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ECOLOGICAL RELATIONSHIPS AT A NEAR-NATURAL TREELINE, ROLWALING VALLEY, NEPAL HIMALAYA: IMPLICATIONS FOR THE SENSITIVITY TO CLIMATE CHANGE

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Summary: At a global scale, heat deficits during the growing season result in growth limitations, which determine the elevation of natural alpine treelines. Thus, the expected response to global warming is a treeline 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. Based on an extensive collection of field data, we analysed population structures and regeneration patterns, investigated population density-environment relationships and correlated tree growth with climate in order to assess the sensitivity to climate warming of a near-natural treeline ecotone in east-central Nepal. The presence of an elevational zone dominated by a gnarled growth form of *Rhododendron campanulatum* physiognomically classifies the treeline as a krummholz treeline. The fraction of juvenile tree 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 also on soil, 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 decreasing moisture availability during the pre-monsoon season has affected *Abies spectabilis'* radial growth. It is evident from our results that to date the treeline has responded to climate warming in terms of stand densities, seed-based regeneration and growth patterns of trees, the treeline position, however, is rather stable. A treeline shift is to be expected in the mid- to long-term only.

Zusammenfassung: Global betrachtet führt Wärmemangel während der Vegetationsperiode zu Wachstumsbeschränkungen, die die Höhenlage der natürlichen alpinen Waldgrenze bestimmen. 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. Basierend auf umfangreichem Datenmaterial zu Vegetations- und Umweltvariablen konnten Populationsstrukturen und Verjüngungsmuster erfasst, Zusammenhänge zwischen Populationsdichten und Standortfaktoren untersucht und Korrelationen zwischen Baumwachstum und Klima ermittelt werden, um die Empfindlichkeit eines naturnahen Waldgrenzökotons im östlichen Zentral-Nepal gegenüber der Klimaerwärmung zu beurteilen. 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. Der Jungwuchs 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 auch von Bodeneigenschaften, 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 unterhalb gelegenen geschlossenen Waldes dominieren dagegen *Abies spectabilis* (Himalaya-Tanne) und *Betula utilis* (Himalaya-Birke). Der dichte Krummholzgürtel verhindert weitgehend die zu erwartende hangaufwärtsgerichtete Wanderung von subalpinen Baumarten. 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. Die Ergebnisse zeigen insgesamt, dass die Waldgrenze auf die Klimaerwärmung im Hinblick auf Bestandsdichte, generativer Verjüngung und Zuwachsmuster der Bäume reagiert, dass die Höhenlage der Waldgrenze jedoch relativ stabil ist. Ein Vorrücken der Waldgrenze ist erst in mittel- bis langfristigen Zeiträumen zu erwarten.

Keywords: feedback, krummholz, Nepal, regeneration, species-environment relationships, tree growth-climate correlation, treeline dynamics, vegetation geography

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1 Introduction

1.1 Treeline dynamics

Mountain ecosystems are considered as highly sensitive to global change, including alterations of climate (Beniston 2003; Löffler et al. 2011; Schickhoff 2011; Palomo 2017; Steinbauer et al. 2018; Immerzeel et al. 2020). The elevational distribution of mountain plant communities is sensitive to climate change with a potential species loss under accelerated warming (Steinbauer et al. 2018). Associated with upward shifting treeline ecotones (Harsch et al. 2009), alpine vegetation habitats might shift upslope as well, or shrink. Shrinking results in potential habitat loss of plant and animal species, amongst them endangered ones like the snow leopard (Gottfried et al. 2012; Forrest et al. 2012; Chhetri et al. 2018). 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 alpine treelines[1)] (e.g., Troll 1973; Stevens and Fox 1991; Miehe and Miehe 2000; Körner 2007; Holtmeier 2009; Körner 2012). In consequence, treelines fluctuated repeatedly because of climate changes during the Holocene (cf. Schickhoff et al. 2016a) and climate warming is expected to cause treelines to advance to higher elevations (e.g., Körner 2012; Lamsal et al. 2017; Holtmeier and Broll 2020). However, 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 were persistent, while 52 % advanced to higher elevations, and only 1 % showed recession. Likewise, recent empirical studies in diverse mountain ranges detected 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; Schickhoff et al. 2015; Shrestha et al. 2015), which is not sufficiently understood. Besides elevational upshift, alpine treelines show responses to climate change by tree densification. Different drivers can control both spatial dynamics (Feuillet et al. 2019). Apart from limitation of tree growth by growing season temperature, regional and local factors and species-specific traits determine treeline positions and dynamics. The latter factors interact and sometimes exceed the influence of climate. In addition, positive feedbacks may decouple spatial patterns and processes within treeline ecotones from basic environmental parameters (Kim and Lee 2015). Seedling establishment is crucial for treeline expansion, and likewise influenced by multiple factors (Holtmeier 2009; Lett and Dorrepaal 2018). In addition, land use and land use changes have modified the spatial patterns at treelines in all historically populated mountains in many ways. Generally, anthropogenic influence lowered treeline elevations. Therefore, a clear signal of climate change can only be detected at near-natural, i.e. climatic treelines (e.g., Miehe and Miehe 2000; Dirnböck et al. 2003; Bolli et al. 2007; Gehrig-Fasel et al. 2007; Rössler et al. 2008; Schickhoff 2011; Penniston and Lundberg 2014; Durak et al. 2015). 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; Brodersen et al. 2019).

Treeline dynamics in the Himalaya are the result of interrelationships between human impact and climatic changes during recent centuries (cf. 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 Himalayan alpine treelines and tree growth-climate relationships have received much attention (e.g., Rana et al. 2017; Yadava et al. 2017; Sigdel et al. 2018; Tiwari and Jha 2018; Mohapatra et al. 2019). Climatic changes will inevitably affect growth patterns, seedling survival and seedling performance, albeit to a regionally differentiated and largely unknown extent (Schickhoff et al. 2015; Schickhoff et al. 2016a; Bürzle et al. 2018).

1.2 Climate change in the Himalaya

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 (ca. 0.75 °C per decade), with a rising trend in extreme values (IPCC 2014; Mountain Research Initiative EDW Working Group 2015;

[1)] We employ the terms 'treeline' and 'treeline ecotone' as synonyms for the transition zone.

Schickhoff et al. 2016b; Krishnan et al. 2019). 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 in east-central Nepal, the target area of this paper, monthly mean surface air 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 temperature trends were identified. Trend analyses of precipitation amounts in the Himalaya do not exhibit 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). Wang et al. (2013) reported an enhanced frequency of winter and pre-monsoon drought events for western Nepal. Additionally, Karki et al. (2017b) found rising precipitation extremes across Nepal.

1.3 Sensitivity indicators and research deficits

Key sensitivity indicators to assess current treeline dynamics include treeline type, treeline form, seed-based regeneration, and growth patterns (Schickhoff et al. 2015). Amongst different treeline types, climatic treelines are considered to show a rather high sensitivity to climate change, notwithstanding the fact that 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 less responsive. Anthropogenic treelines do show distinct directional changes, which have often been attributed to climate warming; however, in the majority of cases, these changes most likely resulted from reduced land-use impacts (Schickhoff et al. 2016a).

According to a worldwide meta-analysis on the responsiveness of different treeline forms (Harsch and Bader 2011), diffuse treelines, which are formed and maintained primarily by growth limitation, exhibit a strong response signal. The same study reports abrupt, island and krummholz treelines to be controlled by seedling mortality and dieback, and they are comparatively less responsive to climate changes. The majority of Himalayan near-natural treelines can be categorised as krummholz treelines, characterized by a dispersed or contiguous band of gnarled and multi-stemmed trees above the subalpine forest (Schickhoff et al. 2016a). With regard to elevational shifts, Himalayan krummholz treelines have shown rather low responsiveness to climate warming over recent decades. However, short- to medium-term responses are expected in terms of tree growth and seedling recruitment (Schickhoff et al. 2016a).

Apart from treeline type and treeline form, tree species composition, population structures, regeneration patterns, and stand structural parameters such as tree density, diameter and height distributions can be indicators of treeline sensitivity to climate change. These parameters provide information about the establishment of recruits and their performance, which is crucial for any treeline advance (Germino et al. 2002; Holtmeier 2009; Körner 2012; Zurbriggen et al. 2013; Schickhoff et al. 2015).

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; Bürzle et al. 2018). Most of the available studies investigated 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; Gaire et al. 2011; Chhetri and Cairns 2015; Shrestha et al. 2015; Singh et al. 2018). Thus, their results can hardly be transferred to near-natural treeline ecotones.

Extensive research deficits persist in terms of the interactions of landscape-scale and local-scale abiotic and biotic factors and processes and their relation to region-wide climate warming inputs (Schickhoff et al. 2016a; Singh et al. 2019). The accumulated knowledge of treeline tree species ecology in the Himalaya remains very limited (Miehe and Miehe 2000; Schickhoff 2005; Miehe et al. 2015), narrowing 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 that respond differently to climate change (Trant and Hermanutz 2014). Most treeline studies in Nepal and the Himalaya focussed on single treeline-forming tree species (e.g., Shrestha et al. 2007; Lv and Zhang 2012; Sujakhu et al. 2013; Gaire et al. 2014) rather than addressing co-occurring tree species and their specific responses. Thus, there is an urgent need for multispecies and multifactorial approaches to treeline dynamics to capture sufficiently the sensitivity of the ecotone to climate change (Schwab et al. 2016; Lett and Dorrepaal 2018; Tiwari and Jha 2018).

To date, various treeline tree species have been analysed 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 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 inferred a limitation of tree growth by winter temperature (e.g., Chhetri and Cairns 2016; Rayback et al. 2017) or by available moisture in dry 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 study areas close to each other (e.g., Gaire et al. 2017b), additional studies are needed to generate denser tree-ring networks of various treeline tree and shrub species and to distinguish tree growth-climate relationships of sites with differing environmental and especially climatic conditions.

The majority of central Himalayan tree-ring studies investigated growth-climate relationships over rather short periods because of the lack of long instrumental records of climate data. Some recent studies employed gridded climate data that cover longer periods. Most studies analysed static correlations that represent the whole data period without investigating the temporal pattern of correlations and addressing its temporal stability (e.g., Thapa et al. 2015). Few recent studies mentioned unstable correlations of *Abies spectabilis* tree growth with climate variables (Shrestha et al. 2015; Sohar et al. 2017; Gaire et al. 2020). To date, hardly any study investigated temporal stability and the so-called 'divergence phenomena' in the Himalaya, pointing to an immense need for further research.

1.4 Objectives

To reduce the aforementioned research deficits, we aim at assessing sensitivity and response of the treeline in the Rolwaling Valley by a series of consecutive and complementary analyses of sensitivity indicators, based on data and results of previous interdisciplinary studies (Supplement I: D) (Schwab et al. 2016; Schwab et al. 2017; Schwab et al. 2018):

1) We detect elevational patterns of tree species distributions in order to analyse species-specific patterns and abruptness of transitions of tree as well as recruit densities and growth parameters along the elevational gradient.
2) We analyse the relations of *Abies spectabilis* radial growth to climate in order to evaluate the sensitivity of tree growth to climate change, and investigate the temporal stability of tree growth-climate relationships.
3) We analyse the relationships of adult and juvenile population densities of tree species with environmental conditions in order to identify crucial site factors for the high competitiveness of *Rhododendron campanulatum*, forming a dense krummholz belt above the treeline, and assess the susceptibility of these variables to climate change.
4) We discuss and summarize results from a system perspective with focus on the treeline migration potential, showing potential feedback processes and equilibrium states under climate change related temperature forcing.

2 Research design and methodology

To examine the treeline ecology and its sensitivity to climate change from an interdisciplinary perspective we applied extensive acquisition of tree species density, tree-ring, soil, topography and climate data across the treeline ecotone. Supplement I: D shows the respective comprehensive research design.

2.1 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 (Province 3), east-central Nepal, adjacent to the border of Tibet Autonomous Region (Supplement I: A, B). The Rolwaling Valley is part of the Gaurishankar Conservation Area, established in 2010 (Bhusal 2012).

The climate of this area is monsoonal, and has a continental character, with dry and cold winter conditions, while the pre-monsoon season is dry and hot. 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 (Supplement I: C) (Müller et al. 2016a; Karki et al. 2017a). At the local scale, the climate shows distinct spatial variability of temperature and precipitation (Böhner et al. 2015; Weidinger et al. 2018). The climate of the study site is considered temperate, with a dry winter and a warm summer (Karki et al. 2016). The warming trend of the study area corresponds to general Himalayan trends (Gerlitz et al. 2014; Schwab et al. 2018). Müller et al. (2016a) classified soils in the treeline ecotone as podzols.

The Rolwaling Himal (mountain) treeline at the north-facing slope exhibits a near-natural state and represents a climatic treeline. The study area has a remote location, which lacks a connection to the road network. To reach the study site, three days of trekking is required. The Rolwaling Valley contains a small human population, and the recurring Buddhist theme of a sacred hidden valley has protected plants and animals to a certain extent (Baumgartner 2015). The study slopes show no signs of fire or grazing by neither herbivores nor domestic animals (cf. Supplement I: E, F). Woodcutting and its influence on stand structures has been negligible in the upper part of the closed forest and above, as concluded from the mapping of stumps (Schwab et al. 2016). Soil physical and chemical conditions, in particular soil bulk densities, atmospheric nitrogen and ammonia deposition (refer to Müller et al. 2017 for the latter) indicate a near-natural state. The Rolwaling Khola (Rolwaling River) separates the uninhabited north-facing study slope from the sparsely populated south-facing slope, where human impact is likewise low. Consequently, considering the fact that land-use effects have disturbed most Himalayan treeline sites (Schickhoff et al. 2015; Schickhoff et al. 2016a), the study slopes provide a unique research opportunity to detect a climate change signal when assessing treeline dynamics.

The studied site comprises three north-facing slopes, which are named NE1, NE2 (both northeast exposure) and NW (northwest exposure) according to their predominant exposition. Each of these sampled slope sectors 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 (Supplement I: E, F).

2.2 Data collection

2.2.1 Vegetation

We stratified the slopes according to the elevational 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. Supplement I: B, E, F). In total, 50 square plots of 20 m × 20 m were randomly selected and sampled. Sampling took place 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 of all vital tree species individuals with dbh $\geq$ 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 $\geq$ 7 cm 'adult trees', whilst smaller ones were categorised as 'juvenile individuals' or 'recruits', regardless of their actual age. In order to analyse tree growth-climate relationships, we followed standard procedures for the collection, preparation and measurement of *Abies spectabilis* tree-ring samples (Speer 2010).

2.2.2 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 for Soil Science and Geoecology at the University of Tübingen (see Müller et al. 2016b for details). To capture the variation in topography between and within plots, several topographic and microtopographic variables were determined (the latter characterising, amongst others, plot surface structure; cf. Schwab et al. 2016). In addition to soil temperature and soil moisture (see Müller et al. 2016b), we used air temperatures from April 2013 to June 2014, recorded through mobile climate stations, which were installed in the lower and upper part of the ecotone (Gerlitz et al. 2016; Weidinger et al. 2018).

To assess tree growth-climate relationships, we consulted climate data from the Climatic Research Unit (CRU) TS4.00 dataset (Harris et al. 2014; CRU 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.

2.3 Data analyses

Unless stated otherwise, all computations and figure plotting were carried out through the functions of packages (see below) in the most recent versions of the program R (R Core Team 2018).

2.3.1 Population structures, regeneration patterns and abruptness of transitions

We calculated stem numbers and stand densities per hectare. To visualise population structures and species compositions, we created bar graphs. To describe and analyse variation in stand structures and characterise abrupt or smooth and gradual transition patterns along the ecotone, the abruptness of transitions between elevational subsequent zones was calculated as the difference between the scaled values of successive zones (Wiegand et al. 2006; Batllori and Gutiérrez 2008; cf. Schwab et al. 2016). We determined abruptness species-wise for the density of trees. In order to compare to abruptness patterns of tree species, we calculated the abruptness of annual and seasonal soil temperatures. We applied functions of the R-packages 'plyr' (Wickham 2011) and 'vegan' (Oksanen et al. 2015).

2.3.2 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, which Schwab et al. (2016) presented in detail. 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. We included all by this procedure selected and all uncorrelated variables in the three final matrices of explanatory variables (Appendix I), which were further reduced by the RDA backward elimination process. We used functions of the R-packages 'PCNM' (Legendre et al. 2013), 'pgirmess' (Giraudoux 2015), 'plyr' (Wickham 2011), 'psych' (Revelle 2015), 'rgdal', 'sp' (Bivand et al. 2013; Bivand et al. 2015), 'vegan' (Oksanen et al. 2015), 'xlsx' (Dragulescu 2014).

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 (cf. Schwab et al. 2016).

2.3.3 Tree growth-climate relationships

The cross-dating of the *Abies spectabilis* 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 CooRecorder and CDendro (Larsson 2016), COFECHA (Holmes 1983) and ARSTAN (Cook 1985). 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 1901–2012. 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 of the present year and the year before ring formation. 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. We applied the R-packages car (Fox and Weisberg 2011) and treeclim (Zang and Biondi 2015).

3 Results

3.1 Elevational boundaries of tree species distributions and regeneration

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. Please refer to Supplement I: E and F for detailed impressions of the elevational vegetation zones. The lower elevational section (zone A; Supplement I: F xiii - xvi) of the upper subalpine forest transitions into its upper section (zone B; Supplement I: F ix - xii) at 3820 m a.s.l. at the NW slope and at 3900 m a.s.l. at NE slopes. The tree species composition differed between these sections. 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 (Fig. 1, Supplement I: F x – xii, xv). Closed forests gave way to a dense and nearly impenetrable *Rhododendron campanulatum* krummholz belt (zone C; Supplement I: F v - viii) 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 (zone D; Supplement I: F i - iv) 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* (Schwab et al. 2016).

The recruit density pattern (Fig. 2) 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 *Juniperus 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.

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 (cf. Schwab et al. 2016).

In general, certain values of stand parameters, such as dbh, tree height and tree density, decreased with elevation. The pattern of tree density 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) (Fig. 3). Annual and all seasons' mean soil temperatures dropped

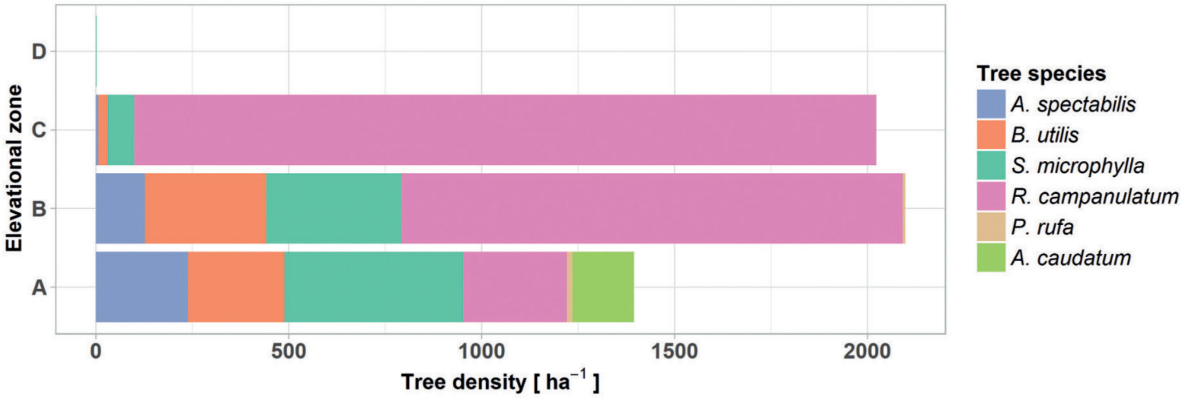

Fig. 1: Tree species population density of adult individuals (≥ 7 cm dbh) across the elevational gradient

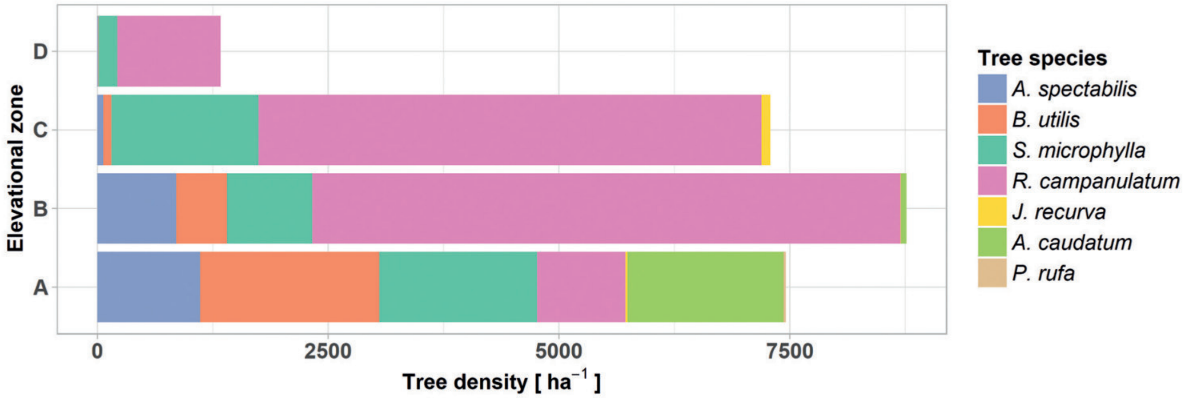

Fig. 2: Tree species population density of juvenile individuals (< 7 cm dbh, 'recruits') across the elevational gradient

most abruptly at the transition from closed forest to krummholz belt (B-C) (Fig. 3) (SCHWAB et al. 2016).

3.2 Population density-environment relationships

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*, which considerably decreases in more nutrient-rich and warmer sites of the upper subalpine forest where other tree species have gained predominance.

3.2.1 Adult trees

Seventeen selected environmental variables explained a total of 77 % of the variation in adult tree species density (cf. Tab. 1 for all selected variables). 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 (Fig. 4). 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 (SCHWAB et al. 2017).

Most environmental variables were correlated with RDA axis one rather than with axis two (Fig. 4). These variables form 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,

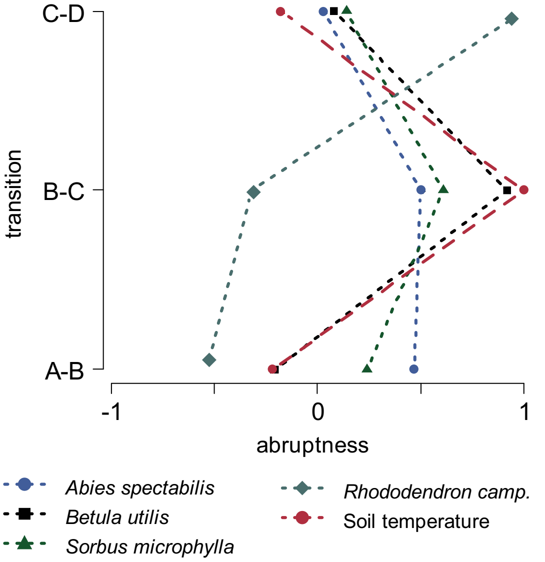

Fig. 3: Species-wise tree density and annual mean soil temperature: abruptness of transitions from lower to upper part of subalpine forest (A-B), from upper part of subalpine forest to krummholz belt (B-C) and from krummholz belt to alpine dwarf shrub heath (C-D). Population densities and soil temperature were generalized across all investigated slopes. A positive abruptness indicates a transition of decreasing values with elevation as it is generally expected in a treeline ecotone, whilst a negative abruptness conveys an increasing value with elevation.

Tab. 1: Explanatory variables and biplot scores of RDA axes 1 and 2 of adult and juvenile tree density RDAs indicating importance of environmental variables and abbreviations used in Figures 4 & 5.

Adult tree density RDA

Variable name	Abbreviation	RDA axis 1	RDA axis 2
Air temperature DJF	Temp DJF	-0.746	-0.181
C/N Ah-horizon	CN Ah	0.688	0.036
Bulk density Of-horizon	BD Of	-0.645	0.154
C/N Ae-horizon	CN Ae	0.489	-0.343
Soil temperature MAM	Soil temp MAM	-0.477	-0.170
Medium size stone cover	Med stone	0.414	0.103
Large stone cover		0.361	0.219
Mn concentration Ah-horizon	Mn Ah	-0.354	0.555
Sand content Ae-horizon	Sand	0.348	0.279
Min. air temperature JJAS	Min temp JJAS	0.320	0.368
Coarse soil cover	Coarse soil	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

Variable name	Abbreviation	RDA axis 1	RDA axis 2
C/N Ah-horizon	CN Ah	0.707	-0.049
Air temperature DJF	Temp DJF	-0.625	-0.433
C/N Ae-horizon	CN Ae	0.468	-0.358
Mn concentration Ah-horizon	Mn Ah	-0.391	-0.319
Bare ground cover	Bare ground	0.334	0.142
Ground cover dissimilarity	Ground diss	0.333	0.295
Medium size stone cover	Med stone	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	Rugged	-0.095	0.320
Eastness		-0.050	0.157
Min. air temperature JJAS		-0.040	-0.102
pH$_{H2O}$		0.038	-0.145

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

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 of variables reflects 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 relates to differences in soil texture and soil fertility as indicated by manganese content and carbon-to-nitrogen (C:N) ratios of Ah and Ae hori-

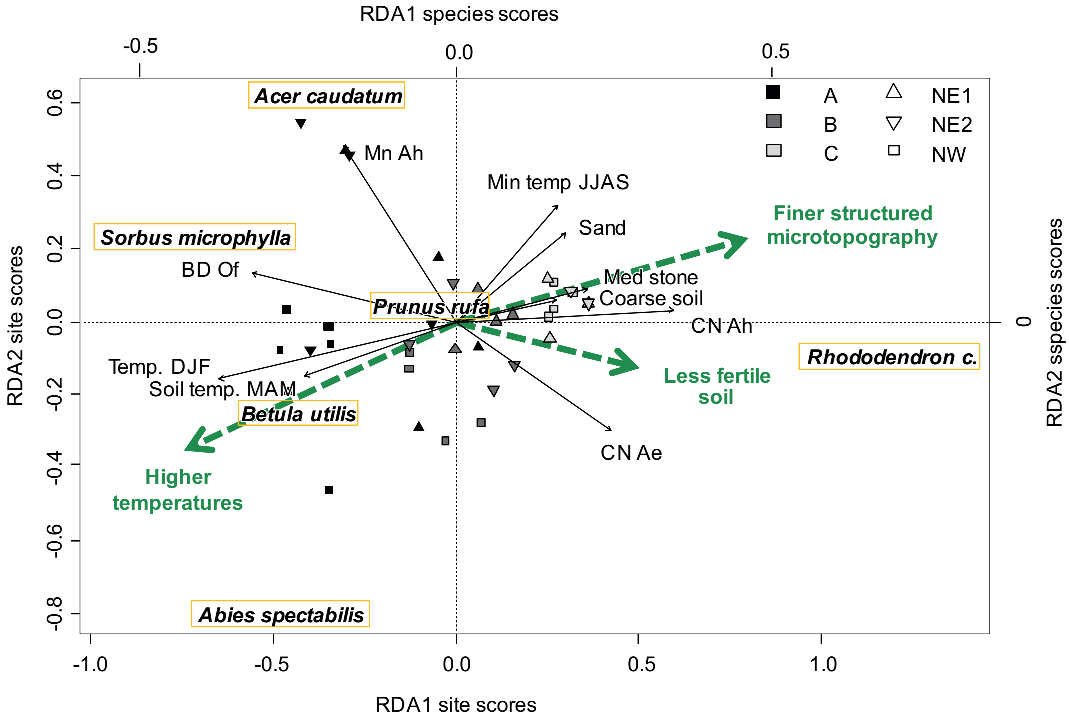

Fig. 4: Ordination diagram of RDA analysis for adult tree density: Vector directions show relation to environmental variables, vector lengths show their importance (for explanation of abbreviations and values see Table 1). Only the most important environmental variables with a biplot score (axis one, 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.

zons. Despite the strong gradient in the ordination, there were no significant disparities in manganese content between the elevational zones. However, the C:N ratios of elevational zones A (closed forest) and C (krummholz belt) were significantly different. 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, which 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 (Schwab et al. 2017).

3.2.2 Recruits

Fourteen selected environmental variables explained a total of 66 % of the variation in juvenile tree species density (cf. Table 1 for all selected variables). 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) (Fig. 5). The groups were separated from each other along the first RDA axis. Compared to the adult tree ordination (Fig. 5), 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 (Schwab et al. 2017).

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

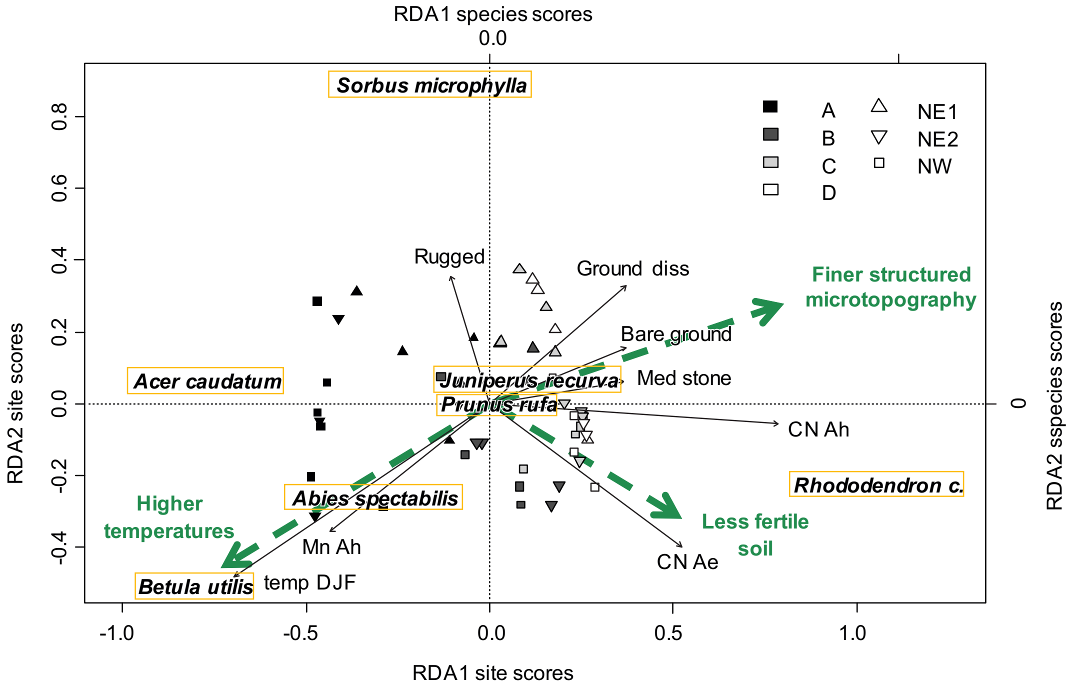

Fig. 5: Ordination diagram of RDA analysis for juvenile tree species density: Vector directions show relation to environmental variables, vector lengths show their importance (for explanation of abbreviations and values see Table 1). Only the most important environmental variables with a biplot score (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.

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 within-plot microrelief 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 (Schwab et al. 2017).

3.2.3 Variance partitioning results

By means of variation partitioning, the explained variability was separated into amounts which were accounted for exclusively by soil, 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 soil 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 %; Fig. 6a), respectively. The analyses revealed that 25 % of the shared variation of adult tree density was explained by soil variables, climate variables or both (Fig. 6a).

As in adult tree density, the soil 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 %; Fig. 6b), 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. Fig. 6). Although topography was of minor importance for adult trees, its share in accounting for the total variation of juvenile density is substantial (Schwab et al. 2017).

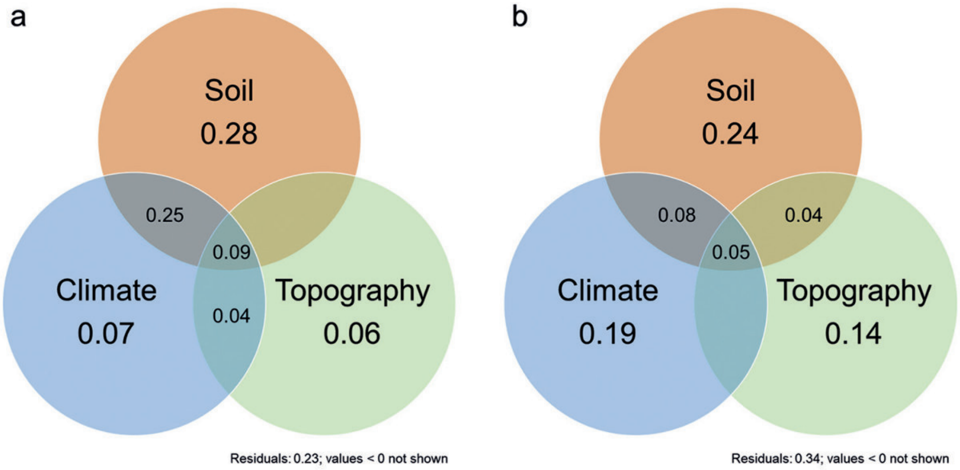

Fig. 6: Variation partitioning of (a) adult tree density using the matrices of soil variables, climate variables and topographic variables and (b) juvenile density using the matrices of soil variables, climate variables and topographic variables. The numbers indicate the percentage of total explained variability, explained exclusively or jointly by the variable matrices.

3.3 Tree growth-climate relationships

The collection and subsequent processing of TRW measurements yielded a chronology that represents the radial growth of *Abies spectablilis* back to 1748 (Fig. 7). The results of the analyses of *Abies spectabilis* tree growth-climate relationships give evidence of 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 (Fig. 8). Previously, the dendroclimatic signal was weaker, which predominantly reflected a positive relationship between tree growth and summer temperature (Fig. 9) (Schwab et al. 2018).

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) (Fig. 8). 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

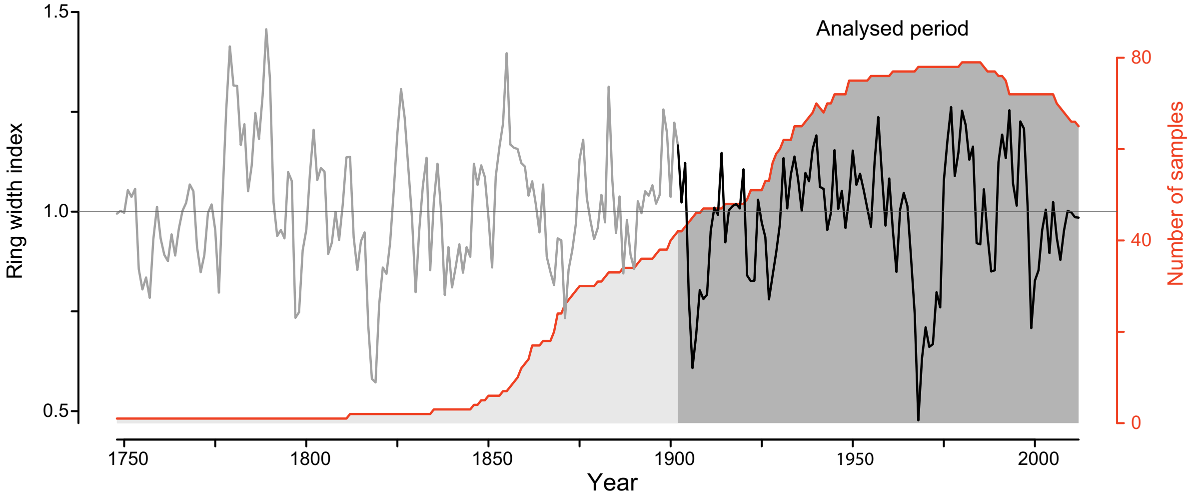

Fig. 7: Tree-ring width standard chronology (black curve) and sample depth (red curve); darker section represents the part of the chronology that was used for tree growth-climate analyses.

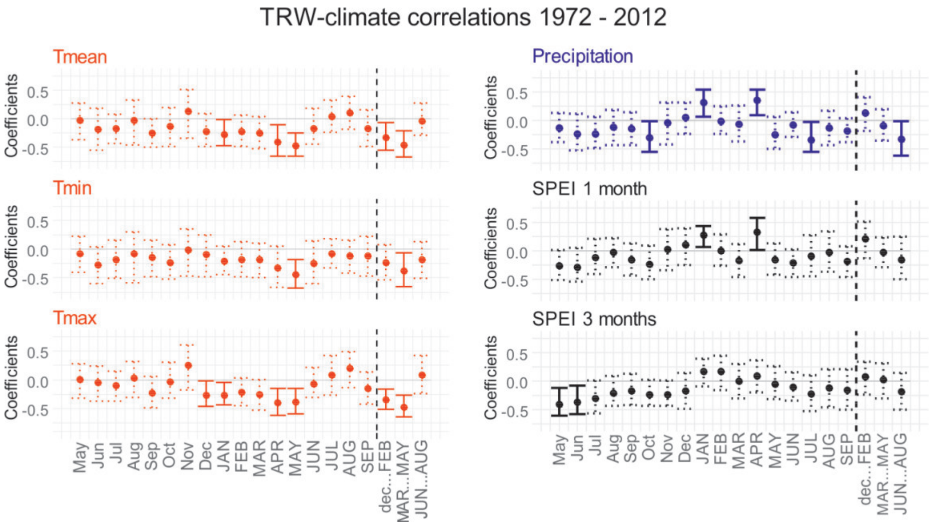

Fig. 8: Static correlations (1972–2012) of the TRW chronology with temperature, precipitation and drought indices (SPEI) for current and previous year's months and current year seasons; solid bars indicate significant correlations ($p < 0.05$).

(Fig. 8). Significantly positive correlations of TRW to one-month SPEI variables (Fig. 8) emphasise pre-monsoon moisture sensitivity, which is in line with the relations of TRW to temperature and precipitation (Schwab et al. 2018).

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. Fig. 9). In summary, both TRW-temperature and TRW-precipitation moving windows exhibit a fragmented pattern of significant tree growth-climate relationships with long insignificant phases (Schwab et al. 2018).

4 Discussion

4.1 Elevational patterns of tree species distributions and regeneration

In general, the tree species composition and elevational position of the Rolwaling Himal treeline ecotone coincides with previous findings for north-facing slopes in central and east Nepal (Miehe 1984; Schickhoff 2005; Miehe et al. 2015). Changes in tree species composition along the elevational gradient are reflected also in several phytosociological communities of the study slopes that were differentiated in detail by Bürzle et al. (2017).

Species-specific and age-specific transition patterns, i.e. varying degrees of abruptness of structural parameters such as diameter at breast height, height and densities, occurred across the treeline ecotone, which resulted in a complex stand structure (cf. Schwab et al. 2016). High standard deviations from mean values of growth and density variables indicated heterogeneous patterns, which differed according to slope, species and elevational zone. *Sorbus microphylla* occurred with high continuity, and its density-diameter distribution indicates an established population in the krummholz belt (zone C), which co-exists alongside the *Rhododendron campanulatum* population. The transition from the uppermost part of the subalpine forest (zone B) to the krummholz belt (zone C) is characterized by the most abrupt change in *Abies spectabilis*, *Betula utilis* and *Sorbus microphylla* tree densities along the elevational gradient (Fig. 3). This abrupt change in species composition coincided with the most abrupt changes in annual, winter and spring mean soil temperature at that transition. Abrupt microenvironmental changes have been associated with abrupt treelines of the southern hemisphere (Harsch and Bader 2011; Cieraad and McGlone 2014). Actually, the abruptness pattern of the Rolwaling Himal treeline at the transition from tall-growing trees to krummholz resembles that of typically abrupt treeline forms to some extent. The latter, however, lack a krummholz belt.

The results of our regeneration studies yielded reverse J-shaped density-diameter distributions and indicate intense, sustainable regeneration and, thus, a considerable potential for upward migrations.

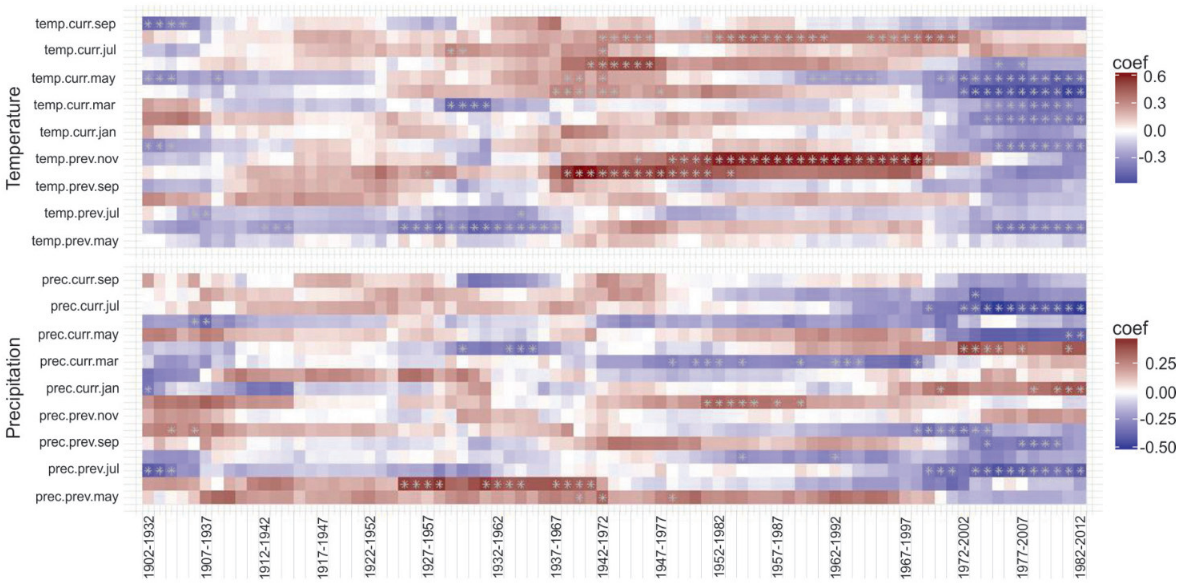

Fig. 9: Moving window correlations of the TRW chronology with mean temperatures and precipitation sums: 31-year windows were shifted in one-year steps throughout the entire period of climate data availability (1901 – 2012); periods with asterisks indicate significant ($p < 0.05$) correlations.

Results of recruit height distributions and regeneration indices (Schwab et al. 2016) support this finding and show that *Abies spectabilis* and *Betula utilis* have the potential to become established (beyond seedling stage) within the krummholz belt and above. Established recruit populations of *Rhododendron campanulatum* and *Sorbus microphylla* in the alpine dwarf shrub heath indicate their potential to sprout and survive in the upper treeline ecotone at least their early life stages. 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; Rana et al. 2016; Bürzle et al. 2018). However, results are hardly comparable since most of these studies were conducted at anthropogenic treelines, which have been depressed and modified by long-lasting human impact.

4.2 Population density-environment relationships

The results support that species-specific variation in adult and juvenile stand density along the treeline ecotone depends, to varying extents, on soil, 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 soil pH limits nutrient availability across the ecotone. Increasing foliar C:N and C:P ratios with elevation suggest decreasing nutrient availability at more elevated sites, i.e. zones C and D (Müller et al. 2017). Low temperature and poor nutrient availability characterise in particular the ecological niche that *Rhododendron campanulatum* occupies. Low temperature decelerates decomposition and reduces nutrient availability in this niche. In addition, *Rhododendron* litter diminishes nutrient availability as well (see below). Plant physiological characteristics associated with evergreenness such as nutrient storage and earlier photosynthetic activity might increase *Rhododendron*'s competitive strength under cool and nutrient poor conditions in the krummholz belt. The dense, evergreen *Rhododendron* canopy reduces insulation in comparison to the mixed forest below and results in the abrupt soil temperature decrease at the transition from closed mixed forest to *Rhododendron campanulatum* krummholz belt. Variation partitioning indicated that apart from thermal limitations soil variables, and nutrient variables in particular, significantly contributed to the total explained variation of adult tree density.

Juvenile population density shows a stronger dependence on the climatic variable of temperature in comparison to adults. In addition, differences in microrelief, 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). Likewise, not merely soil temperature, but also nitrogen supply and availability, and soil moisture differentiated the species composition of phytosociological communities throughout the Rolwaling Himal treeline ecotone (Bürzle et al. 2017). In addition, Bürzle et al. (2018) found species-specific microhabitat preferences for the establishment of seedlings and reported that *Abies spectabilis* seedlings are more associated with a ground cover of litter, whilst *Betula utilis* and *Rhododendron campanulatum* establish preferably on bryophyte mats. Further studies of, inter alia, snowmelt timing, seedling survival facilitating microsite parameters and seedling ecophysiology, focusing on youngest life stages, are badly needed to increase the understanding of response processes at the study site and in treeline ecotones in general (Bader et al. 2018; Brodersen et al. 2019). Spatial pattern analyses of the population densities revealed that environmental variables could not account for some of the variance of spatial patterns (Schwab et al. 2017). This finding as well as general model-based results (Dullinger et al. 2004; Holtmeier and Broll 2010; Nathan et al. 2011; Martínez et al. 2012; Johnson et al. 2017) suggest that species-specific migration potentials, seed-dispersal strategies and ecological drift might contribute to this yet-unexplained variance. In summary, the role of temperature for treeline tree population density and species distributions has to be relativized in favour of topographic and nutrient budget related factors in accordance with the results of Weiss et al. (2015), Müller et al. (2016a; 2016b), Lett and Dorrepaal (2018) and others.

4.3 Tree growth-climate relationships

4.3.1 Moisture deficit during recent decades

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. It indicates a negative relation of growth to temperature-enhanced evapotranspiration. 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. 2017; 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; Gaire et al. 2019). As in our study, the tree growth-climate correlation coefficient values were mostly in a similar, rather low range. To conclude, 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, our results largely match the findings of earlier studies on sites in Nepal and other Himalayan regions. However, certain published results, including those from study sites not far from our site, showed disparate relations of tree growth to temperatures and precipitation in the winter prior to the growing season. The general east-west moisture gradient in the Himalaya and Nepal (Anders et al. 2006; Talchabhadel et al. 2019) 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. 2017; Chhetri and Cairns 2016; Kharal et al. 2017; Rayback et al. 2017; Shrestha et al. 2017; Singh et al. 2018), it can be assumed that deviations in results were due to local variations in the heterogeneous environment. Sparse (and rather short) records of climate data from high elevation sites or derived gridded data might not capture these variations. 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.

4.3.2 Changing long-term tree growth-climate relationships

The static correlation of the whole CRU data period from 1901 onwards yields 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. Similar 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 (cf. Schwab et al. 2018). The period of stable climate conditions (mid-20th century) 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. In contrast, moisture availability did not stress *Abies spectabilis* at a treeline in western Himalaya, most likely in consequence of distinctly higher precipitation and soil moisture in comparison to our site, contrary to the general east-west moisture gradient (cf. Gerlitz et al. 2016; Müller et al 2016; Tewari et al. 2018). Our 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; Gaire et al. 2020), with *Abies spectabilis* trees exhibiting growth plasticity in adaptation to 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 adaptation affects the competitiveness of *Abies spectabilis* and, in a wider sense, also the sensitivity and responsiveness of the Rolwaling Himal treeline to climate change.

4.4 Control of upslope migration by feedback processes

The responsiveness of the Rolwaling Himal treeline to climate warming is currently rather low in terms of a treeline shift (Fig. 10), as assumed for near-natural Himalayan treelines and krummholz treelines in general (Harsch and Bader 2011; Chhetri and Cairns 2015; Schickhoff et al. 2016a; Chhetri and Cairns 2018; Pandey et al. 2018). Aforementioned results contribute to a simplified system perspective to estimate the upward migration potential of tree species qualitatively and to advance towards an approach to model the complex system. Elevational patterns of tree species distributions and regeneration, population density-environment relationships and tree growth-climate correlations point to a *Rhododendron campanulatum* based positive feedback process, which contributes to the currently low responsiveness of the treeline position to climate change.

The system approach and the theory of multiple stable ecosystem states include feedback loops with positive and negative couplings resulting in dynamic alternative stable states. Each negative coupling in a feedback loop reverses the effect of a positive coupling. Thus, the effect an element exerts on itself will be positive in any loop with an even number of negative couplings (Thomas 1981; Thomas and D' Ari 1990; Kump et al. 2004). An external environmental forcing factor such as soil temperature can push the positive feedback system to transient, so-called 'unstable' equilibrium states. Such an unstable equilibrium state separates two or multiple stable states (also called alternative stable states). The system occupies briefly an unstable equilibrium state before either returning to the previous stable state or to an alternative stable state. In opposite to gradual or abrupt phase shifts with two opposing, exclusive stable states, the conditions for alternative stable states are not mutually exclusive. They can exist next to each other at different spatial locations of the system and all alternative states are possible within a range of environmental conditions. In summary, positive feedback loops result in differential regulation and can permit the choice between two or more stable steady states (Thomas and D' Ari 1990; Scheffer et al. 2001; Kump et al. 2004; Schröder et al. 2005; Kim and Lee 2015; Moffett et al. 2015). The outline of the potential positive feedback processes that maintain the competitiveness of *Rhododendron campanulatum* contains an even number of negative couplings (two), that result in a positive feedback loop (Fig. 11). Thus, a forcing such as increasing soil temperature

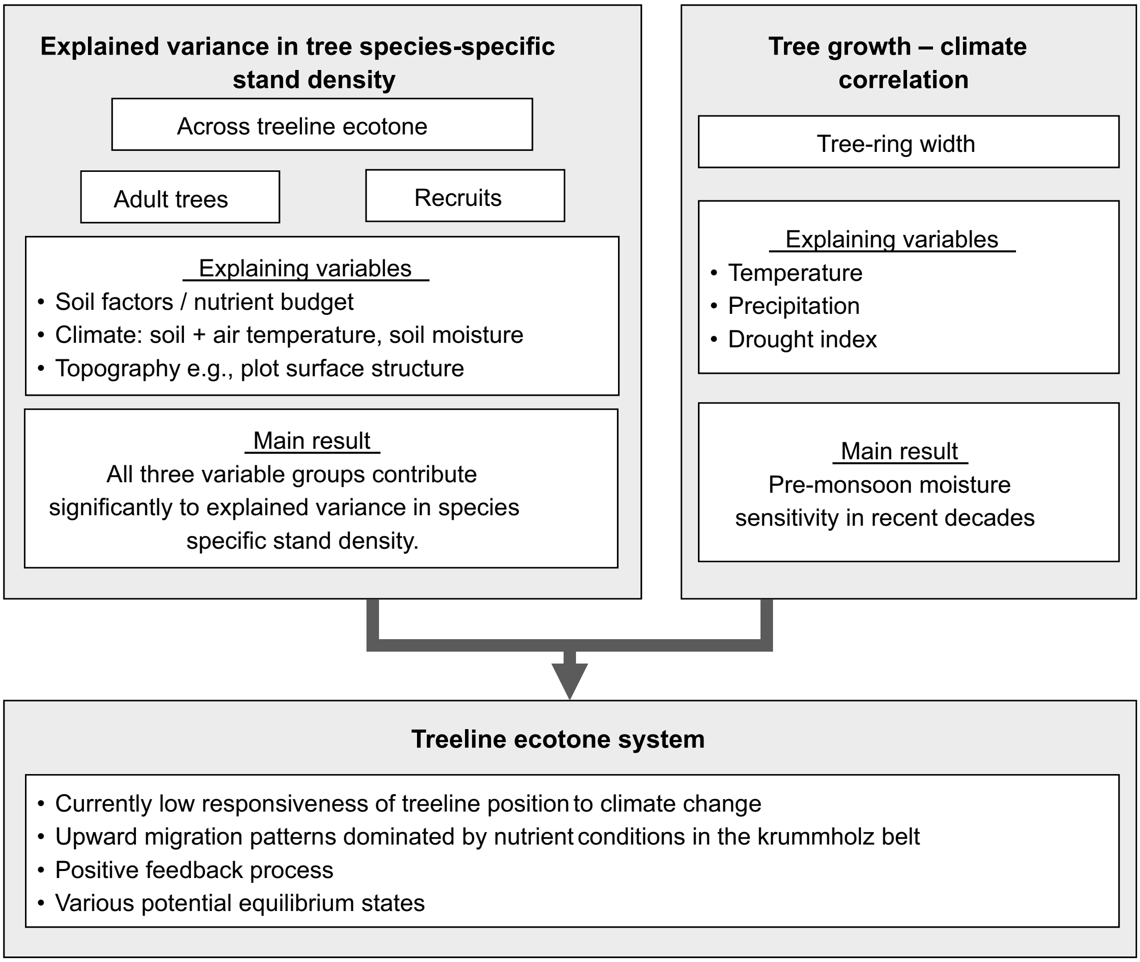

Fig. 10: Analyses of species-specific population densities and tree growth-climate correlations show distinct impacts of thermal and non-thermal factors on upward migration patterns of subalpine tree species.

above a certain threshold (dashed coupling in Fig. 11) might carry the system to a different stable equilibrium state (Kump et al. 2004). Positive and negative external coupling variants are conceivable and both are described below.

Feedback processes most likely consolidate the *Rhododendron* krummholz belt by maintaining *Rhododendron campanulatum*'s high competitiveness compared to *Abies spectabilis* and *Betula utilis* (Fig. 11), as long as external forcing is absent or not crossing a certain threshold. In consequence, the krummholz belt restricts the upward directed migration potential of these tree species. Feedback processes result, inter alia, 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 (Fig. 11) (Northup et al. 1995; DeLuca et al. 2002), thus reducing 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, which grow in soils that are poor in most essential elements and consequently unsuitable to other species; in fact, they are very competitive under poor soil conditions (Cox 1990; Ristvey et al. 2007). The high root-to-shoot ratio of *Rhododendron campanulatum* and its evergreen nature result in nutrient storage and sources as well as in increased photosynthetic capacity in spring (Garkoti and Singh 1994; Garkoti and Singh 1995; Eckstein et al. 1999). These traits enhance the competitive advantages along with some supposed allelopathic effects

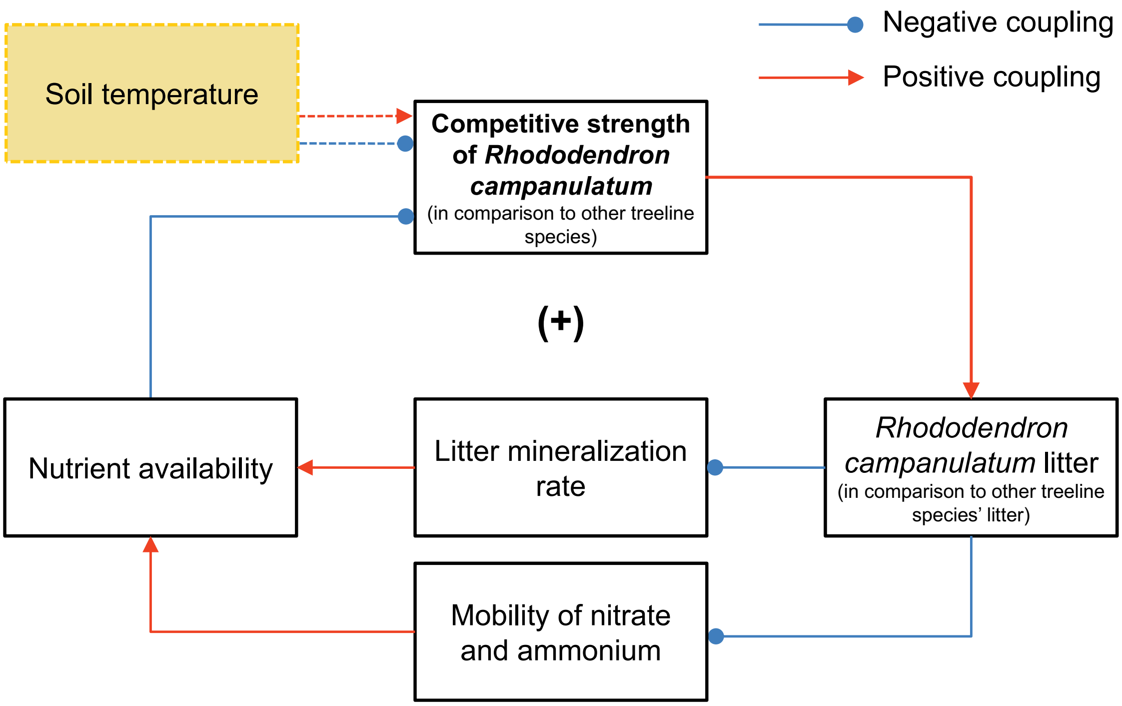

Fig. 11: Potential positive feedback processes that maintain the competitiveness of *Rhododendron campanulatum*

of polyphenol-rich *Rhododendron* litter (Chou et al. 2010; Bürzle et al. 2018). As a consequence of such positive feedback processes, the treeline is not necessarily in equilibrium with climatic conditions. The species dynamics depend more on ecotone internal interaction than on external forcing i.e., the positive feedback buffers the ecotone to some extent against external changes of e.g., climate (Bader et al. 2008). The specific habitat conditions within the krummholz belt, created and maintained by *Rhododendron campanulatum* thickets, constrain the potential establishment of *Abies spectabilis* and *Betula utilis* seedlings, even under a warming climate, and the subsequent shift of the treeline.

In consequence of an external forcing which is not buffered such as distinctly increasing soil temperature and longer growing periods, at least two alternative stable states are possible. The forcing might increase assimilation rates of all species. Thus, *Rhododendron campanulatum* might keep its high competitive strength in the krummholz belt. Its competitive strength might increase in the alpine dwarf shrub heath above the krummholz belt, facilitating *Rhododendron campanulatum*'s establishment and growth in the current alpine dwarf shrub heath ("the more temperature the more *Rhododendron*"; cf. Fig. 11, positive soil temperature coupling). This alternative stable state would result in an upward expansion of the krummholz belt, becoming wider in comparison to the situation before forcing, without a distinct change of treeline position (Supplement I: F ii).

Enhanced recruitment and growth of subalpine tree species to tree size in the krummholz belt, i.e. an upward shift of the treeline, is only to be expected once the competitiveness of *Rhododendron campanulatum* is decreasing and the current krummholz belt will disintegrate. This alternative state might ensue after a substantial temperature increase beyond the present level. After crossing a certain threshold, temperature forcing might lead to reduced competitive strength of *Rhododendron campanulatum* at present day krummholz belt elevation, while the competitiveness of subalpine tree species might reinforce ("the more temperature the less *Rhododendron*"; cf. Fig. 11, negative soil temperature coupling). In this situation, the krummholz belt would not remain at its present position but shift upwards together with the treeline. Nevertheless, the spring moisture sensitivity of tree growth as shown by tree growth-climate correlations and observations in the field (Supplement I: F iii, iv) will remain a crucial factor, affecting the forcing's impact and the likelihood for this scenario in dependence of future pre-monsoon precipitation and soil moisture. Similarily, Barros et al. (2017) showed that drought constrains subalpine forest expansion in the European Alps. The scenario of a positive temperature coupling and a consequent expansion of the krummholz belt into the alpine dwarf shrub heath cannot be excluded in near future.

The degree of stability of states cannot be determined quantitatively by inspecting the heavily simplified feedback diagram. Observations from the field provide only hints of alternative stable states. The system approach would be improved by adding more internal system feedbacks and potential external forcing factors. To obtain definite conclusions, experiment analyses and long-term field data are needed, the feedback loops need to be evaluated mathematically and models are essential for a precise analysis (Scheffer and Carpenter 2003; Kump et al 2004; Schröder et al. 2005; Kim and Lee 2015). Nevertheless, the schematic synthesis of results might be a first step towards a model of the Rolwaling Himal treeline system and more precise predictions of future ecotone states similar to the ones of e.g., Bader et al. (2008) for a tropical and Wiegand et al. (2006) for a Mediterranean alpine treeline.

In summary, the dense krummholz belt effectively controls the upslope migration of subalpine forest tree species *Abies spectabilis* and *Betula utilis*. Gradual changes in climate will not entail gradual linear changes in vegetation. Such non-linearity leads to delays in response to climate change, and to potential abrupt switches once a certain threshold e.g., of soil temperature, is crossed. Feedback processes obviously control spatial patterns and temporal dynamics in many treeline environments (Scheffer et al. 2001; Kim and Lee 2015). In Rolwaling, feedback processes resulted in the establishment of a dense krummholz belt as an alternative stable state, not necessarily in equilibrium with climatic conditions and to some extent decoupled from the regional climate change input.

Above the krummholz belt, the dense and highly competitive alpine dwarf shrub heath vegetation might hinder tree species establishment, even though regeneration is generally intense, and mean annual temperatures in the upper treeline ecotone are comparatively high (Müller et al. 2016a; Müller et al. 2016b; Schickhoff et al. 2016a). 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 comparison to *Abies* and *Betula*, persistent cold, nutrient-poor conditions will probably 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 addition, allelopathic effects of *Rhododendron campanulatum* may prevent juvenile individuals of other tree species from growing to mature, fruiting trees within or above the current krummholz belt, and favour monospecific *Rhododendron* stands (Bürzle et al. 2018). Since the *Rhododendron campanulatum* population of the krummholz belt is firmly established and feedback mechanisms maintain its predominance, this thicket likely constitutes an insurmountable, bottleneck-like barrier for the establishment of *Betula utilis* and *Abies spectabilis* seedlings and saplings even under warmer conditions.

Accordingly, the numbers of *Abies spectabilis* and *Betula utilis* individuals found in the krummholz belt are very low. Their distribution is related to microtopographic features similar to observed establishment patterns in Taiwanese *Abies* and Nepalese *Betula* treelines (Greenwood et al. 2015; Chhetri and Cairns 2018). 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* and *Betula* individuals in and above the krummholz belt illustrate a potential to become established and reach tree dimensions. We assessed high recruit numbers and a considerable upslope migration potential for the shrub or small tree *Sorbus microphylla*, an important component of both the krummholz belt and the dwarf shrub heath. Whether the *Rhododendron campanulatum* belt will shift upslope under more favourable climatic conditions is a matter of debate. Rana et al. (2017) found an upward migration tendency of *Rhododendron campanulatum* at a treeline ecotone in central Nepal.

5 Conclusions

The synthesis of results of the tree species composition analyses along the treeline ecotone, of its environmental drivers and of the tree growth-climate responses facilitates a comprehensive view on the investigated treeline. Key findings show that the elevational position of the Rolwaling Himal treeline has responded to date only slightly to climate warming as supposed for krummholz treelines in general: (i) Treeline position, spatial patterns and dynamics depend on a multitude of environmental factors and ecological interactions at landscape and local scales. (ii) The intense regeneration indicates a potential for upward migration of species. High levels of recruitment within the near-natural treeline ecotone indicate climate-warming-induced stand densification.

(iii) The tree growth-climate relations have changed most likely due to intensified climate warming in recent decades. (iv) The treeline will most probably remain stable at its present position in the coming decades due to the feedback-driven persistence of the *Rhododendron campanulatum* krummholz belt. Soil (nutrient availability) and microtopographic factors influence tree species-environment relationships across the ecotone to a great extent, finally affecting the elevational position of the treeline to a higher degree than current changes of climate, i.e. higher temperatures.

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. Recruits of *Betula utilis* and *Abies spectabilis* illustrate that feedback mechanisms do not completely restrict seed-based regeneration beyond the krummholz belt. However, despite the warming trend, relative low temperatures and low nutrient availability will continue to offer competitive advantages for *Rhododendron campanulatum* and, to some extent, *Sorbus microphylla*. Thus, an upward expansion of the krummholz belt into the alpine dwarf shrub heath 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*. It remains unclear how this limitation affects the 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 krummholz treeline's usefulness as indicator for climate change into perspective.

We assume that the results of this study are largely transferable 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. However, given the ecological complexity of Himalayan treeline ecotones, further detailed studies are needed to better 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. Acquiring information about tree growth-climate relationships for other tree species than *Abies spectabilis* are highly needed. In general, standardised sampling and analytical protocols could improve the comparability of ecological treeline studies at regional and global scales.

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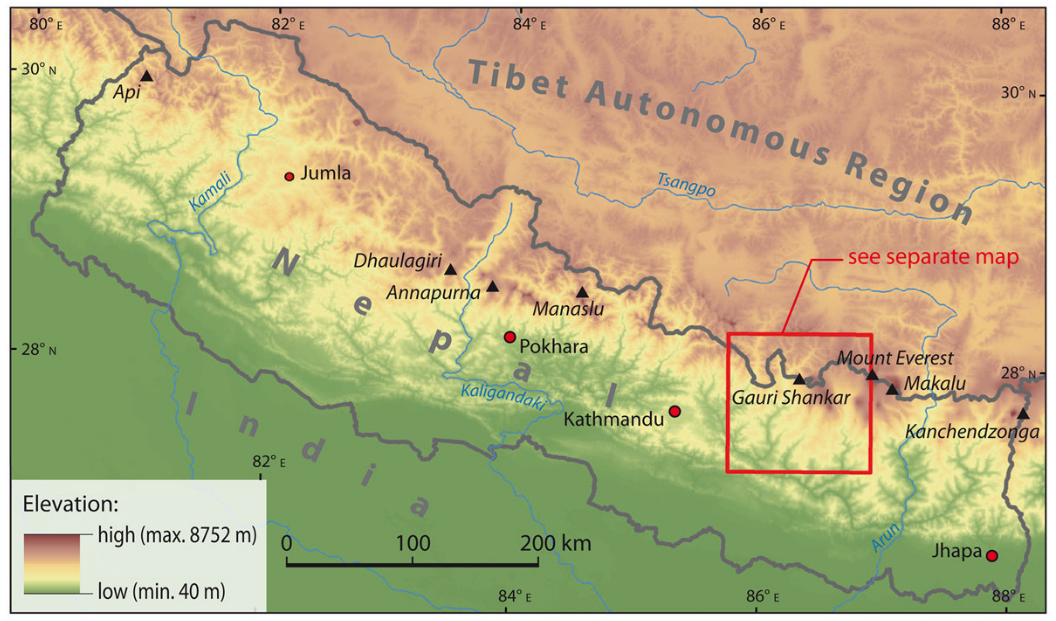
Appendix

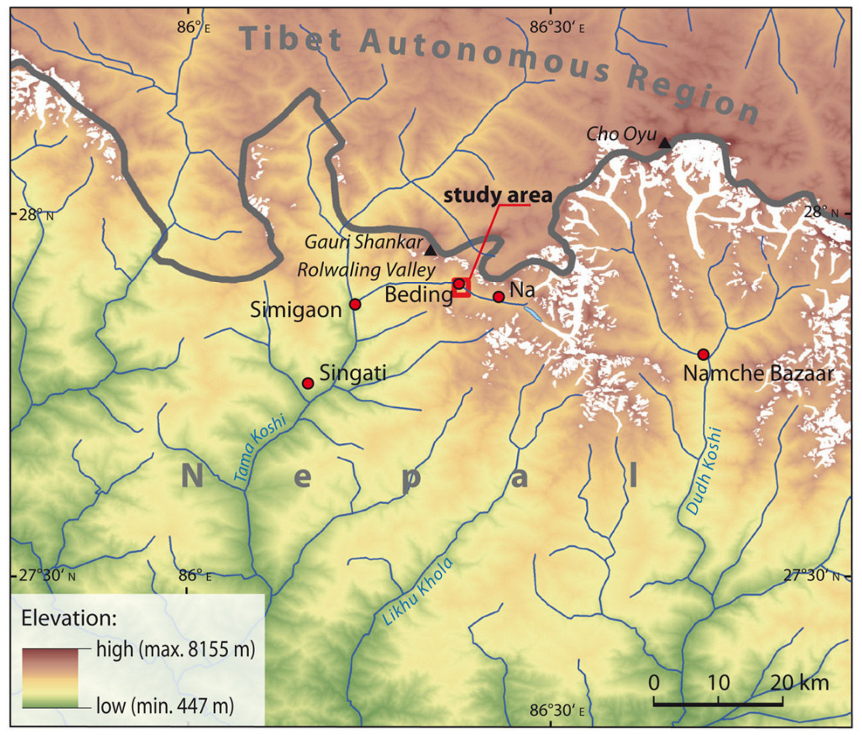
Appendix I : Uncorrelated variables contained in final topographic, soil and climatic explanatory variable matrices

Topography	Soil (Of, Ah, Ae: horizons)	Climate
Aspect dissimilarity	Aluminium concentration (Ah, Ae)	Mean air temperature of DJF season
Bare ground cover	Aluminium stock (Of, Ah)	
Coarse soil cover	Bulk density (Of, Ah)	Minimum air temperature of JJAS season
Curvature dissimilarity	Calcium concentration (Ah, Ae)	
Eastness	Carbon / nitrogen concentration ratio (C/N) (Ah, Ae)	Minimum air temperatures of MAM season
Fine soil cover		
Ground cover dissimilarity	Carbon / nitrogen stock ratio (C/N) (Ah)	Soil moisture of DJF season
Large rock cover	Hydrogen concentration (Ae)	Soil moisture of JJAS season
Large stone cover	Layer thickness (Ae)	Soil moisture of MAM season
Litter cover	Manganese concentration (Ah, Ae)	Soil moisture of ON season
Medium rock cover	Manganese stock (Of, Ah)	Soil temperature of DJF season
Medium stone cover	Mineralised nitrogen concentration (Ae)	
Microrelief and ground cover dissimilarity	pH (H2O) (Ae)	Soil temperature of MAM season
	pH (KCl) (Ae)	
Microrelief dissimilarity	Potassium concentration (Ah)	
Presence of plane rocks	Potassium stock (Of)	
Slope	Sand content (Ae)	
Small rock cover	Sodium concentration (Ah, Ae)	
Surface structure	Sodium stock (Of)	
Surface structure dissimilarity	Total nitrogen (Ah)	
	Total nitrogen concentration (Ae)	
	Total nitrogen stock (Of)	

Insights into the investigated krummholz treeline ecotone

A – Location of study area in east-central Nepal





▲ Mountain peaks

● Settlements

— Rivers

— National border

▨ Glaciers

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

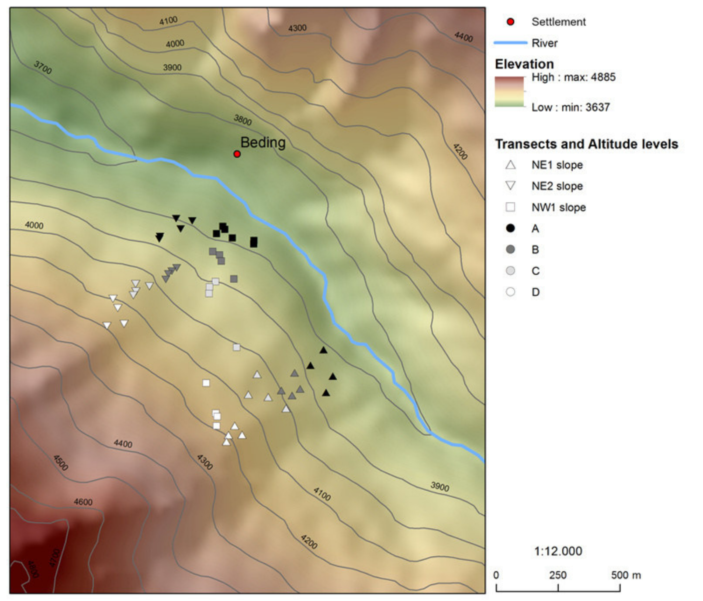
download.geofabrik.de/asia/nepal.html

urs.earthdata.nasa.gov/

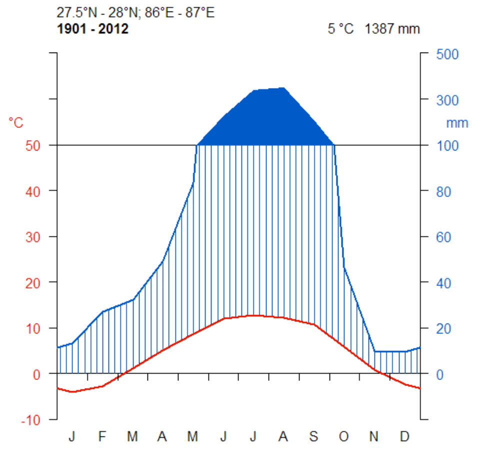
www.naturalearthdata.com

all sources accessed on 2016-03-09

B – Location of sampling plots across the treeline ecotone

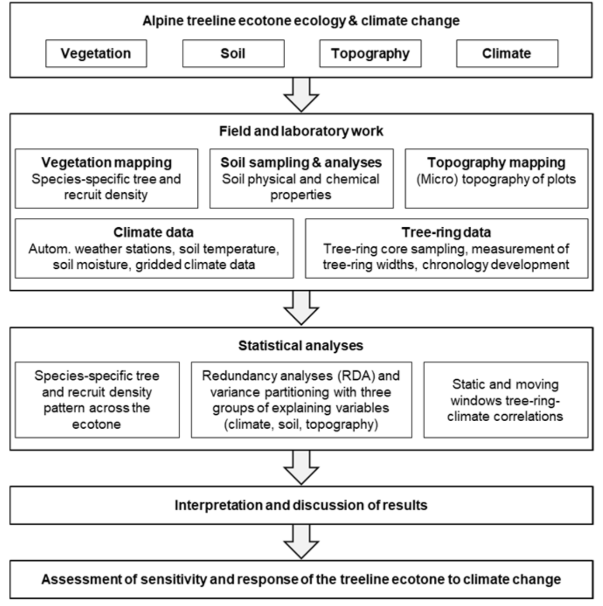


C – Climate of the study area



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 (diagram produced with R package climatol, GUIJARRO 2016)

D – Interdisciplinary approach: multi-faceted insights into the treeline ecotone



Alpine treeline ecotone ecology & climate change

Vegetation | Soil | Topography | Climate

Field and laboratory work

Vegetation mapping Species-specific tree and recruit density

Soil sampling & analyses Soil physical and chemical properties

Topography mapping (Micro) topography of plots

Climate data Autom. weather stations, soil temperature, soil moisture, gridded climate data

Tree-ring data Tree-ring core sampling, measurement of tree-ring widths, chronology development

Statistical analyses

Species-specific tree and recruit density pattern across the ecotone

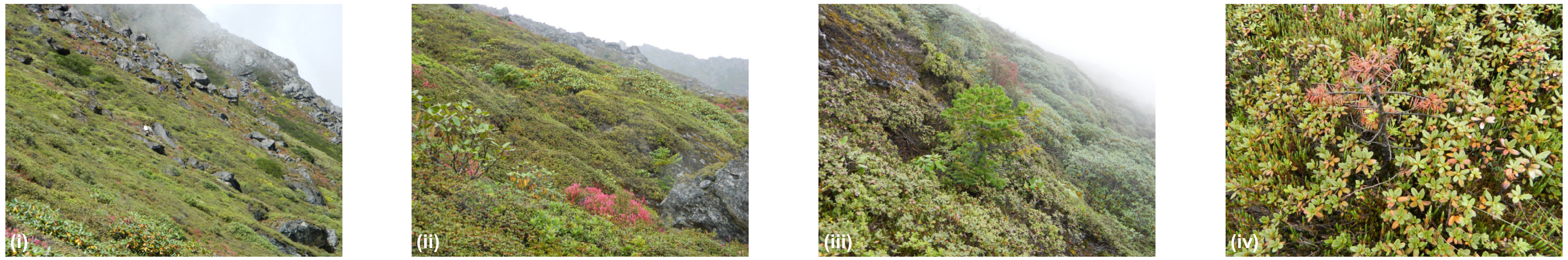
Redundancy analyses (RDA) and variance partitioning with three groups of explaining variables (climate, soil, topography)

Static and moving windows tree-ring-climate correlations

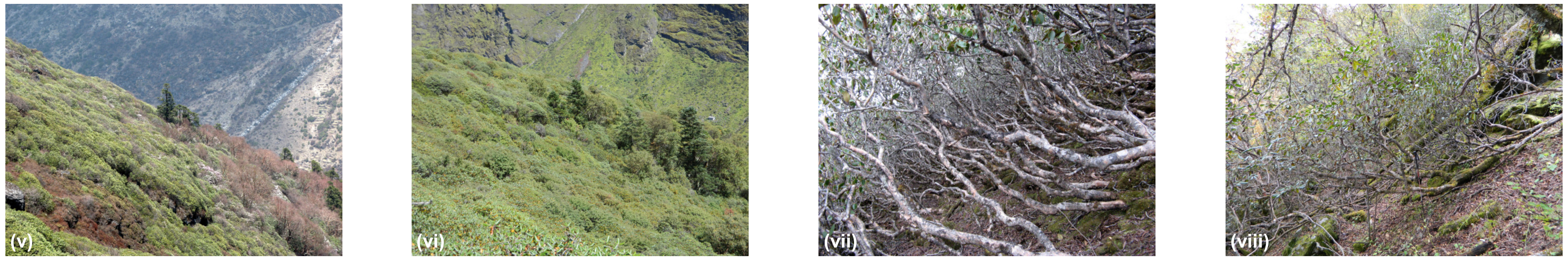
Interpretation and discussion of results

Assessment of sensitivity and response of the treeline ecotone to climate change

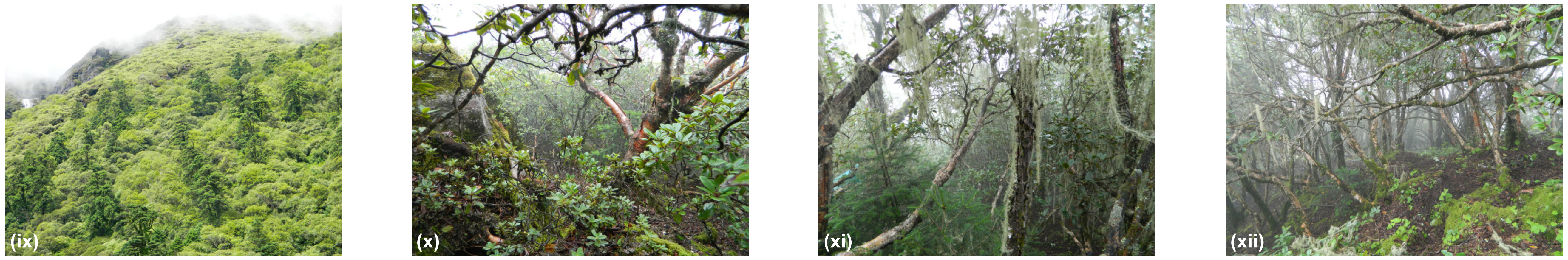
F – Tree species patterns across the treeline ecotone



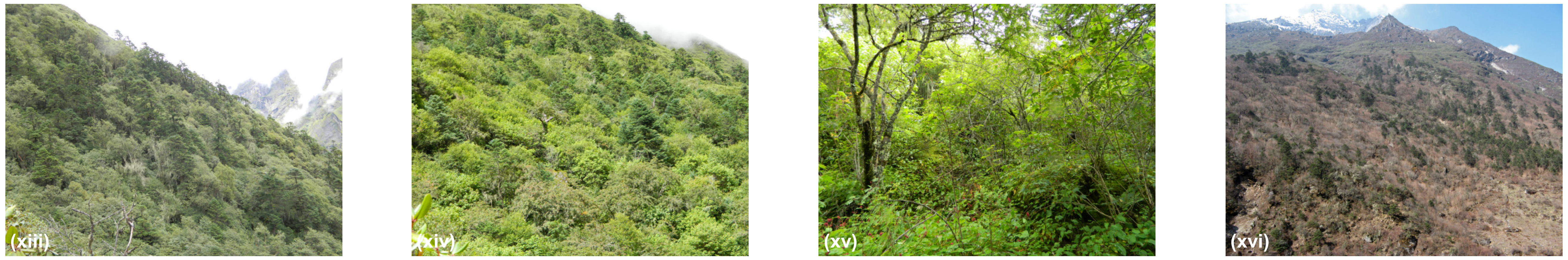
Zone D: Alpine dwarf shrub heath (i) with transition to krummholz belt (ii). Patches of *Rhododendron campanulatum* (ii) at this border show how the krummholz belt might migrate upward in future. Growth conditions for rare and stunted *Abies spectabilis* recruits (iii, iv) are unfavourable at this elevation.



Zone C: Uniform krummholz belt, heavily dominated by *Rhododendron campanulatum* (v, vi) and nearly impenetrable (vii, viii). Photos v and vi show the transition to the upper part of the subalpine forest (zone B) at the right half.

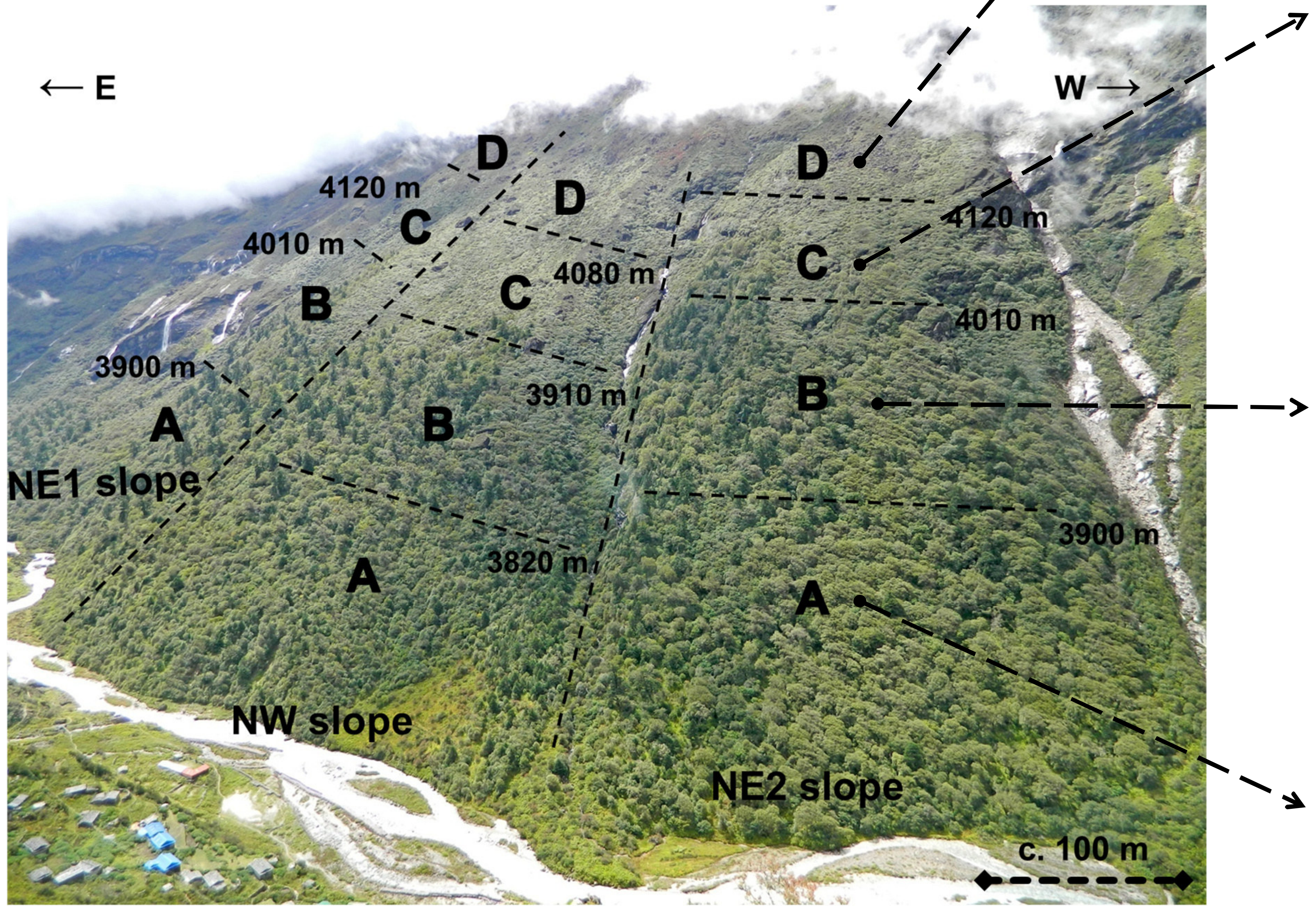


Zone B: Upper part of mixed subalpine forest (ix), characterised by a high percentage of upright growing *Rhododendron campanulatum* trees, mixed with other tree species such as *Abies spectabilis* and *Betula utilis* (x – xii). Beard lichens occur frequently in this part of the upper cloud forest (xi, xii).



Zone A: Lower part of the mixed subalpine forest with equal shares of *Abies spectabilis, Betula utilis, Sorbus microphylla* and *Acer caudatum* trees (xiii – xv). *Rhododendron campanulatum* occurs in relatively small numbers. Moisture deficit characterises spring across the ecotone at beginning of growing season. In consequence, the landscape appears brownish apart from evergreen *Abies* and *Rhododendron* (xvi).

E – Investigated slopes and vegetation zones



Stratification of the study area by elevation (A – D) and aspect (NE, NW); 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. The treeline is located at the border of zone B and C.