



## 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 as well as 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. 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 W and central Himalaya. Ecological niche modelling suggests that bioclimatic conditions for a range expansion of treeline trees will be created during coming decades.

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# 1 Introduction

Since treeline advance to higher elevation results in substantial physiognomic, structural and functional changes of mountain landscapes and ecosystems, sensitivity and response of alpine treelines to climate change has recently seen considerable research (Holtmeier, 2009). Strong general links between climate parameters and tree-line position and repeated climatically caused treeline fluctuations during the Holocene (MacDonald et al., 2000; Tinner and Theurillat, 2003; Reasoner and Tinner, 2009) suggest treelines to be sensitive to and useful indicators of climatic changes (cf. Slatyer and Noble, 1992; Kullman, 1998; Theurillat and Guisan, 2001; Grace et al., 2002; Fagre, 2009; Kullman and Öberg, 2009; Smith et al., 2009). Generally, global warming is expected to cause upper treelines to advance to higher elevations since, at a global scale, the position of natural alpine treelines is controlled mainly by heat deficiency, i.e. insufficient air and soil temperatures during growing season (Körner and Paulsen, 2004; Holtmeier and Broll, 2005, 2009; Holtmeier, 2009; Körner, 2012a; Paulsen and Körner, 2014). The general agreement of the thermal limitation of treeline positions may not, however, hide the fact that there is an ongoing controversial debate on the relevance of various specific abiotic and biotic drivers (e.g. carbon and nitrogen uptake and investment, nutrient availability, soil moisture, species dispersal and recruitment, plant morphology, self-organization) influencing tree growth at its upper limit (e.g. Hoch et al., 2002; Smith et al., 2003; Dullinger et al., 2004; Holtmeier and Broll, 2007; Wieser, 2007, 2012; Bansal et al., 2011; Hoch and Körner, 2012; Körner, 2012a, b).

The current state of knowledge on treelines has been acquired by a wealth of research efforts that can be differentiated into two major conceptual approaches operating at different spatial scales (cf. Malanson et al., 2011). Studies exploring fundamental, global-scale causes of treelines, often characterized by a strong focus on limitations to tree growth from an ecophysiological perspective, can be referred to as the “global approach”. Other studies attempt to understand finer-scale (landscape-scale, local-scale) causes of treelines and variations in spatial and temporal patterns. The focus here is

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on landscape patterns, in particular on the effects of topography and other site conditions and on treeline history. Such studies can be subsumed under the term “landscape approach”. Both research lines have contributed significantly in recent years to answering the key question of treeline response to recent climate change. This response will not linearly follow altitudinal shifts of isotherms, but vary according to the interaction of broad-scale controls (global/regional temperature) and fine-scale modulators of treeline patterns (Holtmeier and Broll, 2005, 2007, 2009; Holtmeier, 2009; Malanson et al., 2011). It has thus become routine to take the scale-dependency of drivers controlling treeline patterns into account (Malanson et al., 2007; Danby, 2011). As treeline heterogeneity increases from global/regional to landscape and local scales, an increasing number of factors and their interactions have to be considered. Effects of varying topography on local site conditions, spatially and temporally variable soil physical and chemical properties, after-effects of historical disturbances (extreme events, fire, insect pests, human impact, etc.), demographic processes, species-specific traits and/or biotic interactions and feedback systems may override or overcompensate the impact of higher average temperatures. It has also to be emphasized that various treeline-forming species will have different growth and regeneration responses to a changing climate. In the long-term, treelines will advance under continued global warming, but not in a closed front parallel to the shift of an isotherm (Holtmeier and Broll, 2005, 2007; Malanson et al., 2011; Körner, 2012a).

The response of treelines to observed climate warming is indeed inconsistent. A recent meta-analysis of treeline response to climate warming, based on a global dataset of 166 sites for which treeline dynamics had been reported since AD 1900, showed advancing treelines at 52 % of the sites, while 47 % did not show any elevational shifts, and only 1 % showed treeline recession (Harsch et al., 2009). Treelines with higher rates of winter warming were more likely to show advance. At many treeline sites in old-settled mountain regions, however, effects of climate warming interfere with those of land use changes (e.g. Bolli et al., 2006; Vittoz et al., 2008; Rössler et al., 2008). Gehrig-Fasel et al. (2007) found land abandonment to be the most dominant driver for

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recent tree line shifts in the Swiss Alps, and attributed only a small fraction of upward shifts to climate change. Some studies documented substantial treeline advances during the twentieth century. Most authors trace it back to climate warming, not always disentangling the effects of land use and climate change. Treeline advances of up to 70–100 m (altitudinal meters) were reported from several mountain ranges in the Northern Hemisphere and attributed to climate changes (e.g. Danby and Hik, 2007; Kharuk et al., 2010; Moiseev et al., 2010). Kullman and Öberg (2009) quantified a maximum treeline advance of 200 m in the southern Swedish Scandes. Other recent empirical studies reported enhanced tree growth, tree establishment and infilling of gaps within the treeline ecotone during recent decades (e.g. Rolland et al., 1998; Camarero and Gutiérrez, 2004; Daniels and Veblen, 2004; Dalen and Hofgaard, 2005; Wang et al., 2006; Kullman, 2007; Roush et al., 2007; Akatov, 2009; Liang et al., 2011). Locally increasing numbers of tree seedlings above the current upper tree limit, occasionally far above, are reported from many mountain ranges (e.g. Kullman, 2008; Hofgaard et al., 2009).

The above cited treeline studies give evidence of both advancing alpine treelines and rather insignificant treeline responses to climate warming. The inconsistency of findings suggests significantly differing sensitivities of global treelines to climate changes. It is known that climate operates at a broad spatial scale and typically exerts a top-down control on local ecological patterns and processes at the treeline (Batllori and Gutiérrez, 2008; Elliott, 2011). It is widely unknown, however, how local-scale site conditions (abiotic site factors, plant interactions associated with facilitation, competition, feedback systems) can modify the treeline response to region-wide climate warming inputs. Thus, it remains unclear how abiotic and biotic factors and processes interact to govern sensitivity and response of the treeline at landscape and local scales (cf. Holtmeier and Broll, 2007; Malanson et al., 2007; Batllori et al., 2009; Smith et al., 2009). Recent studies based on a global treeline dataset suggest a close link between treeline form (spatial pattern) and dynamics. Harsch et al. (2009) and Harsch and Bader (2011) consider treeline form (diffuse, abrupt, island, krummholz) to be an

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indicator of controlling mechanisms and response to climate change. They found the majority of diffuse treelines and about one third of krummholz treelines to be advancing, and abrupt and island treelines to be rather stable. The disjunction of mechanisms and environmental conditions primarily associated with different treeline forms seems to explain this pattern. However, given the nonlinear responses to climate warming caused by various local-scale modulators and their interactions, numerous limitations remain to use treeline form to predict treeline dynamics. In order to analyse the role of local-scale processes in mediating the broader-scale climate inputs, and to improve the model-based prediction ability regarding changing spatial treeline patterns, complex research approaches at local and landscape scales and in different treeline environments are required, focusing on treelines where human impact is negligible and has not resulted in treeline depressions.

Identified research deficits regarding the sensitivity and response of alpine treelines to climate change apply in particular to the Himalaya. While numerous treeline research programs have been carried out in European and North American mountains, related research is still in its infancy in the Himalaya. A recent review of geographical and ecological aspects of the treeline ecotone in the Himalayan mountain system revealed considerable research deficits, in particular with regard to responses to climate change (Schickhoff, 2005). Considering the sensitivity of mountain biota and ecosystems to environmental change on a global scale (e.g. Grabherr et al., 2010; Schickhoff, 2011; Engler et al., 2011; Laurance et al., 2011; Gottfried et al., 2012) and on a Himalayan scale (Xu et al., 2009; Shrestha et al., 2012; Telwala et al., 2013; Aryal et al., 2014), substantial effects on Himalayan treeline ecotones are to be expected. This paper reviews the current state of knowledge regarding sensitivity and response of Himalayan treelines to climate warming, presents novel data from ongoing studies, provides explanations for present findings, and conducts a globally comparative evaluation of Himalayan response patterns.



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than further north. Like in other subtropical high-mountains, treelines considerably vary in their altitudinal position according to aspect and related topoclimatic differences. Under natural conditions, treelines are usually developed at significantly higher elevations on south-facing slopes. Anthropogenic disturbances have blurred this general pattern to a locally different extent since utilisation pressure in southern aspects is disproportionately higher (Schickhoff, 2005).

Interestingly, mean summer temperatures are significantly higher in the more continental NW, the treeline, however, is developed at distinctly lower elevations (Fig. 1). Extremely low winter temperatures with a long snow cover duration and shorter growing seasons obviously overcompensate the effects of favourable summer temperatures. Moreover, the internal preparedness of the predominantly deciduous treeline tree species in the far NW such as *Betula utilis*, *Salix* spp. and of hardy conifers to build new tissue and accumulate dry matter is delayed compared to the evergreen *Rhododendron* species at treelines in the more maritime SE. Increasing treeline elevations along the peripheral–central gradient (Fig. 1) are related to the combined effects of mass-elevation and continentality. As in other extensive mountain massifs, the inner Himalayan highlands provide elevated heating surfaces leading to positive thermal anomalies compared to marginal ranges or free air, and causes altitudinal vegetation limits to rise (cf. Flohn, 1968; Yao and Zhang, 2014). The continentality effect exerts an even stronger influence on treeline elevations (Schickhoff, 2005). Decreasing cloudiness and precipitation, coupled with higher irradiation and sunshine duration, earlier snow melt and higher soil temperatures, results in higher temperature sums and a prolonged growing season. The peripheral–central gradient culminates in SE Tibet, where *Juniperus tibetica* forms the most elevated treeline in the Northern Hemisphere at an altitude of 4900 m (Miehe et al., 2007).

The physiognomy of Himalayan treeline ecotones greatly varies depending on slope aspect. North-facing slopes exhibit a more or less homogeneous physiognomic pattern with closed high coniferous forests giving way to medium-sized broadleaved tree stands and finally to a krummholz belt, interspersed with single small upright trees.

























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by Gaire et al. (2011) at treelines in southern Langtang National Park, who found high levels of recruitment of *Abies spectabilis* in recent decades with seedlings and saplings at much higher elevations than uppermost cone bearing tree individuals. Recent detailed observations in Manaslu Conservation Area (Gaire et al., 2014) indicate a considerable upward shift and excellent recruitment of *Abies spectabilis*, positively correlated with monthly maximum temperature in most of the months of the current year and with May–August precipitation. Another study on treeline fir (*Abies spectabilis*) recruitment in Mt. Everest Nature Reserve (S Tibet) achieved consistent results, with significant tree recruitment in the recent three decades that showed a positive correlation with mean summer air temperature (Lv and Zhang, 2012).

Detailed information on treeline seed-produced regeneration from other Himalayan subregions is hardly available. In the vast Indian Himalaya, some knowledge has been accumulated on regeneration dynamics in lower altitude forests (e.g. Singh and Singh, 1992), but only very scanty information from treeline ecotones has been published. Treeline ecotones in Kumaon/Uttarakhand (Pindar, Sarju, and Ramganga Catchments), heavily influenced by grazing and browsing, showed a low seedling/sapling density of *Abies pindrow*, but a much better regeneration status of *Betula utilis* and *Rhododendron campanulatum* (Rawal and Pangtey, 1994). Gairola et al. (2008) reported intense regeneration from less disturbed upper subalpine forests in Garhwal/Uttarakhand. Dubey et al. (2003) observed increasing establishment of pine saplings (*Pinus wallichiana*) above the treeline zone in Parabati Valley, Himachal Pradesh, India, and ascribed the recruitment pattern to climate warming. Intense regeneration of *Betula utilis* at treelines in Uttarakhand and Himachal Pradesh and invasion of alpine meadows by birch seedlings was highlighted in a recent study by Rai et al. (2013). Information on regeneration at treelines from the Hindu Kush, Karakoram, and W Himalayan ranges of Pakistan is even more meagre. A comprehensive study of high-altitude forests including upper subalpine forest stands in the Karakoram (Schickhoff, 2000) revealed retarded growth processes and slow stand development







### 4.3 Tree physiognomy and growth patterns

Climatic changes affect tree physiognomy at treelines since height growth of trees is very sensitive to decreasing temperatures as one approaches treeline, resulting in climatically shaped growth forms that trees in this harsh environment usually display (Holtmeier, 2009; Körner, 2012a). Varied other abiotic and biotic site factors such as wind, snow, nutrient supply, browsing, etc. also influence the development of growth forms at treelines, but tree physiognomy at least partly reflects changing environmental conditions related to climatic warming. The phenotypical response does not necessarily mirror long-term climatic trends, a few favourable years with undisturbed growth can be sufficient to trigger a change in physiognomy (Holtmeier and Broll, 2005). On the other hand, deteriorating climatic conditions or extreme climatic events may lead to physiognomic changes caused by dieback. While several studies reported accelerated height growth of previously low-growing tree individuals from different treeline ecotones (e.g. Lescop-Sinclair and Payette, 1995; Kullman, 2000; Kullman and Öberg, 2009), no such information from Himalayan treelines is available to date. However, it can be inferred from remote sensing-based studies that the expansion of treeline ecotones, subalpine forests and alpine scrub in recent decades is accompanied by enhanced height growth of individual trees. Rai et al. (2013) detected a substantial increase in fir and birch treeline forests in Himachal Pradesh and Uttarakhand during 1980–2010 that most likely has included positive changes in the physiognomy of single trees. Respective data from ongoing studies in Rolwaling are currently evaluated.

Better evidence can be ascertained for growth responses in the Himalaya in terms of diameter growth. Generally, radial growth is less affected than height growth by decreasing temperatures when approaching the upper treeline, but shows a much more pronounced response to climate warming (Körner, 2012a). It has been shown for *Pinus cembra* and *Picea abies* in the European Alps that the declining trend in tree radial growth toward the treeline that prevailed in the nineteenth century has disappeared in the twentieth century due to rising temperatures, and that mature trees at

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treeline currently grow as fast as trees in the upper montane forest (Paulsen et al., 2000). Other comparable growth enhancements at treelines have been assessed e.g. for *Picea*, *Pinus*, and *Larix* in the Italian Alps (Rolland et al., 1998), for *Pinus longaeva* in western North America (Salzer et al., 2009), for *Nothofagus pumilio* in southern Argentina (Villalba et al., 1997), for *Picea schrenkiana* in the Tianshan Mountains (Qi et al., 2014), or for *Betula ermanii* in Kamchatka (Dolezal et al., 2014). Growth responses to a warming climate, however, tend to be different where lack of available moisture becomes a controlling factor, e.g. in arid or semiarid regions or in regions with seasonal drought periods. Drought stress as a local factor impeding tree growth in recent decades has been supposed for different treeline environments (e.g. Lloyd and Fastie, 2002; Daniels and Veblen, 2004; Dulamsuren et al., 2010; Zhang et al., 2011; Fajardo and McIntire, 2012; Ohse et al., 2012).

In the Himalaya, only very few dendroclimatic studies have been conducted at treeline elevations. However, there is increasing evidence suggesting that growth response of treeline trees to climate change and variability is spatio-temporally differentiated, species-specific and not unidirectional. In general, tree-ring growth in E Himalaya is less sensitive to climate variation compared to W Himalayan sites and trees (Bhattacharyya and Shah, 2009), and most studies reported radial growth of treeline conifers to be more responsive to temperature than precipitation change, with W and central Himalayan conifers being more responsive to winter and pre-monsoon temperatures and E Himalayan conifers often being more responsive to summer temperatures.

Some studies reported consistent responses of tree growth to recent climate warming. Tree-ring width chronologies of *Pinus wallichiana*, *Cedrus deodara* and *Picea smithiana* from high-altitude forests and treeline sites in Kinnaur (Himachal Pradesh) and Gangotri (Uttarakhand) showed an unprecedented growth enhancement during recent decades and a strong positive relationship to the mean annual and winter (DJF) temperatures, the anomalous higher growth was thus ascribed to the overall warming trend over the region (Singh and Yadav, 2000; Borgaonkar et al., 2009, 2011). Ring width chronologies of *Abies georgei* var. *smithii* growing at treeline in the Sygera





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et al. (2004) analysed ring width chronologies of *Abies spectabilis* from four treeline sites in Himachal Pradesh and Uttarakhand and found significantly negative correlations with long-term pre-monsoon temperature series. These findings are in accordance with results from other high-elevation sites in Uttarakhand using *Taxus baccata* tree-ring sequences (Yadav and Singh, 2002) and *Cedrus deodara* tree-ring data (Bhattacharyya and Yadav, 1990), and also correspond to *Abies spectabilis* tree growth-climate relationships analysed near treeline in Humla District (Nepal) (Sano et al., 2005) and at the treeline ecotone in Langtang National Park (Nepal) (Gaire et al., 2011; Shrestha, 2013). Higher temperatures during the relatively dry spring months lead to increased evapotranspiration and to soil moisture deficits, impeding tree growth in particular on sites which are prone to drought stress. A negative correlation of pre-monsoon temperature with total ring width and a positive correlation of pre-monsoon precipitation with ring width are apparently widespread patterns in W and central Himalayan tree growth-climate relationships (cf. Borgeonkar et al., 1999; Pant et al., 2000; Cook et al., 2003; Ram and Borgeonkar, 2013), and have been used accordingly for temperature and precipitation reconstruction (e.g. Yadav et al., 1997, 1999; Singh and Yadav, 2005, 2014; Singh et al., 2006; Ram and Borgeonkar, 2014). A significant negative correlation with May temperature has also been detected for *Juniperus tibetica* on the semiarid southern Tibetan Plateau (He et al., 2013; Liu et al., 2013), a positive relationship, by contrast, for *Larix griffithiana* in humid Arunachal Pradesh (Chaudhary and Bhattacharyya, 2000).

Recently, the pre-monsoon period has been shown to be also critical for broad-leaved treeline trees. After the dendroclimatological potential of the Himalayan birch had been pointed out by Bräuning (2004), Bhattacharyya et al. (2006) reported in a preliminary study of tree-ring data of *Betula utilis*, growing near the snout of Gangotri Glacier (Uttarakhand), that higher temperatures and less rainfall during pre-monsoon months results in lower tree growth. Dawadi et al. (2013) corroborated this finding and assessed for the growth of birch trees at treeline sampling sites in Langtang Valley (Nepal) a positive correlation with March–May precipitation and an inverse relationship

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with pre-monsoon temperatures. Reduced pre-monsoon moisture availability being a primary growth-limiting factor for *Betula utilis* at treeline and the coincidence of years with high percentage of missing rings or narrow rings with dry and warm pre-monsoon seasons was once again confirmed by Liang et al. (2014) for study sites in Sagarmatha National Park, Langtang National Park, and Manaslu Conservation Area (Nepal) (for Manaslu see also Gaire et al., 2014). Recent research by the present authors investigated a ring-width chronology of *Betula utilis* from treeline sites in Langtang Valley dating back to AD 1657, and found a negative correlation of tree-ring width with pre-monsoon temperature and a positive correlation with pre-monsoon precipitation (in review). Pre-monsoon climate definitely affects growth patterns of the Himalayan birch to a large extent, however, contrary to Liang et al. (2014, p. 16) we refrain from concluding that this species is increasingly at risk of survival, and from qualifying respective treelines as “drought-induced alpine timberlines” (op. cit., p. 2) since co-dominant conifer treeline species are more temperature-sensitive, and the altitudinal position of Himalayan birch treelines corresponds more or less to global characteristics of growing season length, thermal sums and mean air and soil temperatures common at treelines induced by heat deficiency (cf. Körner, 2012a). As a pioneer species with relatively wide ecological amplitude, *Betula utilis* also thrives under distinctly drier conditions in the NW Himalaya and Karakoram, and has survived severe drought periods in the past (recently reconstructed by Cook et al., 2010).

## 5 Treeline shifts

As evident from repeated climatically caused treeline fluctuations during the Holocene, treeline shifts are to be expected in response to recent climate change. In most cases, however, the response will be a long-term response, in the order of several decades to hundred or more years. Most likely, treeline positions are always lagging behind climatic fluctuations, and the global treelines we observe today are each in a specific state of climate tracking. Thus, the globally heterogeneous response patterns with

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advancing and stagnating or rather unresponsive treelines come as no surprise. For the Himalaya, stagnating treelines as well as treeline advances of partially significant dimension, mostly attributed to climate warming, have been reported to date. A major difficulty to evaluate currently available observations of treeline shifts in the literature is that they are not based on a comparable treeline concept. E.g. the position of tree seedlings is often hastily taken to calculate treeline shifts without considering that the mere presence of seedlings is not synonymous with an actual treeline advance. Only the sustainable transition into subsequent sapling size classes would increase the potential of a treeline shift (cf. Graumlich et al., 2005).

For the Himalaya, only very few studies on spatio-temporal treeline dynamics are available. Some are based on thorough dendroecological or forest-ecological fieldwork and have been conducted at near-natural treelines. E.g. Liang et al. (2011) analysed Smith fir stands at the treeline in the Sygera Mountains (SE Tibet) and found the treeline position to have moved upslope only slightly and insignificantly, whereas the population density of trees and the number of seedlings have considerably increased after the 1950s. These findings are in line with recent research of the present authors on the treeline in Rolwaling Valley (Nepal) indicating increasing stand densities, but no significant alteration in treeline position (in review). Gaire et al. (2014) have recently investigated upward shifting of tree species limits in the treeline ecotone at Kalchuman Lake (Manaslu, Nepal), and reported extraordinary migration rates of *Abies spectabilis* since AD 1850, while the upper distribution limit of *Betula utilis* remained stagnant in the past decades. Migration rates were calculated on the basis of uppermost seedling position. However, given the generally low survival rate of seedlings in treeline ecotones during the first years after germination, and considering critical later life stages after projecting above the winter snow cover, it is rather unlikely that recorded upper species limits will be persistent ones. A more or less stationary treeline position over recent decades in two study sites in Nepal (Manang, Langtang National Park) was assessed by Gaire et al. (2011) and Shrestha (2013).





scenarios is supported by such model results which also provide insights to decision makers in climate change mitigation and biodiversity conservation.

## 6 Conclusions

Treeline environments in the Himalaya are very heterogeneous, implying limitations for broad generalizations on treeline sensitivity and response to climate change. Nevertheless, several key conclusions emerge from the present study. Anthropogenic treelines are predominant in the Himalaya, i.e. expansions of treeline vegetation and treeline shifts at those treelines are related to declining land use intensity and should not be misunderstood as being primarily triggered by climate change. To distil the climate change signal with high temperature trends over the Himalayan arc, one has to investigate near-natural or less disturbed treelines which have become very rare, and largely confined to north-facing slopes, where they are usually developed as krummholz tree-lines. Strong competition within the krummholz belt and dense dwarf scrub heaths further upslope adversely affects upward migration of tree species and treeline shifts. This prevailing environmental setting suggests a relatively low responsiveness of near-natural Himalayan treelines and a significant move in elevation only in the long-term.

On the other hand, the evaluation of seed-based regeneration showed that recruitment is usually intense with huge amounts of seedling/sapling presence within and beyond the treeline ecotone. These results suggest a high proneness to respond and further suggest that a future treeline advance will be significantly controlled, once seeds have dispersed upslope and germinated, by the species-specific competitive abilities during the recruitment phase or the effectiveness of recruitment suppression in the krummholz and dwarf scrub belts. Tree growth-climate relationships, though species-specific, revealed a high sensitivity of mature treeline trees to temperature. Growth patterns in *W* and central Himalaya are particularly responsive to pre-monsoon temperature and humidity conditions. The future pre-monsoon climate change may, therefore, be an important driver of physiological and morphological responses. Environmental

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niche modelling of *Betula utilis* indicates a probable range expansion in the coming decades, suggesting that the bioclimatic preconditions for a future treeline advance will be existent. Considering species-specific physiological responses and competitive traits, complex and nonlinear responses of individual Himalayan treeline systems to climate change can be anticipated. Treeline shifts are of substantial ecological relevance due to possible implications for regional biodiversity and ecological integrity. A widespread upward encroachment of subalpine forests would displace regionally unique alpine tundra habitats and possibly cause the loss of alpine species.

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**Table 1.** Number of seedlings/saplings (< 7 cm breast height diameter; N ha<sup>-1</sup>) of *Betula utilis*, *Abies spectabilis*, *Rhododendron campanulatum*, and *Sorbus microphylla* in the treeline ecotone in Rolwaling Valley according to slope exposure and altitudinal zone.

	Altitudinal Zone	Altitude (m)	<i>Betula utilis</i>	<i>Abies spectabilis</i>	<i>Rhododendron campanulatum</i>	<i>Sorbus microphylla</i>	Total
NE slope	A	3780–3880	754	100	517	1346	2717
	B	3920–3980	108	1067	7854	233	9262
	C	4020–4080	13	0	5908	500	6421
	D	4120–4220	0	0	379	21	400
Total			875	1167	14 658	2100	18 800
NW slope	A	3760–3780	3788	3488	1129	1133	9538
	B	3820–3880	1067	613	6675	679	9034
	C	3920–3980	58	58	4075	275	4466
	D	4020–4240	8	13	1475	71	1567
Total			4921	4172	13 354	2158	24 605

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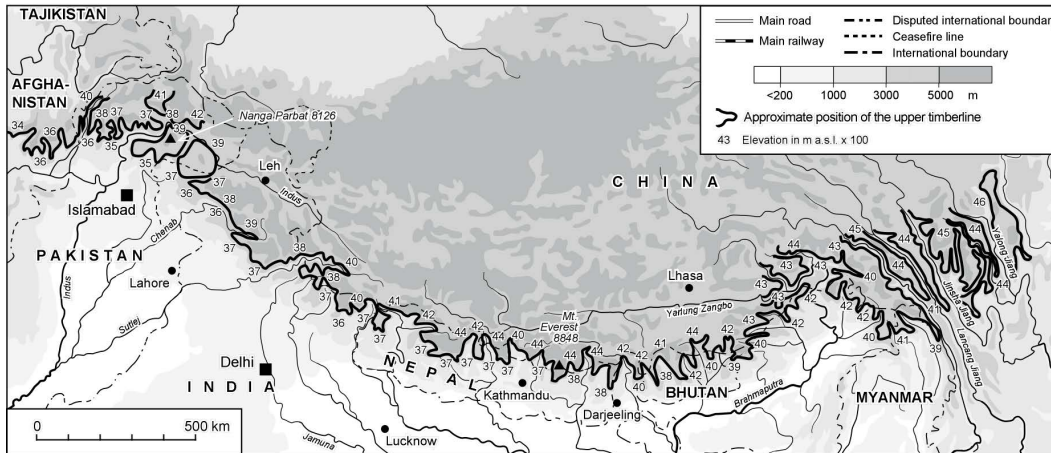
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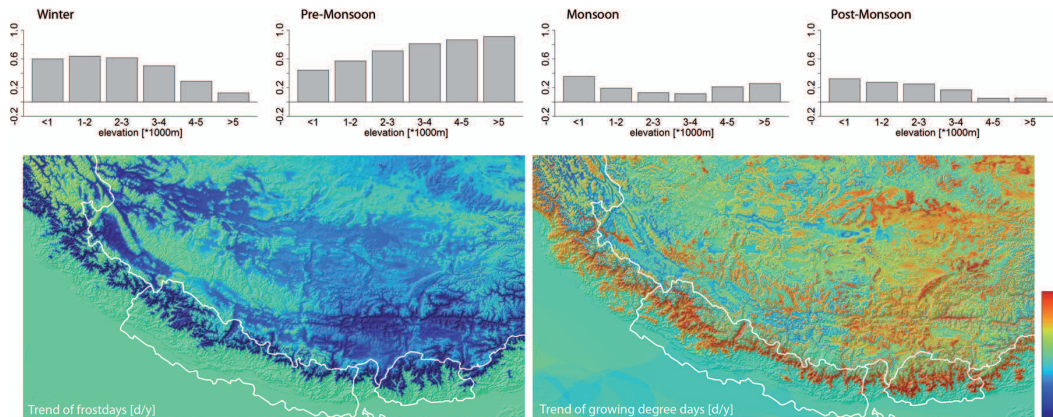
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**Figure 1.** Altitudinal position of alpine treeline in the Himalayan mountain system (north-facing slopes) (after Schickhoff, 2005; modified).

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**Figure 2.** Seasonal temperature trends [°C decade<sup>-1</sup>] for different elevational belts (top panels) and spatial distribution of trends for frost and growing degree days over the Himalaya (bottom panels) (according to Gerlitz et al., 2014).

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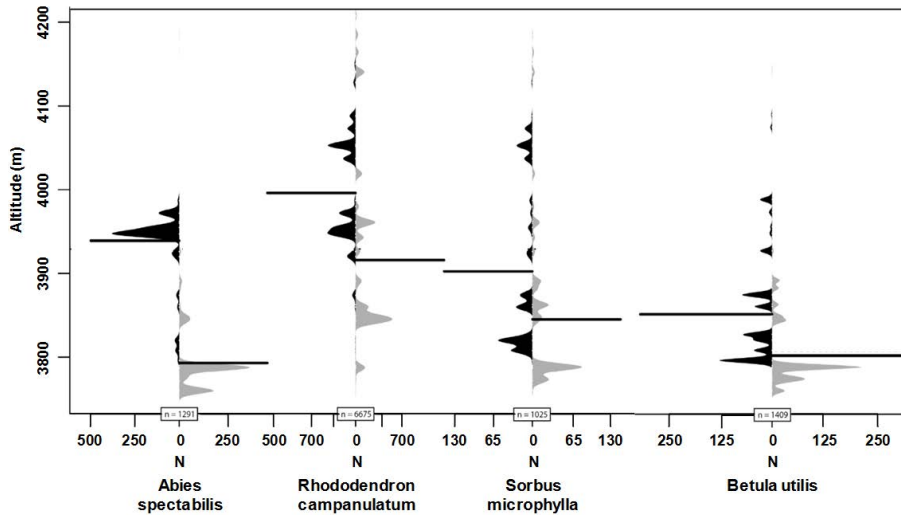
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**Figure 3.** Seedling/sapling density of treeline tree species in the treeline ecotone in Rolwaling Valley according to altitude and slope exposure (black: NE slope; gray: NW slope).

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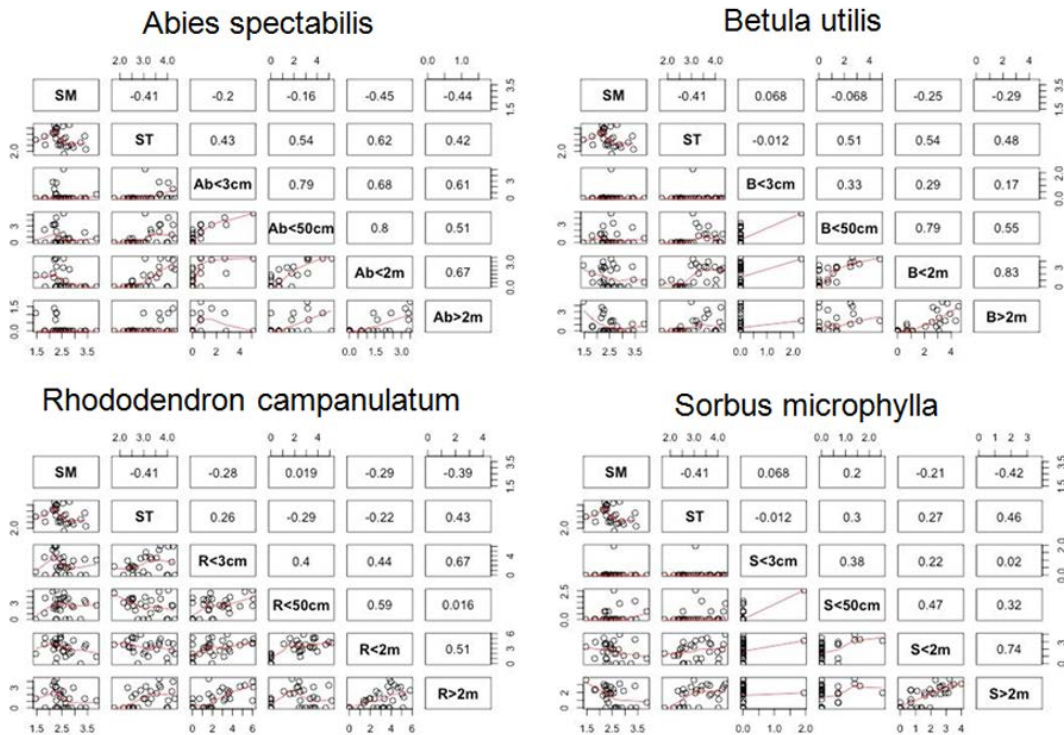
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**Figure 4.** Spearman rank correlations between seedling/sapling abundance and soil temperature and soil moisture in the treeline ecotone in Rolwaling Valley.

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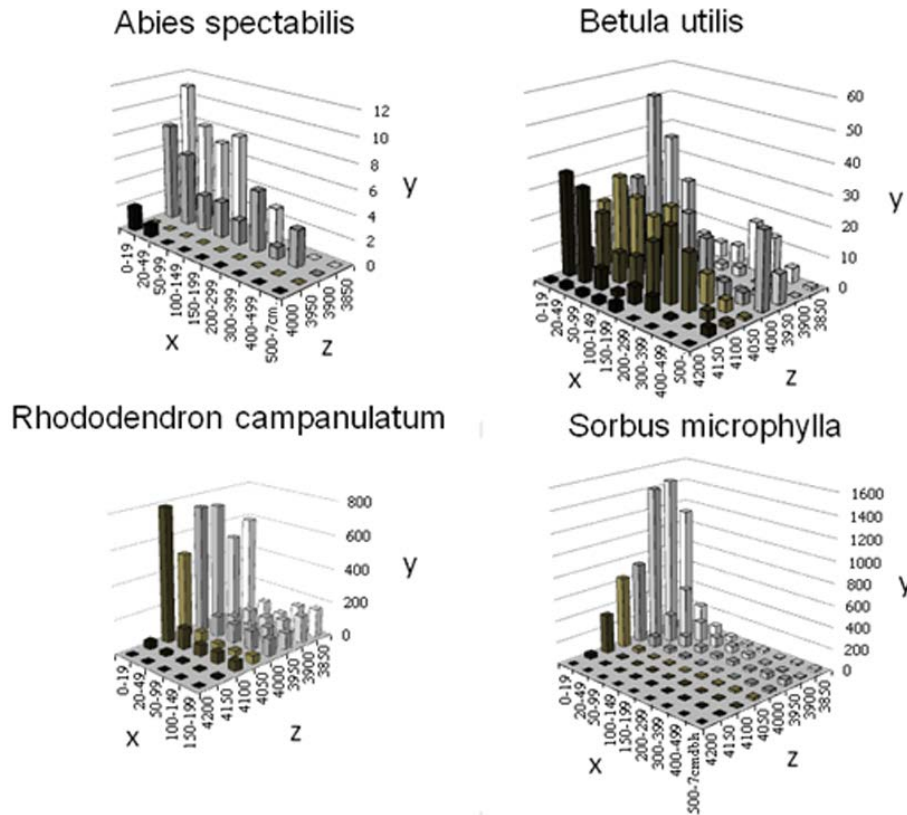
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**Figure 5.** Seedling/sapling density in the treeline ecotone in Langtang Valley according to altitude and size classes (x axis = size class; y axis = quantity; z axis = altitude).

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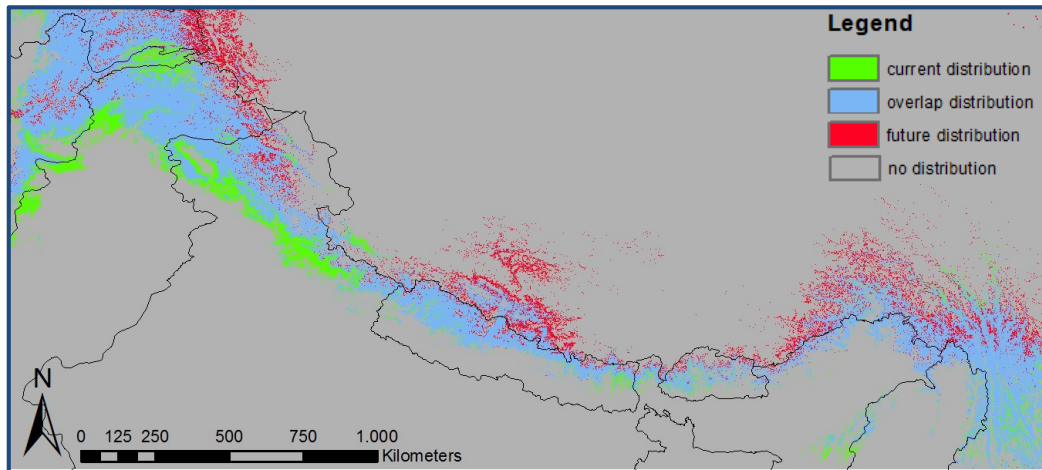
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**Figure 6.** Potential range shift of *Betula utilis* under novel climate conditions in AD 2070, based on ecological niche modelling.

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