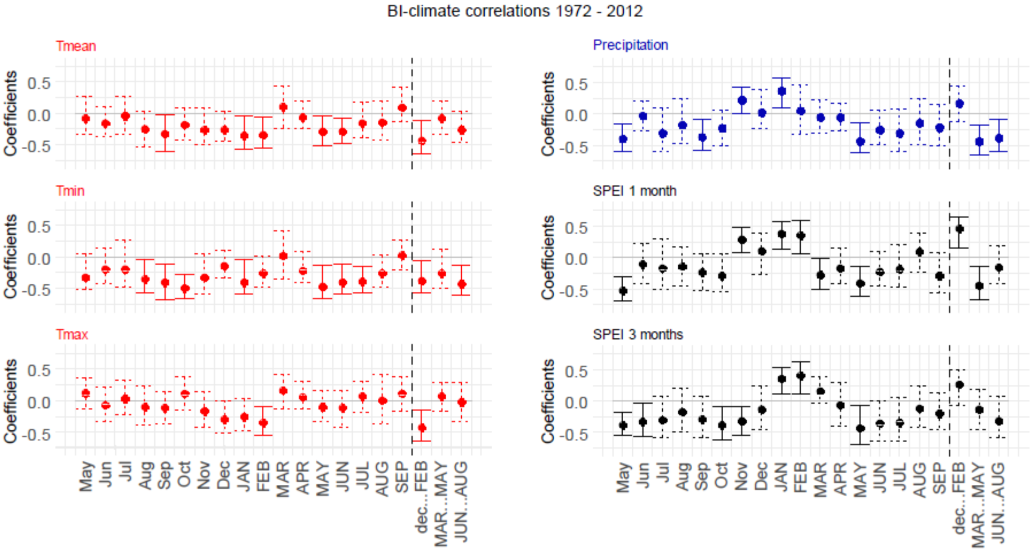


Figure 9. The 1972–2012 static correlations of the Blue Intensity chronology with temperature, precipitation and drought indices for current and previous year's months and current year seasons. Solid bars indicate significant correlations ($p < 0.05$).

The January precipitation influenced BI positively ($r = 0.36$) (Figure 9). There was a strong negative correlation of BI with precipitation during the pre-monsoon ($r = -0.44$; March–May) and monsoon

($r = -0.38$; June–August) periods. BI showed a positive relationship with the one-month SPEI drought index during winter season ($r = 0.46$; December–February), confirmed by correlations of one- and three-month SPEI during single winter months. In contrast to TRW, there was a negative relation of BI and moisture in May and pre-monsoon season (Figure 9).

In summary, these results indicate that both radial growth and BI were influenced positively by low temperature in winter and spring prior to the current growing season. Radial tree growth was influenced positively in years with high precipitation in current January and April and low rain intensity in July. BI results were similar in winter; however, they differ in pre-monsoon and monsoon seasons (Figures 8 and 9). It is particularly remarkable that the results are different from those obtained for the 1902–2012 period (cf. Figure A3).

4. Discussion

4.1. TRW and BI Chronologies

TRW and BI chronologies' descriptive statistics coincidentally indicated their applicability for climate correlations. The chronologies' mean sensitivity showed low interannual variability, an inherent characteristic of Himalayan humid environment TRW chronologies (e.g., [11,33,105]). Mean R-bar values showed a rather low common signal throughout the chronology, pointing to a rather poor agreement between single series. However, this is also a common characteristic of Himalayan chronologies [11,27,106]. The running *R*-bar values varied distinctly over time and the low values in some periods might point to ecological disturbances or stand dynamic processes [36]. The study site is to our knowledge virtually free from direct human intervention. Thus, any disturbances are of natural origin. According to the running EPS values, the chronologies reliably represent the population signal during the entire period that was subjected to growth analyses [90,93]. The autocorrelation values showed that the current year's tree growth was influenced by physiological effects that originate in the previous year [34]. The growth reductions in the TRW chronology in 1818 might be connected to the Mount Tambora eruption in 1815 [24], the reductions in 1968 and 1999 coincide with winter droughts in Nepal [107,108], while the reduction in 1906 followed upon an extreme weak monsoon epoch [109].

4.2. Tree Growth–Climate Relationships during Recent Decades (1972–2012)

Our results for the period with most stable correlations (1972–2012) suggest that *Abies spectabilis* tree growth was sensitive to temperature induced moisture deficits during the pre-monsoon season. We found a negative relationship between radial tree growth and spring temperature, indicating a negative relation of growth with evapotranspiration, which is enhanced by temperature. In addition, the positive correlation of TRW and precipitation of April points to moisture sensitivity during spring [34]. This result is in line with several previous studies on *Abies spectabilis* growth patterns [11,12,24,32,33,59,65,110,111] and those of other coniferous species from sites in the Himalaya and the Tibetan Plateau [58,105,112–115]. Compared to the present study, correlation coefficient values of the aforementioned studies were mostly in a similar, rather low range.

Studies of other tree species in the Himalaya exhibited comparable results. For instance, Ren et al. [116] showed the direct dependence of the onset of xylogenesis of a *Juniperus* species on late spring precipitation. *Betula utilis*, a broadleaved species, showed a positive correlation with spring precipitation and a negative one with spring temperature [8,9,117]. In contrast, Shrestha et al. [28] showed negative influence of May precipitation on *Abies spectabilis* radial increment at a treeline site further west (Langtang National Park). The difference might be attributed to anthropogenic disturbance in Langtang and/or differing micro-climate conditions.

In line with our results, Kharal et al. [111] reported a negative correlation of *Abies spectabilis* tree growth and previous year's December temperature. Several other studies showed relationships to winter temperatures which differ from ours, such as positive correlations of *Abies spectabilis* radial growth, linked to freezing stress and other related processes [10,30,31,110,118]. Similarly, Borgaonkar et al. [113] and Sohar et al. [59] showed a positive relationship to winter temperatures for two conifer species in the western Himalaya.

Results on tree growth–climate relationships at our site during early and mid-20th century more or less corroborate those of other studies highlighting current summer and previous year's autumn temperatures as main limiting factors of *Abies spectabilis*' radial increment [10,12,28,29,110]. These studies used climate records of differing origin and length (station, 1978–2007 [28]; CRU, 1947–2006 [29]; CRU, 1901–2011 [10]; station, 1959–2004 [110]; station, 1970–2013 [12]), exacerbating comparability and causing differences in the temporal variability of correlations cf. [28,29,59], this study.

Tree-ring width correlated positively with January precipitation in our study area. This finding is contrary to results that point to a negative impact of winter moisture availability on the radial tree growth in central Nepal [11,28,31]. The reported negative impact might be a consequence of deeper snowpack that retards the melting process and the soil temperature increase in spring, resulting in a delayed onset of cambial activity [19,119]. Other studies did not assess a negative relation of snow precipitation and following growing season tree growth (e.g., [65,120]). Once melted, snow precipitation might contribute to moisture availability during the dry spring season months [18,19,28,29]. The results of TRW–one-month SPEI correlations show growth limitation due to soil water content deficits in January and April, underpinning the results from correlations of TRW with temperature and precipitation. The significant one-month SPEI correlation points to a short cumulative period of water deficit [121] due to excessive monsoon precipitation occurring each year, resulting in high available water capacity during summer and autumn [18].

In contrast to spring drought-related relationships, we found a significantly negative correlation of radial growth with monsoon season (JJA) precipitation. These results are consistent with those from two rather dry sites located in the Mustang and Manang regions of Nepal [11,111]. The central Himalaya receives the majority of annual precipitation during summer season. The amount of water is by far sufficient to saturate the soil water content, and to cover the water demand of the vegetation, even in years with relatively low amount of precipitation. Thus, we suggest that the negative correlations might indicate that precipitation acts as a proxy for cloud cover and light conditions, respectively, influencing tree growth [122]. If the cloud cover is reduced, trees receive higher insolation, causing enhanced assimilation processes and radial growth. At the same time, the impact of insolation on air temperature might be reduced due to the energy-consuming evaporation process. These linkages might inhibit the TRW–summer temperature correlations to reach the level of significance, while the improved light conditions enhance radial growth, resulting in significantly negative correlation with precipitation.

In contrast to other studies [10,28,29,110], we did not find a significant correlation of TRW with temperature or precipitation of the previous growing season (May–September). Nevertheless, the high first-order autocorrelation value of the TRW chronology points to a distinct influence of previous year's tree growth on current year's growth [34,115]. The negative correlation of TRW with October and September precipitation might indicate a physiological preconditioning for the following year [34]. Reduced precipitation and subsequent higher irradiation might enable trees to gain more carbon and/or cause a larger starting size of the cambial zone for the following year [34,122]. However, this result should be carefully interpreted as we assume the period of cambial activity to end before or early in October according to measured soil and air temperatures [82,123].

In summary, a rather wide spectrum of different radial growth–climate relationships exists at regional and local scales within the Himalayan region of Nepal. With regard to spring moisture sensitivity, our results largely correspond to results of other studies from sites in Nepal and different Himalayan regions. However, some of the published results, including those from study sites near to ours, showed differing relations of tree growth with temperatures and precipitation of the winter prior to growing season. The general east-west precipitation gradient in the Himalaya [124] does explain variations in tree growth–climate relations to a limited extent only. In line with several previous studies [11,28–31,58,59,125], we assume that deviating results are caused by local variations of the heterogeneous environment, which are not captured by sparse (and rather short) records of climate data from high elevation sites or derived gridded data [126]. Moreover, spatially differing characteristics of climate factors at local and regional scales need to be considered when drawing generalized conclusions. For instance, the date of monsoon onset affects radial increment in different intensity at dry and wet sites [28]. Finally, soil conditions, micro-topography, light conditions, land use and other site factors might be reasons for differences in tree growth–climate relationships.

4.3. Changing Long-Term Tree Growth–Climate Relationships (the Entire 20th Century)

The static correlation of the whole CRU data period (Figure A3) showed rather low correlation coefficients, in line with previous studies from the Himalaya (e.g., [10–12]) and other regions [106,127].

The reliability of growth–climate correlation results depends inter alia on the quality of climate data. The warming trend during the 20th century is well reproduced by the gridded CRU climate data used in our study. However, the Rolwaling CRU spring precipitation data might obscure difficulties in modeling precipitation data for complex terrain [78,128] as negative trends of station data [3] and reconstructions [33,115,129,130] for the western and central Himalaya during spring of recent decades are not visible. Since the CRU climate data are based on station data [94,131], length and quality of sparse local climate data records from the region might influence tree growth–climate correlations. The CRU methodology includes measures to produce high quality data in regions with sparse instrumental records. Despite these efforts, the combination of only few stations with long continuous records in vicinity of the grid cells and complex terrain might induce non-significant tree growth correlation results, especially in early periods.

The increase in availability and in quality of station data from Nepal at finer spatial resolution since the 1960s [132] coincides with the beginning of the stable correlation period. Thus, the increasing data quality could play a certain role regarding more stable tree growth–climate relationships during recent decades [59]. However, CRU data are widely used in dendroclimatological studies (e.g., [106,133]), also in mountain regions [54,127,134,135] including the Himalaya [10,29,58,59,136] and their use is recommended for regions with sparse cover of stations despite certain limitations [137].

The detrending method could potentially cause a putative divergence phenomenon [88]. In our study, while using a smoothing spline method for detrending, each individual series was evaluated to preserve low frequency variability but to avoid the artificial increase of the index values of the last years of the chronology. Moreover, the comparison of moving window correlations of tree-ring data detrended in different ways showed no substantial differences (see Figure A6). Thus, we rule out "detrending end effects" as origin of unstable correlations.

Age effects and microsite differences could also cause unstable tree-ring width–climate correlations [46]. Consistent with unstable tree-ring width–climate correlations, the TRW signal strength (*R*-bar) alternated during the period 1902–2012. These variations in *R*-bar over time might indicate disturbances [36] or modulations of the relationships by, e.g., tree age or spatially varying environmental variables such as soil properties and light conditions [138,139].

Changes of the tree growth–climate relationships over time could also point to differentiated responses of groups of trees to climate (e.g., younger vs. older individuals). After splitting the chronology into subsets with old trees (minimum age of 100 years) and young trees, we found similar unstable radial growth–climate correlations for each subset as for the chronologies with all trees of any age (Figures A7 and A8). In addition, the individual tree response to climate (not presented here) is similar to those of the standard chronologies. Thus, temporal changes of the tree growth–climate relationship do not originate from such differences in tree age.

However, despite the cores originate from one site there might be finer-scaled differences of age structure of trees and their relation to climate caused, for instance, by small-scale spatial differences in soil temperature and soil moisture [82]. Small-scale fire, insect outbreaks and geomorphic events or age-related tree deaths might cause disturbances, contributing to variation in tree response. Differences in intra- and inter-specific competition for nutrients or light could also result in varying tree responses. All these environmental factors could cause variance in tree growth which is not explained by climate.

Although effects of non-climatic factors cannot be ruled out, we assume climatic changes to be the root cause for unstable TRW–climate correlations. The observed instability of tree growth–climate correlations and their tendency towards negative relation with temperature and towards moisture sensitivity corroborate various reported divergence phenomena from high latitudes and mountainous environments (e.g., [38,42,46,51,54,140,141]). In the Himalaya, only few studies with significant long-term correlations exist. A dendroclimatic study of *Pinus smithiana* (Wall.) Boiss showed stable negative correlations with spring temperature for the whole analyzed period from the end of 19th to the beginning of 21st century [58]. Sohar et al. [59] found unstable dendroclimatic signals of *Abies spectabilis* growth in the western Himalaya during the CRU data period with climate change effects and potential inaccuracies in the CRU data as potential reasons. However, stable periods do not match with those of the present study. Shrestha et al. [28] showed unstable *Abies spectabilis* and *Pinus wallichiana* A. B. Jackson growth–climate relationships for central Himalayan sites with climatic changes as potential causes for instability. Here, a comparison to our results is complicated by differing window sizes and length of investigated periods. Most studies correlated tree growth and climate over shorter periods of time, based on availability of local station data or chronology length (30–60 years), and did not test correlation results for stability [10,11,28,29,32,33,110,111,115,142].

According to the results of our moving correlations, we assume that *Abies* trees have become more climate-sensitive during the reinforced climate warming period beginning in the 1970s. Similar to the alterations of radial tree growth–climate correlations and of its signal strengths, the climate changed non-linearly, with a temperature increase in the early 20th century, a stable phase during the mid-20th century and pronounced warming during the last decades of the 20th and the beginning of the 21st century. The period of stable climate conditions coincides with a positive relationship of TRW to summer temperature and a negative one to March precipitation, pointing to sufficient moisture availability in spring and growth limitation mostly by low summer temperature. During the climate warming phase earlier in the century, the negative relation of tree growth and May temperature indicated moisture sensitivity. This signal was less significant as during the ca. last 40 years of the investigated period, but already apparent. We suppose that the climate warming-induced increase in evapotranspiration and the consequently intensified moisture stress triggered a shift from summer temperature to spring moisture limited growth response and the stabilization of the correlations towards the end of our investigated period. This is consistent with the change in temperature (Figure 3) and SPEI trends of the study area and intensified spring droughts in the central Himalaya during recent decades [115]. Thus, increased drought might have caused the divergence in growth–climate relationships as observed in other studies [53,143,144], with *Abies spectabilis* trees showing growth plasticity towards the changing environment as other coniferous species do (e.g., [46,48,133,145]). Obviously, this potential adaptation contributed to the rather low responsiveness of the Rolwaling treeline to climate warming [73], and may be crucial for its future sensitivity to climate change.

Until the end of the period of relative stable climate conditions in the mid-20th century (Figure 3), tree growth was limited by previous winter and current spring and summer temperature, and related inversely to winter precipitation and snow height, respectively (Figure 6). These linkages were also found in some studies for the period after the mid-20th century [11,28,31]. Moreover, stable correlations for the whole 20th century exist for a negative relation of tree growth to spring drought [58] as well as for a positive relation to summer temperature [10]. Obviously, some studies neglected information of specific periods or individual trees by the static analysis [48], and/or there might be sites, where climate warming has reached or not reached the potential threshold [43] towards temperature-induced moisture deficits during pre-monsoon season.

4.4. Suitability of Blue Intensity as a Climate Proxy

On the surface, BI–climate correlations exhibited similarities in comparison to correlations of TRW. In detail we found significant differences. BI yielded slightly lower climate correlation coefficients in case of static correlations, but the BI–climate relationships turned out to be generally more stable over time. In line with TRW correlations, BI showed an unstable temporal pattern of climate correlations, however, there were distinctly longer, more significant stable periods. As in the case of TRW–climate correlations, the BI–climate relationships changed towards positive relations with spring precipitation and negative with spring temperature towards the end of the investigated period. This change, however, was less pronounced, and occurred later in comparison to TRW. BI static correlations for the recent four decades did not show spring moisture sensitivity, but a negative relationship to winter and summer temperatures as well as to spring and summer precipitation.

BI correlated positively to spring and summer temperature during a long period, covering nearly the entire 20th century, in line with results of correlations between climate and maximum latewood density (MXD) of *Abies spectabilis* growing near treeline in far western Nepal [65]. The temperature of current year's August played an important role in both cases: MXD correlated positively with August and September temperature [65] while BI was in positive relation to temperatures of July and August. Similarly, *Abies spectabilis* MXD of a study in the NW Himalaya correlated amongst others with September temperature [59]. The slight differences in seasons might result from differences in natural settings between both study areas in terms of micro-climates, soil types, etc. The quality and length of climate data used to perform climate–growth investigations are different as well. Our positive temperature signal for spring and early summer during 20th century was not apparent in the MXD signal, but distinctly visible in correlations of mean and minimum density [65]. Most likely, the latewood formation at our site depends to a greater extent on temperature conditions and consequently carbon acquisition earlier in the year. In contrary to our results for the last decades, Sano et al. [65] did not find any significant correlation of MXD to precipitation. Given the temporal pattern of our correlations, this difference might be attributed to the fact that their MXD chronology ended more than ten years earlier.

Opposite to TRW, BI–climate correlations were not related to moisture conditions during spring. We assume that the formation of latewood cells occurs during the late growing season when moisture and temperature are sufficient. Moreover, latewood density is in general rather related to climate conditions of the entire growing season. BI might be limited by moisture availability in future since the moving window correlation pattern (Figure 7) showed that it already lost its previously positive relation to spring temperature. The different temporal patterns of the correlations of TRW and BI indicate the potential of BI to gain additional information on interannual growth patterns in relation to climatic conditions. Similar to MXD, BI is potentially more useful for climate reconstructions in comparison to TRW [66]. Using BI, additional knowledge could be obtained on, e.g., *Abies spectabilis* biomass acquisition.

5. Conclusions

Abies spectabilis growth–climate correlations in the Rolwaling valley changed during the 20th century, most likely to be attributed to intensified climate warming during the second half of the 20th century. In recent decades, *Abies spectabilis* radial growth has been mostly limited by moisture availability during pre-monsoon season. Winter and pre-monsoon seasons receive the smallest amount of annual precipitation, while sharply rising temperatures in spring increase evaporation, leading to enhanced drought stress when cambial activity starts after winter. Ongoing climate warming will aggravate droughts most likely affecting *Abies spectabilis* more adversely in future and challenging its plasticity.

Blue Intensity of *Abies spectabilis* was shown to be a climate proxy in this study for the first time. The BI signal was more stable and showed higher correlation coefficients compared to radial increment, especially with temperature during the 20th century. It was less affected by spring moisture sensitivity in comparison to tree growth.

Our results accentuate those of most other studies, but show also some differences. To detect underlying mechanisms for temporally and spatially varying results, further studies from different locations are needed to evaluate tree growth response to climatic variables in relation to small-scale climate data and other site properties (e.g., stand structure, gravitational mass movement, geomorphology, slope, aspect, and soil) and their variations. In addition, future studies should analyze individual growth responses to these factors to quantify strategies of single trees or groups of trees. However, the availability of data representing the local climate over sufficient time periods, especially precipitation characteristics of the mountainous terrain at high spatial and temporal resolution, will remain a major challenge.

Author Contributions: N.S., U.S., J.B., R.P.C. and T.S. conceived and designed the experiments; N.S., R.J.K. and K.J. performed the experiments and analyzed the data; and N.S. and U.S. wrote the paper with input from R.J.K., K.J., J.B., R.P.C. and T.S.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix

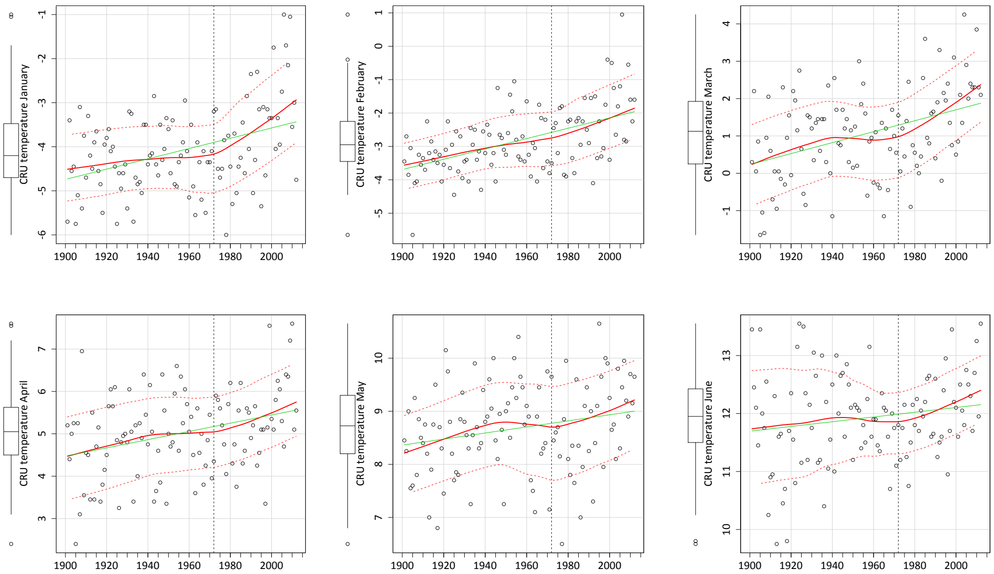

Figure A1. *Cont.*

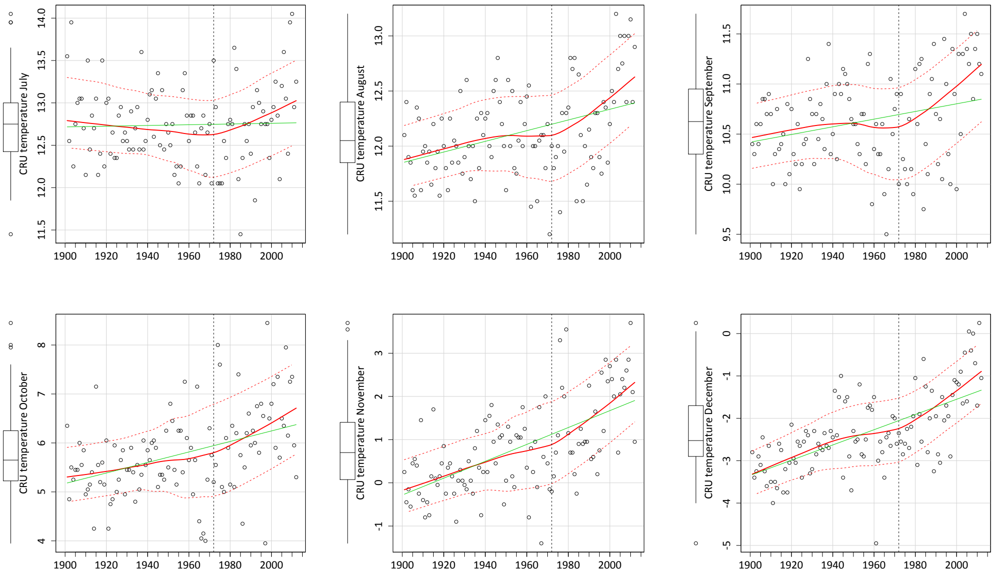

Figure A1. Monthly CRU TS 4.0 temperature non-parametric trends 1901–2012 of the study area. The solid and dashed red lines show locally weighted scatterplot smoothing (LOESS) and corresponding spread smooths, respectively. For comparison, the green line illustrates a linear regression. The dashed black line indicates 1972, i.e., the first year of the period that was analyzed by static tree growth–climate correlations.

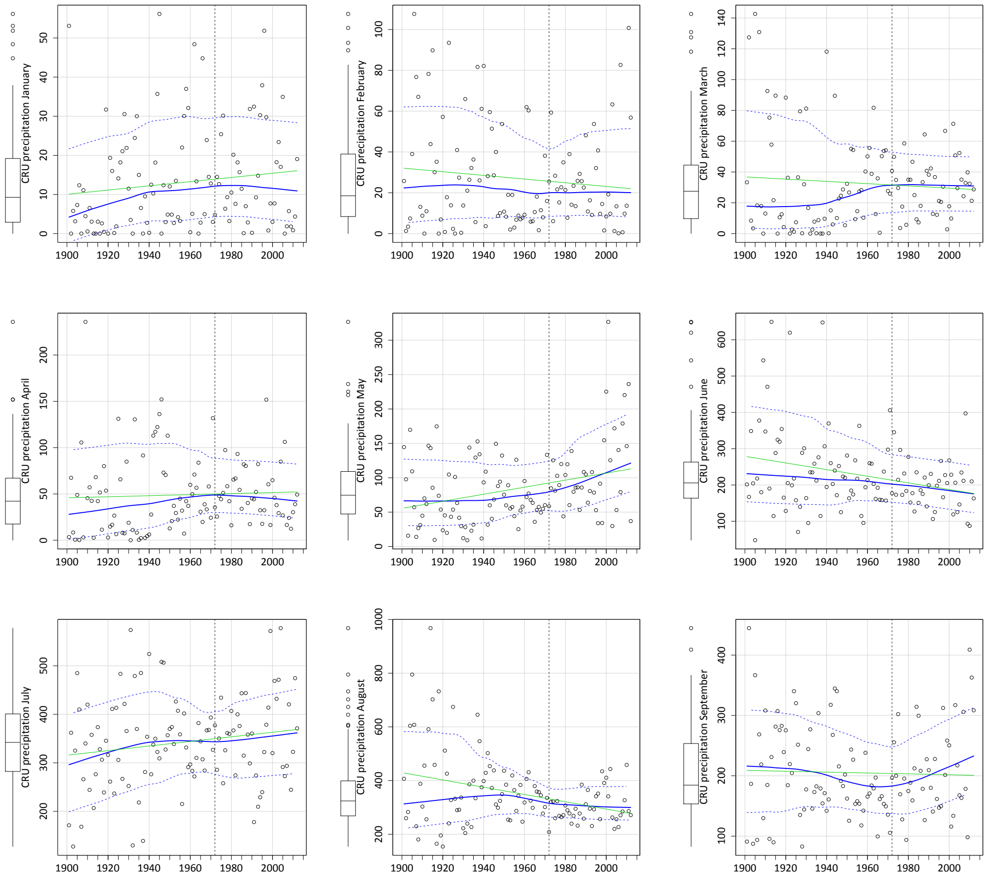

Figure A2. *Cont.*

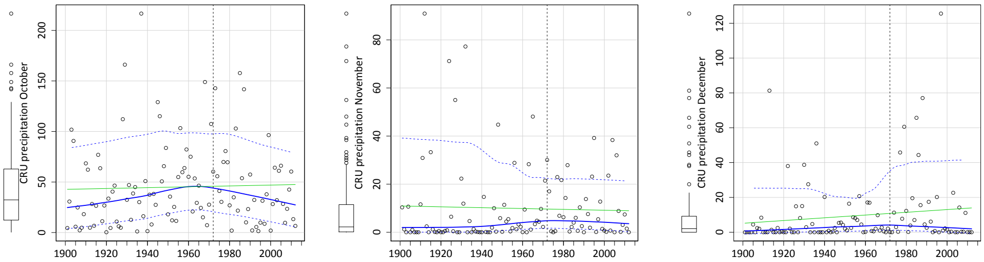

Figure A2. Monthly CRU TS 4.0 precipitation non-parametric trends 1901–2012 of the study area. The solid and dashed red lines show locally weighted scatterplot smoothing (LOESS) and. corresponding spread smooths, respectively. For comparison, the green line illustrates a linear regression. The dashed black line indicates 1972, i.e., the first year of the period that was analyzed by static tree growth–climate correlations.

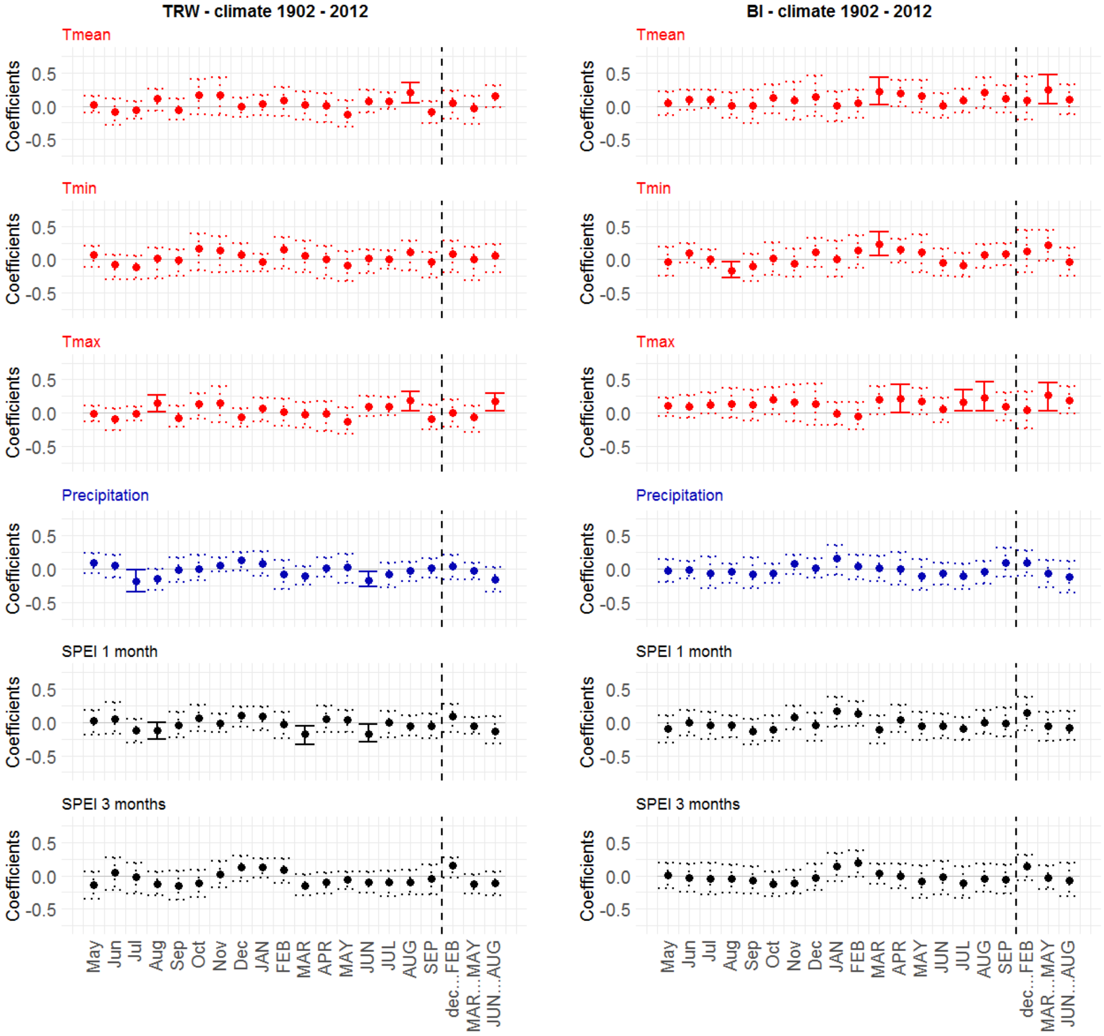

Figure A3. The 1902–2012 static correlations of tree-ring width (TRW, left) and Blue Intensity (BI, right) with temperature, precipitation and drought indices for current and previous year's months and current year seasons. Three-month SPEI correlations were calculated for the period 1903–2012. Solid bars indicate significant correlations ($p < 0.05$).

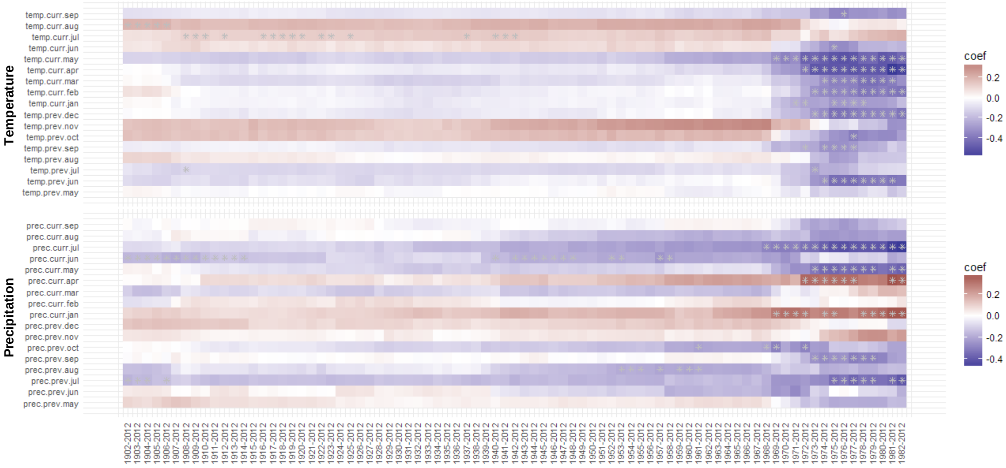

Figure A4. TRW–mean temperatures and TRW–precipitation sums evolving window correlations. Periods with asterisk indicate significant ($p < 0.05$) correlations.

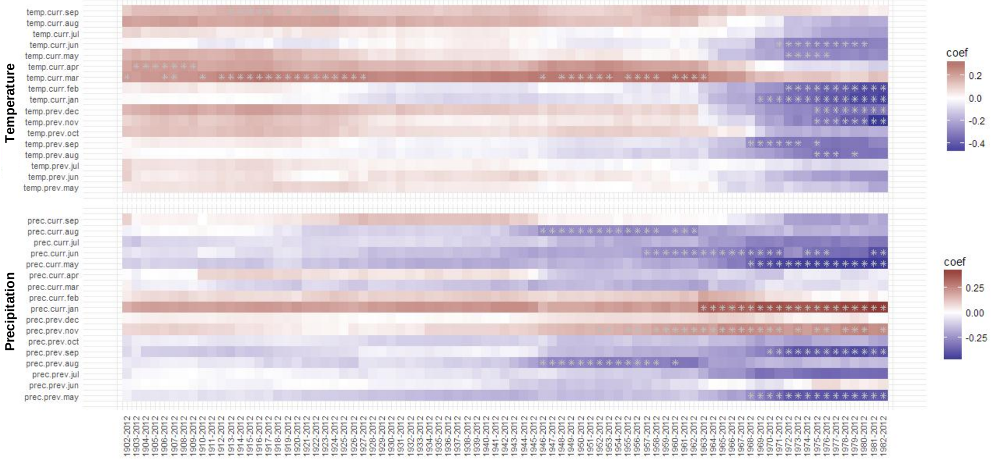

Figure A5. BI–mean temperatures and BI–precipitation sums evolving window correlations. Periods with asterisk indicate significant ($p < 0.05$) correlations.

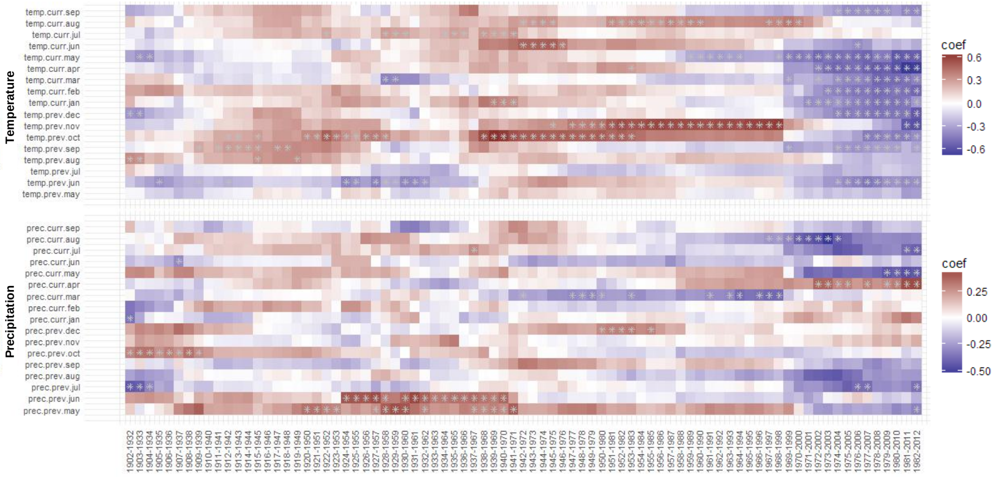

Figure A6. Non-detrended TRW–mean temperatures and non-detrended TRW–precipitation sums moving window correlations. Periods with asterisk indicate significant ($p < 0.05$) correlations.

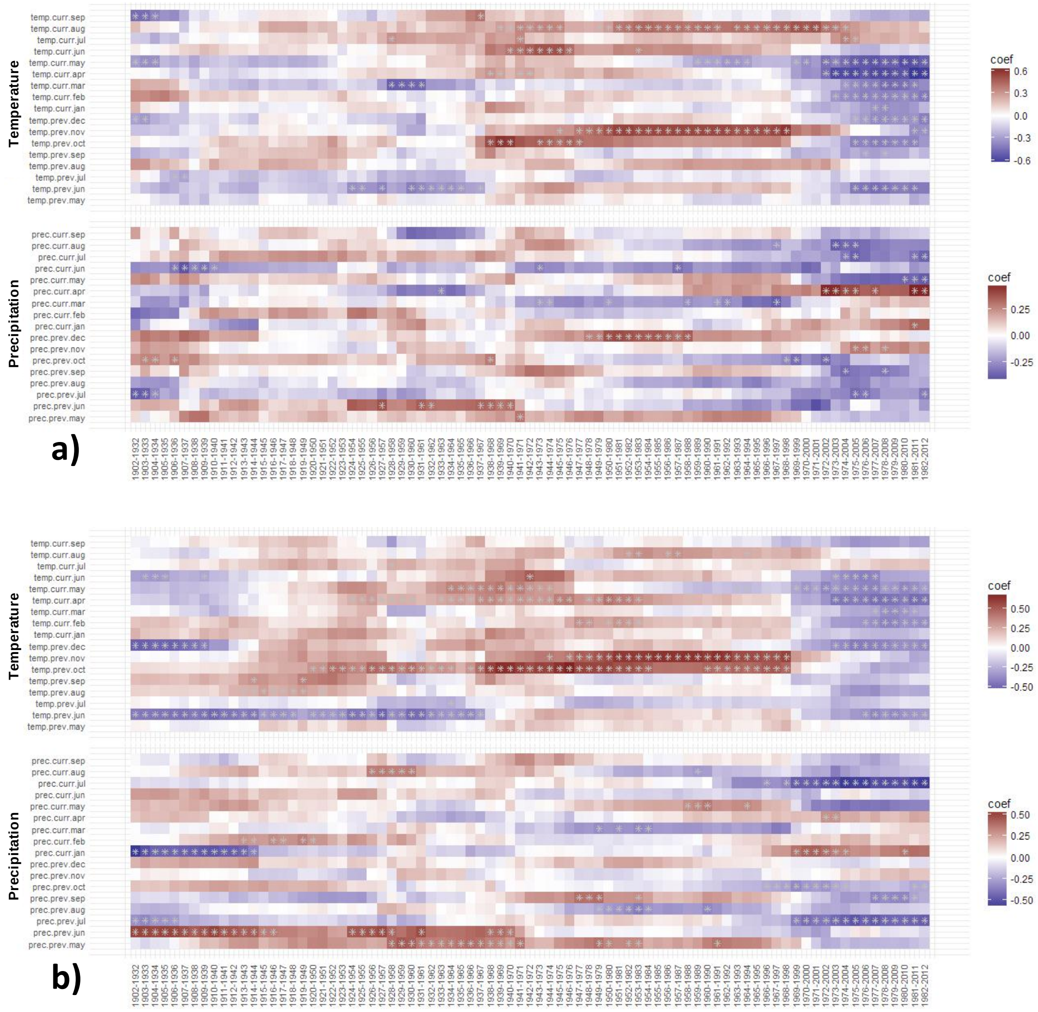

Figure A7. Older trees with minimum age of 100 years (**a**) show unstable radial growth–climate interactions similar to younger trees with an age of less than 100 years (**b**).

Figure A8. *Cont.*

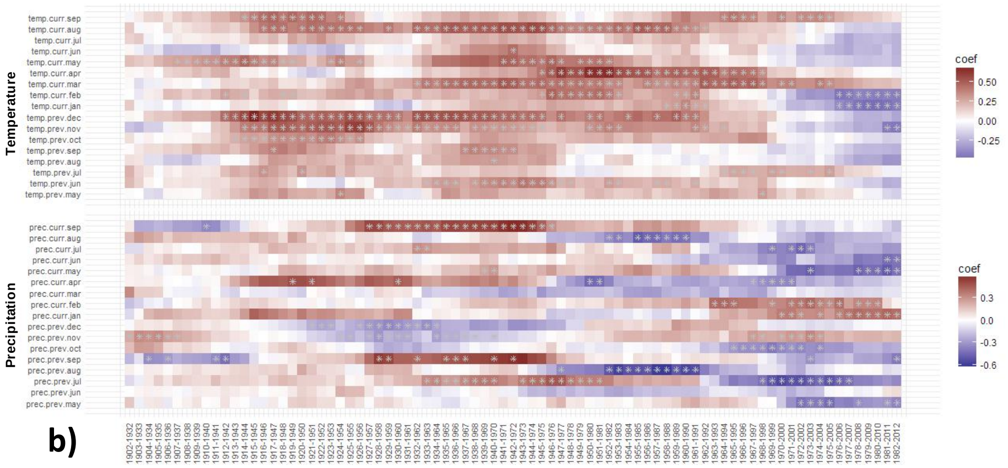

Figure A8. Older trees with minimum age of 100 years (**a**) show unstable Blue Intensity–climate interactions similar to younger trees with an age of less than 100 years (**b**).

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Appendix III: Abstracts of Additional Studies

I contributed as main author to one and as a co-author to seven studies which are closely linked to the main studies of this cumulative thesis. These studies support a more holistic understanding of vegetation, ecological conditions and their interactions within the Rolwaling treeline ecotone. For the sake of completeness, the abstracts of these studies are as follows:

1 'Dendroecological studies in the Nepal Himalaya - review and outlook in the context of a new research initiative (TREELINE)'

Authors: Niels Schwab[1], Udo Schickhoff[1], Birgit Bürzle[1], Julika Hellmold[1], Martin Stellmach[1]

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- The article was published without abstract in the TRACE conference volume -

2 'Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators'

Authors: Udo Schickhoff[1*], Maria Bobrowski[1], Jürgen Böhner[1], Birgit Bürzle[1], R. P. Chaudhary[2], Lars Gerlitz[1], Helge Heyken[1], Jelena Lange[3], Michael Müller[4], Thomas Scholten[4], Niels Schwab[1], Ronja Wedegärtner[4]

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Published 2015 in *Earth System Dynamics* 6:245–265 doi:10.5194/esd-6-245-2015

Abstract. Climate warming is expected to induce treelines to advance to higher elevations. Empirical studies in diverse mountain ranges, however, give evidence of both advancing alpine treelines and rather insignificant responses. The inconsistency of findings suggests distinct differences in the sensitivity of global treelines to recent climate change. It is still unclear where Himalayan treeline ecotones are located along the response gradient from rapid dynamics to apparently complete inertia. This paper reviews the current state of knowledge regarding sensitivity and response of Himalayan treelines to climate warming, based on extensive field observations, published results in the widely scattered literature, and novel data from ongoing research of the present authors.

Several sensitivity indicators such as treeline type, treeline form, seed-based regeneration, and growth patterns are evaluated. Since most Himalayan treelines are anthropogenically depressed, observed advances are largely the result of land use change. Near-natural treelines are usually krummholz treelines, which are relatively unresponsive to climate change. Nevertheless, intense recruitment of treeline trees suggests a great potential for future treeline advance. Competitive abilities of seedlings within krummholz thickets and dwarf scrub heaths will be a major source of variation in treeline dynamics. Tree growth–climate relationships show mature treeline trees to be responsive to temperature change, in particular in winter and pre-monsoon seasons. High pre-monsoon temperature trends will most likely drive tree growth performance in the western and central Himalaya. Ecological niche modelling suggests that bioclimatic conditions for a range expansion of treeline trees will be created during coming decades.

3 ‘Analytic comparison of temperature lapse rates and precipitation gradients in a Himalayan treeline environment: implications for statistical downscaling’

Authors: Lars Gerlitz*[1], Benjamin Bechtel[2], Jürgen Böhner[2], Maria Bobrowski[2], Birgit Bürzle[2], Michael Müller[3], Thomas Scholten[3], Udo Schickhoff[2], Niels Schwab[2], Johannes Weidinger[2]

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Abstract. High mountain regions have been identified as a major hotspot of climate change during recent decades, resulting in a rapid change of local geo- and ecosystems. The ecosystem response to changes of near-surface temperatures and precipitation is often analyzed and simulated by means of statistical or process-based modeling applications. However, these models require high-quality climate input data. Based on the assumption that freely available gridded climate data sets are often not suitable for climate change impact investigation due to their low spatial resolution and a lack of accuracy, this paper aims to suggest adequate statistical downscaling routines in order to facilitate the cooperation of climate and climate impact research. We firstly summarize the requirements of ecological climate impact studies and identify the deficiencies of freely available climate reanalysis and regionalization products. Based on a network of seven recently installed weather stations in the highly structured target area, the seasonal, diurnal, and spatial heterogeneity of near-surface temperatures and precipitation amounts is analyzed, and the major large-scale atmospheric and local-scale topographic forcing are specified. The analysis of observations highly suggests that local-scale climatic conditions are influenced by both large-scale atmospheric parameters and topographic characteristics. Based on related studies in similar environments, we eventually suggest a statistical downscaling approach integrating large-scale atmospheric fields (derived from reanalysis products or large-scale climate models) and GIS-based terrain parameterization in order to generate fully distributed fields of ecologically relevant climate parameters with high spatial resolution.

4 'Climate change and treeline dynamics in the Himalaya'

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Abstract. Treelines are sensitive to changing climatic conditions, in particular to temperature increases, and the majority of global alpine treelines has shown a response to recent climate change. High temperature trends in the Himalaya suggest a treeline advance to higher elevations; it is largely unknown, however, how broader-scale climate inputs interact with local-scale factors and processes to govern treeline response patterns. This paper reviews and synthesizes the current state of knowledge regarding sensitivity and response of Himalayan treelines to climate warming, based on extensive field observations, published results in the widely scattered literature and novel data from ongoing research of the present authors.

Palaeoecological studies indicate that the position of Himalayan treeline ecotones has been sensitive to Holocene climate change. After the Pleistocene-Holocene transition, treelines advanced in elevation to a position several hundred metres higher than today under warm-humid conditions and reached uppermost limits in the early Holocene. Decreasing temperatures below early and mid-Holocene levels induced a downward shift of treelines after c. 5.0 kyr BP. The decline of subalpine forests and treeline elevation in the more recent millennia was coincident with weakening monsoonal influence and increasing anthropogenic interferences.

To assess current treeline dynamics, treeline type, treeline form, seed-based regeneration and growth patterns are evaluated as sensitivity indicators. Anthropogenic treelines are predominant in the Himalaya; upslope movement of these treelines is related to the effects of land-use change. Near-natural treelines, rare nowadays, are usually developed as krummholz treelines which are relatively unresponsive. Strong competition within the krummholz belt and dense dwarf scrub heaths further upslope largely prevents the upward migration of tree species and retards treeline advance to higher elevation. However, intense recruitment of treeline trees within the treeline ecotone and beyond indicates beneficial preconditions for future treeline ascent. Growth patterns of treeline trees are particularly sensitive to higher winter and pre-monsoon temperatures, suggesting that moisture supply in the

pre-monsoon season might be an effective control of future treeline dynamics. Modelled upslope range expansions of treeline trees point to potentially favourable bioclimatic conditions for an upward shift of treelines.

5 'Soil temperature and soil moisture patterns in a Himalayan alpine treeline ecotone'

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Abstract. Soil properties in alpine treeline ecotones are insufficiently explored. In particular, an extensive monitoring of soil moisture conditions over a longer period of time is rare, and the effects of soil moisture variability on alpine treelines have not received adequate attention yet. Soil temperature patterns are generally well documented, and soil temperature is considered a key factor in limiting tree growth at both global and local scales. We performed a 2½-year monitoring in a near-natural treeline ecotone in Rolwaling Himal, Nepal. In this paper, we present new findings on spatiotemporal soil temperature and moisture variability in relation to topographical features and vegetation patterns (variations in stand structures and tree physiognomy). Our results show a growing season mean soil temperature of 7.5 ± 0.6 °C at 10 cm depth at the Rolwaling treeline. Multivariate statistical analyses yield a significant relation between soil temperatures and the variability in tree height, crown length, crown width, and leaf area index (LAI). In turn, soil temperature variability is controlled by the tree physiognomy itself. Soil moisture conditions (available water capacity, 0–10 cm) appear to be less substantial for current stand structures and tree physiognomy. In turn, tree physiognomy patterns control soil moisture, which additionally is affected by snow cover. In Rolwaling, shallow and coarse-grained soils cause low water-holding capacities, and thus a remarkable amount of water percolates from topsoils to subsoils. In the alpine tundra with missing forest canopy, year-round lowest available water capacities are additionally caused by high solar radiation, wind, and thus high evaporation. We assume low soil moisture availability causing largely prevented tree regeneration especially in the alpine tundra.

We conclude that soil temperature and moisture patterns reflect tree physiognomy patterns. The latter cause disparities in soil temperature and moisture conditions inside and outside of the closed forest by shading effects and differences in leaf fall.

6 'Decreasing nutrient concentrations in soils and trees with increasing elevation across a treeline ecotone in Rolwaling Himal, Nepal'

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Abstract. At a global scale, tree growth in alpine treeline ecotones is limited by low temperatures. At a local scale, however, tree growth at its upper limit depends on multiple interactions of influencing factors and mechanisms. The aim of our research was to understand local scale effects of soil properties and nutrient cycling on tree growth limitation, and their interactions with other abiotic and biotic factors in a near-natural Himalayan treeline ecotone. Soil samples of different soil horizons, litter, decomposition layers, and foliage samples of standing biomass were collected in four altitudinal zones along three slopes, and were analysed for exchangeable cations and nutrient concentrations, respectively. Additionally, soil and air temperature, soil moisture, precipitation, and tree physiognomy patterns were evaluated. Both soil nutrients and foliar macronutrient concentrations of nitrogen (N), magnesium (Mg), potassium (K), and foliar phosphorus (P) decrease significantly with elevation. Foliar manganese (Mn) concentrations, by contrast, are extraordinarily high at high elevation sites. Potential constraining factors on tree growth were identified using multivariate statistical approaches. We propose that tree growth, treeline position and vegetation composition are affected by nutrient limitation, which in turn, is governed by low soil temperatures and influenced by soil moisture conditions.

7 'Phytosociology and ecology of treeline ecotone vegetation in Rolwaling Himal, Nepal'

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Abstract. Questions: Species composition and ecology of treeline vegetation types in the Rolwaling Valley is largely unknown to date. The aim of this study is to differentiate plant communities along the elevational gradient in the treeline ecotone, and to identify site factors which cause the differentiation of the treeline ecotone vegetation. **Study area:** Rolwaling Valley (27°52′ N; 86°25′ E) in the central Himalaya, Nepal. **Methods:** We included 91 phytosociological relevés along three elevational transects in this analysis, ranging from 3745 to 4300 m a.s.l. Plant communities were differentiated and vegetation-environment relationships analysed using cluster analysis and ordination. For each community and higher ranked unit, we detected diagnostic species according to their fidelity index (phi coefficient). Ecological preferences of each community were examined using one-way analysis of variance (ANOVA). **Results and conclusions:** We identified five communities, belonging to two different classes: the *Synotis alata-Abies spectabilis* and *Ribes glaciale-Abies spectabilis* communities occupy the upper part of the subalpine forest zone, representing the uppermost forest stands below treeline. These communities are primarily comprised of *Abies spectabilis* and *Betula utilis* in the tree layer, with varying cover of several tree species and distinct differences within the herb layer. Above treeline, the mixed forest stands are replaced by the species-poor *Boschniakia himalaica-Rhododendron campanulatum* community, forming a dense krummholz belt. We assigned the forest and krummholz communities to the class *Betula utilis-Abies spectabilis* forests. In the alpine zone two communities were classified and assigned to the class *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths. The spe-

cies-poor *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community has a less developed herbaceous layer, whereas the *Anaphalis royleana-Rhododendron anthopogon* community is characterized by higher cover and higher species richness of herbs and grasses. Species composition of identified communities is mainly differentiated by soil temperature, nitrogen supply and availability, and soil moisture content.

8 'Seedling recruitment and facilitation dependence on safe site characteristics in a Himalayan treeline ecotone'

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Abstract. Seedling establishment is a crucial factor for spatial dynamics of treelines. However, safe sites for successful tree regeneration which is a basic prerequisite for a supposed treeline advance in response to climate warming have not been fully characterised, especially in the Himalayas. In this study, we aim at analysing safe sites of the tree species *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum*, dominating the near-natural treeline ecotone in Rolwaling Himal, Nepal. We investigated microhabitat ground cover of established seedlings in rectangular plots along the treeline ecotone from subalpine forest stands via the krummholz belt to alpine dwarf shrub heaths (3800–4200 m). We examined protective elements that potentially ameliorate seedlings' growth conditions and quantified the distance of seedlings to the nearest protective element. Our results showed species-specific microhabitat preferences for seedling establishment. While *A. spectabilis* seedlings establish on ground that is covered in average by 70% with litter, *B. utilis* and *R. campanulatum* seedlings

primarily emerge on bryophyte mats (mean site cover 80%). Microhabitat structure did not vary significantly in relation to different vegetation types encompassing the treeline ecotone. The majority of seedlings of all species grew in maximum 2 m distance to at least one potentially protective element. Geomorphic elements and deadwood were the most important shelters for seedling establishment. Our results emphasise the importance of safe sites for successful tree regeneration in harsh environments. As growth conditions in high mountain ecosystems may substantially alter under contemporary climate change, the necessity of safe sites may increase to buffer potential extremes.

Appendix IV: Oral and Poster Presentations

Schwab, N., Janecka K., Kaczka R. J., Böhner, J., Chaudhary, R.P., Scholten, T., Schickhoff, U. (2018): Blue Intensity shows more stable dendroclimatic signal than tree-ring width at a Himalayan treeline. Poster presentation. Jahrestagung des AK Biogeographie. Bonn / Germany

Schwab, N., Janecka K., Kaczka R. J., Böhner, J., Chaudhary, R.P., Scholten, T., Schickhoff, U. (2018): Blue Intensity shows more stable dendroclimatic signal than tree-ring width at a Himalayan treeline. Poster presentation. TRACE 2018 Tree Rings in Archaeology, Climatology and Ecology. Greifswald / Germany

Schwab, N., Kaczka R. J., Janecka K., Böhner, J., Chaudhary, R.P., Scholten, T., Schickhoff, U. (2018): Climate change-induced shift of tree growth sensitivity at a central Himalayan treeline ecotone. Oral presentation. Jahrestagung des AK Hochgebirge „Gebirgsräume im Wandel". Innsbruck / Austria

Schwab, N. (2017): Vegetation dynamics and regeneration on undisturbed slopes related to soil and climate. Oral presentation. Workshop Progress in Gaurishankar Conservation Area: From Monitoring to Carbon Offsetting. Vienna / Austria

Schwab, N., Kaczka R. J., Chaudhary, R.P., Schickhoff, U. (2017): Tree-ring studies of a central Himalayan *Abies spectabilis* treeline ecotone. Oral presentation. MoChWo Mountains in the Changing World. Kathmandu / Nepal

Schwab, N., Kaczka R. J., Schickhoff, U. (2017): Climate-growth relationships of *Abies spectabilis* in a central Himalayan treeline ecotone. Oral presentation. IGU International Geographical Union Thematic Conference on Land Use/Cover Changes, Biodiversity, Health and Environment, Local and Regional Development. Bucharest – Tulcea / Romania

Schwab, N., Kaczka, R.J., Schickhoff, U. (2017): Tree-ring studies of a central Himalayan *Abies spectabilis* treeline ecotone. Oral presentation. Jahrestagung des AK Biogeographie. Erlangen / Germany

Schwab, N., Kaczka R. J., Schickhoff, U. (2017): Climate-growth relationships of *Abies spectabilis* in a central Himalayan treeline ecotone. Oral presentation. TRACE 2017 Tree Rings in Archaeology, Climatology and Ecology. Kaliningrad / Russia

Schwab, N., Kaczka R. J., Schickhoff, U. (2017): Climate-growth relationships of *Abies spectabilis* in a central Himalayan treeline ecotone. Poster presentation. EGU European Geosciences Union General Assembly 2017. Vienna / Austria

Schwab N, Schickhoff U, Bürzle B, Gerlitz L, Müller M, Böhner J, Chaudhary RP, Scholten T (2016): Treeline Responsiveness to Climate Warming: Insights from a Central Himalayan Treeline Ecotone. Oral presentation. 33rd International Geographical Congress - Shaping Our Harmonious Worlds, International Geographical Union (IGU). Beijing / China

Schwab N, Bürzle B, Schickhoff U, Böhner J, Chaudhary RP, Gerlitz L, Müller M, Scholten T (2016) Treeline responsiveness to climate warming: Insights from a Himalayan krummholz treeline ecotone. Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GFÖ). Marburg / Germany

Schwab, N., Schickhoff, U., Böhner, J., Scholten, T., Chaudhary, R. P., Bürzle, B., Gerlitz, L., Müller, M., Schenk, E. (2015): Assessing sensitivity and response of a Himalayan treeline ecotone to climate warming -Introduction to the project TREELINE. Oral presentation. 26th European Dendroecological Fieldweek 2015. Zawoja / Poland

Schwab, N., Gerlitz, L., Müller, M., Schickhoff, U., Heyken, H., Wedegärtner, R., Bürzle, B., Böhner, J., Scholten, T., Chaudhary, Ram P. (2015): How is the spatial pattern of treeline forming tree species in Rolwaling Himal, Nepal, related to siteecological conditions? Oral presentation. Jahrestagung des AK Hochgebirge „Interdisziplinarität in der Hochgebirgsforschung". Hamburg / Germany

Schwab, N., Bürzle, B., Müller, M., Schickhoff, U., Scholten, T., Chaudhary, Ram P. (2015): Near natural treeline ecotone, species patterns and species transitions influenced by soil factors in Rolwaling Himal, Nepal. Poster presentation. International Biogeography Society 7th Biennial Meeting 2015, Bayreuth / Germany

Schwab, N., Schickhoff, U., Böhner, J., Scholten, T., Chaudhary, R. P., Bürzle, B., Gerlitz, L., Müller, M., Schenk, E. (2014): TREELINE: Detecting the response of a Himalayan near-natural treeline ecotone to climate change. Oral presentation. International Geographical Union Regional Conference 2014 „Changes, Challenges, Responsibilities". Krakow / Poland

Schwab, N., Schickhoff, U., Böhner, J., Scholten, T., Chaudhary, R. P., Bürzle, B., Gerlitz, L., Müller, M., Schenk, E. (2014): Assessing sensitivity and response of a Himalayan treeline ecotone to climate warming – the project TREELINE. Poster presentation. Arbeitskreis Biogeographie 2014 „Biogeographie und Ökosystemfunktionen". Karlsruhe / Germany

Schwab, N., Schickhoff, U., Böhner, J., Scholten, T., Chaudhary, R. P., Bürzle, B., Gerlitz, L., Müller, M., Schenk, E. (2014): Assessing sensitivity and response of a Himalayan treeline ecotone to climate warming. Oral presentation. Jahrestagung des AK Hochgebirge „Ressourcen der Gebirgsräume: Nutzung, Wandel, Bewertung". Bern / Switzerland

Schwab, N., Schickhoff, U., Böhner, J., Scholten, T., Chaudhary, R. P., Bürzle, B., Gerlitz, L., Müller, M., Schenk, E. (2014): Dendrochronological analyses at a near-natural Himalayan treeline: detecting the response to climate change. Poster presentation. TRACE 2014 Tree Rings in Archaeology, Climatology and Ecology. Aviemore / Scotland

Appendix V: Science Communication

Neigenfind F, Schwab N, Bürzle B (2017) Stabile Waldgrenze: Wie ein Tal im Himalaya dem Klimawandel trotzt. Neues aus der Klimaforschung. https://www.clisap.de/de/clisap/ueber-uns/news/stabile-waldgrenze:-wie-ein-tal-im-himalaya-dem-klimawandel-trotzt/ (19th April 2017)

Neigenfind F, Schwab N, Bürzle B (2017) Das kleine Tal im Himalaja, das der Erderwärmung trotzt. Hamburger Abendblatt 10th April 2017:18

Appendix VI: Further Scientific Output

The following studies on soil, vegetation and land-use in Nepal are not directly related to the topic of the thesis.

Articles and book chapter

Heider, K, Weinzierl, T, Schwab, N, Bobrowski, M, Schickhoff, U: Future agricultural conditions in the Himalayan Region - A fuzzy logic approach using high resolution climate scenarios. Submitted to Die Erde (under review)

Schick A, Wieners E, Schwab N, Schickhoff U (2018) Sustainable Disaster Risk Reduction in Mountain Agriculture: Agroforestry Experiences in Kaule, Mid-Hills of Nepal. In: Climate Change, Extreme Events and Disaster Risk Reduction. Springer, Cham, pp 249–264. doi 10.1007/978-3-319-56469-2_17

Schwab N, Schickhoff U, Fischer E (2015) Transition to agroforestry significantly improves soil quality: A case study in the central mid-hills of Nepal. Agriculture, Ecosystems & Environment 205:57–69. doi: 10.1016/j.agee.2015.03.004

Oral and Poster Presentations

Schwab, N., Kreipe, L., Wieners, E., Müller, T., Kiese, N., Schickhoff, U. (2017): Transition to sustainable mountain agriculture: Agroforestry experiences in the mid-hills of Nepal. Poster presentation. MoChWo Mountains in the Changing World. Kathmandu / Nepal

Schwab N, Schickhoff U (2016) Does agroforestry protect tree species diversity and reduce soil erosion risk? A comparative study from the mid-hills of Nepal. Poster presentation. 33rd International Geographical Congress - Shaping Our Harmonious Worlds, International Geographical Union (IGU). Beijing / China

Schwab, N., Schick, A., Wieners, E., Kiese, N., Schickhoff, U. (2016) Scaling Sustainable Modernisation in Mountain Agriculture: Agroforestry Experiences in Kaule, Mid-Hills of Nepal. Poster presentation. Tropentag 2016 "Solidarity in a competing world - fair use of resources". Vienna / Austria

Schwab, N., Wieners, E., Schick, A., Kiese, N., Kremer, V., Roth, K., Schickhoff, U. (2015): Transition to Agroforestry in the Mid-Hills of Nepal: Implications for Livelihoods and Environment. Poster presentation. Jahrestagung des AK Hochgebirge „Interdisziplinarität in der Hochgebirgsforschung“. Hamburg / Germany

Schwab, N. & Schickhoff, U (2014): Transition from monoculture to agroforestry: Improving soil con-ditions and phytodiversity for sustainable land use and livelihood security in the mid-hills of Ne-pal. Poster presentation. International Geographical Union Regional Conference 2014 „Changes, Challenges, Responsibilities“. Krakow / Poland

Schwab, N., Wieners, E., Schick, A., Kiese, N., Kremer, V., Roth, K., Borchardt, P., Schickhoff, U. (2014): Transition to Agroforestry in the Mid-Hills of Nepal: Implications for Livelihoods and Environment. Poster presentation. Tropentag 2014 "Bridging the gap between increasing knowledge and decreasing resources". Prague / Czech Republic

Schwab, N. (2013): From monoculture to agroforestry: Towards more resilient land use in the Mid-Hills of Nepal? – Oral presentation, International workshop: Climate Change and Environmental Pressure: Adaptation and Resilience of Local Communities in the Hindu-Kush-Himalaya (HKH). KlimaCampus, University of Hamburg. Hamburg / Germany

Schwab, N. & Schickhoff, U. (2013): Agroforestry for resilient agroecosystems in the Mid-Hills of Nepal. – Poster, Jahrestagung des AK Hochgebirge "Hochgebirge im globalen Wandel", Bonn / Germany

Schwab, N. (2012): Agroforestry's influence on soil conditions and phytodiversity in a mid-hill village of Nepal. – Oral presentation, International Scientific Conference: Sustainable Land Use and Rural Development in Mountain Areas. University of Hohenheim, Stuttgart / Germany

Schwab, N. (2011): Herausforderungen beim Vergleich der Diversität von Agrarökosystemen in den Mid-Hills von Nepal. – Poster, 13. Treffen des Arbeitskreises Biogeographie. Hamburg / Germany

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(Incidentally, I am *not* thankful for the unforgettable experience of 'a few' rainy days during the monsoon seasons of 2013 and 2014.)

Eidesstattliche Versicherung (*Declaration on oath*)

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hamburg, den 31.05.2018