Ecology, syntaxonomy and recruitment of treeline ecotone vegetation in Rolwaling Himal, Nepal -

Vegetation dynamics in response to climate change

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Für Paula

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Summary

Mountains are characterized by a large diversity of plant species and plant communities over short horizontal and vertical distances, primarily corresponding to gradual changes of temperature. Specific zonations of vegetation types along elevational gradients are to be observed in mountains, with the most conspicuous change in mountain vegetation occurring at the alpine treeline ecotone, which represents the transition from closed forest to treeless alpine vegetation. Rapid climate warming at high elevations is predicted to trigger extensive vegetation dynamics within treeline ecotones, primary related to recruitment processes. Vegetation dynamics involve shifts in species distribution, community structure and treeline position. In the Himalayas, species richness as well as rates of climate change are among the highest on earth, yet studies addressing respective relationships are underrepresented in scientific research.

The studies compiled in this thesis investigated the phytosociology and ecology of alpine treeline ecotone vegetation in the Nepalese Himalayas and analysed tree seedling establishment of dominating tree species as a critical component of the dynamics of spatial treeline position. All three parts of this work contribute to assessing vegetation dynamics in alpine treeline ecotones under climate warming conditions. During extensive field research in a near-natural treeline ecotone of Rolwaling Valley in east-central Nepal, we collected data on floristic composition and environmental conditions along three elevational transects. The microhabitat characteristics of naturally germinated tree seedlings of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* were recorded along the altitudinal gradient from subalpine forests via treeline to alpine dwarf shrub heaths.

By applying ordination methods and cluster analysis, 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 the treeline. Above the 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: the species-poor *Pedicularis* cf. *microcalyx – Rhododendron anthopogon* community and the *Anaphalis royleana – Rhododendron anthopogon* community, which is characterised by higher species richness of herbs and grasses. Both communities were assigned to the class *Dasiphora arbuscula – Rhododendron anthopogon* dwarf shrub heaths. The species composition of identified communities is related to an elevational gradient of deteriorating growth conditions, reflecting an increasingly unfavourable constellation of soil temperature, soil moisture and nitrogen supply and availability.

Our research on seedling establishment emphasises the importance of safe sites for successful tree regeneration in mountain environments. We found species-specific microhabitat preferences for seedling establishment. While *Abies spectabilis* seedlings establish on ground that is covered with litter, *Betula utilis* and *Rhododendron campanulatum* seedlings primarily emerge on bryophyte mats. The microhabitat structure did not vary significantly in relation to different vegetation types encompassing the treeline ecotone. The majority of seedlings of all species grew close to at least one potentially protective element. Geomorphic elements and deadwood were the most important shelters for seedling establishment.

The identified critical drivers for community differentiation and for tree seedling establishment - particularly soil temperature, water and nitrogen supply - are directly or indirectly related to climatic conditions. Thus, we suggest distinct alterations to species distribution and treeline position in the Rolwaling treeline ecotone with climate warming. As growth conditions in high mountain ecosystems may substantially alter under contemporary climate change, the need for species-specific safe sites for tree recruitment to buffer potential extremes will likely increase.

This thesis provides novel findings on climate change-induced vegetation dynamics in Himalayan treeline ecotones. The results on seedling establishment serve to enhance the existing knowledge on the prerequisites for successful seedling establishment and spatial alterations of treeline position. The classification of Rolwaling treeline ecotone vegetation also provides a suitable baseline for further phytosociological investigations and for the initiation of a long-term research approach to monitor the effects of climate warming on Himalayan mountain vegetation.

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

Study 1: 'Phytosociology and ecology of treeline ecotone vegetation in Rolwaling Himal, Nepal'
Authors: Birgit Bürzle, Udo Schickhoff, Niels Schwab, Jens Oldeland, Michael Müller, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten and Wolf Bernhard Dickoré
Published in 2017 in *Phytocoenologia* 47:197–220 doi: 10.1127/phyto/2017/0130

Study 2: ‘Seedling recruitment and facilitation dependence on safe site characteristics in a Himalayan treeline ecotone’
Authors: Birgit Bürzle, Udo Schickhoff, Niels Schwab, Lina Marie Wernicke, Yanina Katharina Müller, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten and Jens Oldeland
Published in 2017 in *Plant Ecology* 219:115–132 doi: 10.1007/s11258-017-0782-2

I contributed as a co-author to six additional studies that are closely linked to the objective of this thesis and thereby enhance our understanding on climate change-induced vegetation dynamics in the Rolwaling treeline ecotone. Appendix III includes abstracts of these studies.

Zusammenfassung

Gebirge zeichnen sich durch eine hohe Vielfalt an Pflanzenarten und Pflanzengesellschaften auf kleinstem Raum aus, welche insbesondere auf den höhenabhängigen Temperaturgradienten zurückzuführen ist. Die Gebirgsvegetation ist gekennzeichnet durch eine charakteristische Abfolge von Vegetationstypen entlang des Höhengradienten. Am deutlichsten wird dieser Vegetationswechsel im alpinen Waldgrenzökoton. Dieses stellt den Übergang vom geschlossenen Wald hin zur baumfreien, alpinen Vegetation dar. Aufgrund einer rasanten Klimaerwärmung in den Höhenlagen von Gebirgen sind weitreichende Vegetationsveränderungen innerhalb des Ökotons, welche primär auf Verjüngungsprozessen basieren, zu erwarten. Die ablaufende Vegetationsdynamik zeigt sich in der Veränderung des Verbreitungsareals von Arten und des strukturellen Aufbaus von Pflanzengesellschaften, sowie in der Verschiebung der Waldgrenze. Der Himalaya gehört zu den Hotspots der globalen Artenvielfalt und ist gleichzeitig überdurchschnittlich von klimatischen Veränderungen betroffen. Dennoch ist die Region in der wissenschaftlichen Forschungslandschaft unterrepräsentiert.

Diese Forschungsarbeit untersucht die Pflanzensoziologie und die Ökologie der alpinen Waldgrenzvegetation in der nepalesischen Himalaya-Region und analysiert darüber hinaus die Keimlingsetablierung der vorherrschenden Baumarten als bedeutenden Faktor der Waldgrenzdynamik. Alle drei Teile dieser Arbeit tragen zur Erforschung der klimawandelbedingten Vegetationsdynamik in alpinen Waldgrenzökotonen bei. Basierend auf umfangreichen Feldforschungen in einem naturnahen Waldgrenzökoton im Rolwaling-Tal im östlichen Zentralnepal, haben wir Datenmaterial zur Vegetationszusammensetzung und den Standortbedingungen entlang dreier höhenabhängiger Transekte erhoben. Die Erfassung der Mikrohabitateigenschaften des natürlich gekeimten Baumjungwuchses der Arten *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* erfolgte entlang des Höhengradienten vom subalpinen Wald, über die Waldgrenze bis hin zur alpinen Zwergstrauchheide.

Durch die Anwendung von Ordinationsmethoden und Clusteranalysen, konnten wir fünf Pflanzengesellschaften ermitteln und diese zwei syntaxonomischen Klassen zuordnen: Die *Synotis alata – Abies spectabilis* Gesellschaft und die *Ribes glaciale – Abies spectabilis* Gesellschaft sind im unteren Teil der subalpinen Waldzone, welche die höchste Verbreitung des geschlossenen Waldbestand unterhalb der Waldgrenze darstellt, zu finden. Oberhalb der Waldgrenze löst die artenarme *Boschniakia himalaica – Rhododendron campanulatum* Gesellschaft den Mischwaldbestand ab und bildet einen dichten Krummholzbestand aus. Die Wald- und Krummholz-Gesellschaften haben wir der Klasse der *Betula utilis – Abies spectabilis* Wälder zugeordnet. Im alpinen Bereich des Waldgrenzökotons konnten wir zwei Pflanzengesellschaften klassifizieren: Die artenarme *Pedicularis* cf. *microcalyx – Rhododendron anthopogon* Gesellschaft sowie die *Anaphalis royleana – Rhododendron anthopogon* Gesell-

schaft, welche durch eine hohe Vielfalt an krautigen Arten, insbesondere Gräser, gekennzeichnet ist. Beide Gesellschaften gehören der Klasse der *Dasiphora arbuscula – Rhododendron anthopogon* Zwergstrauchheiden an. Die Artenzusammensetzung der erfassten Pflanzengesellschaften korreliert mit den sich verschlechternden Wachstumsbedingungen entlang des Höhengradienten, insbesondere in Bezug auf Bodentemperatur, Bodenfeuchte, sowie Stickstoffgehalt und Stickstoffverfügbarkeit im Boden.

Unsere Forschungsergebnisse zur Keimlingsetablierung bekräftigen die Bedeutung von geeigneten Mikrohabitaten für die erfolgreiche Verjüngung von Baumarten in Gebirgsregionen. Wir konnten artspezifische Mikrohabitate zur Keimlingsetablierung ermitteln. Während sich die Keimlinge der Art *Abies spectabilis* primär auf streubedeckten Untergrund entwickeln, sind Keimlinge der Arten *Betula utilis* und *Rhododendron campanulatum* vorwiegend auf moosbedecktem Untergrund zu finden. Die artspezifischen Ansprüche an das Mikrohabitat waren unabhängig von den floristischen Veränderungen entlang des Höhengradienten des Waldgrenzökotons. Die Mehrheit der Keimlinge aller untersuchten Arten wuchs in der Nähe von mindestens einem potentiellen Schutzelement. Dabei waren geomorphologische Strukturen sowie Totholz die wichtigsten Schutzelemente für die Keimlingsetablierung.

Die erfassten Hauptfaktoren für die Differenzierung von Pflanzengesellschaften und der Etablierung von Baumkeimlingen, insbesondere die Bodentemperatur, sowie Wasser- und Stickstoffgehalte im Boden, sind direkt oder indirekt klimatisch bedingt. Wir erwarten daher im Waldgrenzökoton des Rolwaling-Tals, im Zuge der Klimaerwärmung, deutliche Veränderungen in der Artenzusammensetzung und der Position der Waldgrenze. Da anzunehmen ist, dass sich die Wuchsbedingungen in Hochgebirgsökosystemen unter dem gegenwärtigen Klimawandel substantiell verändern werden, wird die Bedeutung von artspezifischen Mikrohabitaten weiter zunehmen, um mögliche Extrembedingungen abzumildern.

Diese Arbeit liefert neue Erkenntnisse zur klimawandelinduzierten Vegetationsdynamik in Waldgrenzökotonen des Himalayas. Die Ergebnisse zur Keimlingsetablierung erweitern den Kenntnisstand zu den Voraussetzungen einer erfolgreichen Verjüngung von Baumarten und der Verschiebung der Waldgrenze. Die syntaxonomische Klassifizierung der Vegetation des Waldgrenzökotons im Rolwaling-Tal, stellt einen Ausgangspunkt für weitere pflanzensoziologische Untersuchungen sowie für die Durchführung von Langzeitbeobachtungen, die die Auswirkungen der Klimaerwärmung auf die Vegetation der Himalaya-Region erfassen, dar.

Der vorliegenden kumulativen Dissertation liegen zwei in Peer-Review-Verfahren geprüfte Studien zu Grunde, die in hochrangigen wissenschaftlichen Zeitschriften erschienen sind. In Anhang I dieser Arbeit finden sich die Zusammenfassungen der Studien. Anhang II zeigt die vollständigen Veröffentlichungen.

Studie 1: ‘Phytosociology and ecology of treeline ecotone vegetation in Rolwaling Himal, Nepal’
Authors: Birgit Bürzle, Udo Schickhoff, Niels Schwab, Jens Oldeland, Michael Müller, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten and Wolf Bernhard Dickoré
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Ich habe als Co-Autor zu sechs weiteren Studien beigetragen, die in engem Zusammenhang zu den Forschungszielen dieser Arbeit stehen. Sie tragen damit zum Verständnis der klimawandelinduzierten Vegetationsdynamik im Waldgrenzökotons des Rolwaling-Tals bei. In Anhang III finden sich die Zusammenfassungen der Studien.

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List of Abbreviations

ANOVA	One-way analysis of variance
DCA	Detrended Correspondence Analysis
DJF	winter December to February
JJAS	summer/monsoon June to September
MAM	March to May
ON	autumn/post-monsoon October to November

1. Introduction

1.1. Vegetation dynamics at high elevations

The vegetation zonation of mountains is a compelling subject which has attracted the attention of natural scientists for many years. Primarily due to the temperature regime, high mountains globally demonstrate a specific elevational zonation of vegetation types. Montane and subalpine forest stands give way to dwarf-shrub formations in the subalpine zone and to heaths or arctic tundra in the alpine area. These changes are associated with a reduction of biomass as well as a decline in biodiversity (Nagy and Grabherr 2009). Environmental drivers (e.g. temperature, carbon dioxide partial pressure, solar radiation) change gradually with elevation, preventing trees from establishing beyond certain elevations and critically impacting species composition and community patterns in mountain ecosystems (Whittaker and Niering 1975; Körner 2007; Nagy and Grabherr 2009; Körner 2012a). The most conspicuous change in elevational vegetation zonation is the upper treeline, which forms the lower boundary of the alpine zone. This boundary is rarely sharp, and largely fragmented. Here the dominating life forms change gradually from trees to shrub-only stages over an area of a few meters to several hundred meters (Körner 2012a). This transition zone is called the treeline ecotone. This thesis uses the terms 'treeline' or 'treeline ecotone' to describe the transition zone from closed subalpine forests to the uppermost area of often scattered and stunted individuals of forest-forming tree species (cf. Holtmeier and Broll 2005).

From a global perspective, growing season temperature is widely considered to be the main driver for alpine treeline position (Holtmeier and Broll 2019). The occurrence of mature trees is associated with a growing season that lasts at least 3 months and exhibits a mean ground temperature of at least 6.4 ± 0.7 °C (Körner 2012b). As a result of low temperatures, growth-processes, especially the involved carbon metabolism, are restricted at higher elevations, leading to a gradual decline in mature tree abundance and tree size (Körner 2012a). While photoassimilate production at the treeline position still occurs at a very high level (50-70% at its maximum capacity), apical and cambial growth becomes negligible at around 5°C (Körner 2012a). According to their tall stature, trees are aerodynamically closer linked to the atmospheric conditions and are therefore directly tied to the thermal gradients of the free atmosphere. This results in a general limit on tree growth in relatively low elevations in contrast to lower growing species and tree seedlings, which may be found at several hundred meters above the treeline (Körner 2012b).

The mountains of the world have been subjected to temperature increase that was higher than the global mean during the 20th century (Diaz and Bradley 1997; Beniston 2000; Rangwala and Miller 2012), and temperature increase will most likely continue to be higher than average during the 21st century (Nogués-Bravo et al. 2007; IPCC 2018). Mountain environments are extremely sensitive to climate change due to their cryospheric systems, steep slopes and multifaceted environmental conditions over short geographical distances (Schickhoff 2011; Borsdorf et al. 2014; Schickhoff et al. 2016a). Global warming and the associated changes in precipitation and snow cover have extensive impacts on the physical systems of mountain environments, including permafrost degradation, decline of snow cover and glacier retreat, all of which create a multitude of effects on ecological balance (IPCC 2014; Schickhoff et al. 2016b). As mountain plant species are highly specialised and adapted to a relatively narrow range of environmental conditions, climate changes may already have triggered significant impacts within populations (e.g. changes in phenology, adjustment of phenotype) and on species distribution (Körner 2003; Grabherr et al. 2010; Anderson et al. 2012).

Due to temperature sensitivity, global warming is expected to cause upper treelines to advance to higher elevations (Smith et al. 2003; Holtmeier and Broll 2007; Wieser et al. 2014). The repeated climatically caused treeline fluctuations during the Holocene, which have been explored in many palaeoecological studies, support this thesis (MacDonald et al. 2000; Reasoner and Tinner 2009; Schwörer et al. 2014). However, the results of global and regional studies in different mountain ranges demonstrate mixed responses, from substantially advancing to static and even recessing treelines (e.g. Camarero and Gutiérrez 2004; Danby and Hik 2007; Wieser et al. 2009; Gaire et al. 2011; Zhao et al. 2013). Harsch et al. (2009) conducted a global meta-analysis encompassing data on treeline dynamics from 166 sites for a period of more than 100 years. Fifty-two percent of the treelines had advanced, while 47% did not reveal any altitudinal shifts and 1% regressed. The inconsistency of treeline response to climate warming reflects the local-scale complexity of abiotic and biotic site factors, which is interrelated with broad-scale climate inputs. It is clear from previous research that regional- or landscape-scale climate exerts a top-down control on local ecological patterns and processes at the treeline (e.g. Batllori and Gutiérrez 2008; Elliott 2011). It is widely unknown, however, how local-scale site factors modify the sensitivity and response of treelines to region-wide climate warming (cf. Holtmeier and Broll 2007; Malanson et al. 2007; Smith et al. 2009; Batllori et al. 2009). Furthermore, beyond climate change, land-use change (e.g. land abandonment, changes in livestock grazing patterns, logging) has also influenced treeline position and plant species assemblages, especially in old-settled mountain regions (e.g. Bolli et al. 2007; Gehrig-Fasel et al. 2007; Vittoz et al. 2008; Treml et al. 2016; Bhatta et al. 2018a; Vitali et al. 2018). Thus, it is necessary to disentangle the impact of land-use change and climate warming on treeline dynamics.

Research on treeline position and treeline dynamics can be conducted at different scales (c.f. Malanson et al. 2011). Studies exploring the global-scale causes of treeline position and dynamics primarily focus on the limitations of tree growth from an ecophysiological perspective. These research approaches are subsumed under the term ‘global approach’. Meanwhile, studies investigating the above-mentioned fine-scale variations in treeline patterns focus on landscape patterns, particularly on the effects of site conditions and on treeline history. These studies can be referred to the ‘landscape approach’. Studies of both types have increased considerably in the last decade, seeking to answer key questions on climate change-induced treeline dynamics. In addition to the local-scale complexity of abiotic and biotic site factors, the varied responsiveness of treelines to climate warming may also be related to different treeline forms (e.g. diffuse, abrupt, island, krummholz). Harsch and Bader (2011) found that the majority of diffuse treelines are advancing, while krummholz, abrupt and island treelines are relatively stable. However, Treml and Veblen (2017) highlighted that tree growth sensitivity to climate warming is primarily attributed to tree species and secondarily to treeline form. Given the nonlinear growth-climate response of treelines by species-specific temperature sensitivity and various local scale modulator and their interactions, the significance of treeline forms to predict treeline dynamics remain limited (Schickhoff et al. 2015).

However, treeline position is not solely determined by temperature-sensitive tree growth, but also by regeneration processes. Stable treelines are primarily associated with tree growth and the performance of mature trees, and recruitment is confined to the lower part of the treeline ecotone. Advancing treelines, by contrast, require successful seed germination and seedling establishment beyond the treeline (Harper 1977; Harsch et al. 2012). As habitat conditions and ecophysiologically effective stress factors differ between seedlings and trees, responses to climate warming will as well (Körner 2012a). However, regardless of the importance of tree recruitment for the spatial dynamics of treeline stands, the great majority of field studies on the climatic impacts on treeline position have focused on mature trees. Thus, to understand the differences in treeline dynamics and to form predictions about future treeline position, a deeper knowledge of the underlying processes of tree recruitment in the ecotone is indispensable (Smith et al. 2003).

In addition to the effects on treeline position, rising temperatures will also affect treeline ecotone vegetation on the community level. Due to their multifaceted habitats and environmental conditions, mountainous areas display a rich diversity of plant species communities over short geographical distances (high beta diversity) (Körner 2000; Körner 2007; Nagy and Grabherr 2009; Schickhoff 2011). They are often biodiversity hotspots with a high number of endemic species (Körner 2003). In contrast to the changes of life forms, species turnover and transitions on plant community levels are more continuous (Whittaker 1956; Sundqvist et al. 2011; Sundqvist et al. 2013), usually causing small-scale mosaics of vegetation types. Climate warming triggers an expansion of distribution ranges to higher elevations, which has been observed for a wide range of taxonomic groups and geographical locations (e.g. Walther et al. 2005; Pauli et al. 2007; Gonzalez et al. 2010; Odland et al. 2010; Chen et al. 2011; IPCC 2014; Lenoir and Svenning 2015). Due to the harsh environmental conditions, plant communities in the alpine area are relatively complex, with finely tuned species compositions.

Warming-induced upward range shifts concurrently increase plant species richness in alpine and nival zones and threaten in particular highly specialised nival species through habitat loss (Grabherr et al. 2010; Steinbauer et al. 2018). With further warming, floristic composition will change successively from mutualistic symbionts of slow-growing, cold-adapted and light-demanding plant species to competitive fighters of thermophile/warm-adapted and more or less invasive species (Gottfried et al. 2012). The reduction of suitable habitat and the increase in competing species will lead to declines in alpine plant species, especially at their upper margin of distribution (Theurillat and Guisan 2001). Thus, mountain plant communities will gradually evolve through ongoing climate warming into novel communities with transformed species compositions (Gottfried et al. 2012; Pauli et al. 2012). In contrast, downward shifts or no change in elevational distribution have also been reported in alpine areas (Lenoir et al. 2010; Crimmins et al. 2011; Felde et al. 2012; Bhatta et al. 2018a). These unexpected trends have largely been attributed to biotic interactions, changes in precipitation, dispersal limitation or land-use changes (Bhatta et al. 2018a). Thus, to investigate climatic responses of plant species assemblages, interactions with factors other than warming must be taken into account.

1.2. Climate change in the Himalaya

Temperature trends in the Himalayan region are distinctly higher than the global mean trend of 0.85°C between 1880 and 2012 (Krishnan et al. 2019; cf. IPCC 2013a). This finding is in line with results from most high-mountain environments, showing an amplified warming trend with increasing elevation (Mountain Research Initiative EDW Working Group 2015). The Tibetan Plateau and the Himalaya have been subjected to large warming trends of up to 1.5°C (mean surface air temperature) during the period 1991-2012 (Mountain Research Initiative EDW Working Group 2015; Schickhoff et al. 2016a). Climate change-related trends in the precipitation amounts for the Himalayan region are more difficult to derive, as sub-regions and seasons vary strongly and long-term observations are underrepresented (Schickhoff et al. 2016a; Krishnan et al. 2019). Precipitation in monsoon seasons is expected to rise for the Himalayan region (IPCC 2013b), with some exceptions. Bhutiyani et al. (2010) revealed a decreasing trend in the monsoon precipitation for the northwestern Himalaya in the last 150 years, while Wang et al. (2013) detected an increase in winter and pre-monsoon drought events for western Nepal. Despite an increase in interannual variability, most climate models predict rising precipitation extremes for the Himalayan region (IPPC 2013a; Karki et al. 2017a).

1.3. State of the art and research deficits

1.3.1. Phytosociology and plant diversity in the Nepal Himalaya

Nepal is characterised by a high species diversity and a high degree of endemism due to its steep altitudinal, climatic and ecological gradients. While the interval of maximum species richness is located between 1,500 and 2,500 m a.s.l., the highest numbers of endemic species are found in an altitudinal range between 3,800 and 4,200 m a.s.l. (Vetaas and Grytnes 2002). These differing patterns may particularly result from optimal growth conditions in the sub-montane/montane zone below the treeline and glacial dynamics in the alpine area above the treeline, which may have increased the extinction rate and enhanced niche development and speciation (Colwell and Hurtt 1994; Colwell and Lees 2000). Nepal's high species richness is also the result of the transitional position between two biogeographical realms (Holarctic in the north, Palaeotropic in the south) and between the west Himalayan and east Himalayan floristic provinces (Figure 1). In addition, the country is surrounded by six Asian floristic provinces (cf. Paudel et al. 2012). In the Hindu Kush-Himalayan region, between 8,000 and 10,600 vascular plant species exist, with a proportion of endemic plant species up to 40% (Pandit and Kumar 2013; Pandit et al. 2014). More than 7,000 plant species occur in the eastern Himalaya alone, many of them are endemics with restricted distribution (Chettri et al. 2008). The total number of vascular plants in Nepal is estimated to be at least 6,200, of which 30% are endemic to the Himalayas (Press et al. 2000; Miehe et al. 2015a).

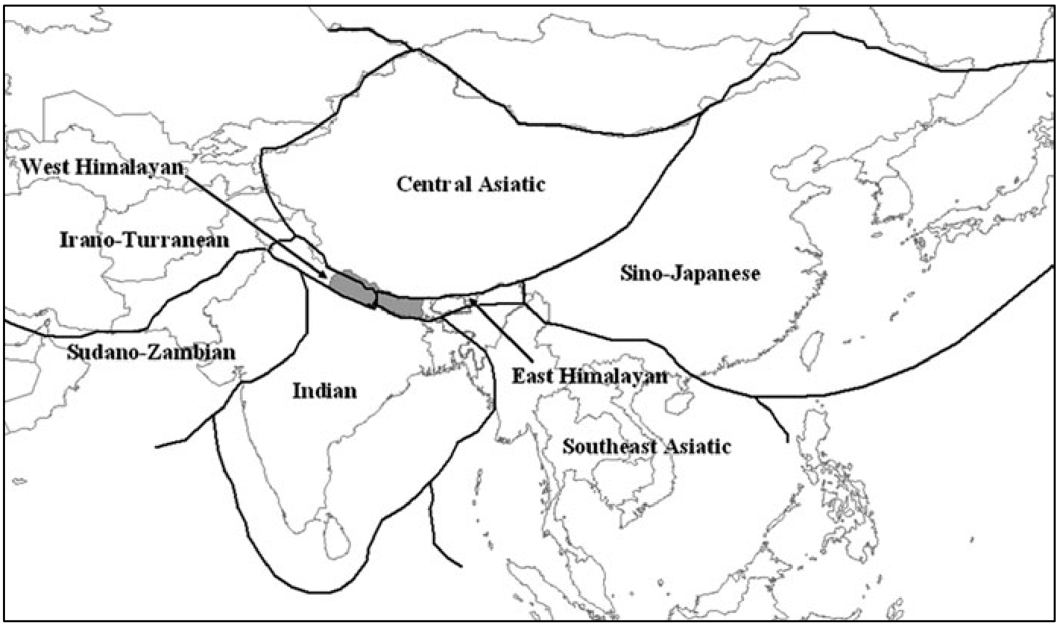


Figure 1. Floristic provinces in Asia (Paudel. et al. 2012)

Description of the vegetation zonation and vegetation types of the Himalayan mountain range has been the subject of several previous studies. (Schweinfurth (1957) first published vegetation maps which illustrated the distribution of vegetation types for the entire Himalayas. Information on altitudinal position, physiognomy and treeline-forming species is also more or less sufficiently documented (Schweinfurth 1957; Troll 1967; Champion and Seth 1968; Stainton 1972; Gupta 1983; Singh and Singh 1987; Puri et al. 1989; Schickhoff 2005; Miehe et al. 2015b). The subalpine areas in the west and central Himalaya are characterised by mixed forest stands dominated by conifers (mainly *Abies* species), with varying proportions of Himalayan birch (*Betula utilis*) and other deciduous trees (Schweinfurth 1957; Miehe 1990;

Schickhoff 1993; Miehe and Miehe 2000; Schickhoff 2005; Miehe et al. 2015b). At the treeline adjacent to the *Abies-Betula*-forests, pure birch stands often form a narrow belt (Miehe 1990; Schickhoff 1993; Schickhoff 2005; Miehe et al. 2015b). Above the treeline, *Betula* forests merge into krummholz thickets mainly composed of *Rhododendron* species, forming the transitional zone to the alpine *Rhododendron* dwarf thickets and *Kobresia* mats further upslope.

Plant species composition in the Himalayan mountain range will be dramatically affected by climate change. Due to the above-average magnitude of climate change in high mountains and the high proportion of endemic species with spatially restricted populations, biodiversity is highly endangered in the Himalaya. The negative impacts of climate change, such as increasing temperature variability and declining precipitation during the dry season, will have substantial effects on plant species distribution patterns (Xu et al. 2009; Shrestha et al. 2012; Telwala et al. 2013; Dolezal et al. 2016; Bhatta et al. 2018a; Chandra et al. 2018; Salick et al. 2019).

However, despite the outstanding plant diversity of the Himalayan mountain range and the threat posed to it by climate change, the phytosociology of Himalayan vegetation types has been widely unexplored. Few notable exceptions of detailed phytosociological studies include the surveys of Hartmann (1968, 1972, 1983, 1987, 1990, 1995, 1997, 1999), Schickhoff (1993, 1996), Eberhardt (2004) and Khan (2012) for the western Himalaya and Karakoram. In the Langtang-Helambu region of central Himalaya, Miehe (1990) undertook in-depth explorations of upper elevational plant communities. Kikuchi and Ohba (1988) offered a first overview of major plant communities in the alpine area near Panch Pokhari Lake in the south-eastern part of Rolwaling Himal (Nepal), the investigation area of the present study. Therefore, there remains an urgent need for further comprehensive studies on the phytosociology of Himalayan mountain areas in order to enable assessments of the climate-induced modifications in species distribution and plant communities.

1.3.2. Vegetation ecology of Himalayan treeline ecotones

Environmental factors (e.g. temperature, carbon dioxide partial pressure, solar radiation), local orographic and edaphic conditions and inter- and intraspecific biotic interactions are crucial for species composition and community patterns. Plant species exhibit individual responses to changing site conditions with increasing elevation, for instance, by adapted photosynthesis, changed metabolism and altered mineralisation rates. By contrast, plant functional traits and types change more or less in parallel with elevational gradients (Hoch and Körner 2012).

Studies on the vegetation-environment relationships of Himalayan vegetation types in general and of Himalayan treeline ecotones in particular are still very limited. While the scientific interest in Himalayan treelines and their reaction to changing climate conditions has increased (Troll, C. 1973; Gupta 1983; Schickhoff 2005; Miehe, et al. 2015b; Schickhoff et al. 2016b), there is a lack of detailed characterisation of treeline vegetation-environment relationships based on correlations of vegetation and site-ecological data for most Himalayan regions. Miehe (1990) provided the most comprehensive account, containing extensive floristic and ecological information, of subalpine and alpine vegetation types to date, based solely on vegetation sampling. Detailed information on treeline floristic, structural and spatial patterns as well as on human impact are provided in the overviews of Miehe and Miehe (2000), Miehe (2004) and Miehe et al. (2015b). However, to estimate the influence of climate change and related environmental factors on Himalayan vegetation types, contemporary and extensive investigations are required. The first study of this PhD thesis therefore aims to analyse the floristic composition, community patterns and environmental relationships of subalpine and alpine vegetation in Rolwaling Valley in east-central Nepal. The study also seeks to relate the results on the sensitivity of treeline ecotone vegetation to climate warming.

1.3.3. Tree recruitment in Himalayan treeline ecotones

The long-term persistence of every plant population and the majority of population dynamics depend on successful recruitment (Harper 1977), which includes successful flowering, pollination, seed maturation, seed dispersal, seed germination and survival of germinated seedlings (Tingstad et al. 2015). As noted above, a deeper knowledge of complex tree recruitment processes in treeline ecotones is necessary to understand present treeline positions and to make predictions about future treeline shifts under accelerated climate warming in the Himalayan mountain range.

Flowering

Flowering in alpine regions is a highly time- and energy-consuming process. Before flowering, alpine species often require several years to build a fully differentiated inflorescence (Billings 1974). The time of flowering is controlled by environmental conditions, with temperature and photoperiod seemingly are the most important factors (Körner 2003). High mountain areas experience an extremely narrow flowering period. In the central Himalayas, more than 70% of all plant species are mid-flowering species, blooming during mid-July (Figure 2) (Ram et al. 1988). Flowering in the middle of the vegetation period reduces the risk of pollen loss by avoiding pollinators (beginning of vegetation period) and the risk of seed loss by immature seeds (end of vegetation period). The flowering phenology of alpine species is due to differences in life history strategies with a r-K continuum from early flowering to late flowering species (Molau 1993).

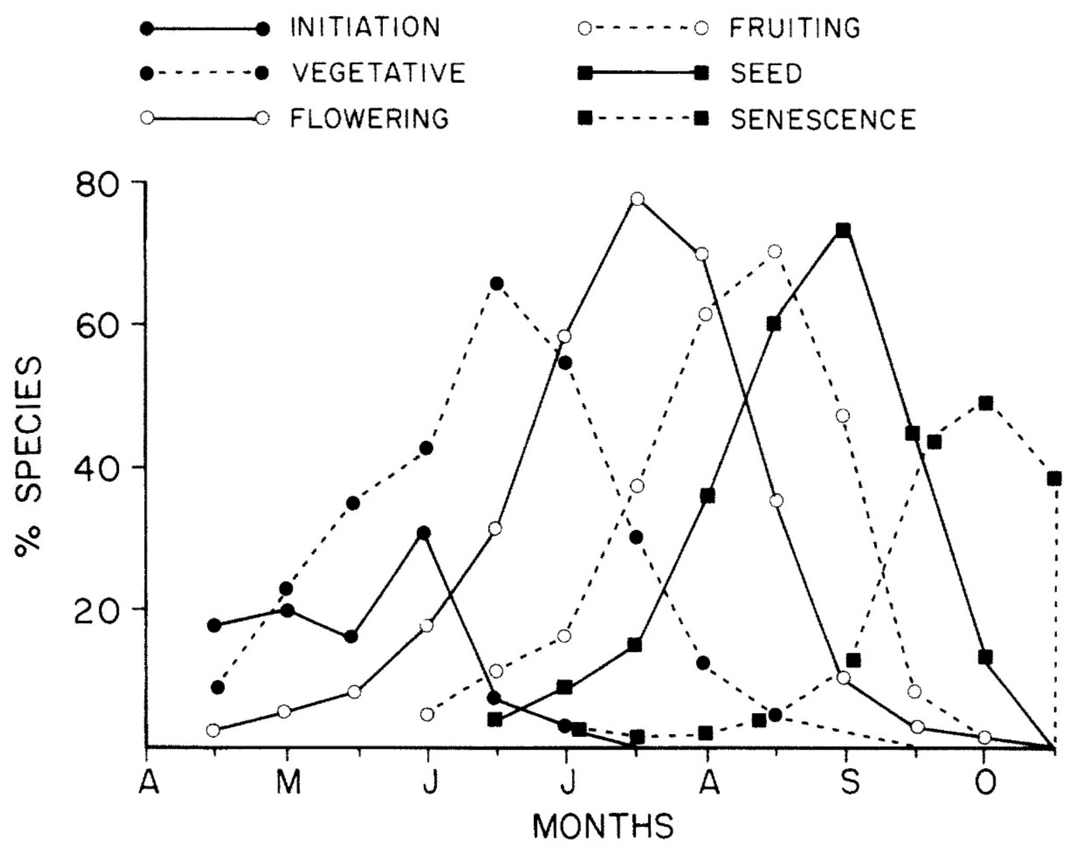


Figure 2. Flowering phenology in the central Himalayas (Ram et al. 1988)

Phenological acceleration (especially flowering) is the first and most pronounced plant reaction to climate change-related temperature increases in alpine regions (Körner 2003). This is primarily the result of a decreasing snow cover and early snow melt, which potentially lead to lengthening of the growing season (Inouye and Wielgolaski 2013; Bhatta et al. 2018b). The consequences of species-specific changes in phenological patterns are extensive, with impacts on species-specific life cycles, plant-to-plant interactions, plant-pollinator relationships and plant-predator relationships. Associated studies for the Himalaya are limited, but have reported a premature onset of flowering for several rhododendron species which is one month earlier than in the past (Xu et al. 2009). Shrestha et al. (2012) found, based on a satellite-derived Normalized Difference Vegetation Index (NDVI) data set, an average advancement of the flowering start and length of 4.7 days between 1982 and 2006 for the Himalayas. The lengthening of phenophases may further lead to greater plant species richness in the Himalayan mountain range, as different alpine species benefit from the increasing number of growing degree days (Adhikari et al. 2018).

Seed maturation

After successful pollination, the development of mature seeds is the next step in the reproduction process, encompassing cell division, differentiation of embryo tissue and testa and the dehydration of the seed (Körner 2003). As seed development is highly time- and energy-consuming, increasing temperatures and prolonged growing seasons may lead to progressive resource accumulation for seed development and a higher reproductive output, especially in the harsh environments of alpine regions (Fenner and Thompson 2005; Briceño et al. 2015). Seed size is genetically restricted and the proportion of resources a plant allocates to seeds is relatively fixed. Thus, the phenotypic plasticity of seed production in response to environmental change is restricted and resource allocation between seed size and seed number is always a trade-off (Fenner and Thompson 2005). Due to the higher amount of absolute nutrient reserves (not concentration), larger seeds better overcome harsh environmental conditions (Fenner and Thompson 2005). Meanwhile, higher seed numbers are able to compensate seeds' or seedlings' failure. Various studies have found an increase in seed numbers and/or seed size through pronounced resource allocation in mountainous regions in response to climate warming (Wagner and Reichegger 1997; Alatalo and Totland 1997; Sandvik and Totland 2000; Cui et al. 2017). However, increasing temperatures and advanced flowering phenology may not necessarily lead to advanced seed production. Liu et al. (2012) recorded reduced seed production after winter warming for different herbal species on the Tibetan Plateau due to plant physiological response (metabolic changes associated with flower production). Warmer temperatures in spring combined with early snow melt may further enhance the risk of freezing damage to reproduction organs (Molau 1996; Gerdol et al. 2013). In addition, seed numbers and seed viability are influenced by dramatic natural year-to-year variation. These variations may increase with ongoing climate warming, making predictions for seed development even more difficult (Laine et al. 1995; Walck et al. 2011).

Dormancy break and germination

The seeds of most alpine plant species are dormant after maturation. To break dormancy, they must undergo several months of quiescence, often in combination with cold temperatures (Körner 2003). The germination of alpine species occurs in spring after snow melt with rising temperatures and soil moisture content. Climate warming may therefore influence seed dormancy and germination in various ways. Accelerated soil warming may fasten germination in spring to some extent, but may also entail the risk of topsoil desiccation (Körner 2003). In addition, warm spells during winter (IPCC 2007) may lead to premature dormancy break and the loss of seeds or seedlings (Walck et al. 2011).

Seedling emergence and seedling establishment

Seedling establishment and survival is the most vulnerable and the most climate-coupled phase in tree recruitment (Fenner 1987; Malanson et al. 2009). As a result of small stature, even small biomass reductions due to environmental stress result in plant death (Fenner and Thompson 2005). Germination on high mountain sites implies a variety of stress factors, including harsh wind, low temperatures, topsoil desiccation, nighttime needle ice and cryogenic soil activity in the winter season (Körner 2003).

A basic prerequisite for seedling survival under extreme conditions is the availability of safe sites, defined as the fine-scale environment immediately surrounding a seedling that has all the necessities for break of dormancy, germination and seedling survival. These necessities include abiotic requirements (water, oxygen and nutrients supply, microclimatic and microtopographic conditions), biotic interactions (surrounding plant species composition, interactions with mycorrhiza and legume bacteria) and the exclusion of hazards (predators, pathogens, competitors) (Harper et al. 1961; Fowler 1988; Callaway 1995). Especially in the harsh environment of high mountains, seedling mortality is often reduced by abiotic sheltering (topographic shelters, rocks and stones) and by sheltering of other plants ('nurse plants'). In treeline ecotones, the nurse effects of tree islands and microtopographic sheltering are well documented (Holtmeier and Broll 1992; Hättenschwiler and Smith 1999; Resler 2006; Batllori et al. 2009). Seedling survival is further tied to the rapid formation of deeply anchored and intensively branched root systems, which enhance water and nutrient supply. Particularly under drought stress and nutrient shortage, root system establishment distinctly exceeds shoot growth in the first years (Körner 2003; Anschlag et al. 2008). Safe site requirements are species-specific, but also vary intraspecifically among genotypes or different seedlings' life stages (Leck et al. 2008). Beyond seed availability, the occurrence of a safe site is the most limiting factor for seedling establishment above the treeline (Jones and del Moral 2005; Batllori et al. 2009). Changing environmental factors due to climate warming - such as soil temperature, soil moisture, soil nutrients and herbivory - may improve and/or deteriorate conditions for seedling establishment (cf. Anschlag et al. 2008; Hofgaard et al. 2009; Batllori et al. 2009; Munier et al. 2010; Lett and Dorrepaal 2018).

Despite the high relevance of tree recruitment for treeline dynamics, few studies on tree recruitment in general, and on small-scale safe site conditions for tree seedlings in particular, have been conducted to date in Himalayan treeline ecotones (Schickhoff 2005; Dutta et al. 2014; Schickhoff et al. 2016b). In upper subalpine forests in Bhutan, spatial pattern analyses of *Abies densa* and *Rhododendron hodgsonii* demonstrated highly positive intraspecific correlations for both species and increasing seedling abundance on bryophyte mats (Gratzer and Rai 2004). In the Sygera Mountains (SE Tibet), (Wang, Camarero, et al. 2012) found microsite-dependent occurrences of Smith fir seedlings (*Abies georgei* var. *smithii*) establishing preferentially on moss-lichen and organic matter substrate, facilitated by juvenile firs and *Rhododendron* mats. The forests of the treeline ecotone in Rolwaling Himal are primarily composed of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum*. At its upper distribution, closed forest stands give way to *Rhododendron campanulatum* krummholz, forming an extensive belt. To our knowledge, neither a study on the prerequisites for seedling establishment nor a study on the implications of climate change for seedling establishment has been conducted to date for any of the three species. Therefore, to address the large gaps in existing research, study 2 of this PhD thesis aims to analyse safe site regeneration of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* in the Rolwaling treeline ecotone. The study gives special emphasis to seedling establishment in the immediate vicinity of *Rhododendron campanulatum*, as study 1 and previous reports in the context of the TREELINE project revealed extensive species impoverishment and low recruit density in the *Rhododendron campanulatum* krummholz belt (Schwab et al. 2016; Schwab et al. 2017).

2. Framework and Objectives

Notwithstanding the existing literature on the high sensitivity of mountain environments to climate change, there are substantial research deficits concerning the impacts of global warming on the biophysical properties of the Himalayan mountain system, and in particular on the Himalayan treeline ecotone (Schickhoff 2005). While the scientific interest in treelines has increased considerably for European and North American mountains, very few studies have been conducted in the Himalaya. Research deficits are most notably present regarding the sensitivity and response of the upper treeline to current climate warming (cf. Schickhoff 2005; Dutta et al. 2014; Schickhoff et al. 2015). As previously stated, there is a significant need for research on vegetation ecology, stand structure and tree recruitment in the Himalayan treeline ecotone. Given that Himalayan treeline ecotones are often strongly modified by human impact (Miehe and Miehe 2000), respective research projects must be undertaken on the few remaining near-natural treeline sites in order to detect a clear climate change effect.

In this context, the project 'Sensitivity and Response of the Treeline Ecotone in Rolwaling Himal, Nepal, to Climate Warming' (TREELINE) was established in 2013 with the aim to reduce the large deficiencies in global-change-related treeline ecotone research in the Himalaya. The objective of the project is to determine the sensitivity and response of the near-natural treeline ecotone in Rolwaling Himal, Nepal to climate warming using a landscape approach. Under consideration of varied landscape- and local-scale site conditions and mechanisms (geomorphic controls; soil, physical and chemical conditions; floristic composition and plant interactions), the project analyses interactions of region-wide climate warming input and finer-scale modulators on treeline response patterns. The interdisciplinary project, funded by the Deutsche Forschungsgemeinschaft (DFG) (SCHI 436/14-1, SCHO 739/14-1, BO 1333/4-1), encompasses three co-operating research groups with focuses on climate (Prof. Dr. Jürgen Böhner, Physical Geography, University of Hamburg), soil (Prof. Dr. Thomas Scholten, Physical Geography and Soil Science, University of Tübingen) and vegetation (Prof. Dr. Udo Schickhoff, Institute of Geography, University of Hamburg). This PhD thesis is embedded in the vegetation group of the TREELINE project, which explores the vegetation-ecological-relationship in the treeline ecotone, particulary under global warming. Based on field work conducted in the Rolwaling Valley in 2013 and 2014, this PhD thesis investigates the phytosociology and ecology of the treeline ecotone vegetation in the remote Rolwaling Valley and also analyses tree seedling recruitment as a prerequisite for dynamics of spatial treeline position.

To reduce the above-mentioned research deficits concerning phytosociology, vegetation ecology and tree recruitment at the treeline ecotone in Rolwaling Valley, this PhD thesis addresses the following research tasks.

1) Identify floristic composition of subalpine and alpine vegetation in the Rolwaling Valley in order to
    - differentiate plant communities of the treeline ecotone and analyse community patterns along the elevational gradient (study 1)

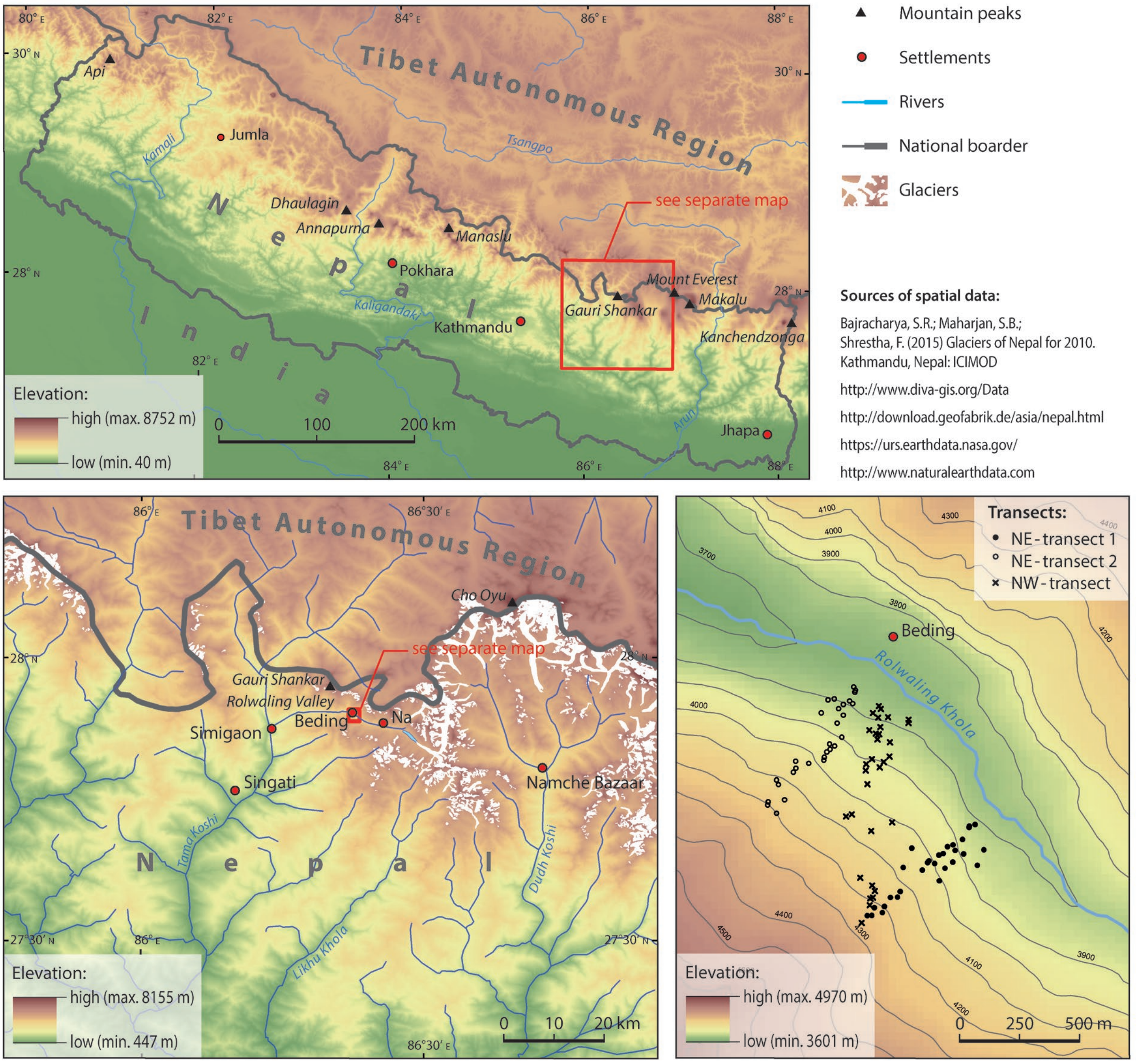
2) Analyse the relationship of treeline ecotone vegetation with environmental conditions in order to
    - identify site factors which cause the differentiation of the treeline ecotone vegetation and, in particular, which induce small-scale differences in species composition (study 1)
    - estimate the sensitivity of these variables to climate warming and the related effects on floristic composition and the development of novel communities in the treeline ecotone (study 1)

3) Analyse safe sites for regeneration of the tree species *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum*, which dominate the treeline ecotone in the Rolwaling Valley, in order to
    - identify key factors for successful seedling establishment along the altitudinal gradient (study 2)
    - investigate the potential inhibiting effect on tree recruitment by *Rhododendron campanulatum* forming a dense krummholz belt above the treeline (study 2)

3. Material and Methods

3.1.Study area

This study was conducted in the Rolwaling valley (27°52’ N; 86°25’ E) located in the Dolakha District in east-central Nepal adjacent to the border of the Tibet Autonomous Region (Figure 3). The Valley is part of the Gaurishankar Conservation Area, which was designated as a protected area in 2010 (Bhusal 2012).



Sources of spatial data:
Bajracharya, S.R.; Maharjan, S.B.;
Shrestha, F. (2015) Glaciers of Nepal for 2010.
Kathmandu, Nepal: ICIMOD
http://www.diva-gis.org/Data
http://download.geofabrik.de/asia/nepal.html
https://urs.earthdata.nasa.gov/
http://www.naturalearthdata.com

Figure 3. Location of the studied treeline ecotone (red rectangles) in the Rolwaling Valley in east-central Nepal. Position of the investigated transects and plots are shown on the third map (lower right).

According to measurements of the TREELINE climate station network (unpublished data), the climate in the study area is classified as subtropical mountainous climate, with dry winter and warm summer conditions (Köppen-Geiger Cwc). During summer, the climate is predominately affected by the Indian Summer Monsoon circulation (June to September) and Mediterranean Westerlies circulation (November to May), resulting in sharp alterations between wet and dry conditions across the four seasons (winter, pre-monsoon, monsoon, post-monsoon) (Böhner 2015; Karki et al. 2016). Winters (December to February) in the study area are cold and dry (Karki et al. 2016). Snow in higher altitudes is mainly induced by extra tropical cyclones/western disturbances (cf. Karki et al. 2017b) and play an important role for generating run-off and agricultural water supply in the hot pre-monsoon period through snow melt (Böhner 2015). In the pre-monsoon season (March to May), incoming solar radiation in the study area is at its highest level, combined with low precipitation amounts and rising temperatures (Karki et al. 2017b). Westerly winds dominate the pre-monsoon period, but are weakened due to rising temperatures of the Tibetan Plateau and subsequent warming of the troposphere. These changes in the troposphere build the transition from winter to summer circulation modes, characterised by abrupt and repeating switches between both circulation modes (Böhner 2015). The ongoing heating of the Tibetan Plateau replaces the westerlies of the winter and pre-monsoon season with a tropical easterly jet: a permanent and important component of the large-scale monsoon system (Böhner 2015). The summer monsoon (June to September) in the Himalayas is dominated by south and southwest winds, bringing moist air and determining summer monsoonal weather patterns along the Himalayas (Böhner 2006; 2015). More than 80% of the annual precipitation is received in that time (Gerlitz et al. 2016). In post-monsoon season (October to November), atmospheric circulation modes alter from summer to winter terms again. As such, dominating wind systems switch discontinuously from tropical westerlies to tropical easterlies, leading to interruptions of the monsoon in the end of August and in September. After a final ‘monsoonal attack’ in late August, western winds are increasingly stabilised during October in conjunction with decreasing temperature on the Tibetan Plateau. At this point circulation modes fully change to winter conditions (Böhner 2015).

The soils of the study area are generally podzols with low pH (from 2.5 to 4) (Müller et al. 2016a). They are developed over bedrocks of granite and gneiss. Soil depths vary from 30 to 70 cm, with maximum skeletal fractions from 75 to 95% for Ae-horizons.

Within the floristic Holarctic Kingdom, the Rolwaling Valley is assigned to the Eastern Himalayan Province of the Sino-Japanese Floristic Region (Meusel and Schubert 1971; Miehe 1990; Miehe 2015a). The ecotone of the study slope encompasses an altitudinal range from 3,745 to 4,300 m a.s.l., extending from the closed subalpine forest (upper cloud forest) with mixed forest stands (primarily composed of *Abies spectabilis*, *Betula utilis*, *Rhododendron campanulatum* and *Sorbus microphylla*) across the treeline and *Rhododendron campanulatum* krummholz belt to the lower alpine vegetation.

The Rolwaling Valley is one of the most remote areas of Nepal, with no connection to the road network. It is sparsely populated by different ethnic groups (Tamang, Sherpa, Gurung and Brahmin) mainly belonging to the Buddhist faith. Due to its seclusion and the fact that plants and animals in this valley are protected to a certain extent by the recurring Buddhist theme of a sacred hidden valley (Baumgartner 2015), vegetation formations are widely undisturbed in Rolwaling. We explored a north-facing slope at Beding village that is separated from the settlement by the Rolwaling River. The slope is steep with an inclination from 26 to 45°, showing no signs of grazing or fire and only negligible signs of logging. The near-natural treeline at the study slope is therefore a climatic one.

3.2.Data collection

We established three altitudinal transects across the studied north slope. The exposition of the transects varies slightly between northeast (two transects) and northwest (one transect) (Figure 1). Vegetation surveys were conducted during the period from July to September 2013 and from July to October 2014.

Vegetation data

Along each transect, we defined four zones (A–D) according to altitudinal differences and changes in vegetation. Altitudinal zones varied from closed upper cloud forests in the upper subalpine belt (zone A and B), to dense krummholz thicket of *Rhododendron campanulatum* (zone C), to alpine dwarf shrub heaths (zone D). Sampling plots were selected randomly in each transect zone due to the homogeneity of physical features and vegetation structure. We completed a total of 91 relevés with a size of 20 m x 20 m (projected on a horizontal plain). We collected phytosociological data along transects following the Braun-Blanquet approach (Braun-Blanquet 1964; Dierschke 1994). Unknown specimens were collected and identified at the herbarium of the Botanische Staatssammlung München (M). In addition, we used determination keys of eFloras (http://www.efloras.org; accessed January 2015), the *Flora of Nepal* (Watson et al. 2011) and the *Flora of Bhutan* (Grierson and Long 1984−2001).

Environmental variables

Environmental data were collected in each plot and included variables referring to topographic position (altitude, slope aspect and inclination) as well as soil chemical and physical parameters. We collected mixed soil samples of the uppermost mineral horizon from three randomly selected points within the plots. Soil sample analyses were conducted via standard methods at the Laboratory of Soil Science and Geoecology of the University of Tübingen (see Müller et al. 2016b for details) and the Laboratory of Physical Geography of the University of Hamburg. In addition, we monitored soil temperature and soil moisture at 10 cm depth and soil surface air temperature (see Müller et al. 2016a for details).

Seedling recruitment

Seedling recruitment was investigated along the northwest exposed transect. We stratified the transect according to the four different vegetation types identified in study 1 of this thesis, and selected plots randomly. In total, we established seven plots with a size of 20 m x 20 m, spread over the elevational range of seedling occurrence of *Abies spectabilis, Betula utilis and Rhododendron campanulatum*. At each plot, we placed five rectangular subplots (35 in total) with a size of 4 m x 4 m along the two diagonal lines of the plot. Field sampling was conducted from July to September 2014.

We examined natural regeneration of *Abies spectabilis, Betula utilis* and *Rhododendron campanulatum* in each subplot. All seedlings ≤ 50 cm in height were measured from ground to shoot tip and were grouped into three height classes (> 0–5 cm, > 5–15 cm, > 15–50 cm). Microhabitat characteristics were analysed for all seedlings. We determined microhabitats as circular sample plots around seedlings with varying diameters in relation to seedlings' height (seedlings' height: diameter microsite; > 0–10 cm: 10 cm diameter, > 10–20 cm: 20 cm diameter, > 20–30 cm: 30 cm diameter, > 30–40 cm: 40 cm diameter, > 40–50 cm: 50 cm diameter) (cf. Duc 1991; Ammer et al. 2004). We analysed vegetation and substrate cover of each microhabitat, including the percentage of vegetation, moss, litter, bare soil, stones and litter of *Rhododendron* species (proportion of total litter amount).

We further sampled shelter elements within a radius of 2 m around each seedling and measured the distance to the nearest element that potentially influences microhabitat and may facilitate germination and growth conditions. We differentiated four types of shelter elements: rocks (> 60 cm diameter), stones (20–60 cm diameter), deadwood and soil depression. We also noted the absence of any shelter element.

3.3.Statistical analysis

Classification of plant communities

For classification, we subjected the complete phytosociological data set to a cluster analysis (linkage method: complete linkage; distance measure: Bray-Curtis). The groups which emerged from cluster analysis were re-sorted iteratively according to the standard relevé method by Braun-Blanquet (1964). We determined diagnostic species of the proposed phytosociological units by calculating the phi-coefficient (Sokal and Rohlf 1995; Chytrỳ et al. 2002) among all units of the same rank. The selection of diagnostic species followed a threshold value at 0.3 and a simultaneous calculation of Fisher's exact test (Tichý 2002) with a significance concentration at 0.05.

The diagnostic species were differentiated into diagnostic (phi > 0.30) and highly diagnostic (phi > 0.50) (Chytrý 2007; Michl et al. 2010). Following Luther-Mosebach et al. (2012), we defined a character species of a syntaxon as a species which is diagnostic and has at least a 0.10 higher phi value than any other syntaxon of the same rank. Species in higher syntaxonomic rank are only regarded as character species if they have positive phi-values for more than half of the subordinated units. If a taxon is a character species in different ranks, we defined the species in the higher syntaxonomic position as a ‘transgressive character species’. In addition to the phi coefficient, percentage frequency was calculated for all species and phytosociological groups. Syntaxa were named using the diagnostic species with highest fidelity phi coefficient and the most important structural tree and shrub species, respectively. The nomenclature of vascular plants largely followed Press et al. (2000) and Watson et al. (2011). In view of the deficit state of knowledge, we consider the proposed classes as provisional, symbolising the higher rank in comparison to the subordinated groups.

Vegetation-environment relationships

We calculated mean values and standard deviation for recorded environmental data to provide an outline of the ecological variability within and between proposed phytosociological units. We assessed significant differences in site conditions between units with one-way analysis of variance (ANOVA). If data did not comply with the terms for ANOVA (normality of distribution, homogeneity of variance), we applied a log10-transformation and used Welch ANOVA (Welch 1951) to account for unequal variances. Pairwise comparison of units was performed by posthoc pairwise t-tests with Holm correction (Holm 1979). Level of significance was applied at $\alpha = 0.05$.

We visualised the compositional pattern of phytosociological units by means of detrended correspondence analysis. Visualised compositional patterns were interpreted by applying post-hoc correlations of the first two ordination axes (with highest eigenvalue) with $\log_{10}$-transformed environmental variables using the non-parametric Kendall rank correlation coefficient (Hill and Gauch 1980; Gauch 1982; Kent 2012).

Species-specific safe sites for regeneration

We computed seedling density per hectare (ha) of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* in all height classes and vegetation types. To analyse seedling habitat preferences, we compared microhabitat characteristics among species in different vegetation types and height classes using the Kruskal–Wallis rank sum test followed by a Dunn’s post hoc test with Bonferroni adjustment of the significance level. We visualised the percentage of different shelter element types by plotting histograms for all species and height classes. To estimate the relevance of shelter elements for seedling establishment, we compared the distances of tree seedlings to the nearest potentially protective structure among species in different vegetation types and height classes.

Cluster analysis and DCA were conducted with PC-ORD 6.255 program (McCune and Mefford 2011). For determination of diagnostic species, we employed JUICE (Tichý 2002). All other analyses and figure plotting were performed using different packages in the most recent version of the program R (R Core Team 2018).

4. Main Results and Discussion

4.1. Phytosociology of treeline ecotone vegetation (study 1)

Results

The treeline ecotone vegetation in Rolwaling Valley, which encompasses the cloud forests in the upper subalpine belt via a dense krummholz belt to alpine dwarf shrub heaths, could be clearly assigned to five phytosociological groups (‘communities’), belonging to two higher ranked units (‘classes’) (Supplement S1). The upper part of the subalpine forest zone is occupied by the *Synotis alata-Abies spectabilis* and the *Ribes glaciale-Abies spectabilis* communities, which adjoined to the krummholz belt further upslope, formed by the *Boschniakia himalaica-Rhododendron campanulatum* community. We assigned the forest and krummholz communities to the class *Betula utilis-Abies spectabilis* forests. In the alpine zone, the two dwarf shrub communities *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community and *Anaphalis royleana-Rhododendron anthopogon* community were differentiated and assigned to the class *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths (Fig. 4). Detrended correspondence analysis (DCA) for the complete data set clearly demonstrates the floristic differentiation of the five communities respectively two classes (Fig. 5), which are clearly separated along Axis1, which primarily represents an elevational gradient. According to a floristic gradient of 3.9 standard deviation units for the data set (length of first axis), the DCA approximately indicates a complete species turnover between the most dissimilar relevés. Relevés of the *Synotis alata-Abies spectabilis* and *Ribes glaciale-Abies spectabilis* communities occupy a considerably narrow range, indicating floristically very homogenous vegetation types. This finding is in contrast to the *Boschniakia himalaica-Rhododendron campanulatum* community, which exhibits the most abrupt change in species composition along the elevational gradient (cf. Fig. 5). Relevés of both treeless dwarf shrub communities (*Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community, *Anaphalis royleana-Rhododendron anthopogon* community) are arranged over a broader space in the ordination diagram, implicating more heterogeneous species compositions and environmental conditions (cf. Fig. 5). In accordance with relevés distribution along the first DCA axis, the dendrogram of the cluster analysis illustrates a clear division into two main groups and five subgroups (Fig. 6), indicated by the early cut off value at approximately 0.25.

Figure 4. Photos of the proposed communities. a: *Synotis alata – Abies spectabilis* community; b: *Ribes glaciale – Abies spectabilis* community; c – d: *Boschniakia himalaica – Rhododendron campanulatum* community; e: *Pedicularis* cf. *microcalyx – Rhododendron anthopogon* community.

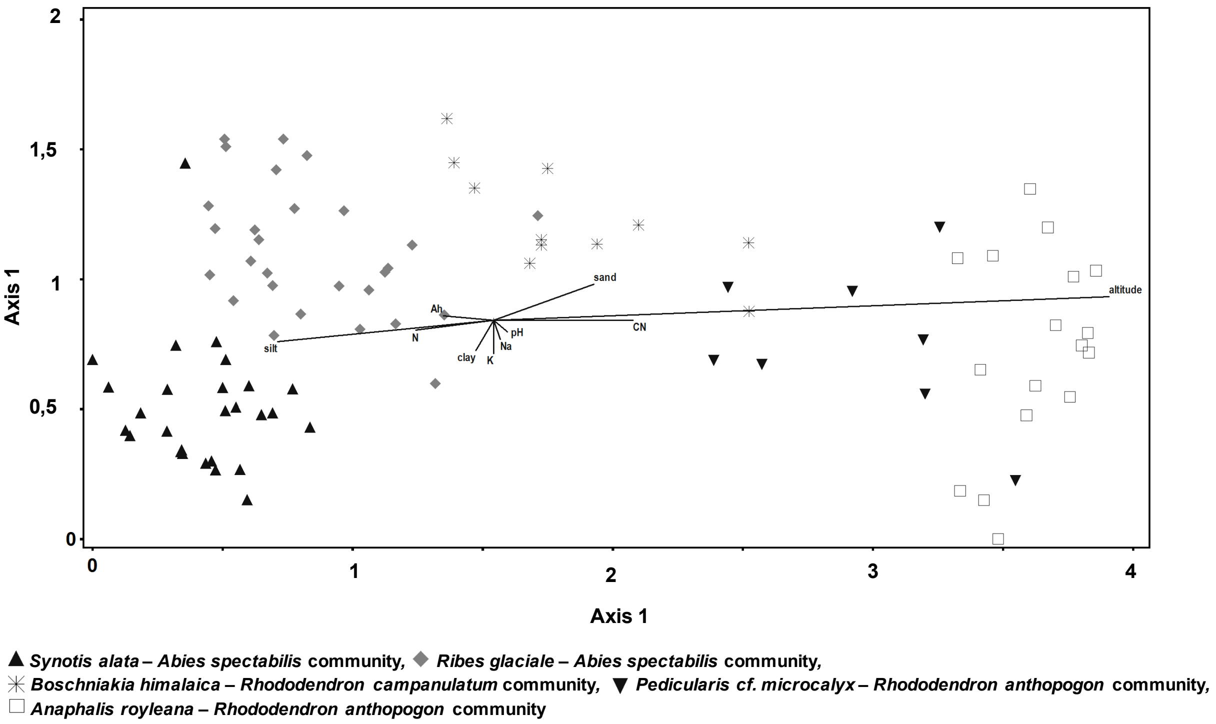


Figure 5. Detrended correspondence analysis (DCA) of relevés recorded in 2013 and 2014 (N = 91) with posthoc correlation of environmental parameters. Relevé symbols refer to clusters of final classification. Eigenvalue Axis 1: 0.69; eigenvalue Axis 2: 0.11; length of gradient Axis 1: 3.857; length of gradient Axis 2: 1.617; total inertia: 2.3713.

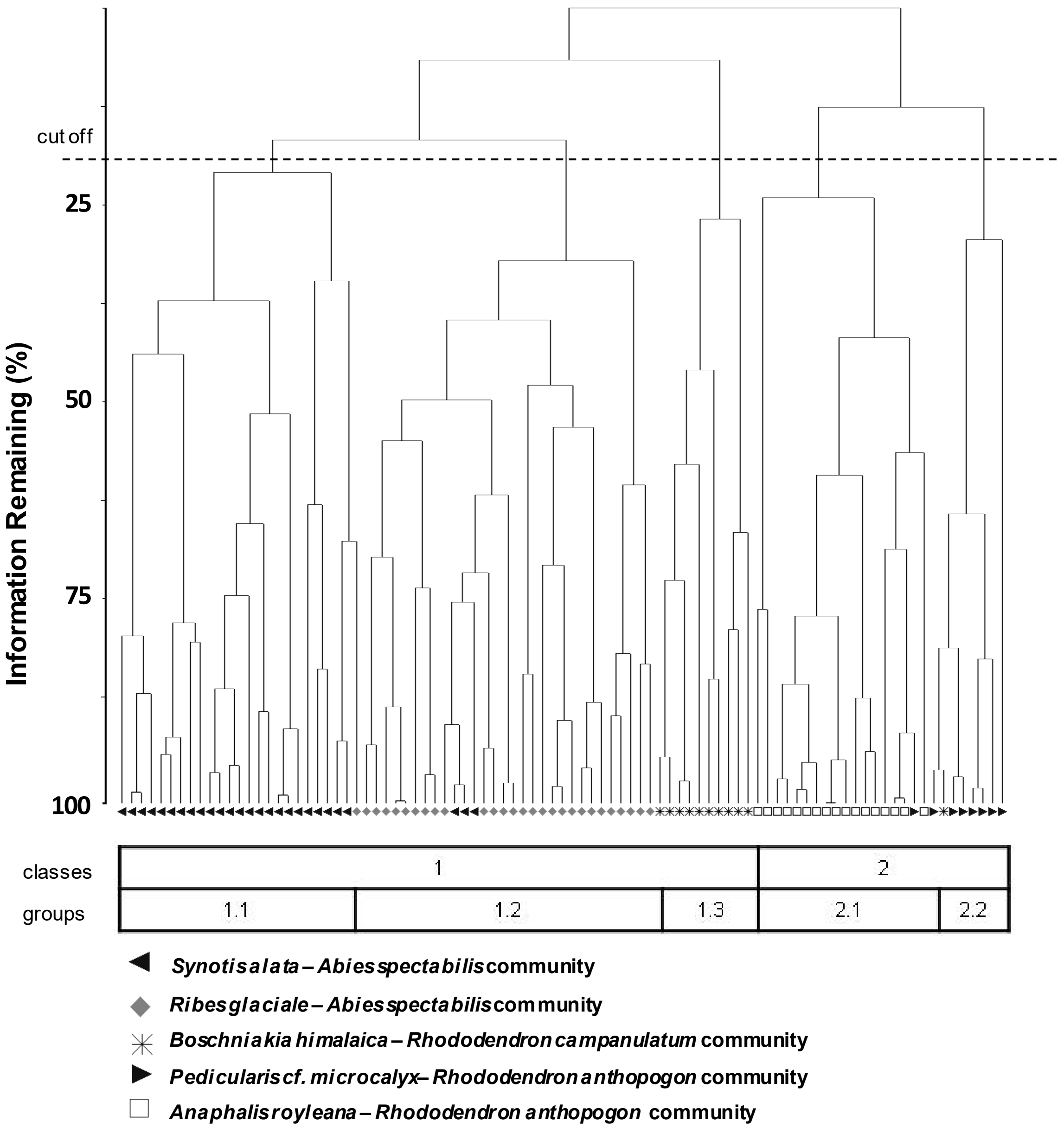


Figure 6. Dendrogram for 91 relevés according to complete linkage cluster analysis, with Bray-Curtis as a distance measure. Clusters at the five-cluster level, closely match with final classification, represented by relevé symbols. Sections below the dendrogram correspond to final phytosociological assignment.

Description of Syntaxa

Class 1: *Betula utilis-Abies spectabilis* forests

In the Rolwaling Valley, *Betula utilis-Abies spectabilis* forests are developed on upper montane and subalpine N/NE-slopes up to an elevation of c. 4,100 m a.s.l. These forest stands are primarily composed of *Abies spectabilis* and *Betula utilis*, with *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer. At the upper distribution, closed forest stands give way to *Rhododendron campanulatum* krummholz, forming an extensive belt between 3,900 and 4,000 m a.s.l. (NW-exposed), and 4000 and 4100 m a.s.l. (NE-exposed). The communities associated to the *Betula utilis-Abies spectabilis* forests contain 91 species. Following a threshold value of 0.3 for the phi coefficient, the classes *Betula utilis-Abies spectabilis* forests and subordinated communities were defined by 30 and 33 diagnostic species, respectively (Table 1).

Group 1.1: *Synotis alata-Abies spectabilis* community

This syntaxon occurs on moderately steep slopes (33°on average) between 3,700 to 3,900 m a.s.l., that is, in the lower subalpine range of the *Betula utilis-Abies spectabilis* forests. These closed forest stands are dominated by *Abies spectabilis, Betula utilis* and *Sorbus microphylla* in the tree layer (mean cover tree layer 1: 40%; tree layer 2: 43%), with regular occurrence of *Acer caudatum* and sporadic occurrence of *Rhododendron campanulatum* and *Prunus rufa.* Most species of the tree layer, which attains a height of c. 16 m, also prevail in the shrub layer (mean cover 38%), accompanied by *Ribes* and *Rosa* species. The productivity of the herb layer is high in comparison to the *Ribes glaciale-Abies spectabilis* community. It includes many tall forbs (e.g. *Synotis alata, Parasenecio quinquelobus, Epilobium* cf. *laxum*) and exhibits a high average cover of 60%. With a mean of 25 species, species richness is highest for *Synotis alata-Abies spectabilis* compared to all other syntaxa of the same rank. This community is marked by a characteristic species combination including 10 highly diagnostic and 14 diagnostic species (Table 1). Eleven diagnostic species are simultaneously diagnostic for the *Ribes glaciale-Abies spectabilis* community, reflecting the close syntaxonomical relation between both communities (Table 1).

Group 1.2: *Ribes glaciale-Abies spectabilis* community

This community of tall mixed forest stands attains a height of c. 17 m and occupies steep slopes (mean of 37°) in the upper subalpine range of the treeline ecotone (3,800 to 4,050 m a.s.l.). *Betula utilis, Abies spectabilis and Rhododendron campanulatum* dominate the tree layer (mean cover tree layer 1: 41%; tree layer 2: 61%), in which *Sorbus microphylla* regularly occurs and *Acer caudatum* occasionally occurs. Compared to the *Synotis alata-Abies spectabilis* community, *Betula utilis* and *Rhododendron campanulatum* tree individuals are more frequent. The shrub layer (mean cover 38%) is mainly composed of tree layer species and of *Ribes glaciale* and *Rosa sericea*. With a mean of 23 vascular plant taxa, the species richness of the *Ribes glaciale-Abies spectabilis* community is slightly lower than of the *Synotis alata-Abies spectabilis* community. The community is defined by four highly diagnostic and 10 diagnostic species (Table 1). Within the forest communities, the *Ribes glaciale-Abies spectabilis* community occupies an intermediate position regarding ground vegetation cover and productivity. Tall forbs are missing and ground vegetation is less dense (average cover of 34%) and less developed compared to the *Synotis alata-Abies spectabilis* community.

Group 1.3: *Boschniakia himalaica-Rhododendron campanulatum* community

The *Boschniakia himalaica-Rhododendron campanulatum* community represents the krummholz belt, located immediately above the *Ribes glaciale-Abies spectabilis* community in an elevational band between 3,900−4,000 m (NW-exposed) and 4,000−4,100 m (NE-exposed). It occupies steep slopes (mean of 35°) and marks the transitional zone between closed forests and alpine dwarf shrub communities. The layer (mean cover 85%) of gnarled and stunted krummholz trees attains a mean height of about 3 m, which gradually decreases upslope. The stems form a dense and largely impenetrable thicket dominated by *Rhododendron campanulatum* with few interspersed, multi-stemmed *Sorbus microphylla* individuals. This species-poor forest community with a mean species number of 12 is marked by a characteristic species combination including one highly diagnostic and one diagnostic species (Table 1). It has the lowest species diversity among the other communities of *Betula utilis-Abies spectabilis* forests. The name-giving, highly diagnostic taxon *Boschniakia himalaica* is parasitic on *Rhododendron* species (Miehe 1990). The shrub and herb layers have low height (2 m and 0.1 m, respectively) and cover (17.5% and 25%, respectively). The low productivity of these layers is further indicated by the low numbers of vascular plant species.

Class 2: *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths

In the Rolwaling Valley, communities of this class occur above the treeline in an elevational range between 3,950 and 4,300 m a.s.l. The *Rhododendron* dwarf thickets are distributed on podzols with pH values of c. 3.0 and are formed by *Rhododendron anthopogon*, *Rhododendron setosum* and *Rhododendron lepidotum*. The communities associated with this class contain 50 species. Following a threshold value of 0.3 for the phi coefficient, the classes *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths and subordinated communities were defined by 19 and 24 diagnostic species, respectively (Table 1).

Group 2.1: *Pedicularis cf. microcalyx-Rhododendron anthopogon* community

This dense dwarf thicket community with grasses in the understory and interspersed low-growing tree individuals is established on steep slopes (37° on average) immediately above the krummholz belt, at elevations between 3,950 and 4,150 m a.s.l. The dwarf scrub heaths reach a mean height of 0.8 m and a mean cover of 80%. Different *Rhododendron* species (*Rhododendron anthopogon, Rhododendron lepidotum*, dwarf individuals of *Rhododendron campanulatum*) dominate the community, with interspersed *Bistorta vacciniifolia* shrubs and *Sorbus microphylla* shrubs or small trees. The herb layer is less developed (mean height 0.1 m, mean cover 45%) and composed of fern species and species of the genera *Kobresia* and *Calamagrostis*. With a mean species number of 11, this community is species poor compared to the other communities of the treeline ecotone. The floristic composition is comparatively inhomogeneous. As apparent from the DCA (Fig. 5), relevés are arranged over a relatively wide range along Axis 1, intersecting the adjacent *Boschniakia himalaica-Rhododendron* *campanulatum* and the *Anaphalis royleana-Rhododendron anthopogon* community. The characteristic species combination is marked by one highly diagnostic and four diagnostic species (Table 1).

Group 2.2: *Anaphalis royleana-Rhododendron anthopogon* community

This open dwarf thicket community occurs in the uppermost zone of the treeline ecotone, extending over an elevational range between 4,100 and 4,300 m a.s.l. The herbaceous layer has a mean cover of 50% and is not as sparse as in the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community. The *Rhododendron* shrub layer has a mean cover of 60% and attains a height of less than 50 cm, interspersed by single higher shrub individuals (*Dasiphora arbuscula, Sorbus microphylla*). The shrub layer is dominated by *Bistorta vacciniifolia, Rhododendron setosum* and *Dasiphora arbuscula*. The comparatively rich herb layer involves the comparatively high species richness mentioned above, where grass taxa are especially frequent (genera *Calamagrostis* and *Kobresia* and others). With a mean species number of 19, the species richness of this dwarf shrub community is distinctly higher compared to the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community adjoining below. The *Anaphalis royleana-Rhododendron anthopogon* community is marked by a characteristic species combination including 13 highly diagnostic and 10 diagnostic species (Table 1).

Table 1. Synoptic table of the proposed vegetation classes and rankless communities. Numbers represent percentage frequencies and modified fidelity phi coefficients multiplied by 100 (superscript). Phi coefficients refer to fidelity among all communities and among classes. Diagnostic species were selected applying a threshold of phi ≥ 0.3 and a significant concentration at $\alpha = 0.05$ according to Fisher's exact test. Character species are highlighted in dark grey at the lowest level where they are diagnostic. Transgressive character species are highlighted in light grey.

Group No.	**1**	**2**	**1.1**	**1.2**	**1.3**	**2.1**	**2.2**
Number of relevés	**66**	**25**	**27**	**28**	**11**	**8**	**17**
Mean species richness	**20**	**15**	**25**	**23**	**12**	**11**	**19**
Number of diagnostic species	**28**	**19**	**24**	**14**	**2**	**5**	**23**
Class 1							
***Betula utilis-Abies spectabilis* forests**							
Betua utilis	88 ^{84}	4 ·	93 ^{43}	100 ^{50}	45 ·	12 ·	--- ·
Circaea alpina subsp. *micrantha*	80 ^{82}	--- ·	89 ^{47}	89 ^{47}	36 ·	--- ·	--- ·
Abies spectabilis	85 ^{77}	8 ·	93 ^{46}	100 ^{54}	27 ·	--- ·	12 ·
Ribes griffithii	67 ^{66}	4 ·	70 ^{34}	79 ^{42}	27 ·	12 ·	--- ·
Rubus fragarioides	38 ^{48}	--- ·	48 ^{39}	43 ^{32}	--- ·	--- ·	--- ·
Class 2							
***Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrubs**							
Cassiope fastigiata	9 ·	84 ^{75}	--- ·	7 ·	36 ·	88 ^{45}	82 ^{40}
Rhododendron anthopogon	26 ·	96 ^{72}	4 ·	29 ·	73 ^{13}	100 ^{41}	94 ^{35}
Group 1.1							
***Synotis alata-Abies spectabilis* community**							
Synotis alata	48 ^{57}	--- ·	93 ^{81}	25 ·	--- ·	--- ·	--- ·

Group No.	**1**	**2**	**1.1**	**1.2**	**1.3**	**2.1**	**2.2**
Number of relevés	**66**	**25**	**27**	**28**	**11**	**8**	**17**
Mean species richness	**20**	**15**	**25**	**23**	**12**	**11**	**19**
Number of diagnostic species	**28**	**19**	**24**	**14**	**2**	**5**	**23**
Clintonia udensis	33^{45}	--- ·	74^{78}	7 ·	--- ·	--- ·	--- ·
Parasenecio quinquelobus	71^{74}	--- ·	96^{65}	75^{43}	--- ·	--- ·	--- ·
Stipa roylei	23^{36}	--- ·	52^{65}	4 ·	--- ·	--- ·	--- ·
Pilea racemosa	70^{73}	--- ·	96^{62}	61 ·	27 ·	--- ·	--- ·
Acer caudatum	56^{62}	--- ·	85^{62}	43 ·	18 ·	--- ·	--- ·
Bistorta amplexicaulis	73^{76}	--- ·	96^{60}	68^{30}	27 ·	--- ·	--- ·
Impatiens racemosa var. *ecalcarata*	15^{29}	--- ·	37^{57}	--- ·	--- ·	--- ·	--- ·
Viola biflora	38^{48}	--- ·	59^{53}	32 ·	--- ·	--- ·	--- ·
Prunus rufa	12 ·	--- ·	30^{50}	--- ·	--- ·	--- ·	--- ·
Koenigia nepalensis	11 ·	--- ·	26^{47}	--- ·	--- ·	--- ·	--- ·
Maianthemum purpureum	17^{30}	--- ·	30^{40}	11 ·	--- ·	--- ·	--- ·
Aruncus dioicus subsp. *triternatus*	14^{27}	--- ·	26^{39}	7 ·	--- ·	--- ·	--- ·
Thalictrum cultratum	33^{45}	--- ·	44^{39}	36 ·	--- ·	--- ·	--- ·
Deparia allantodioides	70^{46}	24 ·	85^{38}	64 ·	45 ·	12 ·	29 ·
Carex munda	47^{24}	24 ·	63^{37}	50 ·	--- ·	--- ·	35 ·
Carex lehmannii	27 ·	24 ·	52^{34}	14 ·	--- ·	25 ·	24 ·
Polygonatum kansuense	11 ·	--- ·	19^{30}	7 ·	--- ·	--- ·	--- ·
Group 1.2							
***Ribes glaciale-Abies spectabilis* community**							
Ribes glaciale	61^{66}	--- ·	48 ·	89^{63}	18 ·	--- ·	--- ·
Rosa sericea	76^{69}	8 ·	78^{38}	96^{57}	18 ·	--- ·	12 ·
Koenigia delicatula	73^{76}	--- ·	59 ·	93^{52}	55 ·	--- ·	--- ·
Saxifraga pallida	14^{27}	--- ·	--- ·	29^{40}	9 ·	--- ·	--- ·
Galium paradoxum	42^{52}	--- ·	33 ·	57^{40}	27 ·	--- ·	--- ·
Scrophularia pauciflora	33^{38}	4 ·	37 ·	43^{34}	--- ·	--- ·	6 ·
Juncus thomsonii	45 ·	36 ·	41 ·	64^{31}	9 ·	12 ·	47 ·
Group 1.3							
***Boschniakia himalaica-Rhododendron campanulatum* community**							
Boschniakia himalaica	20 ·	12 ·	--- ·	21 ·	64^{51}	12 ·	12 ·
Cryptogramma stelleri	18^{32}	--- ·	7 ·	21 ·	36^{35}	--- ·	--- ·
Group 2.1							
***Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community**							
Pedicularis cf. *microcalyx*	--- ·	68^{72}	--- ·	--- ·	--- ·	75^{52}	65^{41}
Rhododendron lepidotum	15 ·	44^{32}	7 ·	18 ·	27 ·	75^{47}	29 ·
Group 2.2							
***Anaphalis royleana-Rhododendron anthopogon* community**							
Anaphalis royleana	--- ·	64^{69}	--- ·	--- ·	--- ·	--- .	94^{96}
Codonopsis thalictrifolia	--- ·	60^{66}	--- ·	--- ·	--- ·	--- .	88^{93}
Rhododendron setosum	2 ·	76^{76}	--- ·	4 ·	--- ·	25 ·	100^{85}
Kobresia nepalensis	--- ·	68^{72}	--- ·	--- ·	--- ·	25 ·	88^{78}
Calamagrostis lahulensis	--- ·	77^{78}	--- ·	--- ·	--- ·	38 ·	94^{77}
Salix calyculata	2 ·	44^{51}	--- ·	4 ·	--- ·	--- ·	65^{65}
Dasiphora arbuscula	3 ·	84^{82}	--- ·	4 ·	9^{9}	50 ·	100^{72}
Pedicularis lachnoglossa	3 ·	40^{45}	4 ·	4 ·	--- ·	--- ·	59^{67}
Lonicera litangensis	9 ·	56^{50}	11 ·	11 ·	--- ·	12 ·	76^{65}
Bistorta vivipara	2 ·	44^{51}	--- ·	4 ·	--- ·	$12^{1.}$	59^{61}
Rhodiola spec.	8 ·	92^{84}	--- ·	7 ·	27^{27}	75^{34}	100^{59}
Anaphalis nepalensis	--- ·	24^{37}	--- ·	--- ·	--- ·	--- ·	35^{55}
Swertia cuneata	--- ·	24^{37}	--- ·	--- ·	--- ·	--- ·	35^{55}
Hierochloe flexuosa	--- ·	20^{33}	--- ·	--- ·	--- ·	--- ·	29^{50}
Calamagrostis spec.	--- ·	16^{30}	--- ·	--- ·	--- ·	--- ·	24^{44}
Rheum australe	33 ·	56^{23}	59^{25}	18 ·	9^{9}	12 ·	76^{43}
Saussurea spec.	--- ·	12^{25}	--- ·	--- ·	--- ·	--- ·	18^{38}
Theropogon pallidus	--- ·	12^{25}	--- ·	--- ·	--- ·	--- ·	18^{38}

Group No.	**1**	**2**	**1.1**	**1.2**	**1.3**	**2.1**	**2.2**
Number of relevés	**66**	**25**	**27**	**28**	**11**	**8**	**17**
Mean species richness	**20**	**15**	**25**	**23**	**12**	**11**	**19**
Number of diagnostic species	**28**	**19**	**24**	**14**	**2**	**5**	**23**
Bistorta vacciniifolia	45 ·	92 ^{50}	22 ·	54 ·	82 ·	75 ·	100 ^{36}
Agrostis inaequiglumis	2 ·	12 ·	--- ·	4 ·	--- ·	--- ·	18 ^{33}
Companion species							
Acanthocalyx nepalensis	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Anaphalis contorta	3 ·	4 ·	--- ·	7 ·	--- ·	--- ·	6 ·
Aconogonon polystachyum	14 ·	4 ·	19 ·	14 ·	--- ·	--- ·	6 ·
Acronema tenerum	91 ^{24}	72 ·	93 ·	89 ·	91 ·	38 ·	88 ·
Agrostis spec. I	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Agrostis spec. II	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Arisaema jacquemontii	3 ·	4 ·	--- ·	7 ·	--- ·	12 ·	--- ·
Athyrium rupicola	23 ·	20 ·	11 ·	32 ·	27 ·	25 ·	18 ·
Carex setosa	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·
Clematis spec.	5 ·	--- ·	7 ·	4 ·	--- ·	--- ·	--- ·
Cremanthodium reniforme	5 ·	--- ·	4 ·	7 ·	--- ·	--- ·	--- ·
Cystopteris cf. *montana*	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Cystopteris fragilis	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·
Dryopteris acutodentata	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Epilobium cf. *laxum*	11 ·	--- ·	15 ·	11 ·	--- ·	--- ·	--- ·
Goodyera fusca	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·
Goodyera repens	11 ·	--- ·	11 ·	14 ·	--- ·	--- ·	--- ·
Hemiphragma heterophyllum	6 ·	--- ·	4 ·	11 ·	--- ·	--- ·	--- ·
Impatiens urticifolia	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Juniperus indica	2 ·	4 ·	--- ·	4 ·	--- ·	--- ·	6 ·
Juniperus squamata	5 ·	4 ·	4 ·	7 ·	--- ·	--- ·	6 ·
Lepisorus cf. *clathratus*	61 ^{46}	16 ·	70 ^{28}	64 ^{22}	27 ·	50 ·	--- ·
Listera pinetorum	3 ·	--- ·	7 ·	--- ·	--- ·	--- ·	--- ·
Lonicera lanceolata	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Malaxis cylindrostachya	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Myriactis nepalensis	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·
Pedicularis furfuracea	3 ·	--- ·	7 ·	--- ·	--- ·	--- ·	--- ·
Phlomis breviflora	5 ·	--- ·	4 ·	7 ·	--- ·	--- ·	--- ·
Phymatopteris malacodon	92 ^{55}	40 ·	89 ·	100 ^{30}	82 ·	75 ·	24 ·
Poa spec. I	17 ·	4 ·	19 ·	18 ·	9 ·	--- ·	6 ·
Poa spec. II	2 ·	--- ·	--- ·	--- ·	9 ·	--- ·	--- ·
Polypodiodes lachnopus	11 ·	--- ·	11 ·	11 ·	9 ·	--- ·	--- ·
Potentilla aristata	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·	6 ·
Primula sikkimensis	6 ·	--- ·	11 ·	4 ·	--- ·	--- ·	--- ·
Rhodiola fastigiata	3 ·	--- ·	4 ·	4 ·	--- ·	--- ·	--- ·
Rhododendron campanulatum	92 ^{31}	68 ·	81 ·	100 ·	100 ·	88 ·	59 ·
Ribes acuminatum	24 ^{37}	--- ·	22 ·	29 ·	18 ·	--- ·	--- ·
Saxifraga granulifera	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Saxifraga hispidula	8 ·	8 ·	--- ·	14 ·	9 ·	--- ·	12 ·
Saxifraga pernes	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Selinum cf. *wallichianum*	17 ·	4 ·	22 ·	18 ·	--- ·	12 ·	--- ·
Sorbus microphylla agg.	100 ^{62}	44 ·	100 ^{23}	100 ^{23}	100 ·	88 ·	24 ·
Spiraea arcuata	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Streptopus simplex	3 ·	--- ·	7 ·	--- ·	--- ·	--- ·	--- ·
Trillium govanianum	18 ^{32}	--- ·	22 ·	21 ·	--- ·	--- ·	--- ·
Utricularia spec.	6 ·	--- ·	--- ·	11 ·	9 ·	--- ·	--- ·
Valeriana hardwickii	2 ·	4 ·	4 ·	--- ·	--- ·	--- ·	6 ·

Discussion

The vegetation zonation and photosociological differentiation assessed in this study for the Rolwaling Valley more or less corresponds to the patterns described in previous studies on subalpine forest vegetation and alpine dwarf shrub vegetation in the west and central Himalaya. Mixed forest stands are dominated by conifers (mainly *Abies* species), with varying proportions of the Himalayan birch (*Betula utilis*) and other deciduous trees (Schweinfurth 1957; Miehe 1990; Schickhoff 1993; Miehe and Miehe 2000; Schickhoff 2005; Miehe, Miehe, et al. 2015b). The forests merge into krummholz thickets, mainly composed of *Rhododendron* species, forming the transitional zone to the alpine *Rhododendron* dwarf thickets and *Kobresia* mats further upslope. As we did not find any evidence of human impact except some logged trees at low elevations, we consider the state of the Rolwaling treeline ecotone and vegetation zonation as near-natural (Schwab et al. 2016). However, a closed belt of pure *Betula utilis* stands above the mixed forest stands of *Abies spectabilis-Betula utilis* - as described by Schickhoff (1993, 2005), Miehe (1990), and Miehe et al. (2015b) for shady slopes in western and central Himalaya - is not developed in the Rolwaling Valley. It could be assumed that *Abies* trees have been eliminated from many treeline forest stands in the Himalaya by logging and cutting for firewood, and that pure *Betula utilis* forests have emerged from former mixed forest stands under devastating human impact (Schickhoff 2005). On the other hand, *Betula utilis* forests are considered climax communities at treelines in inner Himalayan valleys which are currently in the state of regressive successions (Miehe et al. 2015b).

Krummholz thickets are widely distributed at treeline elevations in the Himalaya, consisting of trees with gnarled, stunted growth forms due to deteriorating climatic conditions (Holtmeier 2009). We assigned the *Rhododendron campanulatum* krummholz belt (*Boschniakia himalaica-Rhododendron campanulatum* community) to the class *Betula utilis-Abies* spectabilis forests. The *Rhododendron campanulatum* krummholz belt floristically has a transitional character to some extent, with floristic affinities to both classes separated here. For instance, some diagnostic species of the dwarf shrub communities above the krummholz belt (*Rhododendron anthopogon*, *Bistorta vaccinifolia*) occur with high frequency also in the *Boschniakia himalaica-Rhododendron campanulatum* community. However, the krummholz community and the mixed forest communities exhibit a large number of common highly frequent species which separates them from the dwarf shrub communities (inter alia *Galium paradoxum*, *Koenigia delicatula*, *Deparia allantodioides*, cf. Table 1). Moreover, the krummholz belt has a predominantly forest-like physiognomy, which also suggests a closer relation to the class of *Betula utilis-Abies spectabilis* forests. With regard to classification of treeline forms, the Rolwaling treeline must be assigned to treelines with a krummholz belt sensu Holtmeier 2009 (Schickhoff et al. 2015; Schwab et al. 2016).

The species composition and community structure of Rowaling subalpine mixed forest stands largely corresponds to the description of *Abies spectabilis* forests from the Langtang/Helambu region (Miehe 1990). In correspondence to the provisional class *Abietea himalayae* proposed by Miehe (1990), we assigned the differentiated forest communities (*Synotis alata-Abies spectabilis* community*, Ribes glaciale-Abies spectabilis* community and *Boschniakia himalaica-Rhododendron campanulatum* community) to the class *Betula utilis-Abies spectabilis* forests. However, in contrast to Miehe (1990), we consider more relevé material to be necessary for providing an original diagnosis of a phytosociological class.

Rhododendron dwarf thickets are developed on shady, north-facing slopes along the entire Himalayan arc under cold, semi-humid to sub-humid climatic conditions in the alpine belt (Miehe et al. 2015b). The communities are mainly composed of different small-leaved *Rhododendron* species (*Rhododendron anthopogon, Rhododendron setosum, Rhododendron nivale*) with generally sparsely developed herbaceous layers (Schweinfurth 1957; Kikuchi and Ohba 1988; Miehe 1990; Schickhoff 1993; Miehe, Miehe, et al. 2015b). As very few phytosociological studies in alpine altitudinal zones of the Himalaya have been conducted to date, a syntaxonomical scheme for the respective vegetation units has not been established. The *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* and *Anaphalis royleana-Rhododendron anthopogon* communities are classified here for the first time. Furthermore, on the basis of our study results and the long-term experience of our working group in the alpine belt of many Himalayan regions and in accordance with the synopsis of the lower alpine dwarf shrub communities in European mountains such as *Loiseleurio-Vaccinietea* (cf. Mucina et al. 1993; Dúbravcová et al. 2005; Šibík et al. 2006), we establish the class '*Rhododendretea anthopogonis*', which incorporates Himalayan *Rhododendron* dwarf shrub heaths.

4.2. Vegetation-environment relationships (study 1)

Results

After implementation of the DCA, post-hoc correlation of environmental parameters reveals interrelations between vegetation types and surrounding growth conditions. As mentioned above, the phytosociological groups are arranged and clearly separated along Axis 1 (DCA, Fig. 5), which primarily represents an elevational gradient with complex interrelations of edaphic site factors (Fig. 5, Table 2). The mean annual soil temperature decreases along this gradient, with significant differences between plant communities of lower and upper elevations (Table 3). Moreover, Axis 1 is significantly correlated with the CN ratio, nitrogen and iron content, thickness of the uppermost mineral horizon (Ah) and proportion of silt and sand within the soil texture (Table 2). The communities occupy steep slopes (average inclination between 33° and 37°) without exception. However, we found slope inclination as well as slope aspect to play a negligible role for community differentiation along the treeline ecotone (Table 2, Table 3).

The environmental conditions appear to be similar between *Synotis alata-Abies spectabilis* and *Ribes glaciale-Abies spectabilis* communities, as the relevé groups are arranged in a considerably narrow range along Axes 1 and 2 (Fig. 5). The relevé groups of the dwarf shrub communities *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community and *Anaphalis royleana-Rhododendron anthopogon* community are arranged over a broader space along Axis 1, indicating more heterogeneous environmental conditions (Fig. 5). Beyond elevation, Axis 2 corresponds to an edaphic gradient, with changes in soil nutrient availability and grain size distribution (Table 2). However, while relevés of the class *Betula utilis-Abies spectabilis* forests are separated along this elevational-edaphic gradient (cf. Fig. 5), relevés of the class *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths are more heterogeneously arranged along Axis 2.

Class 1: *Betula utilis-Abies spectabilis* forests

These forest communities are developed on podzol soils with an extremely low pH-value of c. 3.0 (Table 3). As the DCA (Fig. 5, Table 2) and the ANOVA (Table 3) suggest, the altitude and mean soil temperature appear to be the decisive ecological factors for differences in species composition of the three syntaxa. In addition, nutrient storage, water-holding capacity and soil humidity deteriorate towards higher altitudes, as grain size distribution of the soils (sandy loams) changes in favour of the sandy fraction (Table 3).

Group 1.1: *Synotis alata-Abies spectabilis* community

The floristic differentiation of the *Synotis alata-Abies spectabilis* community is highly correlated with the CN ratio and nitrogen and potassium content, as apparent from the DCA (Fig. 5) and associated correlation coefficients (Table 2). In addition, the ANOVA (Table 3) reveals the highest nitrogen and potassium contents (insignificant) in the *Synotis alata-Abies spectabilis* community. At the same time, the CN ratio narrows (insignificant) (Table 3), indicating higher decomposition rates. We measured the highest annual soil temperature (significant) and annual soil humidity (insignificant) values for the *Synotis alata-Abies spectabilis* community (Table 3). The latter is supported by the highly diagnostic species *Clintonia udensis,* which is considered an indicator species for humid soil conditions (Miehe 1990).

Group 1.2: *Ribes glaciale-Abies spectabilis* community

The constellation of site factors (e.g., soil temperatures, nutrient availability) and resulting growth conditions also provide evidence of an intermediate position of the *Ribes glaciale-Abies spectabilis* community. The soil temperature during summer months is significantly lower compared to the *Synotis alata-Abies spectabilis* community, but higher (insignificant) than in the adjoining krummholz belt (Table 3). The same holds true for the CN ratio and content of potassium. However, the nitrogen supply in the *Ribes glaciale-Abies spectabilis* community is the lowest (insignificant) among the three forest communities, though still higher than in the *Rhododendron* dwarf shrub communities (Table 3). As mentioned above, the CN ratio and nitrogen content play an important role for floristic differentiation within the complete treeline ecotone, while potassium is significant only for the floristic dissimilarity between *Ribes glaciale-Abies spectabilis* and *Synotis alata-Abies spectabilis* communities (Fig. 5).

Group 1.3: *Boschniakia himalaica-Rhododendron campanulatum* community

The *Boschniakia himalaica-Rhododendron campanulatum* community has to cope with further deteriorating growth conditions along the elevational gradient (see also Müller et al. 2016a). As the ANOVA revealed (Table 3), annual mean soil temperature and connected growing degree days are lower compared to the downslope communities. At the same time, the CN ratio widens, indicating lower decomposition rates and lower availability of nitrogen.

Class 2: *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths

As explained above, the growth conditions deteriorate along the elevational gradient. Thus, the sites of *Rhododendron* dwarf shrub communities are characterised by lower soil temperatures, wider CN ratios and lower nitrogen content compared to the forest communities of class 1 (Table 3).

Group 2.1: *Pedicularis cf. microcalyx-Rhododendron anthopogon* community

The growth conditions are less favourable in comparison with the forest communities. Mean soil temperatures (insignificant), base saturation (insignificant), and nitrogen contents (insignificant) are reduced (cf. Table 3).

Group 2.2: *Anaphalis royleana-Rhododendron anthopogon* community

Corresponding to the elevational gradient (see DCA, Fig. 3), site conditions are the most unfavourable within the treeline ecotone. The habitats there are characterised by low mean soil temperatures during the vegetation period and a lower number of growing degree days, and soil moisture is comparatively limited owing to a decrease in silt content (significant; Table 3). The decreasing thickness of the Ah-horizon (significant; Table 3) reflects low mineralisation rates on the one hand, and a decrease in biomass and litter production on the other. However, the nitrogen content and CN ratio are in a comparable range as observed for the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community. Mn contents are significantly higher (cf. Table 3).

Table 2. Kendall's r non-parametric correlation coefficients of environmental parameters with ordination scores of plots for the first three axes of the DCA presented in Fig. 2 (*: $P < 0.05$; **: $P < 0.01$).

	Axis1 *r*	Axis 2*r*	Axis 3 *r*
Landscape parameters			
Altitude (m a.s.l.)	0.705^{**}	0.215^{**}	0.274^{**}
Inclination (°)	0.105	0.018	0.199^{**}
Aspect (°)	0.075	0.061	0.109
Soil parameters			
pH (KCl)	0.048	−0.085	−0.066
C_t (%)	−0.069	−0.078	−0.083
N_t (%)	-0.257^{**}	−0.109	-0.190^{**}
CN ratio	0.291^{**}	0.003	0.129
CEC (μmol_c/g)	−0.016	0.011	−0.122
Base saturation (%)	−0.010	0.004	-0.168^{*}
Exchange acidity (μmol_c/g)	−0.025	−0.063	0.132
Na (μmol_c/g)	−0.026	-0.162^{*}	−0.069
K (μmol_c/g)	0.009	-0.158^{*}	−0.090
Mg (μmol_c/g)	−0.007	−0.040	−0.084
Ca (μmol_c/g)	−0.040	0.006	−0.127
Mn (μmol_c/g)	0.006	−0.087	−0.102
Fe (μmol_c/g)	0.145^{*}	−0.080	0.206^{**}
Al (μmol_c/g)	0.036	−0.071	0.196^{**}
Ah (cm)	-0.228^{**}	0.073	−0.063
Organic (%)	−0.067	−0.091	−0.099
Sand (%)	0.298^{**}	0.219^{**}	0.220^{**}
Silt (%)	-0.351^{**}	−0.134	-0.301^{**}
Clay (%)	−0.092	-0.222^{**}	−0.004

Table 3. Mean values (Mean) and standard deviation (SD) for investigated environmental parameters. Differences between phytosociological groups were tested with one-way-ANOVAs. Level of significance (α) was set at 0.05. Superscript letters signify results of *post-hoc* pairwise t-test with Holm correction. The last column shows overall significance pattern abridged with significance codes: < 0.001 '***'; < 0.01 '**'; < 0.05 '*'.

Parameters	*Synotis alata – A. spectabilis* community				*Ribes glaciale – A. spectabilis* community				*Boschniakia himalaica – R. campanulatum* community				*Pedicularis* cf. *microcalyx – R. anthopogon* community				*Anaphalis royleana – R. anthopogon* community				P
	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	
Landscape parameters																					
Altitude (m.a.s.l.)	27	3815.5	44.1	^{a}	28	3928.5	58.0	^{b}	11	4051.4	60.1	^{c}	8	4098.4	72.8	^{c}	17	4215.1	43.3	^{d}	***
Inclination (°)	27	33.2	4.4	^{a}	28	36.9	3.5	^{b}	11	35.1	3.1	^{ab}	8	37.1	3.6	^{ab}	17	33.4	3.3	^{a}	**
Exposition (°)	27	41.4	63.0		28	50.9	62.1		11	91.7	128.4		8	75.3	114.2		17	38.0	17.0		
Soil parameters																					
pH (KCl)	27	3.1	0.4	^{ab}	28	3.0	0.3	^{a}	11	2.8	0.3	^{a}	8	3.0	0.2	^{ab}	17	3.2	0.2	^{b}	**
Ct (%)	27	29.6	12.3		28	25.9	13.6		11	34.4	12.4		8	26.6	13.7		17	23.6	11.8		
Nt (%)	27	1.5	0.6	^{a}	28	1.3	0.6	^{ab}	11	1.4	0.4	^{ab}	8	1.1	0.5	^{ab}	17	1.0	0.3	^{b}	**
CN ratio	27	19.6	3.2	^{a}	28	20.4	2.6	^{a}	11	24.1	4.6	^{b}	8	23.9	3.1	^{b}	17	23.9	4.8	^{b}	***
CEC (µmolc/g)	27	188.0	135.1		28	188.6	116.4		11	234.3	117.4		8	183.7	120.3		17	151.0	68.0		
Base saturation (%)	27	61.1	22.7		28	57.0	24.6		11	66.8	19.7		8	40.5	17.7		17	67.0	20.5		*
Exchange acidity (µmolc/g)	27	67.1	39.7	^{ab}	28	68.2	43.2	^{ab}	11	75.5	45.3	^{ab}	8	106.0	53.2	^{a}	17	45.2	18.6	^{b}	*
Na (µmolc/g)	27	0.3	0.2		28	0.2	0.3		11	0.2	0.1		8	0.2	0.2		17	0.3	0.5		
K (µmolc/g)	27	10.8	7.5		28	8.2	5.3		11	8.9	4.4		8	7.8	4.3		17	10.5	5.4		
Mg (µmolc/g)	27	32.0	25.6		28	29.7	23.3		11	42.3	23.8		8	19.7	12.2		17	30.0	20.4		
Ca (µmolc/g)	27	109.6	119.3		28	107.1	99.1		11	142.0	122.8		8	58.3	71.9		17	86.8	60.8		
Mn (µmolc/g)	27	5.4	12.7	^{ab}	28	3.7	7.3	^{ab}	11	0.9	0.9	^{ab}	8	0.5	0.3	^{a}	17	4.4	4.8	^{b}	***
Fe (µmolc/g)	27	7.7	8.9		28	7.3	7.5		11	11.4	10.0		8	9.3	2.7		17	7.4	5.3		*
Al (µmolc/g)	27	35.4	29.8	^{ab}	28	32.7	26.9	^{ab}	11	34.7	25.5	^{ab}	8	49.6	21.2	^{a}	17	24.2	15.9	^{b}	*
Ah (cm)	27	8.3	7.1	^{a}	28	9.2	6.2	^{a}	11	9.3	5.4	^{a}	8	11.1	10.9	^{a}	17	2.8	2.4	^{b}	***
Organic (%)	27	51.7	21.6		28	44.3	23.4		11	59.2	21.4		8	46.3	22.9		17	41.3	20.0		
Sand (%)	23	56.9	16.9		25	61.1	14.0		9	68.6	10.7		8	69.5	6.2		17	68.0	5.9		
Silt (%)	23	28.0	6.6	^{a}	25	26.0	5.3	^{a}	9	22.1	6.7	^{ab}	8	22.1	5.7	^{ab}	17	19.0	4.1	^{b}	***
Clay (%)	23	15.0	11.3		25	12.9	11.0		9	9.3	5.2		8	8.4	3.6		17	13.0	5.4		
Climate parameters																					
mean soil temp. (year) [°C]	6	3.5	0.6	^{ab}	8	3.6	0.4	^{b}	3	2.7	0.4	^{abc}	6	2.5	0.7	^{ac}	3	2.5	0.8	^{c}	***
mean soil temp. (ON) [°C]	7	3.1	0.7		10	3.3	0.6		3	2.8	0.4		6	2.6	0.8		3	2.7	0.2		
mean soil temp. (DJF) [°C]	7	-2,1	1,4		8	-0,9	0.7		3	-1,9	0.8		6	-2,9	1.5		3	-2,2	0.9		
mean soil temp. (MAM) [°C]	6	1,3	0.6		8	1,3	0.8		3	0.3	0.2		6	0.3	0.5		3	0.0	0.4		*

Parameters	*Synotis alata – A. spectabilis* community				*Ribes glaciale – A. spectabilis* community				*Boschniakia himalaica – R. campanulatum* community				*Pedicularis* cf. *microcalyx – R. anthopogon* community				*Anaphalis royleana – R. anthopogon* community				P
	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	
Climate parameters																					
mean soil temp. (JJAS) [°C]	7	9,5	0.2	a	10	8,8	0.4	b	3	7,8	0.6	ab	6	8,2	0.7	ab	3	7,8	0.7	ab	**
Growing degree days	7	169.6	8.3	a	8	169.3	15.0	ab	3	141.7	4.5	c	6	146.8	11.9	bc	3	137.7	10.7	ac	**
Mean Soil Humidity (year) [pF]	7	2.1	0.5		10	2.3	0.6		3	2.3	0.2		7	2.3	0.4		3	2.6	0.4		

Discussion

The relevant drivers for community differentiation in Rolwaling are soil temperature, nitrogen content and availability, soil nutrient storage and soil water-holding capacity. The soil studies in Rolwaling (Müller et al. 2016a, b) revealed a general decrease in nutrient availability, as well as in annual mean and growing season mean soil temperatures, from closed forest to the krummholz zone and dwarf shrub thickets (Müller et al. 2016a) and concurrently along the altitudinal sequence of communities in Rolwaling. Thus, the spatial patterns of plant communities in Rolwaling reflect an elevational gradient of decreasing soil fertility, parallel to the overall decrease of temperatures in the same direction.

Although nitrogen is the most limiting factor to alpine plant productivity (Larcher 2003), plant communities by themselves are not nitrogen limited, as the species composition is adapted to the prevailing nutrient supply and nutrient enrichment creates modified communities (Körner 2003). We related the lower nitrogen availability (wider CN ratio) in the krummholz and dwarf shrub communities (Table 2) to a low leaf litter quality (wide CN ratio, high lignin content; Maithani et al. 1998; Körner 2003) of ericaceous trees (*Rhododendron* krummholz belt) and shrubs (*Rhododendron* dwarf shrubs). Moreover, the high concentrations of polyphenols in *Rhododendron* leaves (Hegnauer and Hegnauer 1966; Fan et al. 1999) may lead to the binding of N into complex polyphenolic compounds, and further to an increase in $NH4^+$ and NO3 immobilisation (Northup et al. 1995; Schimel et al. 1996; Bradley et al. 2000; DeLuca et al. 2002) and thereby a further decrease of nitrogen availability.

Apart from polyphenols, *Rhododendron* species also contain triterpenes (Hegnauer and Hegnauer 1966; Fan et al. 1999), both of which are known to be potentially allelopathic (Rice 1984; Li et al. 2010; Kadereit et al. 2014). We hypothesise that the impoverished flora of the *Boschniakia himalaica-Rhododendron campanulatum* community and the extremely low productivity of the herbaceous layer can be attributed to the triterpene campanuline in *Rhododendron campanulatum* leaves (Rangaswami and Sambamurthy 1961). The triterpene may directly negatively influence seedling recruitment of other species and favour monospecific *Rhododendron* thickets. However, there is an urgent need for further studies concerning this issue, as to our knowledge, the allelophatic potential of *Rhododendron campanulatum* has not been analysed to date.

We detected soil moisture decreases along the elevational gradient in the Rolwaling treeline ecotone (Table 2, see also Müller et al. 2016a, b), with the lowest values in the *Anaphalis royleana-Rhododendron anthopogon* community. This is remarkable, as plant water supply is often improved at higher altitudes due to reduced evapotranspiration (Körner 2003) as long as increasing wind speed does not overcompensate a decrease in evaporation (cf. Holtmeier

2009). In our study area, the low topsoil moisture may be largely caused by overall low water-holding capacities due to soil texture (Müller et al. 2016b), in combination with low soil depth and a weakly developed, thin Ah-horizon of the *Anaphalis royleana-Rhododendron anthopogon* community (Table 2). Dehydration of the topsoil has strong effects on plant nutrition by interrupting topsoil nutrient cycling and thus reducing nutrient availability (Marschner and Rengel 2012). The effects of this 'drought-enhanced nutrient shortage' on plant life and therefore species distribution are even more appreciable than moisture stress alone (Körner 2003).

The soil studies in Rolwaling Valley (Müller et al. 2016a, b; Drollinger et al. 2017) revealed significantly decreasing nutrient availability (N, K, Mg, P) along the elevational gradient from subalpine forests to krummholz and dwarf shrub thickets. On the level of plant communities, the elevational gradients of soil nutrient contents are, with the exception of nitrogen, less obvious: soil nutrient contents demonstrate either significant differences between single plant communities in the ANOVA (Mn, Al) or significant correlation with DCA axes (Fe, Na, K), never both (Table 2). Moreover, all soil nutrient contents demonstrate relatively wide standard deviations. The differences in the detectability of soil nutrient gradients between altitudinal vegetation zones and the altitudinal sequence of plant communities must be attributed to the mosaic-like pattern of respective habitat patches in the treeline ecotone. Given that alpine soils exhibit pronounced small-scale heterogeneity in terms of fertility and other properties in general (Nagy and Grabherr 2009; Bäumler 2015), further investigations are necessary to detect micro-scale relationships between plant species composition and edaphic properties.

Responsiveness of community patterns to changing environmental conditions

Our data clearly stress the significance of soil temperature, soil moisture and nitrogen (supply and availability) for species distribution along the elevational gradient. As these factors are directly (soil temperature) or indirectly (soil moisture, nitrogen) affected by climatic conditions, we presume that community patterns in the treeline ecotone (species compositions, community structure) will change with ongoing climate warming (Schickhoff et al. 2015; Schickhoff et al. 2016a, b).

Low soil temperatures are the primary constraint for nitrogen availability, which controls alpine plant productivity (Larcher 2003; Baptist and Aranjuelo 2012; Hawkesford et al. 2012). Due to higher rates of decomposition and N mineralisation, increasing temperatures may imply enhanced nitrogen supply (Nadelhoffer et al. 1991). Given the above-average warming in the Himalayan treeline ecotones including the Rolwaling Valley, an increase in plant height and cover within plant communities and a shift in dominance patterns owing to an earlier start of the growing season is to be expected. This is in line with the findings of Chandra et al. (2018), who found a positive correlation between an increase in species richness and soil temperature and greater species richness on most warm summits in the alpine zone of Tungnath, western Himalaya.

Moreover, climate warming involves changes in precipitation patterns, leading to alterations in snow cover and modified soil moisture. Early snow melt in warming climates may affect species diversity, growth and phenology of alpine plants in the Himalayan treeline ecotones. The advancement of snow melt may increase species diversity and plant density due to longer vegetative and flowering phenophases (Adhikari et al. 2018). Plant species assemblages above the treeline may also change in favour of wide-ranging species, as they have more flexible flowering phenology, and may flower longer with earlier snow melt compared to alpine-restricted species (Winkler et al. 2018). However, no clear trend could be detected for precipitation patterns in the greater Himalayan region; observations indicate more decreasing than increasing precipitation trends (Hasson 2016; Schickhoff et al. 2016a). As soil moisture was identified as one of the controlling factors for natural tree regeneration at the Himalayan treeline ecotones (Schickhoff et al. 2015) as well as for species composition in this study, we anticipate shifts in community structure and species composition due to changing precipitation, time of snow melt and soil moisture supply. However, Schwab et al. (2017) found no significant positive correlation between soil moisture and tree population density in the Rolwaling treeline ecotone. This contradiction can presumably be attributed to pronounced time lags in woody plant response to changing environmental conditions (see discussion below).

Lags in plant population and community responses to climate warming

In general, ongoing climatic changes have already triggered shifts in species distributions and abundances in the Himalaya, largely without having been noticed or documented by the science community. For instance, in the alpine Sikkim Himalaya, climate warming is causing species distribution changes, including upward elevation shifts of 87% of 124 endemic plant species studied in the region over the last 150 years (Telwala et al. 2013). Upward range shifts of up to 150 m were also detected in the NW Himalaya by Dolezal et al. (2016), who stressed that plant species responses to ongoing climate change will not be unidirectional upward range shifts, but rather multi-dimensional, species-specific and spatially variable. In the Hengduan Mountains of easternmost Himalaya, Salick et al. (2019) ascertained a distinct increase in plant diversity and the number of Himalayan endemic species over the last seven years, using multi a summit approach as per the global observation research initiative in alpine environments (GLORIA; Grabherr et al. 2000). In sum, studies suggest that present-day plant species composition and community structure in the Himalayan high mountain areas are most likely substantially different from those decades ago. However, while biodiversity changes in alpine regions in the last decades are primarily the result of colonisation of species from lower elevations (Lenoir et al. 2008), the regional extinctions of resident, cold-adapted species have been relatively few (Walther et al. 2005; Pauli et al. 2012; Kulonen et al. 2018). This may support significant lags in plant response to climate warming. Due to ‘dispersal lags’, ‘establishment lags’ and ‘extinction lags’, changes in community composition considerably trail beyond changes in climate conditions (Svenning and Sandel 2013; Corlett and Westcott 2013; Alexander et al. 2018). The magnitude of lags depends on species-specific physiology and demography (i.e. functional traits, life cycle) (Kroiss and HilleRisLambers 2015), biotic interactions (i.e. zoochory, plant-plant interactions, plant-animal interactions, mycorrhizal fungi) (HilleRisLambers et al. 2013), as well as plants’ physical environment (Scherrer and Körner 2011). Dispersal lags become most obvious at the upper treeline. Given their longer life cycles, woody subalpine species are shifting slower towards higher elevations compared to herbaceous plants (Lenoir et al. 2008). This finding is in line with Bolton et al. (2018), who reported that the most significant positive trend in vegetation greening at the alpine treeline ecotones was for herbaceous vegetation, while the trend for woody vegetation was less pronounced. Seed dispersal may be further restricted by physical topographic barriers or a dense krummholz belt (Schwab et al. 2017). Beyond species dispersal, the establishment of shifted species is especially hampered in treeline ecotones, as abrupt bioclimatic transitions at the upper treeline lead to biotic interactions between alpine species, novel competitors and natural enemies (HilleRisLambers et al. 2013). Harsh environmental conditions (extreme temperatures, high irradiance and drought) as well as poorly developed alpine soils may additionally contribute to a lag in establishment (Müller et al. 2016a, b).

Thus, time lags significantly affect the magnitude of climate-change-related species turnover (Bertrand et al. 2011). Nevertheless, the processes contributing to lags in species response to climate warming are poorly understood and are rarely considered for species distribution forecasts from statistical models (e.g. species distribution models) (Wisz et al. 2013; Bertrand et al. 2016). The lack of integration of establishment or extinction lags in particular could lead to divergences between realised community changes and expectations from SDMs (Svenning and Sandel 2013). Future research is therefore needed to understand the underlying processes in delayed species reaction to changing environmental conditions on order to make predictions about future species distribution in alpine treeline ecotones.

4.3. Exploring the regeneration niche of three tree species (study 2)

Results

General pattern and abundances

In total we recorded 784 seedlings of *Abies spectabilis*, 155 seedlings of *Betula utilis* and 1,191 seedlings of *Rhododendron campanulatum*. Table 4 provides an overview of the tree species density of seedlings in different vegetation types, separated according to seedlings' height.

Table 4. Tree species density of seedlings 0-5cm, 5-15cm, 15-50cm in the (I) lower subalpine forest, (II) upper subalpine forest, (III) Rhododendron krummholz belt, (IV) alpine dwarf shrub heath.

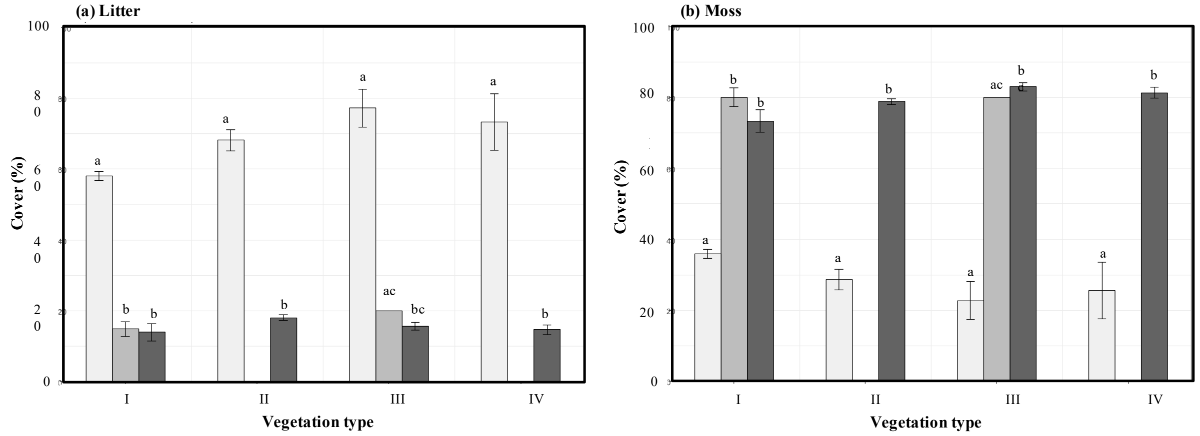
Height (cm)	**Vegetation type**	**Seedling density (N/ha) A. spectabilis**	**Seedling density (N/ha) B. utilis**	**Seedling density (N/ha) R. campanulatum**
0-5	I	34.500	3.313	3.563
0-5	II	6.688	0	39.875
0-5	III	3.125	125	33.750
0-5	IV	875	0	10.813
5-15	I	3.813	4.938	625
5-15	II	313	0	250
5-15	III	0	0	0
5-15	IV	0	0	875
15-50	I	938	1.375	63
15-50	II	188	0	438
15-50	III	250	0	125
15-50	IV	0	0	1.000

Ground cover

The three species in focus demonstrated clear habitat preferences for germination and seedling establishment. The microsite characteristics differed significantly between *Abies spectabilis* on the one hand and *Betula utilis* and *Rhododendron campanulatum* on the other (Fig.7, Table 5).

The youngest seedlings of *Abies spectabilis* (> 0–5 cm) were primarily associated with litter, while moss cover was low (Fig. 3). The microhabitat cover values of the youngest seedlings of *Betula utilis* were significantly different ($p < 0.001$). *Betula* seedlings were most frequently related to moss cover and, to a lower percentage, litter (Fig. 7). The same holds true for the youngest seedlings of *Rhododendron campanulatum*, whose microhabitats had a significantly higher moss cover and lower percentage of litter ($p < 0.001$) compared to *Abies spectabilis* (Fig. 7). These preferences were independent from altitudinal occurrence and the surrounding vegetation, as microsite characteristics of all species did not significantly differ between vegetation types (p < 0.001). Field layer vegetation and the early successional groundcover types ‘bare soil’ and ‘stones’ played a negligible role for seedling establishment of all species with cover values less than 5%.

The taller the seedlings grew, the more the microhabitat preferences converged between the species. Only medium-sized *Abies spectabilis* and *Betula utilis* seedlings (> 5–15 cm) in the lower subalpine forest differed significantly in their microhabitat structure, which showed a significantly higher moss cover for *Betula utilis* seedlings, while litter cover was significantly higher in microhabitats of *Abies spectabilis* (p < 0.001). No clear distinctions could be detected between the microhabitats of medium-sized *Rhododendron campanulatum* seedlings on the one hand and *Abies spectabilis* and *Betula utilis* seedlings on the other (p > 0.001). Tall seedlings (> 15–50 cm) showed no significant differences in their preferred habitat structure between species (p > 0.01).


(a) Litter

(b) Moss

(c) Rhododendron-Litter

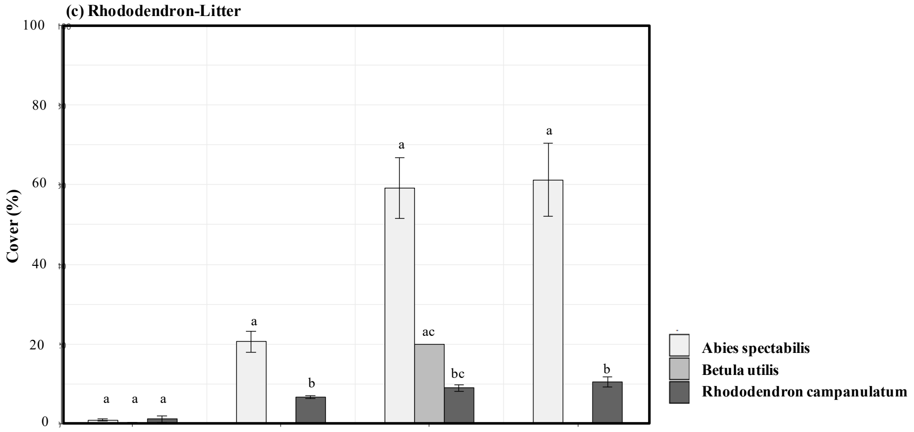


Figure 7. Variations among tree species’ seedlings (0-5 cm) in microhabitat cover of most important cover types (a) Litter, (b) Moss and (c) *Rhododendron*-litter the (I) lower subalpine forest, (II) upper subalpine forest, (III) *Rhododendron* krummholz belt, (IV).

Table 5. Summary of Kruskal-Wallis test and Dunn's post-hoc test on the difference in microhabitat ground cover of *Abies spectabilis* (As), *Betula utilis* (Bu) and *Rhododendron campanulatum* (Rc) seedlings

Cover type	Height	Vegetation	As-Bu	As-Rc	Bu-Rc	H chi-	df	p
Litter	0-5	I	< 2e-16	< 2e-16	1	150.75	2	***
Litter	0-5	II	-	< 2e-16	-	163.99	1	***
Litter	0-5	III	0.92	1.2e-13	1	57.257	2	***
Litter	0-5	IV	-	2.3e-08	-	31.264	1	***
Moss	0-5	I	< 2e-16	2.6e-15	1	134.5	2	***
Moss	0-5	II	-	< 2e-16	-	166.79	1	***
Moss	0-5	III	0.84	2.5e-13	1	55.805	2	***
Moss	0-5	IV	-	1e-07	-	28.372	1	***
Vegetation	0-5	I	0.431	0.138	0.032	6.6985	2	*
Vegetation	0-5	II	-	8.4e-05	-	15.462	1	***
Rhododendron	0-5	II	-	2.3e-07	-	26.723	1	***
Rhododendron	0-5	III	1	3.2e-10	0.88	42.582	2	***
Rhododendron	0-5	IV	-	5.8e-08	-	29.438	1	***
Litter	5-15	I	0.00062	0.90948	1	13.778	2	**
Moss	5-15	I	6e-05	1	0.0098	22.026	2	***
Rhododendron	5-15	I	0.71	1.1e-05	3.3e-	28.193	2	***
Litter	15-50	II	-	0.023	-	5.1429	1	*
Vegetation	15-50	I	8.1e-07	1	0.64	26.989	2	***

*The analysis was conducted for different ground cover types, vegetation types and height classes. For each cover type only significant results (P < 0.001 '***'; < 0.01 '**'; < 0.05 '*') are listed. Df = degrees of freedom, Vegetation types: (I) lower subalpine forest, (II) upper subalpine forest, (III) Rhododendron krummholz belt, (IV) alpine dwarf shrub heaths*

Association with shelter elements

The grand majority of seedlings of all species and all height classes were located close to at least one potential shelter element. However, the percentage of the different shelter elements varied distinctly between species and height classes, with the greatest distinctions between *Abies spectabilis* and *Betula utilis* on the one hand and *Rhododendron campanulatum* on the other (Fig. 8).

The youngest *Abies spectabilis* and *Betula utilis* seedlings (> 0–5 cm) were located most frequently close to rocks (51% and 57% respectively), whereas the youngest *Rhododendron campanulatum* seedlings were largely found near deadwood (48%). Rocks retained their high importance as shelter for medium-sized and tall *Abies spectabilis* and *Betula utilis* seedlings (> 5–15 cm: 52% and 44% respectively;> 15–50 cm: 70% and 71% respectively), while *Rhododendron campanulatum* seedlings were increasingly rarely accompanied by deadwood (> 5–15 cm: 23%;>15–50 cm: 17%) at advanced life stages, increasingly accompanied by rocks (> 5–15 cm: 38%;> 15–50 cm: 42%). In addition, *Rhododendron campanulatum* had the highest proportion of seedlings with no shelter element in all height classes.

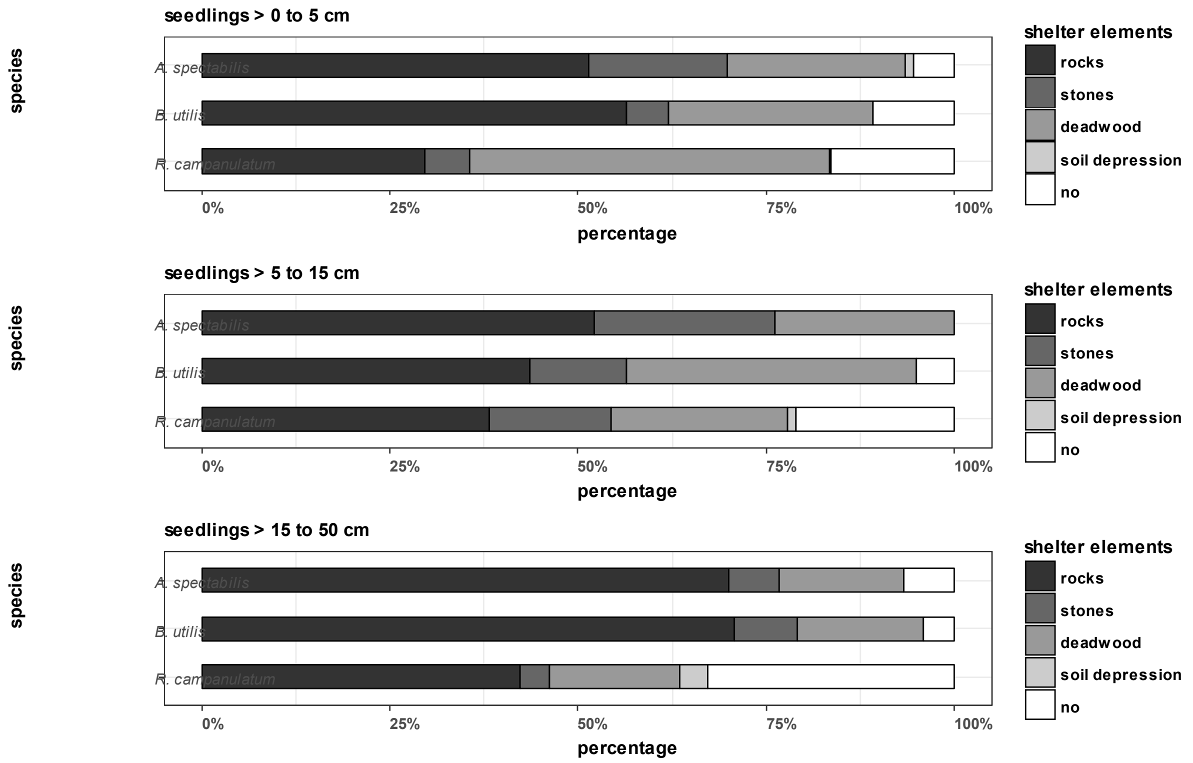


Figure 8. Percentage of shelter element types, associated with tree seedlings of different heights

Influence of Rhododendron campanulatum on Abies spectabilis and Betula utilis recruitment

The *Rhododendron* krummholz belt and the alpine dwarf shrub heaths are largely characterised by a thick layer of *Rhododendron campanulatum* litter, which appeared to be an unsuitable substrate for germination and seedling establishment of *Betula utilis* and *Rhododendron campanulatum*. We did not record *Betula utilis* seedlings in areas covered with *Rhododendron* leaf litter. In microhabitats of *Rhododendron campanulatum* seedlings, the percentage of *Rhododendron* litter was very low. In contrast, the germination and establishment of *Abies spectabilis* seedlings appeared not to be inhibited by *Rhododendron* litter, as the youngest seedlings of *Abies spectabilis* (> 0–5 cm) were associated with *Rhododendron* litter of up to 60% in the krummholz belt and alpine dwarf shrub heaths. These microhabitat cover values were significantly higher than in the microhabitats of *Rhododendron campanulatum* ($p < 0.001$).

Discussion

Our data reveal clear microhabitat preferences of the youngest seedlings of *Betula utilis*, *Rhododendron campanulatum* and *Abies spectabilis* (> 0–5 cm), with remarkable contrasts between the ground cover of the two deciduous species and those of the conifer species. These preferences are largely similar for all vegetation types, reflecting the species-specific requirements for safe sites and the importance of ground cover for safe-site structure. However, we found little variation in microsite cover among older seedlings, similar to the regeneration of other subalpine tree species in other treeline environments (Jones and del Moral 2005; Maher and Germino 2006).

Betula utilis

Bryophytes have often been associated with negative effects on germination and seedling establishment due to their barrier function, shading and toxic leach solution (During and Van Tooren 1990; Van Tooren et al. 1990; Morgan 2006; Jeschke and Kiehl 2008). However, according to our results, moss appears to be a suitable substrate for germination of *Betula utilis* seeds, as we recorded young *Betula* seedlings primarily in moss-covered soils. The suitability may be largely attributed to the high moisture-storage capacity of moss (Groeneveld et al. 2007), which is known to be crucial for seedlings' survival within *Betula* species (Carlton and Bazzaz 1998). The predominant occurrence of *Betula utilis* seedlings in the lower subalpine forest characterised by the highest mean soil humidity values in the treeline ecotone detected by Müller et al. (2016a, b) and in study 1 of this PhD thesis, supports this finding. Facilitative effects of a moss cover for seed germination and seedling establishment have also been reported in previous studies for other *Betula* species, such as *Betula pubescens* ssp. *czerepanovii*, *Betula alba* and *Betula pendula* (Kinnaird 1974; Anschlag et al. 2008; Sanz et al. 2011). We further assume that the bryophyte mats function as a seed trap for *Betula utilis*, as the extremely light seeds are wind-dispersed (mean seed mass 0.209 ± 0.019 mg, Wang et al. 2012).

In contrast, litter appears to be unfavourable for germination and establishment of *Betula utilis*, as abundance of young *Betula* seedlings on the litter layer is low. Seed mass is also positively correlated with seed size. Given the early stage of seedlings' growth depends in large part on nutrient reserves, species-specific seed mass is crucial for successful seedling establishment in environments with dense litter accumulation (Gross 1984; Seiwa and Kikuzawa 1996). Furthermore, autonomous nutrient supply results in a significant gain in time for radical and shoot elongation, and therefore enhances the seedlings' chances to pass through the physical barrier of dense litter mats (Facelli 2008). Snow accumulation and hyphal networks make litter mats even more compressed and impermeable for seedlings' sprouts or radicals (Lei et al. 2002; Facelli 2008). Thus, seedling establishment of small-seeded, pioneer tree species such as *Betula utilis* are largely reduced by litter accumulation, and germinated seedlings may die before establishment (Seiwa and Kikuzawa 1996; Facelli 2008). The germination and establishment of early successional *Betula* species are further promoted by high light intensity (Carlton and Bazzaz 1998; Grime 2006; Hughes et al. 2009). As accumulated litter has a great shading effect on buried seeds and seedlings, similar to those of an established canopy (Vázquez-Yanes et al. 1990), and as small-sized *Betula* seeds may easily get buried below the litter layer, low *Betula* seedling numbers in litter-covered areas may also be an expression of unfavourable light conditions. In deeply shaded forest stands, the survival of first-year-seedlings is positively correlated with seed size and is also influenced by the species-specific relative growth rate (Walters and Reich 2000). This finding is in line with the results of previous studies on optimal light conditions for recruitment of *Betula utilis*, which found high sapling mortality at low light and highest seedling and sapling densities outside tree stands with full solar radiation (Gratzer et al. 2004; Shrestha et al. 2007).

Rhododendron campanulatum

Young *Rhododendron campanulatum* seedlings exhibit comparable microsite preferences to those of *Betula utilis*. Moss is the dominating groundcover type in *Rhododendron campanulatum* microhabitats, while the importance of litter is low. *Similar to Betula utilis, Rhododendron campanulatum* seeds are extremely lightweight *(*0.1060 ± 0.0006 mg, (Wang et al. 2014). High litter accumulation therefore impedes *Rhododendron* seedling emergence. Meanwhile, bryophyte patches may serve as a trap for the lightweight, anemochorous *Rhododendron* seeds and may additionally buffer moisture conditions. Due to the high seedling abundance in the evergreen krummholz belt (Table 4), we suggest that *Rhododendron campanulatum* is more shade-tolerant than *Betula utilis*. These findings generally align with previous studies on other *Rhododendron* species that have indicated humid, low-shaded bryophyte mats as safe sites for *Rhododendron* seedling establishment (Cross 1981; Kameyama et al. 1999; Mejias et al. 2002). Hughes et al. (2009) found a similar pattern of overlapping microhabitat preferences of a birch species (*Betula litwinowii)* and a *Rhododendron* species (*Rhododendron caucasicum*) in the Caucasus region of Georgia.

Abies spectabilis

Although litter has overall negative effects on species germination and seedling establishment (Xiong and Nilsson 1999), the recruitment of *Abies spectabilis* appears to be less affected by litter in comparison to *Betula utilis* and *Rhododendron campanulatum*. We recorded *Abies spectabilis* seedlings predominantly in litter-covered areas, while moss-covered areas played a minor role. As large-sized *Abies spectabilis* seeds are dispersed unassisted or by animals (for example *Ochotona* sp., *Garrulus* sp.) (Fenner and Thompson 2005), bryophyte mats have little or no importance as a seed trap. Moreover, seed size is positively correlated with shade tolerance (Walters and Reich 1996). The high physiological shade tolerance of *Abies spectabilis* and the high amount of seed reserves may enable the species to cope with an impediment by litter (Hewitt 1998; Germino and Smith 1999; Walters and Reich 2000; Maher and Germino 2006). However, microhabitat analyses of other *Abies* species indicate various habitat preferences. While *Abies lasiocarpa* in the subalpine spruce-fir forests of the Rocky Mountains established on thick litter layers (Knapp and Smith 1982), *Abies balsamea* in the Canadian boreal forest avoided litter and were most often recorded on moss layer in well-illuminated microsites (Simard et al. 1998). It is therefore open to debate whether the high seedling abundance of *Abies spectabilis* on litter areas reflects optimal conditions for seedling establishment or results from the short dispersal distance.

Sheltering

We recorded most seedlings for all species near one potential protective element. This finding is in line with previous studies which found that the spatial distributions of established seedlings and saplings were primarily associated with shelter elements, as seedling survival decreased with increasing distance from shelter elements (Germino and Smith 1999; Hättenschwiler and Smith 1999; Moir et al. 1999; Germino et al. 2002; Resler et al. 2005). We found geomorphic elements (rocks, stones) and deadwood to be the most important shelter types for all species and height classes. Both sheltering types ameliorate germination and growth conditions by mediating UV radiation, temperature, wind speed, soil moisture and winter snow accumulation (Holtmeier and Broll 1992; Resler et al. 2005). Thus, our results underline the importance of facilitative elements for tree recruitment in the Rolwaling treeline ecotone.

Rhododendron litter: an impediment for seedling establishment?

Although seedling abundance in the krummholz belt was highest for *Rhododendron campanulatum* (> 0 to 5 cm), only *Abies spectabilis* emerged on *Rhododendron* litter while *Rhododendron campanulatum* itself primarily grew on mossy patches in the litter layer (Fig. 7). We did not record any seedling of *Betula utilis* in the *Rhododendron* krummholz belt. It is widely known that a variety of evergreen shrub species (*Chusquea* sp., *Kalmia* sp., *Rhododendron* sp.) inhibit tree recruitment in forest ecosystems worldwide (Nilsen et al. 2001). However, the precise mechanisms of inhibition remain largely unknown.

Rhododendron species influence tree recruitment through alteration of the N cycle (Hättenschwiler and Vitousek 2000; Wurzburger and Hendrick 2007). Seedlings germinated on *Rhododendron* litter are exposed to low N availability, due to low leaf litter quality and high amounts of polyphenols (cf. chapter 4.2; Maithani et al. 1998; Wurzburger and Hendrick 2007). As nitrogen is the primary limiting soil nutrient for seedling growth (Körner 2003), a shortage may be critical for seedling establishment, in particular for the small, nutrient-limited *Betula* and *Rhododendron* seeds. As previously mentioned, *Rhododendron* leaves contain triterpenes (Hegnauer and Hegnauer 1966; Fan et al. 1999), which are potentially allelopathic

(Rice 1984; Li et al. 2010; Kadereit et al. 2014). In addition, in forests with *Rhododendron* species in the understory, the light availability is greatly reduced, producing a negative impact on carbon gain in seedlings and an increase in seedling mortality (Nilsen et al. 2001; Lei et al. 2006). The lower soil temperatures under existing trees, dwarf trees, or krummholz (Malanson et al. 2019) and the related limitation of mobilisation and carbon reserves transfer are central for restricted seedling establishment and treeline dynamics (Körner 1998, 2015). We suggest that reduced photosynthetically active radiation; low soil temperatures; the thick, recalcitrant litter layer, allelopathic effects, and the altered N cycle may be main causes for the absence of *Betula utilis* seedlings, while *Rhododendron campanulatum* seedlings find a suitable germination substrate on moss in spite of low light conditions. Due to the above-described seed and plant traits, only *Abies spectabilis* is able to establish on *Rhododendron* litter. However, the low abundance of taller *Abies* seedlings (Table 4) and the low number of mature trees in the *Rhododendron* krummholz belt, detected by Schwab et al. (2016) and in study 1 of this PhD thesis suggest a high mortality rate of *Abies spectabilis* seedlings during establishment. The underlying processes of the low rate of tree recruitment in the krummholz belt should be further assessed in detailed species-specific studies.

Responsiveness of seedling establishment to climate warming

Temperature and water supply are critical drivers for plant recruitment, including flowering phenology, pollination, seed maturation, germination and seedling establishment. Temperatures respectively soil temperatures and precipitation respectively soil moisture are simultaneously decisive for species distribution (study 1), adult and juvenile stand density (Schwab et al. 2017), tree physiognomy patterns (Müller et al. 2016b) and radial tree growth of *Abies spectabilis* (Schwab et al. 2018) in the Rolwaling treeline ecotone. As seedlings are even more sensitive to climate alterations than adult stages, climate warming will undoubtedly affect recruitment dynamics in the Rolwaling treeline ecotone. In study 2, we found species-specific microhabitat preferences for seedling emergence of the dominating tree species in the study area. We therefore presume that microhabitats which buffer climatic extremes may become even more important under ongoing climate warming and decreasing precipitation in the Himalaya, especially for small-seeded *Betula* and *Rhododendron* species. We suggest that the availability of safe sites may be the most limiting factor for near-future treeline advance.

5. Conclusions

The aim of this thesis was to investigate the phytosociology and subsequently analyse vegetation ecology and tree seedling establishment in the Rolwaling treeline ecotone. All three research approaches implemented in the course of this study contribute to assessment of vegetation dynamics in the treeline ecotone under climate warming.

Our study provides detailed insights into species compositions of plant communities and vegetation-environment relationships in the treeline ecotone in the Rolwaling Valley for the first time. The study expands on the still limited knowledge of Himalayan subalpine-alpine vegetation with regard to floristic diversity, ecology and syntaxonomy. We classified the treeline ecotone vegetation into five plant communities assigned to two classes. Using DCA and correlation methods, community patterns were successfully related to an elevational gradient of deteriorating growth conditions, reflecting an increasingly unfavourable constellation of soil temperature, soil moisture, and nitrogen supply and availability. Differentiations of species compositions are understood as resulting from complex interrelations between site factors and plant-plant interactions.

When classifying the ecotone vegetation, we had to deal with rank-less communities and a provisional status of classes, because phytosociological studies in the Himalaya are still pioneer studies and a syntaxonomical scheme on a larger scale is missing. This challenge illustrates the urgent need for a complete overview and synopsis of Himalayan vegetation, which would also provide deeper ecological knowledge. Classification of the Rolwaling treeline ecotone vegetation may serve as a suitable baseline for further phytosociological investigations.

Given the high risk of climate-change-induced plant biodiversity loss in mountain areas at high altitudes, additional long-term monitoring studies of Himalayan plant communities are needed in order to detect shifts in vegetations patterns and to assess the vulnerability of flora and vegetation. To improve the comparability between sites, we therefore strongly recommend the application of standardised sampling and analytical protocols along elevational gradients, similar to the global observation research initiative in alpine environments (GLORIA; Grabherr et al. 2000).

Microhabitat analyses suggest species-specific preferences for seedling establishment of the dominating tree species in the Rolwaling treeline ecotone. Predominant substrates for germination and seedling establishment are bryophyte mats (for *Betula utilis* and *Rhododendron campanulatum*) and litter accumulations (for *Abies spectabilis*). The recruitment of all species depends on shelter elements.

We discussed all critical drivers for community differentiation and for tree seedling establishment in light of present climate warming. The identified main environmental variables particularly soil temperature, water and nitrogen supply are directly or indirectly related to climatic conditions, suggesting distinct alterations to species distribution and treeline position. We therefore conclude that buffering climatic extremes by species-specific safe sites may become essential for successful seedling establishment in a warming climate.

Moreover, we recorded an inhibition effect of dense *Rhododendron* stands and *Rhododendron* litter on tree recruitment that may become decisive for future treeline position in the Rolwaling Valley. Low soil temperature and light availability combined with low nutrient availability and the release of toxic compounds by *Rhododendron* litter may specifically be restrictive for upward migration of small-seeded *Betula utilis*. However, scattered recruits of all three tree species in the alpine zone, illustrate that the *Rhododendron* krummholz belt does not completely impede seed-based regeneration beyond the present treeline position.

We assume that our results on seedling establishment are largely transferable to other near-natural treeline ecotones in the Himalaya. The investigated tree species and genera are common in subalpine areas in the Himalaya; thus, our findings on species-specific microhabitat preferences are relevant for assessing subalpine/alpine vegetation dynamics in the broader Himalaya. However, given the large heterogeneity of treeline environments in the vast Himalayan mountain system and the complexity of multi-stage recruitment processes, further studies are required to fully understand the conditions for successful seedling establishment and responsiveness of the Himalayan treeline ecotones to climate change. We propose to conduct in-situ approaches with experimental treatment of naturally germinated seedlings over a period of several years. Further studies should also investigate the sensitivity and response of seedling establishment to variations in snow patterns. In addition, modelling recruitment dynamics could further deepen knowledge on the prerequisites for successful seedling establishment. With consideration of a complete environmental data set as well as time lags on dispersal, establishment and extinction, generalised linear models or species distribution models may contribute to realistic predictions regarding tree recruitment and treeline position.

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Bürzle, B., Schickhoff, U., Schwab, N., Oldeland, J., Müller, M., Böhner, J., Chaudhary, R.P., Scholten, T. and Dickoré, W.B. 2017. Phytosociology and ecology of treeline ecotone vegetation in Rolwaling Himal, Nepal. *Phytocoenologia* **47**: 197-220, dio: 10.1127/phyto/2017/0130

Bürzle, B., Schickhoff, U., Schwab, N., Wernicke, L.M., Müller, Y.K., Böhner, J., Chaudhary, R.P., Scholten and T., Oldeland, J. 2018. Seedling recruitment and facilitation dependence on safe site characteristics in a Himalayan treeline ecotone. *Plant Ecology* **219**: 115-132, dio: 10.1007/s11258-017-0782-2

Additional publications

Gerlitz L.; Bechtel B.; Böhner J.; Bobrowski M.; Bürzle B.; Müller M.; Scholten, T.; Schickhoff, U.; Schwab, N. and Weidinger J. 2016. Analytic comparison of temperature lapse rates and precipitation gradients in a Himalayan treeline environment: Implications for statistical downscaling. In: Singh, R. B.; Schickhoff, U. and Mal, S. (Eds.): Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya. Springer, Switzerland; 49–64. doi: 10.1007/978-3-319-28977-9_3

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Schwab, N., Schickhoff, U., Bürzle, B., Müller, M., Böhner, J., Chaudhary, R.P., Scholten, T. and Oldeland, J. 2017. Implications of tree species – environment relationships for the responsiveness of Himalayan Krummholz treelines to climate change. *Journal of Mountain Science* **14**: 453–473 doi: 10.1007/s11629-016-4257-z

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Bürzle, B. and Schickhoff, U. 2014. Analysis of plant species composition, recruitment processes and seedling establishment in a Himalayan treeline ecotone under experimental warming. Poster presentation. Jahrestagung des AK Hochgebirge „Ressourcen der Gebirgsräume: Nutzung, Wandel, Bewertung". Bern / Switzerland

Bürzle, B., Schickhoff, U., Schwab, N., Oldeland, J., Müller, M., Böhner, J., Chaudhary, R.P., Scholten, T. and Dickoré, W.B. 2016. Phytosociology and ecology of treeline ecotone vegetation in Rolwaling Himal, Nepal. Poster presentation. Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GFÖ). Marburg / Germany

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Bürzle, B., Schwab, N. and Schickhoff, U. 2015. Analysis of plant species composition, recruitment processes and the impact of allelochemicals on seedling establishment in a Himalayan treeline ecotone under ongoing climate warming. Poster presentation. International Biogeography Society 7th Biennial Meeting 2015, Bayreuth / Germany

Bürzle, B., Schwab, N. and Schickhoff, U. 2015. Plant species composition and treeline stand structure in a Himalayan treeline ecotone. Poster presentation. Jahrestagung des AK Hochgebirge „Interdisziplinarität in der Hochgebirgsforschung". Hamburg / Germany

Appendix I: Abstracts and author contributions to original publications

Article I

Bürzle, B., Schickhoff, U., Schwab, N., Oldeland, J., Müller, M., Böhner, J., Chaudhary, R.P., Scholten, T. and Dickoré, W.B. 2017. Phytosociology and ecology of treeline ecotone vegetation in Rolwaling Himal, Nepal. *Phytocoenologia* **47**: 197-220, dio: 10.1127/phyto/2017/0130

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 species-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.

Author contribution

Birgit Bürzle conceived the study, conducted field sampling of vegetation and soils. Birgit Bürzle, Wolf Bernhard Dickoré and Udo Schickhoff dealt with taxonomical issues and determined plant species. Michael Müller and Thomas Scholten conducted field sampling of soils and provided soil data. Birgit Bürzle performed the statistical analyses and led the writing. Niels Schwab and Udo Schickhoff revised the manuscript. Jens Oldeland gave statistical advice. All co-authors copyedited the final version of the manuscript, and Birgit Bürzle acted as the corresponding author.

Appendix I: Abstracts and author contributions to original publications

Article II

Bürzle, B., Schickhoff, U., Schwab, N., Wernicke, L.M., Müller, Y.K., Böhner, J., Chaudhary, R.P., Scholten and T., Oldeland, J. 2018. Seedling recruitment and facilitation dependence on safe site characteristics in a Himalayan treeline ecotone. *Plant Ecology* **219**: 115-132, dio: 10.1007/s11258-017-0782-2

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 *Abies spectabilis* seedlings establish on ground that is covered in average by 70% with litter, *Betula utilis* and *Rhododendron 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.

Author contribution

Birgit Bürzle conceived the study, and conducted the measurement of seedlings and the mapping of microhabitats with the support of student assistants Lina M. Wernicke and Yanina K. Müller. Birgit Bürzle performed the statistical analyses with critical input from Jens Oldeland, she prepared the corresponding figures and tables and wrote the first draft of the manuscript.

Niels Schwab and Udo Schickhoff revised the manuscript. All co-authors copyedited the final version of the manuscript, and Birgit Bürzle acted as the corresponding author.

Appendix II: Original publications

Article I

Bürzle, B., Schickhoff, U., Schwab, N., Oldeland, J., Müller, M., Böhner, J., Chaudhary, R.P., Scholten, T. and Dickoré, W.B. 2017. Phytosociology and ecology of treeline ecotone vegetation in Rolwaling Himal, Nepal. *Phytocoenologia* **47**: 197-220, dio: 10.1127/phyto/2017/0130

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 species-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.

Keywords:
Central Himalaya; classification; climate change; ecology; habitat condition; multivariate analysis; Nepal; ordination; phytosociology; Rolwaling Himal; treeline ecotone; vegetation.

Nomenclature:
The nomenclature of vascular plants follows Press et al. (2000) and Watson et al. (2011).

Abbreviations:
ANOVA = One-way analysis of variance; DCA = Detrended Correspondence Analysis; DJF = winter December to February; JJAS = summer/monsoon June to September; MAM = March to May; ON = autumn/post-monsoon October to November.

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Introduction

Mountains represent an appropriate natural laboratory to investigate community patterns and ecosystem processes along elevational gradients (Körner 2007; Sundqvist et al. 2013). Due to their multifaceted habitats and environmental conditions, mountainous areas display large diversity of plant species and communities over short geographical distances (Körner 2000, 2007; Nagy & Grabherr 2009; Schickhoff 2011). Increasing elevation is associated with a reduction of surface area, a decline in temperature and carbon dioxide partial pressure, as well as an increase in solar radiation and UV-B-radiation (Körner 2007).These elevation-related environmental factors are crucial for species composition and community patterns in mountain ecosystems (Whittaker & Niering 1975; Körner 2007, 2012; Nagy & Grabherr 2009). Local orographic and edaphic conditions as well as inter- and intraspecific biotic interactions are among further significant site factors, affecting in particular the species composition of low-growing vegetation less coupled to the atmosphere than trees and shrubs (Doležal & Šrůtek 2002; Müller et al. 2016a). While plant functional traits and types change along elevational gradients, plant species show individual responses to changing site conditions with increasing elevation, for instance, by adapted photosynthesis, changed metabolism, and altered mineralization rates (Hoch & Körner 2012; Sundqvist et al. 2013). Transformations are most conspicuous at the upper treeline, which represents an almost abrupt alteration of dominating life forms (Körner 1998; Schickhoff 2005). Species turnover and transitions on plant community levels are, however, less abrupt and often more continuous (Whittaker 1956; Sundqvist et al. 2011; Sundqvist et al. 2013), usually causing small-scale mosaics of vegetation types.

In recent decades, vegetation types of mountain regions have been subjected to above-average climate warming. Temperature increase in mountains of the world was higher than the global mean during the 20th century (Diaz & Bradley 1997; Beniston 2000; Rangwala & Miller 2012), and will most likely continue to be higher than average during the 21stcentury (cf. Nogués-Bravo et al. 2007; IPCC 2013). Climate warming triggers an expansion of distribution ranges to higher elevations, which has been observed for a wide range of taxonomic groups and geographical locations (Gonzalez et al. 2010; Chen et al. 2011; Settele et al. 2014; Lenoir & Svenning 2015). Thus, mountain plant communities will gradually alter by ongoing climate warming into novel communities with transformed species compositions (Gottfried et al. 2012; Pauli et al. 2012). Large warming trends (up to 1.2°C per decade at higher altitudes) have been observed in the Himalaya in the past 30-40 years (Shrestha & Aryal 2011; Gerlitz et al. 2014; Schickhoff et al. 2016a), which are expected to have substantial effects on plant species distribution patterns (Xu et al. 2009; Shrestha et al. 2012; Telwala et al. 2013; Dolezal et al. 2016). This suggests that species compositions, community patterns, and the distribution of species and plant communities will be modified at a point in time when ecological and phytosociological knowledge of Himalayan vegetation types is still rather deficient.

In fact, detailed phytosociological studies in the Himalayan region are rare. Notable exceptions for the western Himalaya and Karakoram include the studies of Hartmann (1968, 1972, 1983, 1987, 1990, 1995, 1997, 1999), Schickhoff (1993, 1996), Eberhardt (2004), and Khan (2012). In the central Himalaya, Miehe (1990) presented an in-depth description of upper elevational plant communities based on a complete floristic inventory and numerous phytosociological relevés in the Langtang-Helambu region. Kikuchi & Ohba (1988) conducted a first phytosociological study of major alpine plant communities near Panch Pokhari Lake in the south-eastern part of Rolwaling Himal (Nepal). Studies on the ecology of Himalayan vegetation types are more numerous, however the knowledge of vegetation-environment relationships is still very limited. Standard references which may serve as a basis for future detailed studies include Schweinfurth (1957), Champion & Seth (1968), Stainton (1972), Dobremez (1976), Miehe (1982, 1990), Puri et al. (1983, 1989), Schickhoff (1993, 1996), Dickoré & Nüsser (2000), Eberhardt et al. (2007) and Miehe et al. (2015). In particular, the knowledge of vegetation-environment relationships in Himalayan treeline ecotones is still very deficient. Miehe (1990) provided the most comprehensive account of subalpine and alpine vegetation types to date containing extensive floristic and ecological information which is based solely on vegetation sampling. Detailed information on treeline floristic, structural and spatial patterns as well as on human impact are provided in the overviews of Miehe & Miehe (2000), Miehe (2004), and Miehe et al. (2015). Schickhoff (2005) summarized the available knowledge of geographical and ecological aspects of Himalayan treelines over a decade ago, and pointed out that treeline ecological conditions and processes such as regeneration, carbon balance, frost, drought, snow cover, wind, soil physical and chemical conditions, etc., are still largely unexplored. The growing prominence of climate change issues generated new scientific interest in Himalayan treelines which prompted not only recent studies on vegetation dynamics but also the analysis of microclimatic, soil physical and chemical, regeneration, and paleoecological data (e.g., Gerlitz et al. 2016; Schwab et al. 2016, 2017). Recently, Müller et al. (2016a, b) provided detailed soil-ecological information from a Himalayan treeline ecotone. Schickhoff et al. (2015, 2016b) reviewed the recently accumulated knowledge with a focus on treeline response to climate change. Nevertheless, we still lack a detailed characterization of treeline vegetation-environment relationships based on correlations of vegetation and site-ecological data. This study aims to fill this gap.

As species composition and ecology of treeline vegetation types in the Rolwaling Valley in east-central Nepal is largely unknown to date, the main objective of the present study is to analyse floristic composition, community patterns, and environmental relationships of subalpine and alpine vegetation in this remote valley. We also seek to relate the results to the sensitivity of treeline ecotone vegetation to climate warming.

More specifically, we aim in this baseline study at:

i) differentiating plant communities along the elevational gradient in the treeline ecotone, and

ii) identifying site factors which cause the differentiation of the treeline ecotone vegetation and, in particular, induce small-scale differences in species composition.

Study area

The Rolwaling Valley (27°52’ N; 86°25’ E) is located in Dolakha District, east-central Nepal, adjoining the border to the Tibet Autonomous Region (Fig. 1). It is part of the Gaurishankar

Conservation Area (2035 km²), which was designated as a protected area in 2010 (Shrestha et al. 2010). The area is characterized by a continental climate with dry and cold winters and monsoonal/hyper-humid and cool summer conditions (see Gerlitz et al. 2016 for climatic observations and detailed station data). Within the Holarctic Kingdom, the Rolwaling Valley is assigned to the Eastern Himalayan Province of the Sino-Japanese Floristic Region (Meusel & Schubert 1971; Miehe 1990; Welk 2015). Vegetation formations in Rolwaling Valley are widely undisturbed by land use effects due to its seclusion without connection to the road network, low population density, and the fact that plants and animals in this valley are protected to a certain extent by the recurring Buddhist theme of a sacred hidden valley (Sacherer 1979; Baumgärtner 2015).

In this study we analysed the composition of plant communities and their corresponding site conditions along an entire treeline ecotone located on a north-facing slope. The ecotone encompasses an altitudinal range from 3745 to 4300 m a.s.l., extending from the closed subalpine forest (upper cloud forest) with mixed forest stands across the treeline, and krummholz belt to the lower alpine vegetation. The investigated slope is steep with an inclination from 26 to 45°. Soils in the study area are classified as podzols (IUSS 2015; Müller et al. 2016a). Soil depths vary from 30 to 70 cm, with maximum skeletal fractions from 75 to 95% for Ae-horizons. The Rolwaling River separates the valley into uninhabited north-facing slopes and sparsely populated south-facing slopes where human impact is likewise low. The north-facing study slopes show no signs of fire or grazing by cattle; wood cutting is negligible and confined to lower elevations (Schwab et al. 2016).

Methods

Vegetation sampling

We conducted vegetation surveys during the period from July to September 2013 and from July to October 2014. We collected phytosociological and environmental data along three altitudinal transects (two transects NE-exposed, one transect NW-exposed) across the treeline ecotone, following the Braun-Blanquet approach (Braun-Blanquet 1964; Dierschke 1994). Along each transect, we defined four zones (A–D) according to altitudinal differences and changes in vegetation. Altitudinal zones reaching from closed upper cloud forests in the upper subalpine belt (zone A and B), via a dense krummholz thicket of *Rhododendron campanulatum* (zone C) to alpine dwarf shrub heaths (zone D). Sampling plots were selected randomly in each transect zone under consideration of the homogeneity of physical features and vegetation structure. We completed a total of 91 relevés with a size of 20 m x 20 m (projected on a horizontal plain). In each plot, height and cover of the separate vegetation layers were recorded, followed by a detailed inventarisation of all vascular plants. We estimated species cover using the established cover-abundance scale of Braun-Blanquet (1964). Unknown specimens were collected, and identified at the herbarium of the Botanische Staatssammlung München (M). In addition, we used determination keys of eFloras (http://www.efloras.org; accessed January 2015), the *Flora of Nepal* (Watson et al. 2011), and the *Flora of Bhutan* (Grierson & Long 1984−2001).

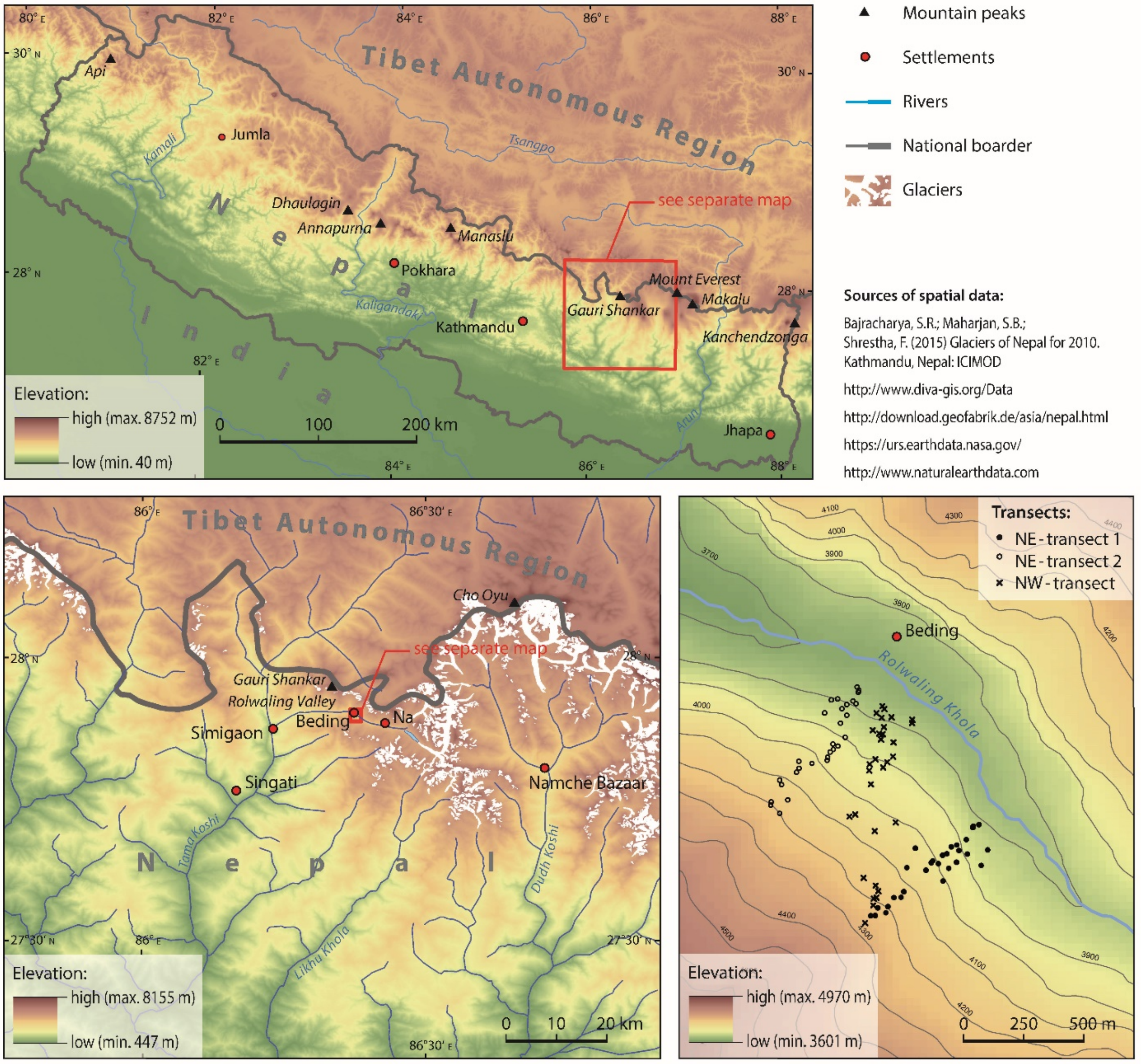
Environmental variables

Environmental data collected in each plot included variables referring to topographic position (altitude, slope aspect and inclination) as well as soil chemical and physical parameters. We collected mixed soil samples of the uppermost mineral horizon from three randomly selected points within the plots.

Fresh field samples were dried at 40°C, sieved with a 2 mm mesh and analysed at the University of Tübingen, Soil Science and Geoecology, and at the University of Hamburg, Institute of Geography. Analysed soil chemical parameters included: i) pH values, measured in KCl-suspension (according to NAW, 1997); ii) organic matter content, determined by a glowing process at 430°C; iii) total carbon and total nitrogen, using a CN analyser (TruMac CN 630. LECO resp. Vario EL II. Elementar); iv) effective cation exchange capacity (cations: Na, K, Mg, Ca, Mn, Fe, Al), analysed with an inductively coupled plasma optical emission spectrometry (ICP-OES, Optima 2100 DV, Perkin Elmer); and v) grain size distribution, determined according to Blume et al. (2011) by using a particle-size analyzer (Sedigraph III Plus. Micromeritics). Grain sizes were classified according to Ad-hoc-AG Boden (2005).

In addition, we installed WiFi Plant Sensors (Koubachi Inc., Switzerland) on 34 plots, which monitored soil temperature and soil moisture at 10 cm depth, respectively, and soil surface air temperature in a 1-hour interval. Modification of sensors enabled logging of soil temperatures from −10 °C to +55 °C, and pF from 0 to 5.75 (Müller et al. 2016a). The sensors were uniformly distributed on plots along two transects (NE-exposed and NW-exposed).

We analysed pedochemical and pedophysical parameters for all 91 plots, except grain size distribution as well as soil temperature and soil moisture, which was analysed or measured for 82 and 34 plots, respectively.



Sources of spatial data:

Bajracharya, S.R.; Maharjan, S.B.; Shrestha, F. (2015) Glaciers of Nepal for 2010. Kathmandu, Nepal: ICIMOD

http://www.diva-gis.org/Data

http://download.geofabrik.de/asia/nepal.html

https://urs.earthdata.nasa.gov/

http://www.naturalearthdata.com

Figure 1 Location of the studied treeline ecotone (red rectangles) in the Rolwaling Valley in east-central Nepal. Position of the 91 relevés is shown on the lower right map (lower right).

Data analysis

Cluster analysis, DCA and computations were carried out with PC-ORD 6.255 program (McCune & Mefford 2011). For determination of diagnostic species we used JUICE (Tichý 2002). ANOVAs were conducted using the statistical software environment R (version 3.2.2; R Core Team 2015) with functions of package *stats* (R Core Team 2013)

Classification

We transformed cover-abundance scale data to mean values of percentage plant cover, in doing so we converted ‘r’ to an arbitrary value of 0.1 and ‘+’ to an arbitrary value of 0.2 (Ellenberg et al. 2001). We merged cover values of species present in different vegetation layers into one using the highest value for each species (Fischer 2003; Walentowski et al. 2014).

In order to reduce significant variations in total abundances and to adjust the contribution of common and rare species, we modified the vegetation data set by logarithmic transformation prior to the following analyses (Kent 2012). Since zeros are present in the data set, we added 1 to all observations before transformation.

For classification, we subjected the complete data set to a cluster analysis (linkage method: complete linkage; distance measure: Bray-Curtis). The groups which emerged from cluster analysis were transferred to JUICE software (Tichý 2002) for further table rearrangement. Re-sorting of relevés was done iteratively, according to the Braun-Blanquet method (1964). A complete relevé table, including all communities and subordinated groups, is shown in Supplement S1. We determined diagnostic species of the proposed phytosociological units by calculating the phi-coefficient (Sokal & Rohlf 1995; Chytrý et al. 2002) among all units of the same rank. As the phi-value is affected by the relative size of groups (Tichý & Chytrý 2006; Tichý et al. 2011), we standardized the size of all site groups before calculation, whereby target groups were of the same size as the others (Tichý et al. 2011). Selection of diagnostic species followed a threshold value at 0.3 and a simultaneous calculation of Fisher's exact test (Tichý 2002) with a significance concentration at 0.05. Diagnostic species were differentiated into diagnostic (phi > 0.30) and highly diagnostic (phi > 0.50) (Chytrý 2007; Michl et al. 2010). According to Luther-Mosebach et al. (2012), we defined a character species of a syntaxon as a species which is diagnostic and has at least a 0.10 higher phi value than any other syntaxon of the same rank. Species in higher syntaxonomic rank are only regarded as character species, if they have positive phi-values for more than half of the subordinated units. If a taxon is a character species in different ranks, we defined the species in the higher syntaxonomic position as a 'transgressive character species'. In addition to the phi coefficient, percentage frequency was calculated for all species and phytosociological groups.

In view of the deficit state of knowledge, we consider the proposed classes as provisional, symbolizing the higher rank in comparison to the subordinated groups.

Vegetation-environment relationships

We calculated mean values and standard deviation for recorded environmental data to give an outline of the ecological variability within and between proposed phytosociological units. Mean soil temperature was determined for all seasons (spring/pre-monsoon March to May: MAM, summer/monsoon June to September: JJAS, autumn/post-monsoon October to November: ON, winter December to February: DJF) (cf. Müller et al. 2016b). In addition, we computed the number of growing degree days, based upon soil temperature, for the different communities according to Körner & Paulsen (2004). We assessed significant differences in site conditions between units with one-way analysis of variance (ANOVA). Environmental factors were checked for normality of distribution and homogeneity of variance by visually examining the distribution of residuals (Quinn & Keough 2002) to verify ANOVA assumption. If tests did not comply with the terms, we applied a $\log_{10}$-transformation and used Welch ANOVA (Welch 1951) to account for unequal variances. Pairwise comparison of units was performed by *posthoc* pairwise t-tests with Holm correction (Holm 1979). Level of significance was applied at $\alpha = 0.05$. As data for grain size distribution, soil temperature and soil moisture were not available for all of the plots, the number of replicates (N) differs between variables.

We visualized compositional pattern of phytosociological units by means of detrended correspondence analysis (DCA; downweighting of rare species; distance measure: chi-squared). Corresponding scatter plots were restricted to two dimensions and showed the diversity in species composition along the first two axes, measured in standard deviation units of species turnover (SD) (Gauch 1982; Kent 2012). Visualized compositional patterns were interpreted applying *post-hoc* correlations of the first two ordination axes (with highest eigenvalue) with $\log_{10}$-transformed environmental variables using the non-parametric Kendall rank correlation coefficient. Because soil temperature and soil moisture data were not available for all plots, both factors were only considered for the ANOVA. For a smaller number of plots without grain size data, we inserted mean values of vegetation units as suggested in McCune et al. (2002).

Nomenclature of plants and syntaxa

Syntaxa were named using the diagnostic species with highest fidelity phi coefficient and the most important structural tree and shrub species, respectively. Diagnostic species, which are not clearly identified (e.g. *Rhodiola* spec.) cannot be name-giving. Nomenclature of vascular plants follows Press et al. (2000) and Watson et al. (2011), with minor adaptations and alterations.

Results

Syntaxonomic classification

In total, we recorded 103 species of vascular plants in 91 relevés along the investigated treeline ecotone (Supplement S1). DCA indicated a floristic gradient of 3.9 standard deviation units for the data set (length of first axis) and thus approximately a complete species turnover between the most dissimilar relevés (Fig. 2). The dendrogram of the cluster analysis shows a clear division into two main groups and five subgroups (Fig. 3), indicated by the early cut off value at approximately 0.25. Clusters match almost perfectly with the relevés' distribution along the first DCA axis (Axis 1 eigenvalue: 0.69, Axis 2 eigenvalue: 0.11).

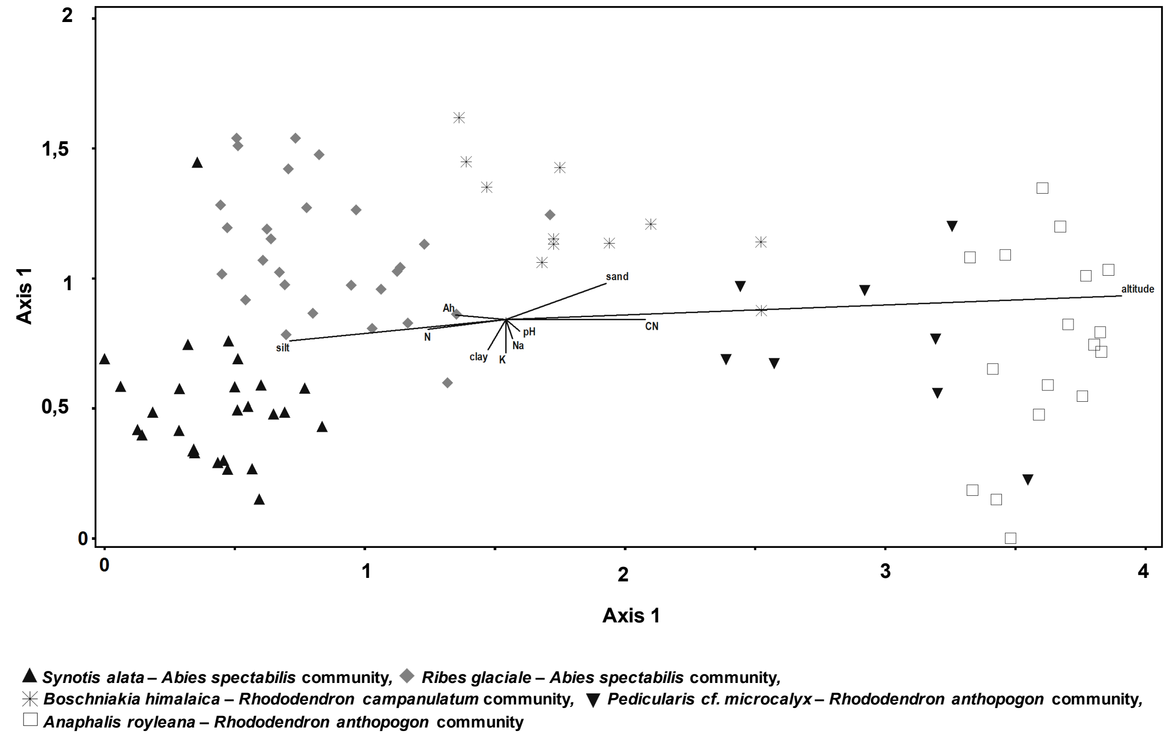


Figure 2 Detrended correspondence analysis (DCA) of relevés recorded in 2013 and 2014 ($N = 91$) with posthoc correlation of environmental parameters. Relevé symbols refer to clusters of final classification. Eigenvalue Axis 1: 0.69; eigenvalue Axis 2: 0.11; length of gradient Axis 1: 3.857; length of gradient Axis 2: 1.617; total inertia: 2.371.

According to the final classification, relevés could be separated into five phytosociological groups, assigned to two higher ranked units. We interpreted the two-cluster level as the classes *Betula utilis-Abies spectabilis* forests and *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths. We interpreted the five-cluster level as lower ranked phytosociological groups below the two classes (Supplement S1, Fig. 3, Table 3), generally termed communities. The floristic differentiation of the five communities is clearly shown in the ordination diagram (Fig. 2). Relevés of community types are arranged and clearly separated along Axis 1, which primarily represents an elevational gradient with complex interrelations of edaphic site factors (Fig. 2, Table 1). Mean annual soil temperature decreases along this gradient with significant differences between plant communities of lower and upper elevations (Table 2). These soil temperature trends are apparent throughout the year, in particular during the vegetation period (spring and summer months); autumn and winter trends are less distinct; mean soil temperatures (ON, DJF) decrease at a lower rate compared to spring and summer seasons (insignificant). Moreover, Axis 1 is significantly correlated with CN ratio, nitrogen and iron content, thickness of uppermost mineral horizon (Ah) and proportion of silt and sand within the soil texture (Table

1). Soils of the communities within the treeline ecotone are generally podzols (Müller et al. 2016a) with extremely low pH-values of c. 3.0 (Table 2). Communities occupy without exception steep slopes (average inclination between 33° and 37°). However, we found slope inclination to play a negligible role for community differentiation along the treeline ecotone (Table 2). Similarly, slope aspect does not visibly affect the floristic composition of plant communities (Table 1, Table 2), since differences in exposition between transects (NW-exposed, NE-exposed) are too low.

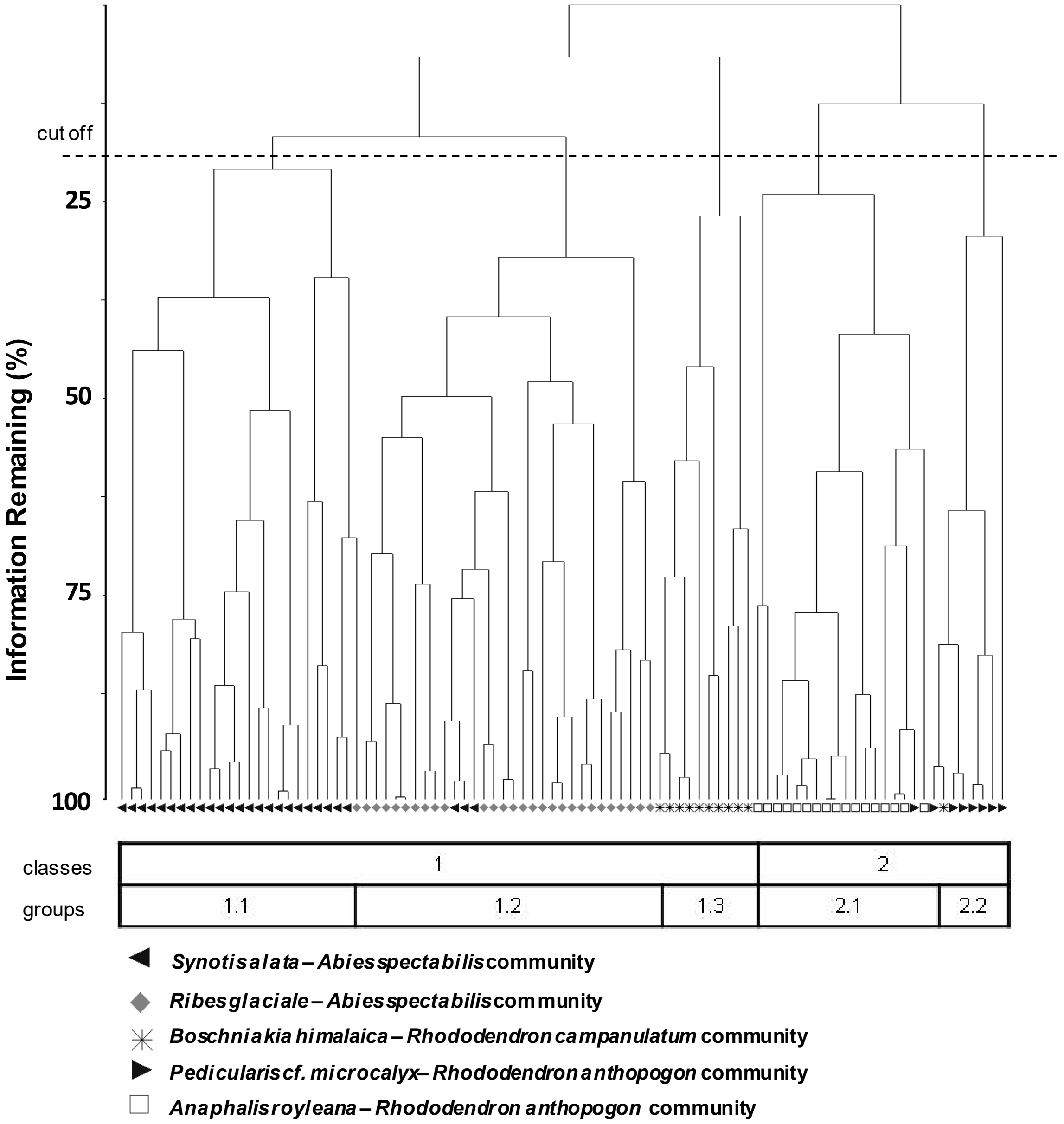


Figure 3 Dendrogram for 91 relevés according to complete linkage cluster analysis, with Bray-Curtis as a distance measure. Clusters at the five-cluster level, closely match with final classification, represented by relevé symbols. Sections below the dendrogram correspond to final phytosociological assignment.

Betula utilis forests-*Abies spectabilis* occupy lower elevations within the treeline ecotone. Accordingly, the first relevé group of Axis 1 represents the *Synotis alata-Abies spectabilis* community (lower left-hand corner in Fig. 2), followed by the *Ribes glaciale-Abies spectabilis* community. Both relevé groups are also vertically arranged along Axis 2. The communities occupy a considerably narrow range, indicating floristically very homogenous vegetation types with comparatively narrow ecological amplitudes. The krummholz belt, formed by the *Boschniakia himalaica-Rhododendron campanulatum* community, follows upslope along the elevational gradient (cf. Fig. 2). This community shows the most abrupt change in species composition along this gradient; it marks the transitional zone between closed forests and alpine dwarf shrub communities. Above the krummholz belt, we differentiated dwarf shrub communities into the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community and the *Anaphalis royleana-Rhododendron anthopogon* community. Relevés of these treeless communities are arranged over a broader space in the ordination diagram, implicating more heterogeneous species compositions and environmental conditions (cf. Fig. 2).

Axis 2 has relatively minor relevance (eigenvalue 0.11, length of gradient 1.62) for floristic differentiation of the community types. However, in addition to a positive correlation with elevational position this axis corresponds to an edaphic gradient with changes in soil nutrient availability and grain size distribution (Table 1). In particular, the *Synotis alata-Abies spectabilis*, *Ribes glaciale-Abies spectabilis*, and *Boschniakia himalaica-Rhododendron campanulatum* communities are separated along this elevational-edaphic gradient (cf. Fig. 2). Relevés of the other communities are more heterogeneously arranged along Axis 2.

The communities associated to the *Betula utilis-Abies spectabilis* forests contain 91 species, while we recorded only 50 species for communities of the *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths above the krummholz belt. Following a threshold value of 0.3 for the phi coefficient, the classes *Betula utilis-Abies spectabilis* forests and *Dasiphora arbuscula-Rhododendron anthopogon dwarf shrub heaths* were defined by 30 and 19 diagnostic species, respectively. For the subordinated communities we identified 33 and 24 diagnostic species, respectively (Table 3).

Table 1. Kendall's *r* non-parametric correlation coefficients of environmental parameters with ordination scores of plots for the first three axes of the DCA presented in Fig. 2 (*: $P < 0.05$; **: $P < 0.01$).

	Axis1 *r*	Axis 2*r*	Axis 3 *r*
Landscape parameters			
Altitude (m a.s.l.)	0.705^{**}	0.215^{**}	0.274^{**}
Inclination (°)	0.105	0.018	0.199^{**}
Aspect (°)	0.075	0.061	0.109
Soil parameters			
pH (KCl)	0.048	−0.085	−0.066
C_t (%)	−0.069	−0.078	−0.083
N_t (%)	-0.257^{**}	−0.109	-0.190^{**}
CN ratio	0.291^{**}	0.003	0.129
CEC (µmol$_c$/g)	−0.016	0.011	−0.122
Base saturation (%)	−0.010	0.004	-0.168^{*}
Exchange acidity (µmol$_c$/g)	−0.025	−0.063	0.132
Na (µmol$_c$/g)	−0.026	-0.162^{*}	−0.069
K (µmol$_c$/g)	0.009	-0.158^{*}	−0.090
Mg (µmol$_c$/g)	−0.007	−0.040	−0.084
Ca (µmol$_c$/g)	−0.040	0.006	−0.127
Mn (µmol$_c$/g)	0.006	−0.087	−0.102
Fe (µmol$_c$/g)	0.145^{*}	−0.080	0.206^{**}
Al (µmol$_c$/g)	0.036	−0.071	0.196^{**}
Ah (cm)	$-,228^{**}$	0.073	−0.063
Organic (%)	−0.067	−0.091	−0.099
Sand (%)	0.298^{**}	0.219^{**}	0.220^{**}
Silt (%)	-0.351^{**}	−0.134	-0.301^{**}
Clay (%)	−0.092	-0.222^{**}	−0.004

Syntaxa and their environmental relationships

Class 1: *Betula utilis-Abies spectabilis* forests

Diagnostic species: *Betula utilis, Circaea alpina* subsp. *micrantha, Abies spectabilis, Ribes griffithii, Rubus fragarioides, Synotis alata, Clintonia udensis, Parasenecio quinquelobus, Stipa roylei, Pilea racemosa, Acer caudatum, Bistorta amplexicaulis, Impatiens racemosa* var. *ecalcarata, Viola biflora, Maianthemum purpureum, Thalictrum cultratum, Deparia allantodioides, Ribes glaciale, Rosa sericea, Koenigia delicatula, Galium paradoxum, Scrophularia pauciflora, Cryptogramma stelleri, Lepisorus* cf. *clathratus, Phymatopteris malacodon, Rhododendron campanulatum, Ribes acuminatum, Sorbus microphylla* agg., *Trillium govanianum*

Character species / Transgressive character species: *Betula utilis, Circaea alpina* subsp. *micrantha, Abies spectabilis, Ribes griffithii, Rubus fragarioides, Parasenecio quinquelobus, Bistorta amplexicaulis, Rosa sericea*

In the Rolwaling Valley, *Betula utilis* - *Abies spectabilis* forests are developed on upper montane and subalpine N/NE-slopes up to an elevation of c. 4100 m a.s.l. These forest stands are primarily composed of *Abies spectabilis* and *Betula utilis*, with *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer. At its upper distribution, closed forest stands give way to *Rhododendron campanulatum* krummholz forming an extensive belt between 3900 and 4000 m a.s.l. (NW-exposed), and 4000 and 4100 m a.s.l. (NE-exposed). We differentiated the *Abies spectabilis* forests into the *Synotis alata-Abies spectabilis* community, the *Ribes glaciale-Abies spectabilis* community, and the *Boschniakia himalaica-Rhododendron campanulatum* community. As the DCA (Fig. 2, Table 1) and the ANOVA (Table 2) suggest, altitude and mean soil temperature appear to be the decisive ecological factors for differences in species composition of the three syntaxa.

These forest communities are developed on podzol soils with an extremely low pH-value of c. 3.0 (Table 2). The sandy fraction dominates the grain size distribution of the soils (sandy loams); its percentage increases slightly towards higher altitudes (Table 2), implying a deterioration of nutrient storage and water-holding capacity (see discussion). Reduced water retention capacity in turn results in decreasing soil humidity along the elevational gradient (Table 2). Slight differences in soil pH do not play a role for the differentiation of species composition, as mean values are extremely low throughout the complete treeline ecotone with slightly higher values in the *Synotis alata-Abies spectabilis* community (Table 2).

Table 2. Mean values (Mean) and standard deviation (SD) for investigated environmental parameters. Differences between phytosociological groups were tested with one-way-ANOVAs. Level of significance (α) was set at 0.05. Superscript letters signify results of *post-hoc* pairwise t-test with Holm correction. The last column shows overall significance pattern abridged with significance codes: < 0.001 '***'; < 0.01 '**'; < 0.05 '*'.

Parameters	*Synotis alata – A. spectabilis* community				*Ribes glaciale – A. spectabilis* community				*Boschniakia himalaica – R. campanulatum* community				*Pedicularis* cf. *microcalyx – R. anthopogon* community				*Anaphalis royleana – R. anthopogon* community				P
	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	N	Mean	SD	Signf.	
Landscape parameters																					
Altitude (m.a.s.l.)	27	3815.5	44.1	a	28	3928.5	58.0	b	11	4051.4	60.1	c	8	4098.4	72.8	c	17	4215.1	43.3	d	***
Inclination (°)	27	33.2	4.4	a	28	36.9	3.5	b	11	35.1	3.1	ab	8	37.1	3.6	ab	17	33.4	3.3	a	**
Exposition (°)	27	41.4	63.0		28	50.9	62.1		11	91.7	128.4		8	75.3	114.2		17	38.0	17.0		
Soil parameters																					
pH (KCl)	27	3.1	0.4	ab	28	3.0	0.3	a	11	2.8	0.3	a	8	3.0	0.2	ab	17	3.2	0.2	b	**
Ct (%)	27	29.6	12.3		28	25.9	13.6		11	34.4	12.4		8	26.6	13.7		17	23.6	11.8		
Nt (%)	27	1.5	0.6	a	28	1.3	0.6	ab	11	1.4	0.4	ab	8	1.1	0.5	ab	17	1.0	0.3	b	**
CN ratio	27	19.6	3.2	a	28	20.4	2.6	a	11	24.1	4.6	b	8	23.9	3.1	b	17	23.9	4.8	b	***
CEC (µmolc/g)	27	188.0	135.1		28	188.6	116.4		11	234.3	117.4		8	183.7	120.3		17	151.0	68.0		
Base saturation (%)	27	61.1	22.7		28	57.0	24.6		11	66.8	19.7		8	40.5	17.7		17	67.0	20.5		*
Exchange acidity (µmolc/g)	27	67.1	39.7	ab	28	68.2	43.2	ab	11	75.5	45.3	ab	8	106.0	53.2	a	17	45.2	18.6	b	*
Na (µmolc/g)	27	0.3	0.2		28	0.2	0.3		11	0.2	0.1		8	0.2	0.2		17	0.3	0.5		
K (µmolc/g)	27	10.8	7.5		28	8.2	5.3		11	8.9	4.4		8	7.8	4.3		17	10.5	5.4		
Mg (µmolc/g)	27	32.0	25.6		28	29.7	23.3		11	42.3	23.8		8	19.7	12.2		17	30.0	20.4		
Ca (µmolc/g)	27	109.6	119.3		28	107.1	99.1		11	142.0	122.8		8	58.3	71.9		17	86.8	60.8		
Mn (µmolc/g)	27	5.4	12.7	ab	28	3.7	7.3	ab	11	0.9	0.9	ab	8	0.5	0.3	a	17	4.4	4.8	b	***
Fe (µmolc/g)	27	7.7	8.9		28	7.3	7.5		11	11.4	10.0		8	9.3	2.7		17	7.4	5.3		*
Al (µmolc/g)	27	35.4	29.8	ab	28	32.7	26.9	ab	11	34.7	25.5	ab	8	49.6	21.2	a	17	24.2	15.9	b	*
Ah (cm)	27	8.3	7.1	a	28	9.2	6.2	a	11	9.3	5.4	a	8	11.1	10.9	a	17	2.8	2.4	b	***
Organic (%)	27	51.7	21.6		28	44.3	23.4		11	59.2	21.4		8	46.3	22.9		17	41.3	20.0		
Sand (%)	23	56.9	16.9		25	61.1	14.0		9	68.6	10.7		8	69.5	6.2		17	68.0	5.9		
Silt (%)	23	28.0	6.6	a	25	26.0	5.3	a	9	22.1	6.7	ab	8	22.1	5.7	ab	17	19.0	4.1	b	***
Clay (%)	23	15.0	11.3		25	12.9	11.0		9	9.3	5.2		8	8.4	3.6		17	13.0	5.4		
Climate parameters																					
mean soil temp. (year) [°C]	6	3.5	0.6	ab	8	3.6	0.4	b	3	2.7	0.4	abc	6	2.5	0.7	ac	3	2.5	0.8	c	***
mean soil temp. (ON) [°C]	7	3.1	0.7		10	3.3	0.6		3	2.8	0.4		6	2.6	0.8		3	2.7	0.2		
mean soil temp. (DJF) [°C]	7	-2,1	1,4		8	-0,9	0.7		3	-1,9	0.8		6	-2,9	1.5		3	-2,2	0.9		
mean soil temp. (MAM) [°C]	6	1,3	0.6		8	1,3	0.8		3	0.3	0.2		6	0.3	0.5		3	0.0	0.4		*
mean soil temp. (JJAS) [°C]	7	9,5	0.2	a	10	8,8	0.4	b	3	7,8	0.6	ab	6	8,2	0.7	ab	3	7,8	0.7	ab	**
Growing degree days	7	169.6	8.3	a	8	169.3	15.0	ab	3	141.7	4.5	c	6	146.8	11.9	bc	3	137.7	10.7	ac	**
Mean Soil Humidity (year) [pF]	7	2.1	0.5		10	2.3	0.6		3	2.3	0.2		7	2.3	0.4		3	2.6	0.4		

Table 3. Synoptic table of the proposed vegetation classes and rankless communities. Numbers represent percentage frequencies and modified fidelity phi coefficients multiplied 100 (superscript). Phi coefficients refer to fidelity among all communities and among classes. Diagnostic species were selected applying a threshold of phi ≥ 0.3 and a significant concentration at $\alpha = 0.05$ according to Fisher's exact test. Character species are highlighted in dark grey at the lowest level where they are diagnostic. Transgressive character species are highlighted in light grey.

Group No.	**1**	**2**	**1.1**	**1.2**	**1.3**	**2.1**	**2.2**
Number of relevés	**66**	**25**	**27**	**28**	**11**	**8**	**17**
Mean species richness	**20**	**15**	**25**	**23**	**12**	**11**	**19**
Number of diagnostic species	**28**	**19**	**24**	**14**	**2**	**5**	**23**
Class 1							
***Betula utilis-Abies spectabilis* forests**							
Betua utilis	88^{84}	4$^{\cdot}$	93^{43}	100^{50}	45$^{\cdot}$	12$^{\cdot}$	---$^{\cdot}$
Circaea alpina subsp. *micrantha*	80^{82}	---$^{\cdot}$	89^{47}	89^{47}	36$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Abies spectabilis	85^{77}	8$^{\cdot}$	93^{46}	100^{54}	27$^{\cdot}$	---$^{\cdot}$	12$^{\cdot}$
Ribes griffithii	67^{66}	4$^{\cdot}$	70^{34}	79^{42}	27$^{\cdot}$	12$^{\cdot}$	---$^{\cdot}$
Rubus fragarioides	38^{48}	---$^{\cdot}$	48^{39}	43^{32}	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Class 2							
***Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrubs**							
Cassiope fastigiata	9$^{\cdot}$	84^{75}	---$^{\cdot}$	7$^{\cdot}$	36$^{\cdot}$	88^{45}	82^{40}
Rhododendron anthopogon	26$^{\cdot}$	96^{72}	4$^{\cdot}$	29$^{\cdot}$	73^{13}	100^{41}	94^{35}
Group 1.1							
***Synotis alata-Abies spectabilis* community**							
Synotis alata	48^{57}	---$^{\cdot}$	93^{81}	25$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Clintonia udensis	33^{45}	---$^{\cdot}$	74^{78}	7$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Parasenecio quinquelobus	71^{74}	---$^{\cdot}$	96^{65}	75^{43}	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Stipa roylei	23^{36}	---$^{\cdot}$	52^{65}	4$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Pilea racemosa	70^{73}	---$^{\cdot}$	96^{62}	61$^{\cdot}$	27$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Acer caudatum	56^{62}	---$^{\cdot}$	85^{62}	43$^{\cdot}$	18$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Bistorta amplexicaulis	73^{76}	---$^{\cdot}$	96^{60}	68^{30}	27$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Impatiens racemosa var. *ecalcarata*	15^{29}	---$^{\cdot}$	37^{57}	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Viola biflora	38^{48}	---$^{\cdot}$	59^{53}	32$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Prunus rufa	12$^{\cdot}$	---$^{\cdot}$	30^{50}	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Koenigia nepalensis	11$^{\cdot}$	---$^{\cdot}$	26^{47}	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Maianthemum purpureum	17^{30}	---$^{\cdot}$	30^{40}	11$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Aruncus dioicus subsp. *triternatus*	14^{27}	---$^{\cdot}$	26^{39}	7$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Thalictrum cultratum	33^{45}	---$^{\cdot}$	44^{39}	36$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Deparia allantodioides	70^{46}	24$^{\cdot}$	85^{38}	64$^{\cdot}$	45$^{\cdot}$	12$^{\cdot}$	29$^{\cdot}$
Carex munda	47^{24}	24$^{\cdot}$	63^{37}	50$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	35$^{\cdot}$
Carex lehmannii	27$^{\cdot}$	24$^{\cdot}$	52^{34}	14$^{\cdot}$	---$^{\cdot}$	25$^{\cdot}$	24$^{\cdot}$
Polygonatum kansuense	11$^{\cdot}$	---$^{\cdot}$	19^{30}	7$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Group 1.2							
***Ribes glaciale-Abies spectabilis* community**							
Ribes glaciale	61^{66}	---$^{\cdot}$	48$^{\cdot}$	89^{63}	18$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Rosa sericea	76^{69}	8$^{\cdot}$	78^{38}	96^{57}	18$^{\cdot}$	---$^{\cdot}$	12$^{\cdot}$
Koenigia delicatula	73^{76}	---$^{\cdot}$	59$^{\cdot}$	93^{52}	55$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Saxifraga pallida	14^{27}	---$^{\cdot}$	---$^{\cdot}$	29^{40}	9$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Galium paradoxum	42^{52}	---$^{\cdot}$	33$^{\cdot}$	57^{40}	27$^{\cdot}$	---$^{\cdot}$	---$^{\cdot}$
Scrophularia pauciflora	33^{38}	4$^{\cdot}$	37$^{\cdot}$	43^{34}	---$^{\cdot}$	---$^{\cdot}$	6$^{\cdot}$
Juncus thomsonii	45$^{\cdot}$	36$^{\cdot}$	41$^{\cdot}$	64^{31}	9$^{\cdot}$	12$^{\cdot}$	47$^{\cdot}$

Group No.	**1**	**2**	**1.1**	**1.2**	**1.3**	**2.1**	**2.2**
Number of relevés	**66**	**25**	**27**	**28**	**11**	**8**	**17**
Mean species richness	**20**	**15**	**25**	**23**	**12**	**11**	**19**
Number of diagnostic species	**28**	**19**	**24**	**14**	**2**	**5**	**23**
Group 1.3							
***Boschniakia himalaica-Rhododendron campanulatum* community**							
Boschniakia himalaica	20 ·	12 ·	--- ·	21 ·	64^{51}	12 ·	12 ·
Cryptogramma stelleri	18^{32}	--- ·	7 ·	21 ·	36^{35}	--- ·	--- ·
Group 2.1							
***Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community**							
Pedicularis cf. *microcalyx*	--- ·	68^{72}	--- ·	--- ·	--- ·	75^{52}	65^{41}
Rhododendron lepidotum	15 ·	44^{32}	7 ·	18 ·	27 ·	75^{47}	29 ·
Group 2.2							
***Anaphalis royleana-Rhododendron anthopogon* community**							
Anaphalis royleana	--- ·	64^{69}	--- ·	--- ·	--- ·	--- .	94^{96}
Codonopsis thalictrifolia	--- ·	60^{66}	--- ·	--- ·	--- ·	--- .	88^{93}
Rhododendron setosum	2 ·	76^{76}	--- ·	4 ·	--- ·	25 ·	100^{85}
Kobresia nepalensis	--- ·	68^{72}	--- ·	--- ·	--- ·	25 ·	88^{78}
Calamagrostis lahulensis	--- ·	77^{78}	--- ·	--- ·	--- ·	38 ·	94^{77}
Salix calyculata	2 ·	44^{51}	--- ·	4 ·	--- ·	--- ·	65^{65}
Dasiphora arbuscula	3 ·	84^{82}	--- ·	4 ·	9^{9}	50 ·	100^{72}
Pedicularis lachnoglossa	3 ·	40^{45}	4 ·	4 ·	--- ·	--- ·	59^{67}
Lonicera litangensis	9 ·	56^{50}	11 ·	11 ·	--- ·	12 ·	76^{65}
Bistorta vivipara	2 ·	44^{51}	--- ·	4 ·	--- ·	$12^{1.}$	59^{61}
Rhodiola spec.	8 ·	92^{84}	--- ·	7 ·	27^{27}	75^{34}	100^{59}
Anaphalis nepalensis	--- ·	24^{37}	--- ·	--- ·	--- ·	--- ·	35^{55}
Swertia cuneata	--- ·	24^{37}	--- ·	--- ·	--- ·	--- ·	35^{55}
Hierochloe flexuosa	--- ·	20^{33}	--- ·	--- ·	--- ·	--- ·	29^{50}
Calamagrostis spec.	--- ·	16^{30}	--- ·	--- ·	--- ·	--- ·	24^{44}
Rheum australe	33 ·	56^{23}	59^{25}	18 ·	9^{9}	12 ·	76^{43}
Saussurea spec.	--- ·	12^{25}	--- ·	--- ·	--- ·	--- ·	18^{38}
Theropogon pallidus	--- ·	12^{25}	--- ·	--- ·	--- ·	--- ·	18^{38}
Bistorta vacciniifolia	45 ·	92^{50}	22 ·	54 ·	82 ·	75 ·	100^{36}
Agrostis inaequiglumis	2 ·	12 ·	--- ·	4 ·	--- ·	--- ·	18^{33}
Companion species							
Acanthocalyx nepalensis	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Anaphalis contorta	3 ·	4 ·	--- ·	7 ·	--- ·	--- ·	6 ·
Aconogonon polystachyum	14 ·	4 ·	19 ·	14 ·	--- ·	--- ·	6 ·
Acronema tenerum	91^{24}	72 ·	93 ·	89 ·	91 ·	38 ·	88 ·
Agrostis spec. I	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Agrostis spec. II	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Arisaema jacquemontii	3 ·	4 ·	--- ·	7 ·	--- ·	12 ·	--- ·
Athyrium rupicola	23 ·	20 ·	11 ·	32 ·	27 ·	25 ·	18 ·
Carex setosa	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·
Clematis spec.	5 ·	--- ·	7 ·	4 ·	--- ·	--- ·	--- ·
Cremanthodium reniforme	5 ·	--- ·	4 ·	7 ·	--- ·	--- ·	--- ·
Cystopteris cf. *montana*	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Cystopteris fragilis	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·
Dryopteris acutodentata	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Epilobium cf. *laxum*	11 ·	--- ·	15 ·	11 ·	--- ·	--- ·	--- ·
Goodyera fusca	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·

Group No.	**1**	**2**	**1.1**	**1.2**	**1.3**	**2.1**	**2.2**
Number of relevés	**66**	**25**	**27**	**28**	**11**	**8**	**17**
Mean species richness	**20**	**15**	**25**	**23**	**12**	**11**	**19**
Number of diagnostic species	**28**	**19**	**24**	**14**	**2**	**5**	**23**
Goodyera repens	11 ·	--- ·	11 ·	14 ·	--- ·	--- ·	--- ·
Hemiphragma heterophyllum	6 ·	--- ·	4 ·	11 ·	--- ·	--- ·	--- ·
Impatiens urticifolia	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Juniperus indica	2 ·	4 ·	--- ·	4 ·	--- ·	--- ·	6 ·
Juniperus squamata	5 ·	4 ·	4 ·	7 ·	--- ·	--- ·	6 ·
Lepisorus cf. *clathratus*	61 ^{46}	16 ·	70 ^{28}	64 ^{22}	27 ·	50 ·	--- ·
Listera pinetorum	3 ·	--- ·	7 ·	--- ·	--- ·	--- ·	--- ·
Lonicera lanceolata	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Malaxis cylindrostachya	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Myriactis nepalensis	3 ·	--- ·	--- ·	7 ·	--- ·	--- ·	--- ·
Pedicularis furfuracea	3 ·	--- ·	7 ·	--- ·	--- ·	--- ·	--- ·
Phlomis breviflora	5 ·	--- ·	4 ·	7 ·	--- ·	--- ·	--- ·
Phymatopteris malacodon	92 ^{55}	40 ·	89 ·	100 ^{30}	82 ·	75 ·	24 ·
Poa spec. I	17 ·	4 ·	19 ·	18 ·	9 ·	--- ·	6 ·
Poa spec. II	2 ·	--- ·	--- ·	--- ·	9 ·	--- ·	--- ·
Polypodiodes lachnopus	11 ·	--- ·	11 ·	11 ·	9 ·	--- ·	--- ·
Potentilla aristata	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·	6 ·
Primula sikkimensis	6 ·	--- ·	11 ·	4 ·	--- ·	--- ·	--- ·
Rhodiola fastigiata	3 ·	--- ·	4 ·	4 ·	--- ·	--- ·	--- ·
Rhododendron campanulatum	92 ^{31}	68 ·	81 ·	100 ·	100 ·	88 ·	59 ·
Ribes acuminatum	24 ^{37}	--- ·	22 ·	29 ·	18 ·	--- ·	--- ·
Saxifraga granulifera	2 ·	--- ·	4 ·	--- ·	--- ·	--- ·	--- ·
Saxifraga hispidula	8 ·	8 ·	--- ·	14 ·	9 ·	--- ·	12 ·
Saxifraga pernes	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Selinum cf. *wallichianum*	17 ·	4 ·	22 ·	18 ·	--- ·	12 ·	--- ·
Sorbus microphylla agg.	100 ^{62}	44 ·	100 ^{23}	100 ^{23}	100 ·	88 ·	24 ·
Spiraea arcuata	2 ·	--- ·	--- ·	4 ·	--- ·	--- ·	--- ·
Streptopus simplex	3 ·	--- ·	7 ·	--- ·	--- ·	--- ·	--- ·
Trillium govanianum	18 ^{32}	--- ·	22 ·	21 ·	--- ·	--- ·	--- ·
Utricularia spec.	6 ·	--- ·	--- ·	11 ·	9 ·	--- ·	--- ·
Valeriana hardwickii	2 ·	4 ·	4 ·	--- ·	--- ·	--- ·	6 ·

Figure 4. Photos of the proposed communities.a: *Synotis alata* – *Abies spectabilis* community; b: *Ribes glaciale* – *Abies spectabilis* community; c – d: *Boschniakia himalaica* – *Rhododendron campanulatum* community; e: *Pedicularis cf. microcalyx* – *Rhododendron anthopogon* community; f: *Anaphalis royleana* – *Rhododendron anthopogon* community.

Group 1.1: Synotis alata-Abies spectabilis community

Diagnostic species: *Betula utilis, Circaea alpina* subsp. *micrantha, Abies spectabilis, Ribes griffithii, Rubus fragarioides, Synotis alata, Clintonia udensis, Parasenecio quinquelobus, Stipa roylei, Pilea racemosa, Acer caudatum, Bistorta amplexicaulis, Impatiens racemosa* var. *ecalcarata, Viola biflora, Prunus rufa, Koenigia nepalensis, Maianthemum purpureum, Aruncus dioicus* subsp. *triternatus, Thalictrum cultratum, Deparia allantodioides, Carex munda, Carex lehmannii, Polygonatum kansuense, Rosa sericea.*

With a mean number of 25 species, species richness is highest for *Synotis alata-Abies spectabilis* compared to all other syntaxa of the same rank. This community is marked by a characteristic species combination including ten highly diagnostic and 14 diagnostic species (Table 3). Eleven diagnostic species are at the same time diagnostic for the *Ribes glaciale-Abies spectabilis* community, reflecting the close syntaxonomical relation between both communities (Table 3; Supplement S1).

This syntaxon occurs on moderately steep slopes (33° on average) between 3700 to 3900 m a.s.l., i.e. in the lower subalpine range of the *Betula utilis* - *Abies spectabilis* forests. These closed forest stands are dominated by *Abies spectabilis*, *Betula utilis*, and *Sorbus microphylla* in the tree layer (mean cover tree layer 1: 40%; tree layer 2: 43%), with regular occurrence of *Acer caudatum* and sporadic occurrence of *Rhododendron campanulatum* and *Prunus rufa*. Most species of the tree layer, which attains a height of c. 16 m, also prevail in the shrub layer (mean cover 38%), accompanied by *Ribes* and *Rosa* species. Productivity of the herb layer is high in comparison to the *Ribes glaciale-Abies spectabilis* community. It includes many tall forbs (e.g. *Synotis alata, Parasenecio quinquelobus, Epilobium* cf. *laxum*) and shows high average cover of 60%. This can be attributed to the more favourable growth conditions with higher temperature sums and better nutrient supply (see discussion). As is apparent from the ANOVA (Table 2), annual soil temperature (significant) and nitrogen and potassium contents (insignificant) show highest values in the *Synotis alata-Abies spectabilis* community. At the same time the CN ratio narrows (insignificant) (Table 2), indicating higher decomposition rates. The DCA (Fig. 2) and associated correlation coefficients (Table 1) confirm the relevance of CN ratio, nitrogen and potassium for the floristic differentiation of the *Synotis alata-Abies spectabilis* community. CN ratio and nitrogen levels are significant for the arrangement of relevés along Axis 1, representing the floristic dissimilarity along the elevational gradient. We measured the highest annual soil humidity values for the *Synotis alata-Abies spectabilis* community (Table 2). This is supported by the highly diagnostic species

Clintonia udensis, which is considered an indicator species for humid soil conditions (Miehe 1990). Relevés of the *Synotis alata-Abies spectabilis* and the *Ribes glaciale-Abies spectabilis* community are additionally arranged along Axis 2 of the DCA. According to the correlation of ordination scores with environmental parameters, Axis 2 corresponds to a gradient of potassium and sodium. Soils of *Synotis alata-Abies spectabilis* communities are also characterized by the highest mean content of manganese (insignificant, Table 2). The values are, however, extremely heterogeneous according to the high standard deviation.

Group 1.2: Ribes glaciale-Abies spectabilis community

Diagnostic species: *Betula utilis, Circaea alpina* subsp. *micrantha, Abies spectabilis, Ribes griffithii, Rubus fragarioides, Parasenecio quinquelobus, Bistorta amplexicaulis, Ribes glaciale, Rosa sericea, Koenigia delicatula, Saxifraga pallida, Galium paradoxum, Scrophularia pauciflora, Juncus thomsonii*

With a mean number of 23 vascular plant taxa, species richness of the *Ribes glaciale-Abies spectabilis* community is slightly lower than of the *Synotis alata-Abies spectabilis* community. The community is defined by four highly diagnostic and ten diagnostic species (Table 3).

This community of tall mixed forest stands attains a height of c. 17 m, and occupies steep slopes (mean of 37°) in the upper subalpine range of the treeline ecotone (3800 to 4050 m a.s.l.). *Betula utilis*, *Abies spectabilis* and *Rhododendron campanulatum* dominate the tree layer (mean cover tree layer 1: 41%; tree layer 2: 61%), in which *Sorbus microphylla* regularly occurs and *Acer caudatum* occasionally. Compared to the *Synotis alata-Abies spectabilis* community, *Betula utilis* and *Rhododendron campanulatum* tree individuals are more frequent. The shrub layer (mean cover 38%) is mainly composed of tree layer species and of *Ribes glaciale* and *Rosa sericea*.

Within the forest communities, the *Ribes glaciale-Abies spectabilis* community takes an intermediate position regarding ground vegetation cover and productivity. Tall forbs are missing and ground vegetation is less dense (average cover of 34%) and less developed compared to the *Synotis alata-Abies spectabilis* community. However, in contrast to the *Boschniakia himalaica-Rhododendron campanulatum* community, the herbaceous layer is much more luxuriant. The constellation of site factors (e.g., soil temperatures, nutrient availability) and resulting growth conditions also give evidence of an intermediate position of the *Ribes glaciale-Abies spectabilis* community. Soil temperature during summer months is significantly lower compared to the *Synotis alata-Abies spectabilis* community, but higher (insignificant) than in the adjoining krummholz belt (Table 2).The same holds true for CN ratio and content of potassium. However, nitrogen supply in the *Ribes glaciale-Abies spectabilis* community is lowest (insignificant) within the three forest communities, but still higher than in the *Rhododendron* dwarf shrub communities (Table 2). As mentioned above, CN ratio and nitrogen content play an important role for floristic differentiation within the complete treeline ecotone, while potassium is significant only for the floristic dissimilarity between *Ribes glaciale-Abies spectabilis* and *Synotis alata-Abies spectabilis* communities (Fig. 2).

Group1.3: Boschniakia himalaica-Rhododendron campanulatum community

Diagnostic species: *Boschniakia himalaica, Cryptogramma stelleri*

This species-poor forest community with a mean species number of 12 is marked by a characteristic species combination including one highly diagnostic and one diagnostic species (Table 3). It has the lowest species diversity in comparison to the other communities of *Betula utilis-Abies spectabilis* forests.

The *Boschniakia himalaica-Rhododendron campanulatum* community represents the krummholz belt, located immediately above the *Ribes glaciale-Abies spectabilis* community in an elevational band between 3900−4000 m (NW-exposed) and 4000−4100 m (NE-exposed). It occupies steep slopes (mean of 35°) between the treeline and the dwarf scrub heaths.

The layer (mean cover 85%) of gnarled and stunted krummholz trees attains a mean height of about three meters, which gradually decreases upslope. The stems form a dense and largely impenetrable thicket dominated by *Rhododendron campanulatum* with few interspersed, multi-stemmed *Sorbus microphylla* individuals. The name-giving, highly diagnostic taxon *Boschniakia himalaica* is parasitic on *Rhododendron* species (Miehe 1990). Shrub and herb layers have low height (2 m and 0.1 m, respectively) and cover (17.5% and 25%, respectively). Low productivity of these layers is further indicated by the low numbers of vascular plant species. The *Boschniakia himalaica-Rhododendron campanulatum* community has to cope with further deteriorating growth conditions along the elevational gradient (see Discussion). As the ANOVA revealed (Table 2), annual mean soil temperature and connected growing degree days are lower compared to the downslope communities. At the same time, CN ratio widens, indicating lower decomposition rates and lower availability of nitrogen. Mean pH value marginally decreases to 2.8 (insignificant).

Class 2: *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrub heaths

Diagnostic species: *Cassiope fastigiata, Rhododendron anthopogon, Pedicularis* cf. *microcalyx, Rhododendron lepidotum, Anaphalis royleana, Codonopsis thalictrifolia, Rhododendron setosum, Kobresia nepalensis, Calamagrostis lahulensis, Salix calyculata, Dasiphora arbuscula, Pedicularis lachnoglossa, Lonicera litangensis, Bistorta vivipara, Rhodiola discolor, Anaphalis nepalensis, Swertia cuneata, Hierochloe flexuosa, Bistorta vacciniifolia*

Character species / Transgressive character species: *Cassiope fastigiata*, *Rhododendron anthopogon*, *Pedicularis* cf. *microcalyx*, *Rhodiola discolor*.

In the Rolwaling Valley, communities of this class occur above the treeline in an elevational range between 3950 and 4300 m a.s.l. The *Rhododendron* dwarf thickets are distributed on podzols with pH values of c. 3.0 and formed by *Rhododendron anthopogon*, *Rhododendron setosum* and *Rhododendron lepidotum*. As mentioned above, growth conditions deteriorate along the elevational gradient (see also Müller et al. 2016a). Thus, sites of *Rhododendron* dwarf shrub communities are characterized by lower soil temperatures, wider CN ratios and lower nitrogen contents compared to the forest communities of class 1 (Table 2).

Group 2.1: Pedicularis cf. microcalyx-Rhododendron anthopogon community

Diagnostic species: *Cassiope fastigiata, Rhododendron anthopogon, Pedicularis* cf. *microcalyx, Rhododendron lepidotum, Rhodiola discolor*

With a mean species number of eleven, this community is species-poor compared to the other communities of the treeline ecotone. Floristic composition is comparatively inhomogeneous. As apparent from the DCA (Fig. 2), relevés are arranged over a relatively wide range along Axis 1, intersecting the adjacent *Boschniakia himalaica-Rhododendron campanulatum* and the *Anaphalis royleana-Rhododendron anthopogon* community. The characteristic species combination is marked by one highly diagnostic and four diagnostic species (Table 3). This dense dwarf thicket community with grasses in the understory and interspersed low-growing tree individuals is established on steep slopes (37° on average) immediately above the krummholz belt at elevations between 3950 and 4150 m a.s.l. The dwarf scrub heaths reach a mean height of 0.8 m and a mean cover of 80%. Different *Rhododendron* species (*R. anthopogon*, *R. lepidotum*, dwarf individuals of *R. campanulatum*) dominate the community, with interspersed *Bistorta vacciniifolia* shrubs and *Sorbus microphylla* shrubs or small trees.

The herb layer is less developed (mean height 0.1 m, mean cover 45%) and composed of fern species and species of the genera *Kobresia* and *Calamagrostis*. Growth conditions are less favourable with reduced mean soil temperatures (insignificant), base saturation (insignificant), and nitrogen contents (insignificant) (cf. Table 2).

Group 2.2: Anaphalis royleana-Rhododendron anthopogon community

Diagnostic species: *Cassiope fastigiata, Rhododendron anthopogon, Pedicularis* cf. *microcalyx, Anaphalis royleana, Codonopsis thalictrifolia, Rhododendron setosum, Kobresia nepalensis, Calamagrostis lahulensis, Salix calyculata, Dasiphora arbuscula, Pedicularis lachnoglossa, Lonicera litangensis, Bistorta vivipara, Rhodiola discolor, Anaphalis nepalensis, Swertia cuneata, Hierochloe flexuosa, Calamagrostis* spec.*, Rheum australe, Saussurea* spec.*, Theropogon pallidus, Bistorta vacciniifolia, Agrostis inaequiglumis*

With a mean species number of 19, species richness of this dwarf shrub community is distinctly higher compared to the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community adjoining below. The *Anaphalis royleana-Rhododendron anthopogon* community is marked by a characteristic species combination including 13 highly diagnostic and 10 diagnostic species. This open dwarf thicket community occurs in the uppermost zone of the treeline ecotone, extending over an elevational range between 4100 and 4300 m a.s.l. The herbaceous layer has a mean cover of 50%, and is not as sparse as in the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community. The *Rhododendron* shrub layer has a mean cover of 60% and attains a height of less than 50 cm, interspersed by single higher shrub individuals (*Dasiphora arbuscula*, *Sorbus microphylla*). The shrub layer is dominated by *Bistorta vacciniifolia*, *Rhododendron setosum* and *Dasiphora arbuscula*. The comparatively rich herb layer involves the comparatively high species richness mentioned above, grass taxa are especially frequent (genera *Calamagrostis* and *Kobresia* and others).

Corresponding to the elevational gradient (see DCA, Fig. 2), site conditions are the most unfavourable within the treeline ecotone. Habitats are characterized by low mean soil temperatures during the vegetation period and a lower number of growing degree days, and soil moisture is comparatively limited owing to a decrease in silt content (significant; Table 2). Decreasing thickness of the Ah-horizon (significant; Table 2) reflects low mineralisation rates on the one hand, and a decrease in biomass and litter production on the other. However, nitrogen content and CN ratio are in a comparable range as observed for the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community. Mn contents are significantly higher (cf. Table 2).

Discussion

Floristic composition and community patterns

Previous accounts of subalpine forest vegetation in the West and Central Himalaya indicate mixed forest stands dominated by conifers (mainly *Abies* species), with varying proportions of the Himalayan birch (*Betula utilis*) and other deciduous trees (Schweinfurth 1957; Miehe 1990; Schickhoff 1993; Miehe & Miehe 2000; Schickhoff 2005; Miehe et al. 2015). A gradual upslope increase in the proportion of birch occurrences has often been observed by these authors, with pure birch stands forming a narrow belt at many treelines. The treeline *Betula* forests merge into krummholz thickets, mainly composed of *Rhododendron* species, interspersed by isolated *Betula* or *Sorbus* trees. The krummholz belt forms the transitional zone to the alpine *Rhododendron* dwarf thickets and *Kobresia* mats further upslope.

The vegetation zonation and phytosociological differentiation assessed in this study for the Rolwaling Valley more or less corresponds to the patterns described in the above cited previous studies. However, a closed belt of pure *Betula utilis* stands above the mixed forest stands of *Abies spectabilis-Betula utilis* stands, as described in Schickhoff (1993, 2005), Miehe (1990), and Miehe et al. (2015) for shady slopes in the western and central Himalaya, is not developed in the Rolwaling Valley. In Rolwaling, subalpine mixed forests directly merge into the *Rhododendron campanulatum* krummholz belt (*Boschniakia himalaica-Rhododendron campanulatum* community) without an intermediate *Betula utilis* belt. These findings coincide with the results of Kikuchi & Ohba (1988), who found similar vegetation zonation in a southeastern range of the Rolwaling Himal. Whether this altitudinal zonation reflects a natural pattern is open to debate. We consider the Rolwaling treeline ecotone a near-natural treeline ecotone since we did not find any evidence of human impact except some wood cutting at lower elevations (Schwab et al. 2016). It could be assumed that *Abies* trees (and thus seed sources) have been eliminated from many treeline forest stands in the Himalaya by logging and cutting for firewood, and that pure *Betula utilis* forests have emerged from former mixed forest stands under devastating human impact (Schickhoff 2005). On the other hand, *Betula utilis* forests are considered climax communities at treelines in inner Himalayan valleys which are currently largely in the state of regressive successions (Miehe et al. 2015).

Subalpine mixed forest stands with prevailing *Abies* spp. and varying proportions of *Betula utilis,* as well as *Rhododendron campanulatum* in the understorey, are widespread from the West to the East Himalaya on euhumid to subhumid slopes (Schickhoff 2005; Miehe et al. 2015). Several fir species mostly dominate the tree layer of this upper cloud forest belt (*Abies pindrow* [Afghanistan to W Nepal], *A. spectabilis* [Afghanistan to Bhutan], *A. densa* [E Nepal to SE Tibet]; distribution ranges after Polunin & Stainton 1984). *A. pindrow* and *A. spectabilis* are considered by some not to be distinct species, and the latter is often confused with *A. densa*. Since species composition and community structure identified in this study largely corresponds to the comprehensive description of *Abies spectabilis* forests from the Langtang/Helambu region, c. 100 km to the west (Miehe 1990), we assign the differentiated forest communities (*Synotis alata-Abies spectabilis* community and *Ribes glaciale-Abies spectabilis* community) to a class of Himalayan fir forests (upper cloud forests). We term this class '*Betula utilis-Abies spectabilis* forests' on the basis of our material. It corresponds to the provisional class *Abietea himalayae* proposed by Miehe (1990). We agree with Miehe's (1990) assessment that the closely related Himalayan fir species (*A. pindrow*, *A.spectabilis*, *A. densa*) are dominant in upper montane/subalpine forests along the Himalayan South Slope and most suitable to characterize these forests, and that the genus *Abies* should be the name-giving taxon of a phytosociological rank unit at class level. We refrain, however, from providing here an original diagnosis of a phytosociological class and from applying the respective nomenclature since we consider the available relevé material as still not sufficient. Whether the Himalayan *Betula utilis-Abies spectabilis* forests prove to be a 'good' class is a matter that must be determined by further research.

Krummholz thickets are widely distributed at treeline elevations in the Himalaya, consisting of trees with gnarled, stunted growth forms due to deteriorating climatic conditions (Holtmeier 2009). We assigned the *Rhododendron campanulatum* krummholz belt (*Boschniakia himalaica-Rhododendron campanulatum* community) to the class *Betula utilis-Abies spectabilis* forests. The *Rhododendron campanulatum* krummholz belt has floristically to some extent a transitional character, with floristic affinities to both classes separated here. For instance, some diagnostic species of the dwarf shrub communities above the krummholz belt (*Rhododendron anthopogon, Bistorta vaccinifolia*) occur with high frequency also in the *Boschniakia himalaica-Rhododendron campanulatum* community. However, the krummholz community and the mixed forest communities show quite a high number of common highly frequent species which separates them from the dwarf shrub communities (inter alia *Galium paradoxum, Koenigia delicatula, Deparia allantodioides,* cf. Table 3). Moreover, the krummholz belt has a predominantly forest-like physiognomy which also suggests a closer relation to the class *Betula utilis-Abies spectabilis* forests. *Boschniakia himalaica* regularly occurs in Rhododendron krummholz thickets in the Himalaya (Miehe et al. 2015). This is in line with our phytosociological analysis, which *Boschniakia himalaica* turned out to be highly diagnostic and therefore the name-given species in the studied krummholz belt.

The largely impenetrable *Rhododendron campanulatum* krummholz belt in the Rolwaling Valley (with interspersed multi-stemmed *Sorbus* shrubs and trees) gives way to alpine *Rhododendron anthopogon* dwarf shrub communities. We assigned the differentiated *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* and *Anaphalis royleana-Rhododendron anthopogon* communities to the class *Dasiphora arbuscula-Rhododendron anthopogon* dwarf shrubs.

In Rolwaling, both dwarf shrub communities are mainly comprised of *Rhododendron anthopogon*, with interspersed *Rhododendron lepidotum* and *Rhododendron setosum*. Dwarf shrub cover of the *Pedicularis* cf. *microcalyx-Rhododendron anthopogon* community adds up to more than 80%, while the species composition of the *Anaphalis royleana-Rhododendron anthopogon* community is characterized by a strong graminoid and herbaceous component. Previous studies in Rolwaling Himal (Kikuchi & Ohba 1988), Langtang Valley (Miehe 1990), and Kaghan Valley in the West Himalaya (Schickhoff 1993) provide evidence that the species composition of *Rhododendron anthopogon* communities varies in different regions due to the variation of local site conditions and severity of human impact. Even within one investigation area the species turnover is rather high. In general, human impact on upper subalpine forests and krummholz seems to facilitate the expansion of dwarf shrub communities (Schickhoff et al. 2015). According to our observations in several Himalayan valleys, Rhododendron dwarf shrub communities extend their range into areas where the natural krummholz belt has been destroyed. Such replacement communities add to the floristic heterogeneity of the syntaxa of this class.

Pedicularis cf. *microcalyx-Rhododendron anthopogon* and *Anaphalis royleana-Rhododendron anthopogon* communities are classified here for the first time. Their species compositions deviate to some extent from previous descriptions of *Rhododendron anthopogon* communities in the literature (cf. Kikuchi & Ohba 1988; Miehe 1990; Schickhoff 1993). *Rhododendron* dwarf thickets are developed on shady, north-facing slopes along the entire Himalayan arc under cold, semi-humid to sub-humid climatic conditions in the alpine belt (Miehe et al. 2015). Communities are mainly comprised of different small-leaved *Rhododendron* species (*Rhododendron anthopogon, Rhododendron setosum, Rhododendron nivale*) with generally sparsely developed herbaceous layers (Schweinfurth 1957; Kikuchi & Ohba 1988; Miehe 1990; Schickhoff 1993; Miehe et al. 2015). As only very few phytosociological studies in alpine altitudinal zones of the Himalaya have been conducted so far, a syntaxonomical scheme for the respective vegetation units has not been established to date. Miehe (1990) proposed a provisional class '*Kobresietea nepalensis*' into which he integrated lower alpine *Rhododendron* dwarf shrub heaths as well as high alpine *Kobresia* mats. Due to insufficient relevé material, however, this scheme is hypothetical. Miehe (1990) conceded that it might be appropriate to separate the provisional '*Kobresietea nepalensis*' into two classes once an enlarged phytosociological database is made available. On the basis of our field experience in the alpine belt of many Himalayan regions and in accordance with the synopsis of the lower alpine dwarf shrub communities in European mountains such as *Loiseleurio-Vaccinietea* (cf. Mucina et al. 1993; Dúbravcová et al. 2005; Šibík et al. 2006), it is reasonable to assume that a syntaxonomical unit at class level which incorporates Himalayan *Rhododendron* dwarf shrub heaths and might be called '*Rhododendretea anthopogonis*' can be established.

Vegetation-environment relationships

Our study reveals distinct relationships of communities with various soil physical and chemical properties. Relevant drivers for community differentiation are soil temperature, nitrogen content and availability, as well as soil nutrient storage and soil water-holding capacity. Annual mean and growing season mean soil temperatures generally decrease from closed forest to the krummholz zone and dwarf shrub thickets (Müller et al. 2016a) and concurrently along the altitudinal sequence of communities in Rolwaling. Corresponding relationships with edaphic properties were identified for tree species density along the same transect (Schwab et al. 2017). The spatial pattern of nitrogen content and availability, soil nutrient storage and soil water retention capacity represents an elevational gradient of decreasing soil fertility, parallel to the overall decrease of temperatures in the same direction. However, the effect of dense tree canopies preventing soil heat flux and radiative warming of soil temperatures was observed on the NE-exposed slope during certain periods of the year, resulting in temporarily higher soil temperatures under dwarf shrub thickets compared to the krummholz zone (Müller et al. 2016a). Nitrogen is the most limiting factor to alpine plant productivity, whereas the supply of plant available nitrogen is primarily determined by soil temperature (Larcher 2003; Baptist & Aranjuelo 2012; Hawkesford et al. 2012). Nevertheless, plant communities by themselves are not nitrogen limited, as species composition is adapted to the prevailing nutrient supply, and nutrient enrichment creates modified communities (Körner 2003). Lower nitrogen availability (wider CN ratio) prevails in the krummholz and dwarf shrub communities (Table 2). The dense cover of ericaceous trees (*Rhododendron* krummholz belt) and shrubs (*Rhododendron* dwarf shrubs, Supplement S1), associated with a low leaf litter quality (wide CN ratio, high lignin content; Körner 2003), may contribute to this nutrient deficiency. Thick layers of recalcitrant *Rhododendron* litter are associated with low N mineralization rates and N availability (Maithani et al. 1998). Moreover, *Rhododendron* leaves contain high amounts of polyphenols (Hegnauer & Hegnauer 1966; Fan et al. 1999), which are an important C source for microorganisms in forest ecosystems (Schimel et al. 1996; Souto et al. 2000; DeLuca et al. 2002). High concentration of polyphenols may lead to the binding of N into complex polyphenolic compounds, and further to an increase in NH_4^+ and NO_3 immobilization (Northup et al. 1995; Schimel et al. 1996; Bradley et al. 2000; DeLuca et al. 2002) and thus to a decrease of nitrogen availability.

In addition to nitrogen deficiency, we hypothesize the impoverished flora of the *Boschniakia himalaica-Rhododendron campanulatum* community, and the extremely low productivity of the herbaceous layer, can be attributed to allelopathic effects of *Rhododendron campanulatum*. Apart from polyphenols, ericaceous vegetation contains triterpenes, inter alia ursolic acid (Hegnauer & Hegnauer 1966; Fan et al. 1999). Both classes of chemical compounds are known to be potentially allelopathic (Rice 1984; Li et al. 2010; Kadereit et al. 2014). *Rhododendron campanulatum* leaves contain the triterpene campanuline (Rangaswami & Sambamurthy 1961), which may directly negatively influence seedling recruitment of other species and favour monospecific *Rhododendron* thickets. To our knowledge, unlike other species of the genus *Rhododendron* (Nilsen et al. 1999; Chou et al. 2010), the allelopathic potential of *Rhododendron campanulatum* has not been analysed until now. Aside from allelopathic effects and competition for nutrients, plant-plant interference in the evergreen, dense *Rhododendron*-stands involves a strong competition for light.

Soil studies in Rolwaling Valley (Müller et al. 2016a, b) showed significantly decreasing nutrient availability (N, K, Mg, P) along the elevational gradient from subalpine forests to krummholz and dwarf shrub thickets. On the level of plant communities, elevational gradients of soil nutrient contents are, with the exception of nitrogen, less obvious: Soil nutrient contents show either significant differences between single plant communities in the ANOVA (Mn, Al) or significant correlation with DCA axes (Fe, Na, K), never both (Table 2). Moreover, all soil nutrient contents show relatively wide standard deviations. Differences in the detectability of soil nutrient gradients between altitudinal vegetation zones and the altitudinal sequence of plant communities have to be attributed to the mosaic-like pattern of respective habitat patches in the treeline ecotone. Since alpine soils show pronounced small-scale heterogeneity in terms of fertility and other properties in general (Nagy & Grabherr 2009, Bäumler 2015), further investigations are necessary to detect micro-scale relationships between plant species composition and edaphic properties.

Analyses of soil moisture indicated a decreasing trend along the elevational gradient (Table 2, see also Müller et al. 2016a, b). Lowest values were detected in the *Anaphalis royleana-Rhododendron anthopogon* community at the front edge of the ecotone. This is remarkable, as plant water supply is often improved at higher altitudes due to reduced evapotranspiration (Körner 2003) as long as increasing wind speed does not overcompensate a decrease in evaporation (cf. Holtmeier 2009). In spite of increasing solar radiation, evaporation often decreases along the elevational gradient, conditioned by temperature, solar intensity, atmospheric pressure, soil moisture, the degree of saturation of the air, and wind (Nullet & Juvik 1994; Nagy & Grabherr 2009; Kuhn 2012; Bach & Price 2013). In our study area, low topsoil moisture might be mainly caused by overall low water-holding capacities, according to a high proportion of sand within the soil texture (Müller et al. 2016b). In addition, the soil depth of the *Anaphalis royleana-Rhododendron anthopogon* community is low and the profile shows only weakly developed, thin Ah-horizons (Table 2). Dehydration of topsoil has strong effects on plant nutrition by interrupting topsoil nutrient cycling and thus reducing nutrient availability (Marschner & Rengel 2012). Effects of this 'drought-enhanced nutrient shortage' on plant life and therefore species distribution are even more appreciable than moisture stress by itself (Körner 2003).

Deteriorating site conditions with increasing elevation as assessed in soil studies in Rolwaling Valley (Müller et al. 2016a, b) can be confirmed for the elevational sequence of plant communities, especially in terms of soil temperature, nitrogen supply and availability, and soil moisture. These factors are crucial for differences in species composition along the steep environmental gradient in the treeline ecotone. Multifaceted interrelations between environmental factors make it difficult to rank them in order of their importance for species composition. Neither the DCA nor the ANOVA (Table 1, Table 2) give evidence of distinctly differing significance between main environmental variables. Apart from parent material and litter fall, nitrogen supply, for instance, is influenced by temperature and soil moisture. Moisture deficits in plants, in turn, can be strengthened by low soil temperatures (Tranquillini 1982; Larcher 2003). Low temperatures also affect life processes of plants directly by freezing stress and low temperature limit of net photosynthesis (Sakai & Larcher 1987; Larcher 2003; Taiz & Zeiger 2010).

Responsiveness of community patterns to climate warming

Accumulated knowledge of climate change-induced alteration of Himalayan ecosystems in terms of plant cover, plant functional type dominance, species distributions, species compositions and community structure is still very deficient. The sensitivity of species compositions and community structure in treeline ecotones is likewise largely unknown. For the Rolwaling Valley, our data clearly stress the significance of soil temperature, soil moisture and nitrogen (supply and availability) for species distribution along the elevational gradient. Since these factors are directly (soil temperature) or indirectly (soil moisture, nitrogen) affected by climatic conditions, we presume that community patterns in the treeline ecotone (species compositions, community structure) will change with ongoing climate warming (Schickhoff et al. 2015, 2016a,b).

Increasing temperatures might imply enhanced nitrogen supply. Low soil temperatures are the main constraint for nitrogen availability which controls alpine plant productivity (Larcher 2003; Baptist & Aranjuelo 2012; Hawkesford et al. 2012). Given the above-average warming in Himalayan treeline ecotones including the Rolwaling Valley, an increase in plant height and cover within plant communities and a shift in dominance patterns owing to an earlier start of the growing season is to be expected. Moreover, climate warming involves changes in precipitation patterns, leading to alterations in snow cover and modified soil moisture. No clear trend could be detected for precipitation patterns in the greater Himalayan region; observations show more decreasing than increasing precipitation trends (Hasson et al. 2016; Schickhoff et al. 2016a). As soil moisture was identified as one of the controlling factors for tree regeneration and stand structural patterns (Schickhoff et al. 2015, 2016b; Müller et al. 2016b) as well as for species composition in this study, we anticipate shifts in community structure and species composition due to changing precipitation and soil moisture supply.

In general, ongoing climatic changes will already have triggered shifts in species distributions and abundances in the Himalaya, widely without having been noticed or documented by science. For instance, Telwala et al. (2013) provided evidence of warming-driven elevational range shifts in 87% of 124 studied endemic plant species in the alpine zone Sikkim over the last 150 years. Upward range shifts of up to 150 m were detected in the NW Himalaya by Dolezal et al. (2016), who stress at the same time that plant species responses to ongoing climate change will not be unidirectional upward range shifts but rather multi-dimensional, species-specific and spatially variable. Thus, present-day plant assemblages and community structures are definitely different from those of the 19th century.

Conclusions and outlook

Our study provides first detailed insights into species compositions of plant communities and vegetation-environment relationships in the treeline ecotone in the Rolwaling Valley, an area not previously studied. The study expands on the still very limited knowledge of Himalayan subalpine-alpine vegetation with regard to floristic diversity, ecology, and syntaxonomy. When classifying the ecotone into five plant communities assigned to two classes, we had to deal with rank-less communities and a provisional status of classes. Thus, phytosociological studies in the Himalaya are still pioneer studies, illustrating the need for a complete overview and synopsis of Himalayan vegetation which would simultaneously provide deepened ecological knowledge. Differences in species composition of subalpine forests and dwarf shrub communities between the Rolwaling Valley and other Himalayan study areas, point to the importance of detailed local studies. Community patterns are distinctly correlated to a deterioration of growth conditions along the elevational gradient, reflected in an increasingly unfavorable constellation of soil temperature, soil moisture, and nitrogen supply and availability. Differentiations of species compositions are understood as resulting from complex interrelations between site factors. Though identified main environmental variables are directly or indirectly related to climatic conditions, long-term studies are necessary to evaluate the sensitivity of treeline ecotone vegetation to climate warming. However, this study provides a suitable baseline for monitoring plant communities in order to detect climate change-induced shifts in vegetation patterns and to assess the vulnerability of Himalayan treeline flora and vegetation.

Author contributions

B.B. conceived the study, conducted field sampling of vegetation and soils, determined plant species, performed the statistical analyses and led the writing with critical input from N.S; U.S. contributed expert knowledge, supported the field sampling, determined plant species, and provided major revision of the manuscript; J.O. gave statistical advise; M.M and T.S. conducted field sampling of soils, contributed soil expertise and provided soil data; W.B.D. dealt with taxonomical issues and determined the majority of plant species; all authors critically revised the manuscript.

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Electronic Supplements

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Supplement S1. Relevé table of communities in the treeline ecotone

Appendix II: Original publications

Article II

Bürzle, B., Schickhoff, U., Schwab, N., Wernicke, L.M., Müller, Y.K., Böhner, J., Chaudhary, R.P., Scholten and T., Oldeland, J. 2018. Seedling recruitment and facilitation dependence on safe site characteristics in a Himalayan treeline ecotone. *Plant Ecology* **219**: 115-132, dio: 10.1007/s11258-017-0782-2

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 *Abies spectabilis* seedlings establish on ground that is covered in average by 70% with litter, *Betula utilis* and *Rhododendron 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 two meter distance to at least one potentially protective element. Geomorphic elements and deadwood were the most important shelters for seedling establishment. Our results emphasize 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.

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Keywords:

Abies spectabilis; *Betula utilis*; microhabitat; Nepal; *Rhododendron campanulatum*; seedling establishment.

Introduction

It is generally supposed that alpine treelines migrate to higher elevations in response to contemporary climate change, at least in the long term (Smith 2003; Holtmeier and Broll 2007; Wieser et al. 2014). Current observations show quite inconsistent and sometimes contradictory responses, including substantially advancing as well as static treelines (Harsch et al. 2009). These variations reflect the local-scale complexity of abiotic and biotic site factors, interrelated with broad-scale climate inputs, species-specific traits as well as differences in local land use (Hofgaard 1997; Holtmeier and Broll 2005; Malanson et al. 2007; Hofgaard et al. 2009).

The majority of population dynamics within treeline ecotones are related to regeneration processes (Harper 1977). Treelines are stable if recruitment is confined to the lower part of the treeline ecotone, while treeline expansion to higher elevations requires the successful seedling establishment in the contiguous treeline ecotone, i.e. beyond the uppermost tree individuals or tree groups. A constantly low regeneration rate within the upper subalpine forest results in a contraction of the ecotone and a treeline shift towards lower elevations (Smith et al. 2009).

Regardless of the outstanding importance of seedling establishment for the spatial dynamics of treeline stands and the high mortality in pre-established life stages (e.g. Grubb 1977; Fenner and Thomson 2005), the far majority of field studies on the climatic impact on treeline position focused on mature trees (Smith et al. 2009). As habitat conditions and ecophysiologically effective stress factors differ distinctly between seedlings and trees, responses to climate warming will likewise do (Körner 2012). Thus, to understand differences in treeline dynamics and to make predictions about future treeline position, a deeper knowledge of the underlying processes of seedling establishment in the treeline ecotone and the required microhabitat conditions for successful recruitment is necessary (Germino et al. 2002; Smith et al. 2003, 2009).

A basic prerequisite for seedling recruitment is the availability of safe sites, defined as the fine-scale environment immediately surrounding a seedling that has all the necessities for germination and survival (Harper et al. 1961; Fowler 1988). Besides seed availability, the occurrence of a safe site is the most limiting factor for seedling establishment above the treeline (Jones and del Moral 2005; Batllori et al. 2009). Safe site requirements are species-specific, but also vary intraspecifically among genotypes or different seedlings' life stages (Leck et al. 2008). In harsh environments at high elevations, seedlings often require additional recruitment facilitation by abiotic sheltering (topographic shelters, rocks and stones) and/or positive biotic interactions (nurse plants, interactions with mycorrhiza and legume bacteria) that result in an amelioration of unfavourable site conditions (Callaway 1995). In treeline ecotones seedling microhabitat may be facilitated by microtopographic sheltering, positive inter-/intraspecific interrelations and nurse effects of tree islands (Resler 2006; Batllori et al. 2009; Greenwood et al. 2015).

Large warming trends in the Himalaya (up to 0.7 °C per decade at higher altitudes), which have been observed in the past 20 years (Pepin et al. 2015), are expected to have substantial effects on plant species distribution patterns, tree species density and treeline position (Xu et al. 2009; Shrestha et al. 2012; Telwala et al. 2013; Schickhoff et al. 2015; Dolezal et al. 2016, Schwab et al. 2017). However, despite the relevance of tree regeneration for treeline dynamics, only few studies on tree recruitment in Himalayan treeline ecotones have been conducted so far (Dutta et al. 2014; Schickhoff 2005; Schickhoff et al. 2016). Some studies on age stand distribution reported recruitment patterns of tree species in different parts of the Himalaya. Continuous recruitment of *Abies spectabilis*, *Pinus wallichiana* and *Betula utilis* was observed in treeline forests in Manang Valley, Annapurna Conservation Area (Nepal) (Ghimire and Lekhak 2007; Ghimire et al., 2010; Shrestha et al. 2007; Shrestha 2013). Corresponding recruitment patterns of *Abies spectabilis* were detected at treelines in the southern Langtang National Park, Nepal (Gaire et al. 2011), the Manaslu Conservation Area (Gaire et al. 2014) and in the Mt. Everest Nature Reserve, Tibet (Lv and Zhang 2012).

However, small-scaled safe site conditions of tree seedlings in Himalayan treeline ecotones are hardly explored. At upper subalpine forests in Bhutan spatial pattern analyses of *Abies densa* and *Rhododendron hodgsonii* showed highly positive intraspecific correlations for both species and increasing seedling abundance on bryophyte mats (Gratzer and Rai 2004). In the Sygera Mountains (SE Tibet), Wang et al. (2012a) found microsite-dependent occurrence of Smith fir seedlings (*Abies georgei* var. *smithii*) establishing preferentially on moss-lichen and organic matter substrate, facilitated by juvenile firs and *Rhododendron* mats.

In order to reduce the still large deficiencies in research this study aims at analysing safe sites for regeneration of the tree species *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum*, dominating the treeline ecotone in Rolwaling Himal, Nepal. We particularly focus on potential contrasts in safe site requirements between the three tree species. Since the ecotone displays a large diversity of species compositions and environmental conditions over a short geographical distance (Müller et al. 2016b; Bürzle et al. 2017; Schwab et al. 2017), our objective is to identify key factors for successful seedling establishment along an altitudinal gradient from upper subalpine closed forests via a dense *Rhododendron campanulatum* krummholz belt to alpine dwarf shrub heaths. We further focus on seedling establishment in the *Rhododendron* krummholz belt, as earlier studies indicate that the krummholz belt prevents the upslope migration of tree species (Schwab et al. 2017). To address these issues we:

1) analyse microhabitat substrate and vegetation cover of naturally established *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* seedlings in different stages of establishment;

2) examine facilitative elements (stones, rocks, microtopographic shelters, shrubs, trees) that potentially provide safe sites for regeneration of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* seedlings; and quantify the distance of seedlings to the nearest protective elements.

Study site

The study was conducted in the Rolwaling Valley (27°52’ N; 86°25’ E), which is located in Dolakha District, east-central Nepal, adjacent to the border to Tibet Autonomous Region (Fig. 1). It is part of the Gaurishankar Conservation Area, which was designated as a protected area in 2010 (Shrestha et al. 2010). The area is characterised by a continental climate with dry and cold winter and monsoonal/hyper-humid and cool summer conditions (Böhner et al. 2015; Gerlitz et al. 2016; Karki et al. 2017). Vegetation formations in the Rolwaling Valley are widely undisturbed by land use effects due to its seclusion without connection to the road network, low population density, and the Valley’s status as a sacred place in the Buddhist philosophy (Baumgartner 2015).

We investigated the treeline ecotone on a north-facing slope, extending from the closed subalpine forest to the lower alpine vegetation (3745 to 4300 m). The slope is steep with an inclination of 26 to 45°. The ecotone is composed of four vegetation types that succeed each other along the elevational gradient. (cf. Bürzle et al. 2017). Since transitions between vegetation types are fluent, the altitudinal dispersal of types is overlapping. The **lower subalpine forest [I]** (3700 to 3900 m) are primarily composed of *Abies spectabilis*, *Betula utilis* and regularly interspersed *Acer caudatum*, with *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer. Ground vegetation has a high diversity and cover. The **upper subalpine forest [II]** (3800 to 4050 m) shows a higher frequency of *Betula utilis* and *Rhododendron campanulatum* tree individuals and a less diverse and dense herb layer. In an elevational range between 3900 and 4000 m, the mixed forest stands are replaced by a species-poor ***Rhododendron*** **krummholz belt [III]**. The largely impenetrable thicket of

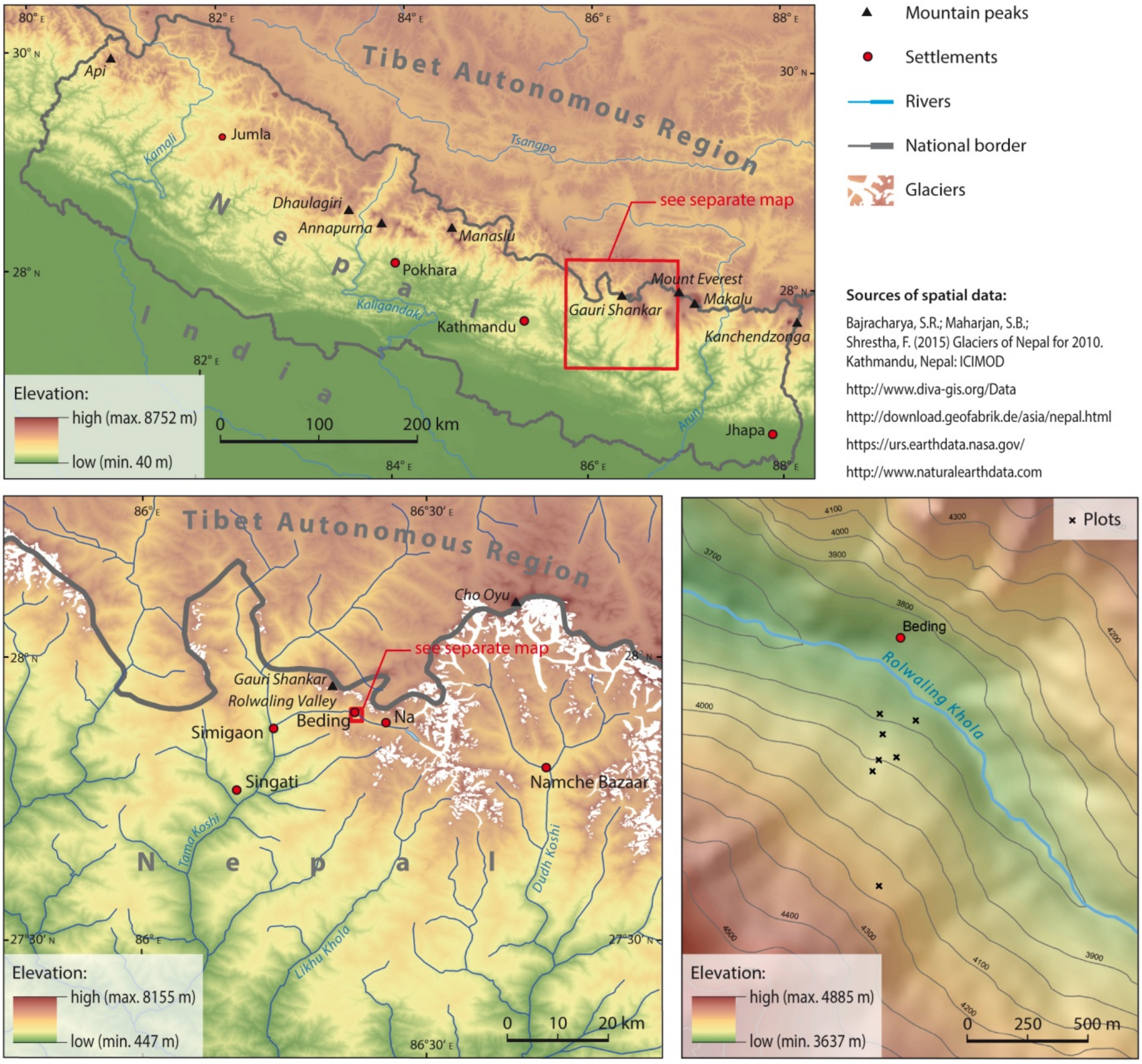

Fig. 1 Location of the studied treeline ecotone (red rectangles) in the Rolwaling Valley in east-central Nepal. Position of the 7 plots (35 subplots) is shown on the third map (lower right).

gnarled and stunted krummholz trees is dominated by *Rhododendron campanulatum* with few interspersed *Sorbus microphylla* individuals. The ground is characterised by a thick layer of *Rhododendron* litter and a sparse plant cover. Above the krummholz belt, **alpine dwarf shrub heaths [IV]** (3950 to 4300 m) represent the uppermost part of the treeline ecotone. The heaths are dominated by *Rhododendron* dwarf shrub species with different grass species in the understory. For detailed information on phytosociology of the treeline ecotone vegetation see Bürzle et al. (2017). Relevant drivers for the differentiation of vegetation types are soil temperature, nitrogen and other nutrient availability as well as soil water-holding capacity (Müller et al. 2016a, b, 2017; Bürzle et al. 2017). Soils in the study area are classified as podzols (IUSS 2015; Müller et al. 2016a).

Methods

Field data

We stratified the slope according to the different vegetation types encompassing the treeline ecotone and selected plots randomly by Microsoft Excel function RANDBETWEEN. In total, we established seven plots with a size of 20 m x 20 m, spread over the elevational range of seedling occurrence of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum.* At each plot we placed five rectangular subplots (35 in total) with a size of 4 m x 4 m along the two diagonal lines of the plot. Field sampling was conducted from July to September 2014.

We examined natural regeneration of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* in each subplot. All seedlings ≤ 50cm in height were measured from ground to shoot tip and grouped into three height classes (> 0 to 5cm, > 5 to 15cm, > 15 to 50cm). Seedlings' height decreases to a small extent along the elevational gradient in relation to their age (counts of internodes, unpublished data). Since seedlings were grouped in height classes with a relatively wide range, height variability of individuals of the same age is negligible. As *Betula utilis* exhibits seed-based regeneration as well as vegetative reproduction, we carefully checked their nature of propagation. All *Betula utilis* individuals reported here had developed from seeds.

Microhabitat characteristics were analyzed for all seedlings. We determined microhabitats as circular sample plots around seedlings with varying diameter in relation to seedlings' height (seedlings' height : diameter microsite; > 0 to 10cm : 10cm diameter, > 10 to 20cm : 20cm diameter, > 20 to 30cm : 30cm diameter, > 30 to 40cm : 40cm diameter, > 40 to 50cm : 50cm diameter) (cf. Duc 1991, Ammer et al. 2004). We analysed vegetation and substrate cover of each microhabitat, including the percentage of vegetation, moss, litter, bar soil, stones and litter of *Rhododendron* species (proportion of total litter amount).

We additionally sampled shelter elements within a radius of two meter around each seedling and measured the distance to the nearest element that potentially influences microhabitat and may facilitate germination and growth conditions. We differentiated four types of shelter elements: rocks (> 60cm diameter), stones (20-60cm diameter), deadwood and soil depression. We also noted the absence of any shelter element.

Statistical analysis

We computed seedling density per hectare (ha) of *Abies spectabilis*, *Betula utilis* and *Rhododendron campanulatum* in all height classes and vegetation types. To analyse seedling habitat preferences, we compared microhabitat characteristics of the tree species in focus. Microhabitat mean cover values were checked for normality of distribution and homogeneity of variance by visually examining the distribution of residuals (Quinn & Keough 2002). Since data failed the test, we used Kruskal-Wallis rank sum test followed by a Dunn's *post-hoc* test with Bonferroni adjustment of the significance level to check for significant differences among tree species in different vegetation types and height classes.

We visualised percentage of different shelter element types by plotting histograms for all species and height classes. To estimate the relevance of shelter elements for seedling establishment, we compared distances of tree seedlings to the nearest potentially protective structure. Differences of mean ranked distances were tested for significance by running a Kruskal-Wallis rank sum test followed by a Dunn's *post-hoc* multiple comparison test with Bonferroni adjustment of the significance level, since data were non-normally distributed. Compared group levels were likewise defined according to 'species', 'height class and 'vegetation type'.

Kruskal-Wallis tests were performed using the function 'kruskal.test' of the package 'stats' (R Core Team 2016). Dunn's tests were performed using the function 'posthoc.kruskal.dunn.test' of the package 'PMCMR' (Pohlert 2014). All graphs were created using the package 'ggplot2' (Wickham 2009). We performed all analysis using the statistical software environment R (version 3.2.4; R Core Team 2015).

Results

General pattern of abundance

In total we recorded 784 seedlings of *Abies spectabilis*, 155 seedlings of *Betula utilis* and 1191 seedlings of *Rhododendron campanulatum*. In correspondence to the high mortality rate during recruitment, seedlings' density was highest at early stages of establishment (> 0 to 5cm and > 5 to 15cm) (Table 1). Seedling distribution was not uniform among vegetation types. We recorded highest numbers of *Abies spectabilis* seedlings of all height classes in the lower and upper subalpine forest. *Betula utilis* seedlings of all height classes were most frequent in the lower subalpine forest. Small and medium sized *Rhododendron campanulatum* seedlings primarily occurred in the upper subalpine forest and in the krummholz belt, while we recorded highest density for taller *Rhododendron* seedlings (> 15 to 50cm) in the alpine dwarf shrub heaths.

Table 1 Tree species density of seedlings 0-5cm, 5-15cm, 15-50cm in the (I) lower subalpine forest, (II) upper subalpine forest, (III) *Rhododendron* krummholz belt, (IV) alpine dwarf shrub heath.

Height (cm)	Vegetation type	Seedling density (N/ha) A. spectabilis	Seedling density (N/ha) B. utilis	Seedling density (N/ha) R. campanulatum
0-5	I	34.500	3.313	3.563
0-5	II	6.688	0	39.875
0-5	III	3.125	125	33.750
0-5	IV	875	0	10.813
5-15	I	3.813	4.938	625
5-15	II	313	0	250
5-15	III	0	0	0
5-15	IV	0	0	875
15-50	I	938	1.375	63
15-50	II	188	0	438
15-50	III	250	0	125
15-50	IV	0	0	1.000

Ground cover

The three species in focus showed clear habitat preferences for germination and seedling establishment. Microsite characteristics differed significantly between *Abies spectabilis* on the one hand and *Betula utilis* and *Rhododendron campanulatum* on the other (Fig. 2, Table 2).

The youngest seedlings of *Abies spectabilis* (> 0 to 5cm) were mostly associated with litter, whereas moss cover was low (Fig. 3). Microhabitat cover values of the youngest seedlings of *Betula utilis* were significantly different ($p < 0.001$). *Betula* seedlings were most frequently related to moss cover and to a lower percentage to litter (Fig. 4). The same holds true for the youngest seedlings of *Rhododendron campanulatum* whose microhabitats had a significantly higher moss cover and lower percentage of litter ($p < 0.001$) compared to *Abies spectabilis* (Fig. 5). These preferences were independent from altitudinal occurrence and the surrounding vegetation, as microsite characteristics of all species did not significantly differ between vegetation types ($p > 0.001$). Field layer vegetation and the early successional groundcover types ‘bare soil’ and ‘stones’ played a negligible role for seedling establishment of all species with cover values less than 5%.

The taller the seedlings grew, the more the microhabitat preferences converged between the species. Only medium-sized *Abies spectabilis* and *Betula utilis* seedlings (> 5 to 15cm) in the lower subalpine forest differed significantly in their microhabitat structure that showed a significantly higher moss cover for *Betula utilis* seedlings, whereas litter cover was significantly higher in microhabitats of *Abies spectabilis* ($p < 0.001$). No clear distinctions could be detected between microhabitats of medium-sized *Rhododendron campanulatum* seedlings on the one hand and *Abies spectabilis* and *Betula utilis* seedlings on the other ($p > 0.001$). Tall seedlings (> 15 to 50cm) showed no significant differences in their preferred habitat structure between species ($p > 0.01$).

The *Rhododendron* krummholz belt and the alpine dwarf shrub heaths are largely characterised by a thick layer of *Rhododendron campanulatum* litter. *Rhododendron* litter seemed to be an unsuitable substrate for germination and seedling establishment of *Betula utilis* and *Rhododendron campanulatum*. We recorded no *Betula utilis* seedlings in areas covered with *Rhododendron* leaf litter. In microhabitats of *Rhododendron campanulatum* seedlings, percentage of *Rhododendron* litter was very low. In contrast, germination and establishment of *Abies spectabilis* seedlings appeared not to be interfered by *Rhododendron* litter, as youngest seedlings of *Abies spectabilis* (> 0 to 5cm) were associated with *Rhododendron* litter up to 60% in the krummholz belt and in the alpine dwarf shrub heaths. These microhabitat cover values were significantly higher than in microhabitats of *Rhododendron campanulatum* ($p < 0.001$).

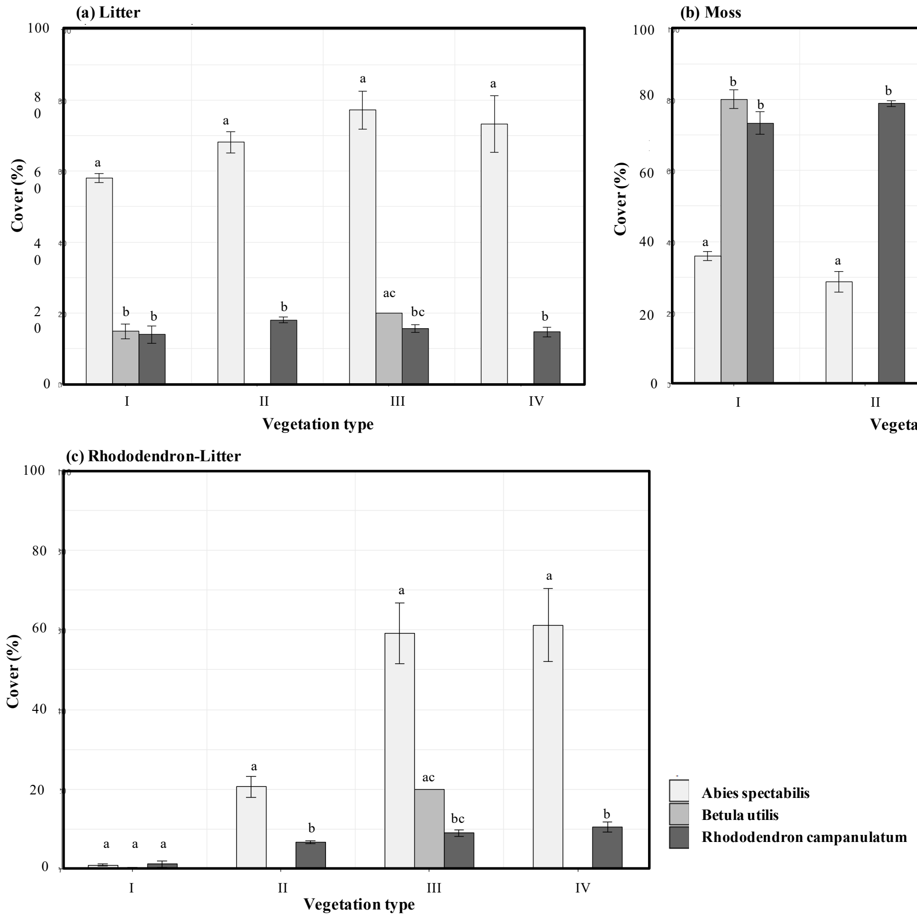

Fig. 2 Variations among tree species' seedlings (0-5 cm) in microhabitat cover of most important cover types (a) Litter, (b) Moss and (c) Rhododendron-litter the (I) lower subalpine forest, (II) upper subalpine forest, (III) *Rhododendron* krummholz belt, (IV) alpine dwarf shrub heath. Lower case letters indicate significant differences detected by Dunn's *post-hoc* test (P < 0.01)

Association with shelter elements

The far majority of seedlings of all species and all height classes was located close to at least one potential shelter element. However, the percentage of the different shelter elements varied distinctly between species and height classes, with greatest distinctions between *Abies spectabilis* and *Betula utilis* on the one hand and *Rhododendron campanulatum* on the other (Fig. 6).

Youngest *Abies spectabilis* and *Betula utilis* seedlings (> 0 to 5cm) were located most frequently close to rocks (51% respectively 57%), whereas youngest *Rhododendron campanulatum* seedlings were mostly found near deadwood (48%). Rocks retained their high importance for medium-sized and tall *Abies spectabilis* and *Betula utilis* seedlings (> 5 to 15cm: 52% respectively 44%; > 15 to 50cm: 70% respectively 71%), while *Rhododendron* *campanulatum* seedlings were increasingly rarely accompanied by deadwood (> 5 to 15cm: 23%; > 15 to 50cm: 17%) at advanced life stages, but more often by rocks (> 5 to 15cm: 38%; > 15 to 50cm: 42%). Additionally, *Rhododendron campanulatum* had the highest proportion of seedlings with no shelter element in all height classes.

Table 2 Summary of Kruskal-Wallis test and Dunn's post-hoc test on the difference in microhabitat ground cover of *Abies spectabilis* (As), *Betula utilis* (Bu) and *Rhododendron campanulatum* (Rc) seedlings.

Cover type	Height	Vegetation	As-Bu	As-Rc	Bu-Rc	H chi-	df	p
Litter	0-5	I	< 2e-16	< 2e-16	1	150.75	2	***
Litter	0-5	II	-	< 2e-16	-	163.99	1	***
Litter	0-5	III	0.92	1.2e-13	1	57.257	2	***
Litter	0-5	IV	-	2.3e-08	-	31.264	1	***
Moss	0-5	I	< 2e-16	2.6e-15	1	134.5	2	***
Moss	0-5	II	-	< 2e-16	-	166.79	1	***
Moss	0-5	III	0.84	2.5e-13	1	55.805	2	***
Moss	0-5	IV	-	1e-07	-	28.372	1	***
Vegetation	0-5	I	0.431	0.138	0.032	6.6985	2	*
Vegetation	0-5	II	-	8.4e-05	-	15.462	1	***
Rhododendron	0-5	II	-	2.3e-07	-	26.723	1	***
Rhododendron	0-5	III	1	3.2e-10	0.88	42.582	2	***
Rhododendron	0-5	IV	-	5.8e-08	-	29.438	1	***
Litter	5-15	I	0.00062	0.90948	1	13.778	2	**
Moss	5-15	I	6e-05	1	0.0098	22.026	2	***
Rhododendron	5-15	I	0.71	1.1e-05	3.3e-	28.193	2	***
Litter	15-50	II	-	0.023	-	5.1429	1	*
Vegetation	15-50	I	8.1e-07	1	0.64	26.989	2	***

The analysis was conducted for different ground cover types, vegetation types and height classes. For each cover type only significant results (P < 0.001 '***'; < 0.01 '**'; < 0.05 '*') are listed. Df = degrees of freedom, Vegetation types: (I) lower subalpine forest, (II) upper subalpine forest, (III) *Rhododendron* krummholz belt, (IV) alpine dwarf shrub heaths.

In accordance with these differences between species, the distance of seedlings from the nearest potential facilitative object varied greatly between *Abies spectabilis* and *Betula utilis* on the one hand and *Rhododendron campanulatum* on the other (Fig. 7, Table 3). In all height classes and vegetation types, *Rhododendron campanulatum* seedlings germinated and established closer to a protective element than seedlings of *Abies spectabilis* and *Betula utilis*. We found significant differences for youngest seedlings of the lower subalpine forest, the krummholz belt and the alpine dwarf shrub heaths ($p < 0.05$).

Discussion

Ground cover

Our data show clear microhabitat preferences of youngest seedlings of *Betula utilis*, *Rhododendron campanulatum* and *Abies spectabilis* (> 0 to 5cm) with remarkable contrasts between the ground cover of the two deciduous species and those of the conifer species. These preferences are largely similar for all vegetation types, reflecting the species-specific requirements for safe sites and the importance of ground cover for safe site structure. However, we found little variation in microsite cover among older seedlings, similar to the regeneration of other subalpine tree species in other treeline environments (Jones and del Moral 2005; Maher and Germino 2006).

Our results stress the great importance of litter and moss for describing patterns of tree regeneration in the Rolwaling treeline ecotone. Litter modifies seeds' and seedlings' physical and chemical environment directly and indirectly. Litter decomposition increases nutrient availability for plants, but may also release phytotoxic substances into the soil (Facelli and Pickett 1991). In addition, litter creates a physical barrier for seedlings, both germinated beneath or on the litter layer. Compressed and impermeable litter mats due to snow accumulation and hyphal network impede sprouting of seedlings and radical growth in particular (Lei et al. 2002; Facelli et al. 2008). Moreover, accumulated litter has a great shading effect on buried seeds and seedlings, similar to those of

Fig. 3 *Abies spectabilis* seedling, growing on litter layer in the study area (September 2014)

Fig. 4 *Betula utilis* seedling, growing on a bryophyte mat in the study area (August 2014)

Fig. 5 *Rhododendron campanulatum* seedlings that germinated on bryophyte mats in the study area (August 2014)

an established canopy (Vazquez-Yanes et al. 1990). Litter accumulations further reduce the thermal amplitude of soils by insulating them from air temperature (Facelli and Picket 1991). Thus, the protective effect of litter may protect seedlings from frost damage in late winter and early spring (Dzwonko and Gawroński 2002). On the other hand, reduced soil temperatures during vegetation period may negatively affect seedling establishment since seedlings' growth is positively correlated to soil temperature (Weih and Karlsson 2001). Additionally, water availability for seedlings' growth may decrease when litter retains precipitation (Facelli and Pickett 1991). According to a meta-analysis of Xiong & Nilsson (1999), the negative effects of plant litter on germination and seedling establishment generally outweigh the positive ones.

Influences of the moss cover on seeds' and seedlings' physical and chemical environment are comparable to those of litter. Leach solutions from bryophytes may negatively affect germination and seedlings establishment (Van Tooren 1990). Similar to litter, a thick moss cover impedes radical growth and reduces soil temperature amplitudes as well as light intensity (Van Cleve et al. 1983; Haeussler and Tappeiner 1993; Morgan 2006). On the other hand, bryophyte mats may have positive effects for germination and seedling establishment that has been attributed to a seed trap effect, reduced predation of seeds, improved soil moisture, and reduced wind speed (Bell and Bliss 1980; Sohlberg and Bliss 1984; During and van Tooren 1990; Groeneveld et al. 2007; Jeschke and Kiehl 2008). The magnitude of negative and positive impacts varies with litter/moss depth, litter origin, moss species target species and related species-specific seed and seedling traits (Sydes & Grime 1981; Xiong & Nilsson 1999).

Betula utilis

Moss seems to be a suitable substrate for germination of *Betula utilis* seeds, as we recorded young *Betula* seedlings primarily in moss-covered soils. The suitability might be largely attributed to the high moisture storage capacity of moss, which is known to be crucial for seedlings' survival of *Betula* species (Carlton and Bazzaz 1998). The predominant occurrence of *Betula utilis* seedlings in the lower subalpine forest characterised by highest mean soil humidity values in the treeline ecotone (Müller et al. 2016a, b; Bürzle et al. 2017) supports this

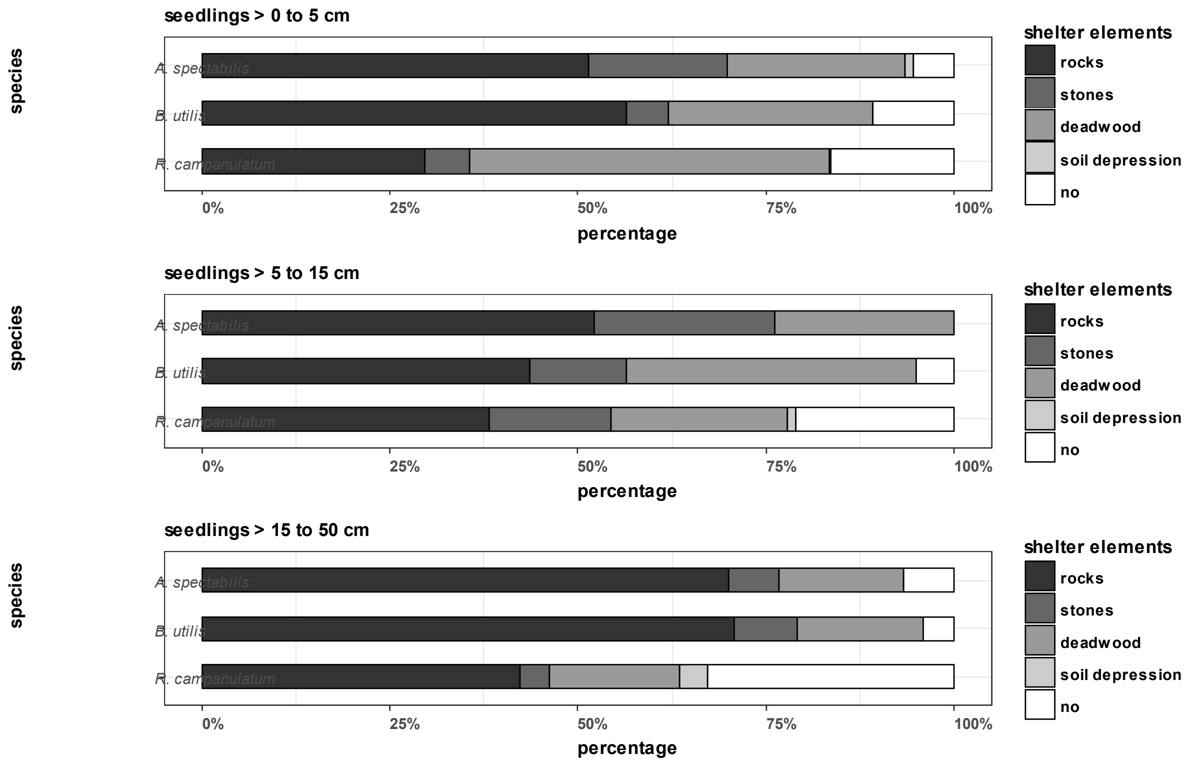

Fig. 6 Percentage of shelter element types, associated with tree seedlings of different heights

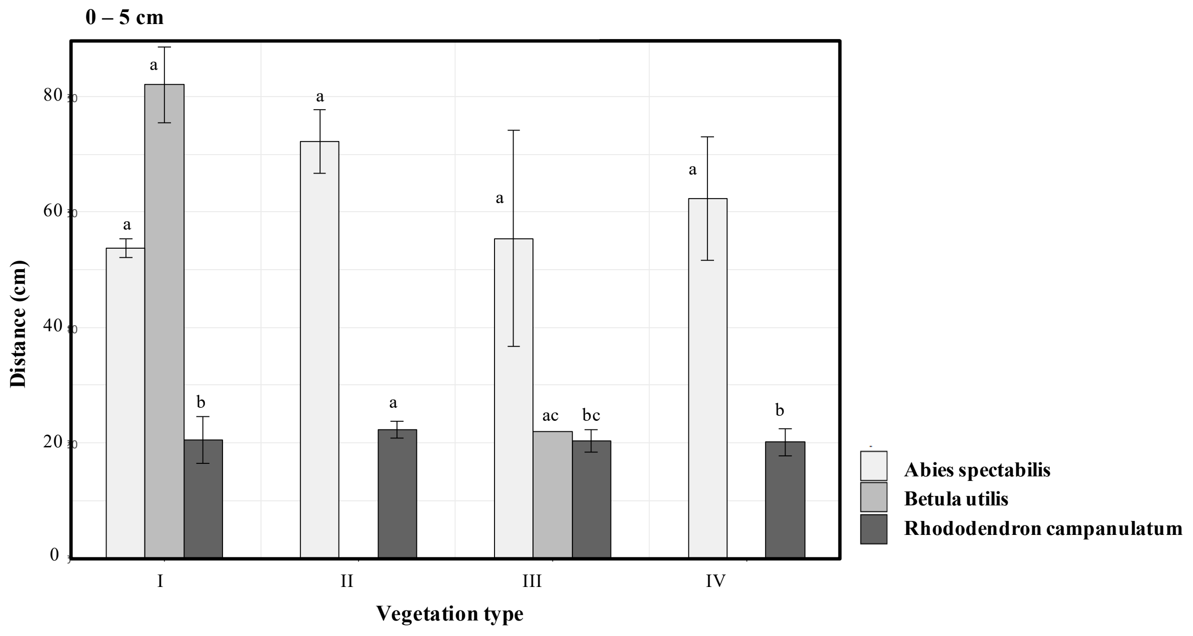

Fig. 7 Variations among tree seedlings (0-5 cm) in mean distance (cm) to shelter elements in the (I) lower subalpine forest, (II) upper subalpine forest, (III) *Rhododendron* krummholz belt, (IV) alpine dwarf shrub heath. Lower case letters indicate significant differences detected by Dunn's *post-hoc* test ($P < 0.05$)

finding. Facilitative effects of a moss cover for seed germination and seedling establishment have also been reported in previous studies for other *Betula* species, e.g., *Betula pubescens* ssp. *czerepanovii*, *Betula alba* and *Betula pendula* (Anschlag et al. 2008; Sanz et al. 2011; Kinnaird 1974). We further assume that the bryophyte mats function as a seed trap for *Betula utilis*, since the extremely light seeds are wind-dispersed (mean seed mass 0.209 ± 0.019 mg, Wang et al. 2012b).

By contrast, litter seems to be unfavorable for germination and establishment of *Betula utilis*, since abundance of young *Betula* seedlings on the litter layer is low. Seed mass is positively correlated with seed size. Since the early stage of seedlings' growth predominately depends on nutrient reserves, species-specific seed mass is crucial for successful seedling establishment in environments with dense litter accumulation (Gross 1984; Seiwa and Kikuzwawa 1991). Autonomous nutrient supply implies a significant gain in time for radical and shoot elongation, and therefore enhances the seedlings' chances to pass through dense litter mats (Facelli 2008). Thus, seedling establishment of small-seeded, pioneer tree species like *Betula utilis* are largely reduced by litter accumulation; germinated seedlings may die before establishment (Seiwa and Kikuzawa 1996; Facelli 2008). Germination and establishment of early successional *Betula* species are further favoured by high light intensity (Carlton and Bazzaz 1998; Grime 2006; Hughes et al. 2009). As small-sized *Betula* seeds may easily get buried below the litter layer, and high litter accumulation may be caused by dense tree canopy with associated reduced light intensity, low seedling numbers in litter-covered areas may also be an expression of unfavorable light conditions. In deeply shaded forest stands, survival of first-year-seedlings is positively correlated with seed size and additionally influenced by the species-specific relative growth rate (Walters and Reich 2000). This is in line with the results of previous studies on optimal light conditions for recruitment of *Betula utilis* that have shown high sapling mortality at low light and highest seedling and sapling densities outside tree stands with full solar radiation (Gratzer et al. 2004; Shrestha et al. 2007).

Table 3 Summary of Kruskal-Wallis test and Dunn's post-hoc test on the difference in mean distance of *Abies spectabilis* (As), *Betula utilis* (Bu) and *Rhododendron campanulatum* (Rc) seedlings to nearest shelter elements. The analysis was conducted for different vegetation types and height classes. For each cover type only significant results (P < 0.001 '***'; < 0.01 '**'; < 0.05 '*') are listed. Df = degrees of freedom, Vegetation types: (I) lower subalpine forest, (II) upper subalpine forest, (III) *Rhododendron* krummholz belt, (IV) alpine dwarf shrub heaths.

Height (cm)	Vegetation type	As-Bu	As-Rc	Bu-Rc	H chi-squared	df	p
0-5	I	0.3895	0.0042	0.0016	13.465	2	**
0-5	III	0.49	2e-06	1.00		2	***
0-5	IV	-	0.019	-	5.4674	1	*

Rhododendron campanulatum

Young *Rhododendron campanulatum* seedlings show comparable microsite preferences to those of *Betula utilis*. Moss is the dominating groundcover type in *Rhododendron campanulatum* microhabitats, whereas the importance of litter is low. Similar to *Betula utilis*, *Rhododendron campanulatum* seeds are extremely lightweight (0.1060 ± 0.0006 mg, Wang et al. 2014). Thus, following the above line of argumentation, high litter accumulation impedes *Rhododendron* seedling emergence. On the other hand, bryophyte patches may serve as a trap for the lightweight, anemochorous *Rhododendron* seeds and may additionally buffer moisture conditions. According to the high seedling abundance in the evergreen krummholz belt (Table 1), we suggest that *Rhododendron campanulatum* is more shade-tolerant compared to *Betula utilis*. These findings generally agree with previous studies on other *Rhododendron* species that indicated humid, low-shaded bryophyte mats as safe sites for *Rhododendron* seedling establishment (Cross 1981; Kaneyama et al. 1999; Mejías et al. 2002). Hughes et al. (2009) found a similar pattern of overlapping microhabitat preferences of a birch species (*Betula litwinowii)* and a *Rhododendron* species (*Rhododendron caucasicum*) in the Caucasus, Georgia.

Abies spectabilis

Although litter has in general negative effects on species germination and seedling establishment (Xiong and Nilsson 1999), recruitment of *Abies spectabilis* seems to be less affected by litter in comparison to *Betula utilis* and *Rhododendron campanulatum*. We recorded *Abies spectabilis* seedlings predominantly in litter-covered areas, whereas moss-covered areas played a minor role. Since large-sized *Abies spectabilis* seeds are dispersed unassisted or by animals (for example *Ochotona* sp., *Garrulus* sp.) (Wang et al. 2014), bryophyte mats have less or no importance as a seed trap. Moreover, seed-size is positively correlated with shade tolerance (Walters und Reich 1996). The high physiological shade-tolerance of *Abies spectabilis* and the high amount of seed reserves may enable the species to cope with an impediment by litter (Hewitt 1998; Germino and Smith 1999; Walters and Reich 2000; Maher and Germino 2006). However, microhabitat analyses of other *Abies* species indicate various habitat preferences. While *Abies lasiocarpa* in the subalpine spruce-fir forests of the Rocky Mountains established on thick litter layers (Knapp and Smith 1982), *Abies balsamea* in the Canadian boreal forest avoided litter and were most often recorded on moss layer in well-illuminated microsites (Simard et al. 1998). It is therefore open to debate whether high seedling abundance of *Abies spectabilis* on litter areas reflects optimal conditions for seedling establishment or results from short dispersal-distance.

Rhododendron litter

Tree species' microhabitat preferences in the krummholz belt were similar to those in the subalpine forests and alpine dwarf shrub heaths. The *Rhododendron* krummholz belt is characterised by the evergreen shrub respectively tree *Rhododendron campanulatum* and a thick, recalcitrant layer of *Rhododendron* litter. Seedling abundance in the krummholz belt was highest for *Rhododendron campanulatum* (> 0 to 5cm), while abundance of *Abies spectabilis* seedlings was low. We did not record any seedling of *Betula utilis*. However, only *Abies spectabilis* emerged on *Rhododendron* litter while *Rhododendron campanulatum* itself was mainly growing on mossy patches in the litter layer (Fig. 2).

It is known, that a variety of evergreen shrub species (*Chusquea* sp., *Kalmia* sp., *Rhododendron* sp.) inhibit tree recruitment in forest ecosystems worldwide (Nilsen et al. 2001). However the precise mechanisms of inhibition are largely unknown. *Rhododendron* species influence tree recruitment by alteration of the N cycle (Hättenschwiler and Vitousek 2000; Wurzburger and Hendrick 2007). Seedlings germinated on *Rhododendron* litter are exposed to low N availability, due to low leaf litter quality (Maithani et al. 1998, Wurzburger and Hendrick 2007). High amounts of polyphenols in *Rhododendron* leaves (Hegnauer & Hegnauer 1966; Fan et al. 1999) lead to further decrease of N availability by binding N into complex polyphenolic compounds (Northup et al. 1995; Bradley et al. 2000). Since nitrogen is the primary limiting soil nutrient for seedling growth (Körner 2003), shortage may be critical for seedling establishment, in particular for the small, nutrient-limited *Betula* and *Rhododendron* seeds.

Apart from polyphenols, *Rhododendron* leaves contain triterpenes (Hegnauer & Hegnauer 1966; Fan et al. 1999), which are both known to be potentially allelopathic (Rice 1984; Li et al. 2010; Kadereit et al. 2014). The triterpene campanuline in *Rhododendron campanulatum* leaves (Rangaswami & Sambamurthy 1961) may influence tree seedling recruitment in the *Rhododendron* krummholz belt. However, Nilsen et al. (1999) could not find any significant allelopathic effect of *Rhododendron maximum* on germination and seedling establishment of socialized tree species in the Appalachian Mountains, North America.

In forests with *Rhododendron* species in the understory, light availability is greatly reduced with negative impact on carbon gain in seedlings and an increase in seedling mortality (Nilsen et al. 2001; Lei et al. 2006). We suggest that reduced photosynthetically active radiation, the thick, recalcitrant litter layer, and the altered N cycle may be main causes for the absence of *Betula utilis* seedlings; while *Rhododendron campanulatum* seedlings find a suitable germination substrate on moss in spite of low light conditions. Due to the above described seed and plant traits, only *Abies spectabilis* is able to establish on *Rhododendron* litter. However, the low abundance of taller *Abies* seedlings (Table 1) and the low number of mature trees in the *Rhododendron* krummholz belt (Schwab et al. 2016; Bürzle et al. 2017) suggest a high mortality rate of *Abies spectabilis* seedlings during establishment. The underlying processes of the low rate of tree recruitment in the krummholz belt and should be further assessed in detailed species-specific studies.

Sheltering

We recorded most seedlings of all species near one potential protective element, in line with findings in other extreme environments (Kitzberger et al 2000; Resler 2005; Batllori et al. 2009). We found geomorphic elements (rocks, stones) and deadwood to be the most important shelter types of all species and height classes. Both sheltering types ameliorate germination and growth conditions by mediating UV radiation, temperature, wind speed, soil moisture and winter snow accumulation (Holtmeier and Broll 1992; Resler 2005). The distance of *Rhododendron* seedlings to the nearest protective element was distinctly shorter compared to *Abies* and *Betula* seedlings. As *Rhododendron campanulatum* is dispersed by wind, deadwood may serve as a seed trap; it additionally provides an ideal germination habitat covered by moss. The same holds true for anemochorous *Betula utilis* seeds that may accumulate close to present facilitative elements (Anschlag et al. 2008) and preferentially germinate on bryophyte layers. In previous studies, the spatial distribution of established seedlings and saplings were primarily associated with shelter elements, since seedling survival decreased with increasing distance from shelter elements (Germino and Smith 1999; Hättenschwiler and Smith 1999; Moir et al. 1999; Germino et al. 2002; Resler 2005). Our results underline the high importance of facilitative elements for tree recruitment in the Rolwaling treeline ecotone. The amount of data, however, cannot quantify the influence of different habitat conditions on plant physiological growth parameters. Light, temperature and moisture conditions to which seedlings are subjected to highly affect their photosynthesis and carbon balance in alpine regions (Germino and Smith 1999; Moyes et al. 2013). Since rising temperature and negative precipitation trends in the Himalaya will lead to enhanced drought stress especially in the pre-monsoon season (Wang et al. 2013; Schickhoff et al. 2015), further studies in the region should focus on the implications of changing plant ecological parameters for plant physiological processes.

Conclusion

Our results suggest species-specific microhabitat preferences for seedling emergence of the dominating tree species in the Rolwaling treeline ecotone. Predominant substrates for germination and seedling establishment are bryophyte mats (for *Betula utilis* and *Rhododendron campanulatum*) and litter accumulations (for *Abies spectabilis*). The recruitment of all species depends on shelter elements. Temperature and water supply are critical drivers for seedling establishment, thus microhabitats that buffer climatic extremes may become even more important under ongoing climate warming and decreasing precipitation in the Himalaya. Therefore we suggest that the availability of safe sites may be the most limiting factor for near future treeline advance.

Acknowledgements

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Appendix III: Abstracts of additional studies

Article I

Gerlitz L.; Bechtel B.; Böhner J.; Bobrowski M.; Bürzle B.; Müller M.; Scholten, T.; Schickhoff, U.; Schwab, N. and Weidinger J. 2016. Analytic comparison of temperature lapse rates and precipitation gradients in a Himalayan treeline environment: Implications for statistical downscaling. In: Singh, R. B.; Schickhoff, U. and Mal, S. (Eds.): Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya. Springer, Switzerland; 49–64. doi: 10.1007/978-3-319-28977-9_3

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 analysed 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.

Article II

Schickhoff, U., Bobrowski, M., Böhner, J., Bürzle, B., Chaudhary, R.P., Gerlitz, L., Heyken, H., Lange, J., Müller, M., Scholten, T., Schwab, N. and Wedegärtner, R. 2015. Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators. *Earth System Dynamics* **6**: 245-265, dio: 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.

Article III

Schickhoff, U., Bobrowski, M., Böhner, J., Bürzle, B., Chaudhary, R.P., Gerlitz, L., Lange, J., Müller, M., Scholten, T. and Schwab, N. 2016. Climate change and treeline dynamics in the Himalaya. In: Singh, R.B., Schickhoff, U. and Mal, S. (Eds.): Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya. Springer, Switzerland: 271-306, doi: 10.1007/978-3-319-28977-9_15

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 warmhumid 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 sub-alpine 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.

Article IV

Schwab, N., Schickhoff, U., Bobrowski, M., Böhner, J., Bürzle, B., Chaudhary, R.P., Gerlitz, L., Müller, M. and Scholten, T. 2016. Treeline responsiveness to climate warming: Insights from a krummholz treeline in Rolwaling Himal, Nepal. In: Singh, R.B., Schickhoff, U. and Mal, S. (Eds.): Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya. Springer, Switzerland: 307-345, doi: 10.1007/978-3-319-28977-9_16

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 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.

Article V

Schwab, N., Schickhoff, U., Bürzle, B., Hellmold, J and Stellmach, M. 2015. Dendroecological studies in the Nepal Himalaya - review and outlook in the context of a new research initiative (TREELINE). In: Wilson, R, Helle, G and Gaertner, H (Eds.): TRACE - Tree Rings in Archaeology, Climatology and Ecology. Scientific Technical Report, GFZ German Research Centre for Geosciences, Potsdam, Germany. **13**: 86–95 doi: 10.2312/GFZ.b103-15069

Abstract

The article was published without abstract in the TRACE conference volume

Article VI

Schwab, N., Schickhoff, U., Bürzle, B., Müller, M., Böhner, J., Chaudhary, R.P., Scholten, T. and Oldeland, J. 2017. Implications of tree species – environment relationships for the responsiveness of Himalayan Krummholz treelines to climate change. *Journal of Mountain Science* **14**: 453–473 doi: 10.1007/s11629-016-4257-z

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 con-

straints 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.

Supplementary Material

S1

Complete relevé table of communities characterized by diagnostic species according to phi-value. Abundance of listed species are determined using the 7-degree-cover-abundance scale of Braun-Blanquet (1964). Cover values of species present in different layers (H: herb layer, S: shrub layer, T: tree layer) were merged into one using the highest value for each species.

Supplement S1 Complete relevé table of communities characterized by diagnostic species according to phi-value. Abundance of listed species are determined using the 7-degree-cover-abundance scale of Braun-Blanquet (1964).

Taxon or field name	Layer	***Abies spectabilis* – *Betula utilis* – forest**																																																					***Rhododendron campanulatum* - krummholz belt**											**Rhododendron dwarf shrub heath**																									**Total Frequency [%]**
		Group 1: Synotis alata – *Abies spectabilis* community																											**Group 2: Ribes glaciale – *Abies spectabilis* community**																												**Group 3: *Boschniakia himalaica – Rhododendron campanulatum* community**											**Group 4: *Pedicularix* cf. *microcalyx - Rhododendron anthopogon* community**								**Group 5: *Anaphalis royleana - Rhododendron anthopogon* community**																	
Nr.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	
Plot_ID		1_NE1	2_NE1	4_NE1	5_NE1	16_NW1	17_NW1	18_NW1	19_NW1	20_NW1	21_NW1	31_NE2	32_NE2	33_NE2	34_NE2	35_NE2	36_NE2	55_NW1	56_NW1	57_NW1	68_NE2	69_NE2	70_NE2	71_NE2	88_NE1	89_NE2	90_NE2	91_NE2	3_NE1	6_NE1	7_NE1	8_NE1	9_NE1	10_NE1	12_NE1	22_NW1	23_NW1	24_NW1	25_NW1	26_NW1	37_NE2	38_NE2	39_NE2	40_NE2	54_NW1	58_NW1	59_NW1	65_NE2	66_NE2	67_NE2	82_NE1	83_NE1	84_NE1	85_NE1	86_NE1	87_NE1	11_NE1	13_NE1	14_NE1	27_NW1	42_NE2	46_NW1	51_NW1	52_NW1	53_NW1	75_NE1	76_NE1	28_NW1	29_NW1	41_NE2	43_NE2	63_NE2	64_NE2	72_NE2	73_NE2	15_NE1	30_NW1	44_NW1	45_NW1	47_NW1	48_NW1	49_NW1	50_NW1	60_NE2	61_NE2	62_NE2	74_NE1	77_NE1	78_NE1	79_NE1	80_NE1	81_NE1	
Relevé area [m²]		400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	400	
Date		2013-07-23	2013-07-25	2013-07-26	2013-07-28	2013-07-15	2013-07-15	2013-07-15	2013-07-16	2013-07-22	2013-07-22	2013-07-18	2013-07-18	2013-07-18	2013-07-19	2013-07-20	2013-07-20	2014-08-08	2014-08-07	2014-08-06	2014-08-05	2014-08-03	2014-08-02	2014-08-01	2014-08-25	2014-09-28	2014-09-27	2014-09-27	2013-07-25	2013-07-28	2013-07-29	2013-07-31	2013-07-28	2013-07-28	2013-08-01	2013-08-07	2013-08-07	2013-08-07	2013-08-08	2013-08-08	2013-08-11	2013-08-11	2013-08-11	2013-08-12	2013-08-12	2014-08-06	2014-08-07	2014-09-16	2014-09-18	2014-09-16	2014-08-29	2014-08-29	2014-08-27	2014-08-27	2014-08-26	2014-08-25	2013-07-31	2013-08-01	2013-08-01	2013-08-09	2013-08-13	2014-08-11	2014-08-12	2014-08-12	2014-08-09	2014-09-06	2014-09-06	2013-08-09	2013-08-20	2013-08-12	2013-08-13	2014-09-19	2014-09-19	2014-09-21	2014-09-21	2013-08-02	2013-08-20	2013-08-30	2014-08-16	2014-08-19	2014-08-18	2014-08-17	2014-08-16	2014-09-24	2014-09-22	2014-09-22	2014-09-05	2014-09-01	2014-08-31	2014-08-31	2014-09-02	2014-09-01	
Latitude [°]		27,896107	27,895149	27,895536	27,895998	27,900476	27,900580	27,900158	27,900317	27,900072	27,899942	27,900771	27,900849	27,900472	27,900316	27,900815	27,900638	27,898455	27,899204	27,900138	27,899389	27,899922	27,900228	27,900672	27,896037	27,901109	27,901180	27,901302	27,894547	27,895258	27,894667	27,894431	27,894612	27,894713	27,895199	27,899663	27,899537	27,899317	27,898669	27,898560	27,899054	27,898931	27,898833	27,898626	27,898254	27,899786	27,899520	27,898626	27,898507	27,899129	27,894648	27,894982	27,895115	27,894991	27,894933	27,895317	27,893952	27,894362	27,894449	27,898371	27,898462	27,896169	27,896381	27,896466	27,897613	27,893316	27,893541	27,898133	27,893766	27,898386	27,898197	27,897757	27,898055	27,897585	27,897004	27,893308	27,895836	27,892344	27,893311	27,893010	27,893271	27,893553	27,894055	27,896491	27,896926	27,896811	27,892614	27,892733	27,892970	27,893308	27,892626	27,892920	
Longitude [°]		86,379536	86,379920	86,379005	86,379275	86,375447	86,375370	86,375768	86,375108	86,376652	86,376639	86,374110	86,373444	86,373637	86,372889	86,373181	86,373838	86,375588	86,375847	86,375344	86,373785	86,373572	86,373840	86,374240	86,379284	86,374335	86,374348	86,374281	86,379650	86,378349	86,378582	86,378258	86,377812	86,377555	86,376817	86,374965	86,375244	86,375318	86,375834	86,375084	86,373481	86,373287	86,373136	86,373035	86,375414	86,375438	86,375380	86,373035	86,373013	86,373258	86,377502	86,379044	86,378686	86,378171	86,377982	86,378591	86,378009	86,377269	86,376458	86,374837	86,371794	86,375961	86,373980	86,374225	86,374889	86,376215	86,376323	86,374819	86,375120	86,372365	86,371806	86,370981	86,371712	86,371070	86,371333	86,375908	86,375067	86,374673	86,375147	86,375019	86,375035	86,375238	86,374603	86,370990	86,370631	86,370605	86,374917	86,375567	86,375649	86,375908	86,375112	86,375212	
Altitude [m a.s.l.]		3831	3844	3895	3844	3772	3776	3790	3788	3782	3794	3796	3808	3827	3866	3827	3829	3916	3844	3767	3881	3844	3830	3793	3827	3753	3745	3749	3860	3919	3939	3973	3987	3990	4046	3843	3849	3863	3891	3926	3926	3947	3972	3987	3941	3828	3841	3987	3971	3933	4003	3869	3885	3953	3973	3895	4017	4046	4078	3943	4054	4019	4083	4058	3990	4165	4112	3962	4164	4037	4073	4145	4088	4150	4168	4182	4185	4300	4208	4223	4112	4180	4180	4223	4223	4224	4264	4245	4225	4182	4265	4236	
Inclination [°]		37	28	44	38	37	35	38	35	29	29	31	32	34	34	35	30	30	33	40	34	36	34	26	35	28	28	27	31	41	36	36	37	34	32	37	36	39	37	32	41	40	36	38	32	37	38	38	38	45	33	37	36	32	43	40	38	38	33	35	40	32	32	32	34	33	39	30	40	35	41	39	36	40	36	34	29	33	35	35	30	27	27	35	36	36	34	38	37	34	33	34	
Exposition [°]		63	50	65	44	48	27	26	31	5	17	31	24	22	17	11	50	0	7	340	50	70	26	40	40	5	5	5	45	65	63	42	42	53	67	13	22	10	25	0	53	67	69	50	20	350	0	54	40	35	50	30	30	30	30	70	37	26	50	346	26	354	30	30	10	60	40	352	12	31	44	0	37	51	75	31	15	65	22	37	44	33	10	60	65	52	20	45	25	52	30	40	
Height tree layer1 [m]		15	12	18	25	18	18	15	15	15	20	16	20	18	18	20	15	18	18	12	12	18	12	15	24	15	18	18	13	15	18	15	18	18	10	12	13	11	18	12	15	15	18	15	14	18	15	17	16	16	15	25	12	22	20	18	8	6	5	6	4,5	6	6	5	6	3,5	5	5	-	-	5	3,5	-	3,5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Height tree layer2 [m]		9	7	12	12	12	10	12	10	9	12	12	15	12	9	15	8	10	10	10	7	10	6	10	15	-	12	12	8	10	8	7	8	12	5	6	8	6	12	8	6	6	9	10	9	12	10	10	10	10	10	16	8	12	12	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Height shrub layer1 [m]		5	4	4	5	4	5	4	5	5	3,5	5	8	6	6	4	4	1,5	4	4	3	5	3	4	5	5	7	7	4	4	3,5	4	4	6	5	3	3	3	3	2	2,5	3	2,5	3,5	3	5	4	4	4	3	4	7	4	5	7	5	1,5	2	3	2,5	1	1,5	3	3	0,8	1,8	4	2,5	1,5	5	3	0,6	2	0,5	0,4	1,5	0,6	0,2	0,5	0,3	3,5	1	1,8	0,5	0,4	0,4	0,4	1,5	1,5	3,5	0,4	0,4	
Height shrub layer2 [m]		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,3	-	0,4	0,25	0,7	0,4	0,25	0,5	2	0,2	0,3	0,2	-	0,3	-	0,4	0,4	0,45	0,25	0,25	0,25	0,2	0,3	0,3	0,3	0,2	0,25	
Height herb layer [m]		0,2	0,2	0,25	0,2	0,25	-	0,2	0,2	30	0,2	0,25	0,25	0,25	0,2	0,2	0,2	0,2	0,15	0,25	0,25	0,25	0,15	0,2	0,4	0,4	0,45	0,35	0,25	0,15	0,2	0,05	0,15	10	0,2	0,15	0,2	0,15	0,15	0,1	0,2	0,2	0,15	0,15	0,15	0,15	0,15	0,2	0,25	0,25	0,2	0,3	0,25	0,3	0,2	0,3	0,05	0,05	0,15	0,15	0,2	0,05	0,15	0,1	0,15	0,2	0,2	0,2	0,15	0,15	0,1	0,2	0,2	0,2	0,3	0,2	0,15	0,2	0,25	0,2	0,2	0,15	0,25	0,2	0,3	0,3	0,4	0,25	0,2	0,2	0,3	0,3	
Cover tree layer1 [%]		40	70	50	30	<5	10	5	25	25	20	5	50	50	60	15	70	15	15	50	40	10	65	20	30	65	60	40	25	40	40	40	20	25	30	30	50	60	25	15	25	40	30	55	40	40	30	60	70	45	40	45	25	40	35	40	90	90	90	80	90	90	90	80	85	75	90	20	-	-	35	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Cover tree layer2 [%]		40	5	50	50	70	60	80	70	65	50	60	50	35	20	40	<5	80	60	35	30	50	20	40	60	-	35	60	70	50	50	60	70	40	85	60	50	40	60	70	60	70	70	40	70	75	45	50	50	35	85	60	80	60	70	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Cover shrub layer1 [%]		30	30	20	40	40	30	35	30	45	60	10	15	25	30	20	30	20	40	20	30	30	30	40	45	35	70	70	20	30	30	30	10	60	10	30	30	30	20	25	30	30	25	25	20	30	40	60	35	55	25	55	40	35	50	30	10	10	10	25	15	15	15	10	15	20	30	70	30	80	70	50	40	75	40	30	25	70	20	70	5	35	30	55	-	30	30	15	10	40	30	15	
Cover shrub layer2 [%]		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	-	40	70	30	30	60	75	20	80	70	70	-	80	-	70	70	70	75	-	70	45	90	80	70	40	75	
Cover herb layer [%]		60	30	60	60	40	70	40	40	85	60	80	85	80	35	70	70	35	35	60	70	70	60	70	65	80	65	50	10	30	70	10	10	50	5	10	10	20	15	5	25	15	20	25	15	25	15	50	55	20	35	50	35	65	30	40	5	<5	20	5	5	15	20	15	35	40	25	20	15	5	30	20	60	60	40	15	20	30	40	50	50	40	20	40	-	40	70	65	60	40	75	45	
Cover moss layer [%]		20	60	5	30	70	80	60	40	35	80	40	40	35	70	70	80	30	50	50	45	15	60	20	25	65	60	40	40	20	60	40	-	50	60	40	30	70	30	40	20	20	-	40	60	20	60	40	45	60	60	20	50	40	60	25	70	80	40	40	70	50	40	5	65	40	-	40	60	70	50	70	80	70	80	70	70	50	80	70	80	90	80	80	-	70	45	65	70	70	80	65	
Species number		26	32	27	29	20	28	27	28	33	30	25	24	21	16	24	23	20	21	25	28	23	27	27	29	25	22	25	29	26	28	18	24	26	25	15	22	22	21	13	24	22	18	22	22	21	21	20	21	18	27	31	30	27	26	38	14	7	9	17	7	9	11	16	20	15	12	14	8	6	11	15	10	15	12	20	25	22	22	21	21	20	19	18	12	12	25	22	21	18	20	20	
***Clintonia udensis - Abies spectabilis* community**																																																																																														
Synotis alata	H	2	.	2	2	2	2	2	1	3	1	1	2	3	.	1	2	1	1	1	2	4	1	3	2	1	1	2	1	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	3	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37
Clintonia udensis	H	1	r	.	.	1	1	.	+	+	.	2	1	1	.	2	1	.	.	1	1	2	r	1	1	1	1	1	+	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24
Stipa roylei	H	+	.	.	.	.	1	1	.	1	1	+	.	.	.	+	.	.	1	1	.	.	.	+	+	+	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16
Parasenecio quinquelobus	H	2	.	2	2	2	2	2	2	+	2	2	2	1	1	2	2	2	2	3	3	1	2	2	3	2	1	2	+	2	2	+	+	1	.	1	.	.	1	.	2	2	2	.	.	1	1	.	r	1	r	2	3	3	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	52
Impatiens racemosa var. *ecalcarata*	H	.	1	.	1	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	r	.	1	.	1	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
Acer caudatum	T, S, H	.	2	.	.	2	1	2	1	2	2	2	2	2	1	2	4	3	2	1	2	3	3	2	.	3	3	2	2	.	2	.	.	+	.	1	+	2	1	.	.	.	.	.	r	+	+	.	.	.	.	.	r	.	r	.	.	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	41
Carex lehmannii	H	.	.	1	1	.	1	1	+	.	1	.	.	.	.	1	.	.	.	.	+	+	r	r	.	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	1	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	r	.	.	.	.	.	.	.	.	.	1	.	.	2	.	1	.	+	.	26
Pilea racemosa	H	2	2	1	.	2	1	2	2	1	2	2	2	1	1	2	2	2	+	+	2	2	2	2	1	3	4	3	1	.	2	3	1	2	.	.	.	.	.	.	1	.	1	2	+	.	+	2	+	.	1	.	1	2	1	1	1	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	51
Bistorta amplexicaulis	H	.	1	3	2	2	3	2	2	3	2	3	2	3	3	2	2	2	2	3	1	1	1	3	1	4	3	3	1	2	1	.	+	.	.	.	.	.	2	.	2	2	2	2	2	2	2	2	3	1	.	1	1	2	1	.	.	.	.	2	.	.	.	.	2	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	53
Prunus rufa	T, S	2	2	2	1	+	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
Viola biflora	H	.	1	.	.	.	1	1	.	1	1	2	1	1	.	1	1	.	.	.	+	.	1	1	.	1	+	1	1	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	27
Koenigia nepalensis	H	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	.	.	.	.	+	r	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Carex munda	H	1	1	1	1	+	1	.	1	1	1	+	.	+	.	1	.	+	1	.	.	.	.	+	1	.	.	1	+	1	1	.	.	+	.	1	1	+	.	.	.	.	.	.	.	1	+	.	.	1	+	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	+	r	.	.	.	.	.	.	1	+	.	.	.	.	41
Aruncus dioicus subsp. *triternatus*	H	1	.	.	1	.	.	r	.	.	.	.	1	+	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
Maianthemum purpureum	H	2	1	1	1	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
Saxifraga pallida - Abies spectabilis community																																																																																														
Ribes glaciale	S, H	r	2	.	.	.	+	.	.	2	2	1	1	1	+	.	1	.	.	.	.	1	.	1	r	.	.	.	1	.	2	1	+	2	1	.	1	1	1	+	+	1	1	2	.	r	1	2	r	r	1	1	r	r	r	r	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	44
Rosa sericea	S, H	2	1	2	2	+	.	+	+	1	1	r	2	1	.	.	.	r	1	1	1	r	1	1	r	.	.	r	1	2	1	1	.	2	1	1	1	1	2	1	1	+	2	1	1	2	2	1	+	1	2	2	1	2	2	2	.	.	1	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	57
Abies spectabilis	T, S, H	3	1	2	3	2	2	2	2	2	2	r	1	r	1	1	.	2	2	2	+	2	r	2	3	+	.	r	2	2	3	2	3	2	2	2	2	2	2	2	2	3	3	1	2	3	1	1	1	3	2	4	+	2	+	2	.	.	.	2	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	64
Juncus thomsonii	H	1	.	.	.	.	.	+	+	1	1	.	+	.	.	1	.	.	.	+	+	+	+	.	.	.	.	.	.	1	1	.	.	+	.	.	.	1	.	.	1	+	1	1	+	.	+	+	+	.	+	+	+	+	+	r	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	1	+	+	.	+	+	43
Koenigia delicatula	H	.	1	1	1	.	.	1	.	1	1	.	.	.	.	1	1	1	1	+	+	1	r	.	1	+	.	.	1	1	1	2	1	1	1	.	1	1	1	.	1	1	1	2	1	+	+	2	2	+	2	+	1	2	1	1	1	.	.	1	.	.	2	1	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	53
Betua utilis	T, S, H	2	.	3	2	3	2	2	2	2	1	1	3	3	3	3	.	4	3	2	2	1	2	2	3	3	3	3	2	3	3	3	2	2	3	3	3	3	3	2	2	2	2	4	3	3	3	4	4	2	3	2	2	2	3	3	r	.	.	.	.	r	r	r	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	65
Saxifraga pallida	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
***Boschniakia himalaica - Rhododendron campanulatum* community**																																																																																														
Rhododendron anthopogon	S, H	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1	2	2	2	.	1	2	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	1	1	.	2	2	2	.	.	1	2	+	3	4	2	3	5	4	4	4	.	4	2	4	4	3	4	3	3	4	3	3	4	4	4	3	4	45
Boschniakia himalaica	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	r	.	.	r	+	.	.	.	.	.	.	.	.	r	1	.	.	.	.	.	.	1	.	1	1	r	.	.	1	1	1	+	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18
Cassiope fastigiata	S, H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	+	1	.	2	3	.	2	4	3	2	2	3	3	2	2	3	3	4	2	.	.	.	2	3	4	3	2	3	30
Bistorta vacciniifolia	S	.	.	.	.	2	1	1	2	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2	1	1	2	.	.	1	1	.	1	2	.	.	+	2	.	r	.	.	+	+	.	1	1	1	1	2	.	.	2	2	2	1	2	.	2	3	3	.	3	3	1	2	2	2	2	2	2	3	3	3	3	3	2	2	1	3	2	58
Rhodiola discolor	S, H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	r	1	.	.	r	1	1	1	1	1	2	1	2	1	1	1	2	1	1	1	+	1	1	+	1	1	31
***Rhododendron lepidotum - Rododendron anthopogon* community**																																																																																														
Sorbus microphylla	T, S, H	2	3	2	2	2	2	2	2	2	2	2	1	2	1	2	2	2	2	2	2	2	2	2	2	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	3	2	2	2	1	1	2	2	3	3	2	3	2	3	2	+	2	2	2	2	2	.	.	1	.	+	.	r	.	.	.	.	.	.	r	.	.	.	.	85
Lepisorus df. clathratus	H	.	1	1	1	1	.	1	1	1	1	1	+	.	.	1	1	.	+	1	.	+	r	+	+	1	.	.	1	1	1	1	1	1	.	.	1	1	1	.	1	.	.	1	+	.	.	.	+	.	r	+	+	+	+	.	1	.	.	.	.	.	.	+	+	.	.	.	.	.	1	.	1	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	48
Phymatopteris malacodon	H	1	1	1	1	1	+	1	1	1	1	1	1	.	1	1	1	+	+	+	+	+	+	+	.	1	.	2	1	1	1	1	1	1	+	1	+	1	1	1	1	1	1	1	1	1	+	1	+	1	+	+	+	+	+	+	1	1	.	1	1	.	+	1	+	+	1	1	.	1	1	r	1	+	.	+	.	.	.	+	.	r	.	.	.	.	1	.	.	.	.	.	78
Rhododendron lepidotum	S, H	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	2	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	r	.	.	2	2	2	2	2	2	2	.	.	.	.	.	.	.	.	2	2	.	.	1	.	1	.	23
***Codonopsis thalictrifolia - Rhododendron athopogon* community**																																																																																														
Anaphalis royleana	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	1	1	1	+	+	3	.	2	2	1	2	1	1	1	18
Codonopsis thalictrifolia	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	2	1	1	1	+	1	.	.	1	2	2	1	1	2	16
Rhododendron setosum	S, H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	2	3	3	3	2	3	3	2	2	2	2	2	2	2	2	1	2	22
Salix calyculata	S, H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	3	2	2	3	1	.	.	.	1	.	.	2	1	+	13
Pedicularis lachnoglossa	H	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.	.	r	.	+	.	.	.	r	1	1	1	.	1	13
Rheum australe	H	1	.	1	2	2	.	.	.	1	2	2	2	2	2	2	2	.	3	.	2	+	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	+	1	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	+	1	1	r	.	.	2	1	2	2	1	1	1	.	1	1	40
Lonicera litangensis	S, H	.	.	.	r	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	+	2	1	1	1	1	.	.	.	2	1	r	1	.	1	22
Kobresia nepalensis	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	1	2	2	2	1	1	+	1	+	+	2	1	1	.	3	2	19
Calamagrostis lahulensis	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	2	1	1	2	1	1	+	1	+	1	1	1	2	1	1	.	1	1	21
Dasiphora arbuscula	S, H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	2	1	3	3	2	2	2	2	2	2	1	3	3	3	3	3	2	2	1	3	2	25
Acronema tenerum	H	+	1	1	1	.	.	1	1	1	1	1	1	1	1	1	1	1	1	+	+	+	+	+	+	1	+	+	1	1	1	1	1	1	.	1	1	1	1	1	.	1	1	1	1	+	+	+	1	1	+	+	+	+	+	.	1	1	1	1	.	2	1	1	1	+	1	1	.	.	.	.	.	+	+	1	1	1	+	+	1	r	1	+	+	.	+	r	+	.	+	+	86
Bistorta vivipara	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	1	2	2	1	1	1	.	.	.	.	1	.	.	+	1	1	13
Companion species																																																																																														
Rhododendron campanulatum	T, S, H	1	1	3	2	1	1	2	1	2	r	1	1	2	2	2	.	2	3	2	2	1	.	1	3	.	.	.	4	3	3	3	4	3	5	3	3	2	3	2	4	3	3	3	4	3	3	3	3	3	4	3	4	3	4	3	5	5	5	4	5	5	5	5	5	2	5	4	2	4	4	2	2	2	.	4	2	+	2	.	r	3	2	.	.	.	.	r	2	3	.	.	86
Circaea alpina subsp. *micrantha*	H	.	1	1	1	+	.	1	1	1	.	1	1	1	1	1	2	2	2	1	1	1	2	1	2	2	2	2	2	1	3	1	1	3	1	1	1	1	2	.	1	.	1	2	2	1	1	2	3	.	2	1	2	2	1	1	.	.	.	1	.	.	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	58
Deparia allantodioides	H	2	1	2	2	1	1	1	.	1	1	2	2	2	1	1	2	+	1	.	1	1	1	.	2	3	2	.	1	.	.	.	1	2	.	.	1	+	1	+	1	1	1	1	1	1	+	+	1	.	.	+	.	1	.	.	1	.	.	1	.	.	r	+	+	.	.	.	.	.	.	.	.	.	r	.	.	.	+	2	.	r	.	2	.	1	.	.	.	.	.	.	57
Ribes griffithii	S, H	r	2	1	1	.	.	.	+	.	.	.	.	.	1	+	2	2	2	+	2	r	1	2	1	2	2	+	.	1	1	.	+	.	1	+	+	1	2	1	1	.	.	r	r	1	1	.	2	r	+	r	2	1	+	r	.	.	.	.	.	+	r	.	r	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	49
Galium paradoxum	H	.	1	1	1	.	.	1	.	1	.	.	.	.	.	.	1	.	.	.	r	.	.	.	.	+	+	.	1	1	1	2	1	1	1	.	1	1	1	.	1	1	1	1	.	.	.	.	.	.	.	.	+	+	.	.	1	.	.	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	31
Rubus fragarioides	H	1	.	1	1	.	.	r	+	+	1	.	1	.	.	.	.	.	.	+	+	+	.	.	1	.	1	.	1	1	1	.	.	.	.	.	+	.	.	1	.	1	1	.	+	1	.	.	.	+	.	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	27
Scrophularia pauciflora	H	.	1	+	+	.	+	.	+	+	1	.	.	.	.	.	.	.	.	.	+	.	.	+	1	.	.	.	+	1	1	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	+	1	1	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	25
Thalictrum cultratum	H	.	1	.	.	.	+	+	.	+	1	1	.	.	.	.	1	.	.	.	.	.	1	+	.	r	+	r	2	1	2	1	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	1	r	.	.	r	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24
Athyrium rupicola	H	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2	.	2	1	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	+	.	2	3	.	.	2	2	.	.	.	.	.	2	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	1	22
Pedicularis cf. *microcalyx*	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	1	r	.	1	r	.	.	.	+	+	+	r	+	1	+	+	+	r	1	.	.	.	19
Ribes acuminatum	S, H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	2	.	2	.	.	2	3	4	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	r	.	.	r	.	2	r	r	.	.	.	.	.	.	r	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18
Cryptogramma stelleri	H	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	+	1	.	1	.	1	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13
Poa spec. I	H	.	1	.	.	.	.	.	.	+	.	.	.	+	.	.	1	.	.	.	.	.	.	.	.	.	r	.	+	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	13
Selinum cf. *Wallichianum*	H	.	1	1	.	.	1	.	+	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13
Trillium govanianum	H	.	1	.	.	.	+	.	1	.	.	.	.	.	.	.	+	.	.	.	.	.	r	1	.	.	.	.	1	.	*	.	.	1	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13
Aconogonon polystachyum	H	1	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	11
Epilobium spec.	H	.	.	.	+	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Goodyera repens	H	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Polygonatum kansuense	H	.	.	1	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Polypodiodes lachnopus	H	.	1	.	.	.	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Saxifraga hispidula	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	8
Anaphalis nepalensis	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	+	.	.	.	.	.	1	.	.	.	1	1	7
Swertia cuneata	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	.	1	.	.	.	1	.	1	.	1	.	7
Hierochloe flexuosa	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	r	+	.	.	.	.	.	.	.	.	.	.	5
Agrostis inaequiglumis	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	4
Calamagrostis spec.	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	1	4
Hemiphragma heterophyllum	H	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Juniperus squamata	S, H	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	4
Primula sikkimensis	H	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Urticularia spec.	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Anaphalis contorta	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Arisaema jacquemontii	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Clematis spec	S, H	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Cremanthodium reniforme	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Phlomis breviflora	H	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Saussurea spec.	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	3
Theropogon pallidus	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	r	.	.	.	.	.	.	.	r	.	.	3
Juniperus indica	T, S	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	2
Carex setosa	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Cystopteris fragilis	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Goodyera fusca	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Listera pinetorum	H	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Myriactis nepalensis	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Pedicularis furfuracea	H	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Rhodiola fastigiata	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
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Valeriana hardwickii	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	2
Acanthocalyx nepalensis	H	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
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Cystopteris cf. montana	H	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Dryopteris acutodentata	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
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Lonicera lanceolata	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
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Potentilla aristata	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1
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Spiraea arcuata	H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1

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