

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

U. Schickhoff<sup>1</sup>, M. Bobrowski<sup>1</sup>, J. Böhner<sup>1</sup>, B. Bürzle<sup>1</sup>, R.P. Chaudhary<sup>2</sup>, L. Gerlitz<sup>1</sup>, H. Heyken<sup>1</sup>, J. Lange<sup>3</sup>, M. Müller<sup>4</sup>, T. Scholten<sup>4</sup>, N. Schwab<sup>1</sup>, and R. Wedegärtner<sup>4</sup>

<sup>1</sup>CEN Center for Earth System Research and Sustainability, Institute of Geography, University of Hamburg, Germany

<sup>2</sup> Research Centre for Applied Science and Technology, Tribhuvan University, Kathmandu, Nepal

<sup>3</sup> Institute of Botany and Landscape Ecology, University of Greifswald, Germany

<sup>4</sup> Institute of Physical Geography and Soil Science, University of Tübingen, Germany

*Correspondence to:* U. Schickhoff (udo.schickhoff@uni-hamburg.de)

**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.

## 1 Introduction

Treeline advance to higher elevation results in substantial physiognomic, structural and functional changes of mountain landscapes and ecosystems. Thus, sensitivity and response of alpine treelines to climate change is increasingly being discussed among scientists and by the general public (Holtmeier, 2009). Strong general links between climate parameters and treeline 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 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 (e.g., Körner, 1998), 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 (e.g., Holtmeier, 2009). The focus here is 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 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 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. They should focus on treelines which do not show substantial treeline depressions as a result of human impact.

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 in the Himalaya is still in the early stages. 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.

## **2 Geography and ecology of Himalayan treeline ecotones**

The Himalayan mountain system occupies a vast territory, extending from Afghanistan in the NW (c. 36° N and 70° E) to Yunnan in the SE (c. 26° N and 100° E). It encompasses a geographic relief of enormous dimensions, including the Tibetan Plateau in the north, all fourteen of earth's summits above 8000 m, and the outer foothills of the Indo-Gangetic Plain in the south. As indicated by the vegetation of its immediate forelands, the Himalaya crosses several horizontal climatic zones. Subtropical semi-desert and thorn steppe formations in the NW are replaced by tropical evergreen rainforests in the SE along a pronounced gradient of increasing humidity. A steep gradient of decreasing humidity is developed across the mountain system from S to N. The staggered mountain ranges act as climatic barrier for moisture-bearing monsoonal air masses, and cause a sharp decline in precipitation in peripheral-central direction. Along this gradient the densely forested Himalayan south slope strongly contrasts with steppe lands on the Tibetan Plateau.

According to the complex three-dimensional geocological differentiation with a high diversity of hygric, thermal, edaphic and biotic conditions, Himalayan treeline ecotones show considerable differences in altitudinal position as well as in physiognomy and species composition (Schickhoff, 2005). Along the two gradients described above, treeline elevations increase in accordance with increasing higher mean annual temperatures at same altitudes (Fig. 1). Along the mountain arc from NW to SE, the latitude-related temperature increase causes an upward shift of treelines of about 1000 m. At the northwestern range limit of monsoon-dependent Himalayan forests (Central Hindu Kush), treeline elevations reach 3400-3600 m (north-facing slopes). In the northern mountain ranges of Yunnan and in SE Tibet in the SE, the upper limit of tree growth attains elevations of c. 4600 m in northern aspects. The more or less linear ascent of treeline elevations along the peripheral-central gradient from the Himalayan south slope to the Tibetan highlands, which can be up to 600 m, is modified at single high-mountain massifs (e.g., Dhaulagiri and Annapurna Himal) with treelines located at higher altitudes 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 (cf. 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 (Fig. 2). Remnant forest stands on south-facing slopes are usually open coniferous forests that dissolve into isolated patches or single crippled trees over a broad altitudinal zone (Fig. 3). North- and south-facing slopes also show pronounced differences with regard to treeline-forming tree species. In the NW and W Himalaya, montane and subalpine vegetation in northern aspects primarily consists of coniferous forests (*Abies pindrow*, *Pinus wallichiana*, *Picea smithiana*, *Cedrus deodara*) which show an increasing proportion of birch (*Betula utilis*) in the upper subalpine belt and finally turn into a narrow band of more or less pure birch stands. *Rhododendron campanulatum*, *Sorbus* spp., and *Salix* spp. are principal understory species. Further upslope, *Betula utilis* and *Sorbus* spp. grow scattered in a crippled growth form and merge into a *Rhododendron* and/or *Salix* krummholz belt, which delimits the treeline ecotone and marks the transition to the alpine belt. Along the NW-SE gradient, increasingly more maritime climatic conditions with strongly decreasing winter cold and higher monsoonal humidity levels increase the competitiveness of evergreen trees and large shrubs of the genus *Rhododendron* (*Rh. campanulatum*, *Rh. barbatum*, *Rh. wightii*, *Rh. fulgens*, *Rh. lanatum*, *Rh. bhutanense*, a.o.) which replace the deciduous birch belt in the E Himalaya. Concomitantly, the hardy fir, spruce and pine species give way to other coniferous trees in high-altitude forests in Nepal, Sikkim and further to the east. Species such as *Abies spectabilis*, *Abies densa*, *Picea spinulosa*, *Larix griffithiana* a.o. ascend from closed forests in the upper montane and lower subalpine belt into the *Rhododendron*-dominated treeline ecotone with uppermost *Rhododendron* stands turning into krummholz and *Rhododendron* dwarf shrubs further upslope (Miehe and Miehe, 2000; Miehe, 2004; Schickhoff, 2005).

Along the entire mountain arc, *Juniperus* spp. are the principal treeline tree species on south-facing slopes. Below the treeline ecotone, coniferous forests (mostly *Pinus wallichiana* forests, in more humid areas even *Abies* forests) cover southern aspects if they have not been transformed into grazing lands. Several juniper species

(*Juniperus excelsa*, *J. semiglobosa*, *J. turkestanica*, *J. recurva*, *J. wallichiana*, *J. indica*, *J. tibetica* a.o.) are able to grow as upright trees in the subalpine belt, forming stands of varying density. Most common are very open woodlands, in particular in the NW Himalaya. In pasture areas junipers often occur as single isolated individuals. South-facing slopes often lack a distinct and easily recognizable altitudinal zonation of vegetation mainly due to excessive human impact. Scattered junipers may change their growth form from tree to (dwarf) shrub with increasing altitude (e.g., *J. indica*, *J. recurva*), and are generally less suitable for the delimitation of treeline ecotones. The potential natural stand structure of juniper groves is hard to reconstruct since south-facing slopes are strongly modified by human impact for centuries, if not millennia (Miehe, 1990; Miehe and Miehe, 2000; Schickhoff, 2005).

### 3 Regional climate change

The climate of the Himalayan Arc is triggered by the seasonal shift of the major pressure cells over Asia and the adjacent oceans and the accompanying change of large scale circulation patterns, which lead to a distinct hygric seasonality, referred to as „monsoon“. Due to the strong establishment of the Asian Heat Low, the summer season is characterized by a south-westerly flow, originating over the Bay of Bengal, which advects moist air masses into the Eastern Himalayas and leads to summer precipitation amounts of up to 5000 mm at the windward Himalayan slopes. A minor monsoonal current from the Arabian Sea transports moist air masses into the western part of the Himalaya. In contrast the winter climate is determined by a uniform westerly flow. The upper tropospheric jetstream at the 200 hPa level determines the trajectories of extratropical western disturbances, which lead to occasional precipitation events, particularly in the western Himalaya (Böhner, 2006; Maussion et al., 2013). While the eastern Himalaya receives more than 80 % of the annual precipitation during summer season, the winter precipitation over the far western parts reaches up to 50 % of the annual amount. The transition seasons are characterized by mainly dry conditions throughout the Himalaya, although infrequent convective precipitation events occur at south facing slopes (Romatschke et al., 2010).

On regional and local scales the climate of the Himalaya is distinctly modified by the vast topography. While the climate of the lowlands and foothills is characterized by warm conditions throughout the year, the very high elevations stand out due to extremely cold conditions with temperatures below 0°C even during summer season. The distinct topographic characteristics lead to varying solar insolation rates and the development of autochthonous local-scale circulation systems, resulting in a rather complex near surface temperature distribution. The local-scale distribution of precipitation rates is mainly influenced by wind- and leeward positions and again by topographically induced local scale circulation patterns (Gerlitz, 2014).

Many studies show that high mountain regions are particularly sensitive to climatic changes (e.g., Kohler et al., 2010). The enhanced radiative forcing due to anthropogenic greenhouse gas emissions and the albedo-feedback due to shrinking glaciers and reduced snow cover rates during winter and spring result in an accelerated response to recent global warming. Observations show that temperature trends over the Himalaya by far exceed the global mean trend of 0.74 °C during the previous century. For high elevations, temperature trends between 0.6°C and 1°C per decade were detected (Shrestha et al., 1999; Liu and Chen, 2000). Based on elevation- and bias-adjusted ERA-Interim reanalysis data, Gerlitz et al. (2014)

analyzed spatial high resolution temperature trends over the Himalaya for the period since 1989. During winter season, high temperature trends of up to +0.8 °C per decade were detected over the eastern Himalaya. In pre-monsoon season, high temperature trends were found for the entire Himalayan Arc. Estimated temperature trends show a clear elevational gradient with maximum values of up to 1°C per decade at higher altitudes (Fig. 4). During monsoon season, temperature trends were found to be reduced throughout the target area. High temperature trends during post-monsoon season were detected only over the eastern Indus-Ganges lowlands. The study further indicates a decrease of frost days (up to -17 days per decade) in the Nepal Himalaya at elevations between 3000 and 3500m. A significant positive trend of growing degree days was detected for the southern slopes of the Himalaya at elevations between 2000 and 3500 m (cf. Fig. 4).

Based on rain gauge observations, negative trends of annual precipitation (up to 20 % for the previous century) over the western Himalaya were identified by Duan et al. (2006), Bhutiyani et al. (2010) and Jain et al. (2013). This trend mainly results from decreasing summer precipitation rates after the 1960s, and is associated with a weakening of the Southern Oscillation and a decrease of temperature gradients over southern Asia due to high warming rates over the Indian Ocean during recent decades (Basistha et al., 2009; Naidu et al., 2009). Long-term trends of winter precipitation rates are slightly negative, but not statistically significant (Bhutiyani et al., 2010). Particularly for western Nepal, an enhanced frequency of winter and pre-monsoon drought events has been reported by Wang et al. (2013). No statistically significant trends of annual precipitation rates could be detected for the eastern Himalaya (Jain et al., 2013). In combination with rising temperatures and accompanying increase of evapotranspiration rates, the decrease of precipitation over the Himalaya very likely leads to enhanced drought stress, particularly in the pre-monsoon season. Thus, recent climatic changes will inevitably affect growth patterns and seedling performance at Himalayan treelines, albeit to a regionally differentiated extent.

## **4 Assessing sensitivity of Himalayan treelines**

### **4.1 Susceptibility of treeline types and treeline forms**

The occurrence of certain treeline types and treeline forms in a mountainous region indicates to some extent the susceptibility to respond to changing climatic conditions. Treeline types (climatic, orographic/edaphic, anthropogenic) are distinguished in this paper according to the environmental factors which control their altitudinal position (cf. Holtmeier and Broll, 2005). Climatic treelines are caused mainly by heat deficiency and, in extratropical regions, the duration of the growing season. It is the common alpine treeline type in zonal habitats under natural undisturbed conditions. By contrast, orographic treelines are always located below the climatically caused altitudinal limit, and are prevented from reaching their potential upper limit by factors such as steep topography, rock walls, talus cones, slope debris, or avalanche chutes. Edaphic treelines are often difficult to distinguish from orographic treelines, in particular when the steepness of slopes or the substrate on precipitous slopes prevents the accumulation of sufficient fine material and pedogenesis. On volcanic substrates, lack of soil moisture may also prevent the treelines from reaching their upper climatic limit (Gieger and Leuschner, 2004). Anthropogenic treelines have been lowered from their natural position, often by several hundred meters, through a variety of human uses such as pastoral use, fire clearing, logging, collecting firewood,

charcoal production, mining, salt works, etc. They are particularly common in old-settled mountain regions in Europe and Asia where the average treeline depression is 150-300 m (Holtmeier, 2009).

The predisposition to respond to recent climate change varies considerably among the different treeline types. Climatic treelines show a comparatively high susceptibility and are more likely to reflect climate tracking since increases in temperature sums and growing season length will be inevitably reflected by growth patterns, regeneration, and treeline position, at least in the long-term (Holtmeier and Broll, 2007; Körner, 2012a). However, the direct influence of climate warming is variegated in complex ways by local-scale abiotic and biotic site factors and their manifold interactions that act as thermal modifiers. For instance, broad-scale climatic inputs are mediated at local scales by the varying microtopography in treeline ecotones and will exert a modified influence on soil temperatures, soil moisture, or the distribution of trees (Holtmeier and Broll, 2005, 2012; Case and Duncan, 2014). Thus, the sensitivity of climatic treelines varies with a considerable scope in the medium-term (several years to a few decades). The long-term response in terms of treeline shifts might be more homogeneous, but the treeline position will adjust to present climatic conditions only after a time lag of several decades to hundreds of years.

Unlike climatic treelines, orographic treelines are resistant to the effects of climate warming. As long as orographic factors such as debris slides, rockfalls, snow avalanches, etc. prevent the establishment of trees, the fragmented spatial pattern of orographic treelines will not change significantly. Edaphic treelines will become more sensitive to a warming climate once pedogenetic processes accelerate and favour the establishment of tree seedlings and tree invasion. Anthropogenic treelines show considerable dynamics in recent decades with prolific regeneration, increased tree establishment within the treeline ecotone, and invasion into treeless areas above the anthropogenic forest limit. These directional changes are readily attributed to effects of global warming, they result, however, in most cases from the cessation of pastoral use or other human impact (Holtmeier, 2009; Schickhoff, 2011). It is imperative to disentangle the effects of decreasing land use and climate warming (cf. Gehrig-Fasel et al., 2007; Vittoz et al., 2008) in order to assess the potential for treeline advance beyond the current climatically determined upper limit. Nevertheless, anthropogenic treelines do not basically differ from climatic treelines in terms of sensitivity to climate warming, the potential effects of which, however, may be reduced due to radically altered site conditions and other after-effects of historical forest removal (Holtmeier and Broll, 2005).

The various treeline types occur in different frequencies in the vast Himalayan mountain system. According to our extensive field experience along the entire mountain arc, we estimate 85-90 % of treelines to be anthropogenic (Fig. 5), and only 10-15 % to be orographic/edaphic and climatically determined. Since the beginning of human occupation that started in many subregions thousands of years ago, yet in some valleys only a few centuries ago, animal husbandry, timber logging, fuelwood collection and the like are integral parts of village economies. Thus, treeline ecotones have been transformed to a locally and regionally varying extent, and present landscape patterns at treeline elevations are cultural landscape patterns. Overgrazing and fire have been the main agents for lowering treelines (Beug and Miehe, 1999). Treelines at north- and south-facing slopes reflect contrasting utilization intensity. As land use pressure is unevenly higher at south-facing slopes, in particular with regard to pastoral use, downslope extension of alpine pastures, depression of treelines, or even complete removal of forest cover are widespread



phenomena at southern aspects throughout the mountain system (Miehe and Miehe, 2000; Schickhoff, 2005). Treeline depressions may be up to 500-1000 m (Miehe, 1997), in particular in localities where extensive alpine grazing grounds are not available. Treelines on south slopes are thus almost exclusively anthropogenic.

North-facing slopes have a lower utilization potential for pastoral use. Nevertheless, a considerable depression of alpine treelines can be observed on shaded slopes as well, resulting from the extension of alpine grazing grounds and the over-utilization of subalpine forests (Schmidt-Vogt, 1990; Schickhoff, 2002). A representative example for the western Himalaya is Kaghan Valley, Pakistan, where the birch belt has been largely decimated, and uppermost coniferous forests depleted, resulting in a difference between current and potential treeline of up to 300 m (Schickhoff, 1995). In most Himalayan regions we still witness a growing importance of the primary sector with land use intensification by local mountain farmers as a consequence of internally (population growth) and externally (lowland markets) generated pressure. Cessation of land use and subsequent landscape change in treeline ecotones has been observed to date only to a limited extent. Respective changes are largely confined to protected areas such as national parks and biosphere reserves.

The percentage of anthropogenic treelines on north-facing slopes is lower than on south-facing slopes, i.e., some near-natural treeline ecotones, more or less undisturbed by human impact, still persist on northern aspects in remote valleys which are sparsely populated, not connected to the road network, and/or where plants and animals are protected for religious reasons. These climatic treelines have to be considered unique research opportunities for detecting a clear climate change signal as a driver for treeline dynamics. Examples include treeline ecotones in the Black Mountains of Bhutan (Miehe and Miehe, 2000), in the Sygera Mountains in SE Tibet (Liang et al., 2011), and in the Rolwaling Valley, Nepal (Fig. 6). The latter is the location of a new treeline research programme from which first data are presented below. Due to the widespread steep and rugged terrain in the Himalaya, orographic/edaphic treelines are not uncommon, but make up only a small percentage of all treelines. Summing up, the proportional distribution of treeline types in the Himalaya suggests that sensitivity and response to climate warming must be assessed cautiously. The vast majority are anthropogenic treelines which, in addition, will be subjected to continued intensive land use in the foreseeable future. Thus, a substantial medium-term response is to be expected from the tiny fraction of climatic treelines only, and from those anthropogenic treelines which are no longer exposed to important human disturbance.

Recently, Harsch and Bader (2011) discussed how treeline spatial patterns (treeline forms) are controlled by different mechanisms (at the levels of direct tree performance, causative stresses, and modifying neighbour interactions), and how the varying dominance of these controlling mechanisms modulate climate change responses of different treeline forms. They distinguished four primary treeline forms with a wide geographic distribution: i) Diffuse, with a gradual decrease in tree height and density along the treeline ecotone; ii) Abrupt, with forest stands directly bordering low alpine vegetation; iii) Island, with clumped patches or linear strips of krummholz or trees above closed forests; iv) Krummholz, with a dispersed or contiguous belt of severely stunted or deformed trees above the upright forest. Applying this framework to alpine treelines globally, Harsch and Bader (2011) found diffuse treelines, formed and maintained primarily by growth limitation, to exhibit an earlier, stronger response signal, whereas abrupt, island, and krummholz treelines, controlled by seedling mortality and dieback, are comparatively unresponsive. They confirmed the link

between treeline form and dynamics established earlier (Lloyd, 2005; Harsch et al., 2009), and supported the general suitability of treeline form for explaining the variability of response to climate warming.

Although the present understanding of treeline pattern-process relationships is not sufficiently advanced to use treeline form to predict dynamics, and although land use effects on treelines are not explicitly addressed in Harsch and Bader's approach, transferring their conclusions to Himalayan treelines (not included in their dataset of 195 treeline sites with one or two exceptions) may give an additional indication of sensitivity and response. As indicated above, treeline forms in the Himalaya are predominantly controlled by anthropogenic disturbances, and cannot easily be classified into discrete classes. However, according to our field experience the occurrence of abrupt and island treelines under natural conditions can be virtually excluded. Abrupt treelines do occur (e.g., *Betula* treelines in Manang Valley, Nepal), they are however caused by land use (Shrestha et al., 2007). The far majority of less disturbed or near-natural Himalayan treelines, mainly confined to north-facing slopes, has to be categorized as krummholz treelines (cf. Sect. 2). Diffuse treelines are largely limited to less disturbed or near-natural sites in southern aspects which have become very rare. As treeline advances have been less commonly observed in krummholz treelines (Harsch and Bader, 2011), and responsive diffuse treelines are rare, sensitivity and response of Himalayan treelines need to be assessed with reluctance again, at least in terms of treeline shifts. In addition, near-natural Himalayan krummholz treelines give way at their upper limit to a very dense alpine dwarf scrub heath so that tree seedlings are subjected to a strong competition. Nevertheless, increased vertical stem growth and enhanced recruitment of seedlings have been reported from many krummholz treelines worldwide (cf. Lescop-Sinclair and Payette, 1995; Harsch et al., 2009), presumably more related to a change in snow and winter climate conditions, and can also be expected at Himalayan treelines.

#### **4.2 Seed-based regeneration**

Any upward elevational shift of alpine treelines depends on the establishment of seedlings and their performance during early life stages (Germino et al., 2002; Holtmeier, 2009; Smith et al., 2009; Zurbriggen et al., 2013). Hence, as an indicator of treeline sensitivity, successful regeneration is considered to have higher significance than morphological or physiological responses of mature trees (Holtmeier and Broll, 2005). Interpreting tree recruitment as evidence of response to recent environmental change, however, has to take into account site, climate and species-specific regeneration cycles and should be backed by robust cause and effect analysis (Körner, 2012a). To understand underlying mechanisms of treeline dynamics, a multitude of environmental factors and processes controlling seed-based regeneration have to be included in respective analyses and correlated with seedling establishment, survival and growth. In recent years, an increasing number of studies have investigated the response of treeline seedlings to changing environmental factors such as soil temperature, soil moisture, soil nutrients, light conditions, herbivory, and competition/facilitation (e.g., Maher and Germino, 2006; Anschlag et al., 2008; Batllori et al., 2009; Hofgaard et al., 2009; Kabeya, 2010; Munier et al., 2010), some studies explicitly addressed the relative importance of multiple factors (Barbeito et al., 2012; Zurbriggen et al., 2013).

In the Himalaya, only very few studies on treeline seedlings have been conducted so far, and tree recruitment in treeline ecotones is not well understood (Schickhoff, 2005; Dutta et al., 2014). However, some preliminary evidence with regard to using regeneration as indicator for treeline sensitivity can be inferred. The majority of studies on seed-based regeneration were carried out in Nepal. Shrestha et al. (2007) found *Betula utilis* treeline forests in Manang Valley, Annapurna Conservation Area, sufficiently generating with a reverse J-shaped diameter distribution. Along vertical transects, *Betula* seedlings and saplings were common up to an altitudinal distance of 50 m above the treeline. Seedlings could not establish, however, under their own canopy when tree density and basal area exceeded certain threshold values. Canopy cover (light) and soil moisture largely determined reproductive success. Seedlings of *Abies spectabilis* were abundant up to 3900 m, but absent above 4000 m. Continuous regeneration as indicated by reverse J-shaped density-diameter curves and high densities of seedlings and saplings was also assessed in other studies in treeline forests in Manang, focusing on *Abies spectabilis* (Ghimire and Lekhak, 2007), and *Pinus wallichiana* (Ghimire et al., 2010). *Abies* seedling abundance was positively correlated to soil moisture and nutrients (phosphorus), whereas altitude was the only significant predictor of *Pinus* seedling density. Shrestha (2013) also observed continuous tree recruitment of *Pinus wallichiana* in Ngawal/Manang (south-facing slope) and *Abies spectabilis* in Lauribinayak/Langtang National Park (north-facing slope), with seedlings occurring up to 60 m above current treelines in 4120 m/3910 m. Corresponding results were obtained 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 cycles with generally low regeneration rates, associated with low site productivity rather than grazing impact.

Research on treeline seedlings performance in the eastern Himalaya is in its infancy as well. Some detailed studies on *Abies densa* regeneration and its controlling factors near alpine treelines in Bhutan showed intense recruitment (Gratzer et al., 2002; Gratzer and Rai, 2004). Expanding treeline populations of Smith fir (*Abies georgei* var. *smithii*) and infilling of treeline ecotones with intense, microsite-dependent clumping of abundant seedlings were reported from the Sygera Mountains (SE Tibet) (Ren et al., 2007; Wang et al., 2012), in accordance with observations from Liang et al. (2011), who assessed considerably increased Smith fir recruitment in recent decades, significantly positively correlated with both summer and winter temperatures. First experimental studies (transplant experiment) in an adjacent study area indicated early-season freezing events to be the major limiting factor determining mortality of fir seedlings above the current treeline (Shen et al., 2014). High rates of regeneration with the percentage of seedlings/saplings increasing upslope across the treeline ecotone was assessed in the Hengduan Mountains (NW Yunnan) by Wong et al. (2010).

First results from ongoing research projects of the present authors in two study areas in Nepal (Rolwaling Valley, Gaurishankar Conservation Area; Langtang Valley, Langtang National Park) corroborate the emerging pattern of a generally intense regeneration at Himalayan treeline sites, as long as pastoral use is not the major force determining seedling performance. The alpine treeline in Rolwaling Valley, located in east-central Nepal (27°52'N; 86°25'E) and virtually undisturbed by human impact, corresponds to the krummholz treeline form (north-facing slope). Upper subalpine forests are primarily composed of *Betula utilis* and *Abies spectabilis*, with *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer. Closed forests give way to an extensive krummholz belt of *Rh. campanulatum* at 3900 m (NW-exp.) / 4000 m (NE-exp.), which turn into alpine *Rhododendron* dwarf scrub heaths at c. 4000 m / 4100 m. We analysed seedling density on NW and NE slopes in upper Rolwaling across the treeline ecotone, divided into four altitudinal zones (Tab. 1). Within each zone, 12 plots (20 m x 20 m) were randomly selected. We assessed largely prolific regeneration with seedling establishment of *Betula*, *Abies*, and *Sorbus* to some extent far above the upper limit of adult trees (Fig. 7). Some individuals of more than 2 m height even grow vigorously above the krummholz belt, a small birch tree of 2.4 m height was found in 4140 m. Maximum seedling/sapling density occurs in elevational zone B (more than 9000 N/ha) where *Rh. campanulatum* has its most intense recruitment (cf. Tab. 1). Young growth density sharply decreases towards the alpine tundra, in particular with *Abies* and *Betula*, which also show considerably higher seedling/sapling abundance on the NW slope. The average elevation a.s.l. of maximum seedling/sapling density is distinctly higher on the NE slope (Fig. 8), which experiences higher sunshine duration and heat sum. *Rhododendron* and *Sorbus* seedlings/saplings are distributed along the entire treeline ecotone. We found a negative correlation between abundance and density of *Rh. campanulatum* and recruitment of other tree species (unpubl. data), the seedling establishment of which is obviously impeded by the permanently dense foliage of evergreen *Rhododendron* and by potential allelopathic effects that have been shown for other species of this genus (Chou et al., 2010). Thus, the dense krummholz belt appears to be an effective barrier for upslope migration of other tree species. Reproductive success was also found to be generally positively correlated with a finely structured microtopography.

A first evaluation of the importance of soil temperature and soil moisture for seedling/sapling density of *Abies*, *Betula*, *Rhododendron*, and *Sorbus* has been conducted on the basis of 32 plots, on which these variables were recorded in 10 cm soil depth from May 2013 to April 2014 (Fig. 9). The results show significantly positive correlations of seedling/sapling abundance with soil moisture for *Abies*, *Betula*, and *Rhododendron*, and with soil temperature for *Abies*, *Betula*, and *Sorbus*, in each case over almost all size classes. Thus, higher soil moisture and soil temperatures indicate higher recruitment density of the majority of treeline tree species. A negative correlation with soil moisture was merely assessed for germinants and small saplings of *Sorbus microphylla*, in contrast to larger recruits of this species. *Rh. campanulatum* saplings (up to a height of 2 m) were found to be negatively correlated with soil temperature, germinants and large shrubs, however, showed a positive correlation (cf. Fig. 9). Total soil moisture values did not differ much between NE and NW slopes.

The treeline physiognomy and vegetation zonation of the study sites in Langtang Valley, c. 100 km to the west, is more or less in accordance with that of Rolwaling. The *Rh. campanulatum* krummholz belt, however, is not as dense and often disintegrated so that uppermost birch forest stands are occasionally adjoining *Rhododendron* dwarf scrub heaths that may have invaded downslope into former krummholz sites. Langtang treeline ecotones and its vegetation patterns, though near-natural, have been and still are affected to a much larger extent by pastoral and forest use compared to those in Rolwaling. We studied regeneration dynamics on 70 plots along elevational transects across the treeline ecotone with a stratified-random sampling. In accordance with the observations in Rolwaling, the production of viable seeds and the supply of treeline ecotones with fertile seeds are obviously sufficient to generate relatively high rates of seedling establishment, even beyond the actual upper limit of contiguous forests between 4000 and 4100 m. Maximum seedling/sapling density occurs at 3900 and 3950 m with 10665 N/ha and 10075 N/ha respectively, before the recruit abundance sharply decreases above 4100 m, slightly above the transition from cloud forests to dwarf scrub heaths (Tab. 2). The far majority of all seedlings/saplings are *Sorbus microphylla* (54 %) and *Rh. campanulatum* individuals (40 %), they occupy in particular the size class 0-19 cm (98 %) (Fig. 10). In contrast, recruitment of *Abies spectabilis* is relatively sparse, and obviously related to grazing impact and the removal of adult trees as seed sources. Regeneration of *Betula utilis* is also less intense. However, *Betula* seedlings/saplings are far more homogeneously distributed across the size classes compared to the other species (cf. Fig. 10). Numerous saplings of greater size classes became established at the treeline and above the upper limit of contiguous forests (Fig. 11). The uppermost *Betula* tree individual was found at 4215 m, c. 150 m above the current treeline, with a height of 4.5 m and a breast height diameter of 14.5 cm. Summing up, seed-based regeneration within and beyond treeline ecotones of Rolwaling and Langtang valleys does not appear to restrict the proneness to respond to climate warming.

### 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 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., 2015), 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 Mountains (SE Tibet) revealed accelerated growth in the past decades and significantly positive correlations with monthly mean and minimum temperatures of most months, particularly in summer (Liang et al., 2009, 2010). However, the significant extension of the growing season at the same treeline by c. 21 days during the past 50 years has not directly affected the radial growth of Smith fir to date (Liu et al., 2013). Zhu et al. (2011) reported a similar response to summer temperatures for *Picea likiangensis* var. *balfouriana* at adjacent treelines.

Recent accelerated growth has not been confirmed in the Karakoram Mountains, but it has been established for near-treeline sampling locations of *Juniperus turkestanica*, *Pinus wallichiana*, and *Picea smithiana* that temperature variation predominantly limits tree growth (Esper et al., 2002, 2007). High-elevation junipers in semiarid Lahul (Himachal Pradesh) are obviously more responsive to precipitation during winter and spring months (Yadav et al., 2006; see also Yadav et al. 2011). Gaire et al. (2014) found tree growth of *Abies spectabilis* in Manaslu Conservation Area (Nepal) to be positively correlated with higher winter temperatures prior to growing season, and stressed the positive effects of earlier snow melt and increased melt water supply for growth. Similarly, Bräuning (2004) reported a strong positive relationship between *Abies spectabilis* ring width and November-January temperature in Dolpo (W Nepal). The ring width of several treeline conifers in SE Tibet and NW Yunnan was also found to be sensitive to winter season temperature, while their maximum latewood density was positively correlated with summer temperature (Bräuning and Mantwill, 2004; Bräuning, 2006; Bräuning and Grießinger, 2006; Fan et al., 2009). Warmer conditions during winter season facilitate the storage of higher levels of hydro-carbonates and are beneficial to root system activity and carbon absorption and transportation (He et al., 2013). A positive relationship to winter temperatures was also ascertained for *Abies densa* near treelines in Sikkim and Arunachal Pradesh, while summer temperatures were inversely related to tree growth (Bhattacharyya and Chaudhary, 2003).

An increasing number of studies in W and central Himalaya have revealed a strong sensitivity of tree growth to pre-monsoon temperature and humidity conditions. Yadav 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* [now *Taxus wallichiana*] 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. Borgaonkar et al., 1999; Pant et al., 2000; Cook et al., 2003; Ram and Borgaonkar, 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 Borgaonkar, 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 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 (Lange et al. unpubl.). 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). 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 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 (unpubl. data). 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).

Other studies on treeline shifts are based on remote sensing. Bharti et al. (2012) used Landsat imagery and found an overall increase in the green biomass of treeline ecotone in Nanda Devi Biosphere Reserve (Uttarakhand) during 1980-2010, in particular of the subalpine forest's canopy, but no shift of the upper treeline. In contrast, two other studies in the same area reported globally exceptional and unprecedented treeline advances of more than 300 m in recent decades (Panigrahy et al., 2010; Singh et al., 2012), these results, however, have been criticized as unreliable due to methodological shortcomings (cf. Bharti et al., 2011; Negi, 2012; Rawat, 2012). Another Landsat-based change detection study of the treeline ecotone in Himachal Pradesh and Uttarakhand indicated an expansion of fir and birch forests in recent decades (Rai et al., 2013). Based on repeat photography, Baker and Moseley (2007) documented a significant infilling of the tree-limit ecocline and an upward shift of the timberline of almost 70 m in elevation at a slope in the Hengduan Mountains (NW Yunnan) since AD 1923, and argued that climate warming contributed to the elevational advance of the alpine treeline. However, the expansions and shifts, when detected at anthropogenically depressed treelines, are rather an effect of the cessation of land use and other human disturbances than a result of climate change.

Recently, an increasing number of modelling approaches are applied to gain a better understanding of treeline dynamics in response to climate and land use change and of underlying process-pattern relationships (e.g., Dullinger et al., 2004; Wallentin et al., 2008; Paulsen and Körner, 2014). In the Himalaya, neither modelling approaches to predict the response of individual treeline systems nor modelling studies to project future geographic distribution of treeline tree species have been conducted so far. Recently, initial modelling studies with regard to environmental niches of the genus *Rhododendron* in Sikkim and of *Betula utilis* in Uttarakhand were published (Kumar, 2012; Singh et al., 2013).

Ecological niche models have proven to be a valuable tool of linking the occurrence or abundance of a species to environmental and/or geographical variables, providing predictions of species distribution ranges or potential habitat suitability (e.g., Elith et al., 2010). They are usually calibrated based on current environmental conditions and extrapolated to future scenarios, based on the assumption of niche conservatism (Wiens et al., 2010). We used ecological niche modelling to forecast the range shift of *Betula utilis* under novel climate conditions in AD 2070 (Fig. 12). All models were calculated using the maximum entropy algorithm (Phillips et al., 2006), implemented in the software Maxent, Version 3.3.3k. Presence-only occurrence data of *Betula utilis* were accessed via the Global Biodiversity Information Facility (gbif.org). The database hosted 193 georeferenced records (1970-2014) with non-known coordinate issues for the Himalayan region. 93 records were added compiled from the present author's database. After filtering the occurrence points to reduce spatial autocorrelation, 173 records were used for model analysis. We used bioclimatic raster data and a digital elevation model (DEM) obtained from Worldclim (worldclim.org; Hijmans et al., 2005). For future climate scenario, 19 bioclimatic variables of MIROC5 rcp60 were used and projected to 2070 (downscaled IPCC5 (CMIP5) data (Hijmans et al., 2005). Spatial resolution of all grids was 30 arc seconds (~1km). We used a geographically structured approach with 3 bins, accordingly occurrence data were split in 138 training data points and evaluated with the remaining 35 data points. Models were fitted and projected to both current and future climate using all features and different regularization parameters. Models were evaluated using the Receiver Operating Characteristic (area under the curve, ROC, AUC). Consistently with current scientific knowledge, the averaged models (AUC 0.922) mapped upslope distribution range shifts.

Driven by significant bioclimatic variables such as mean diurnal range (monthly temperature: min-max), minimum temperature of coldest month, slope and annual precipitation, mean temp of wettest month and the like, the potential habitat of *Betula utilis* is predicted to shift from lower to higher elevations and to expand into new habitats north of the Himalayan range (cf. Fig. 12). Significant upslope expansions are modelled for Transhimalayan ranges in S Tibet. Range contractions are forecasted for the Lesser W Indian Himalaya, the S Hindukush, and the Wakhan Corridor. Gaining a better understanding of potential range shifts of alpine treeline species under climate change 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 treelines. 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 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 sub-alpine forests would displace regionally unique alpine tundra habitats and possibly cause the loss of alpine species.

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## References

- Akatov, P.V.: Changes in the upper limits of tree species distribution in the western Caucasus (Belaya River basin) related to recent climate warming, *Russ. J. Ecol.* 40, 33-38, 2009.
- Anschlag, K., Broll, G. and Holtmeier, F.K.: Mountain birch seedlings in the treeline ecotone, subarctic Finland: Variation in above-and below-ground growth depending on microtopography, *Arct., Antarct., Alp. Res.* 40, 609-616, 2008.
- Aryal, A., Brunton, D. and Raubenheimer, D.: Impact of climate change on human-wildlife-ecosystem interactions in the Trans-Himalaya region of Nepal, *Theor. Appl. Climatol.* 115, 517-529, 2014.
- Baker, B.B. and Moseley, R.K.: Advancing treeline and retreating glaciers: Implications for conservation in Yunnan, P.R. China, *Arct., Antarct., Alp. Res.* 39, 200-209, 2007.
- Bansal, S., Reinhardt, K., and Germino, M.J.: Linking carbon balance to establishment patterns: Comparison of whitebark pine and Engelmann spruce seedlings along an herb cover exposure gradient at treeline, *Plant Ecol.* 212, 219-228, 2011.
- Barbeito, I., Dawes, M. A., Rixen, C., Senn, J. and Bebi, P.: Factors driving mortality and growth at treeline: A 30-year experiment of 92 000 conifers, *Ecology* 93, 389-401, 2012.

- Basistha, A., Arya, D.S. and Goel, N.K.: Analysis of historical changes in rainfall in the Indian Himalayas, *Int. J. Climatol.* 29, 555–572, 2009.
- Batllori, E. and Gutiérrez, E.: Regional tree line dynamics in response to global change in the Pyrenees, *J. Ecol.* 96, 1275-1288, 2008.
- Batllori, E., Camarero, J.J., Ninot, J.M. and Gutiérrez, E.: Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming, *Global Ecol. Biogeogr.* 18, 460-472, 2009.
- Beug, H.J. and Miehe, G.: *Vegetation History and Human Impact in the Eastern Central Himalaya (Langtang and Helambu, Nepal)*, Diss. Bot. 318, Berlin-Stuttgart, 1999.
- Bharti, R.R., Rai, I.D., Adhikari, B.S. and Rawat, G.S.: Timberline change detection using topographic map and satellite imagery: A critique, *Trop. Ecol.* 52, 133-137, 2011.
- Bharti, R.R., Adhikari, B.S. and Rawat, G.S.: Assessing vegetation changes in timberline ecotone of Nanda Devi National Park, Uttarakhand, *Int. J. Appl. Earth Observ. Geoinform.* 18, 472-479, 2012.
- Bhattacharyya, A. and Chaudhary, V.: Late-summer temperature reconstruction of the eastern Himalayan region based on tree-ring data of *Abies densa*. *Arct., Antarct., Alp. Res.* 35, 196-202, 2003.
- Bhattacharyya, A. and Shah, S.K.: Tree-ring studies in India, past appraisal, present status and future prospects, *IAWA J.* 30, 361-370, 2009.
- Bhattacharyya, A. and Yadav, R.R.: Growth and climate relationship in *Cedrus deodara* from Joshimath, Uttar Pradesh, *Paleobotanist* 38, 411-414, 1990.
- Bhattacharyya, A., Shah, S.K. and Chaudhary, V.: Would tree-ring data of *Betula utilis* have potential for the analysis of Himalayan glacial fluctuations? *Curr. Sci.* 91, 754–761, 2006.
- Bhutiyan, M.R., Kale, V.S. and Pawar, N.J.: Climate change and the precipitation variations in the northwestern Himalaya: 1866–2006, *Int. J. Climatol.* 30, 535–548, 2010.
- Böhner, J.: General climatic controls and topoclimatic variations in Central and High Asia, *Boreas* 35, 279–295, 2006.
- Bolli, J.C., Rigling, A. and Bugmann, H.: The influence of changes in climate and land-use on regeneration dynamics of Norway Spruce at the treeline in the Swiss Alps, *Silva Fennica* 41, 55-70, 2006.
- Borgaonkar, H.P., Pant, G.B. and Rupa Kumar, K.: Tree-ring chronologies from western Himalaya and their dendroclimatic potential, *Int. Assoc. Wood Anat. J.* 20, 295-309, 1999.
- Borgaonkar, H.P., Ram, S. and Sikder, A.B.: Assessment of tree-ring analysis of high-elevation *Cedrus deodara* D. Don from western Himalaya (India) in relation to climate and glacier fluctuations, *Dendrochronologia* 27, 59–69, 2009.
- Borgaonkar, H.P., Sikder, A.B. and Ram, S.: High altitude forest sensitivity to the recent warming: a tree-ring analysis of conifers from western Himalaya, India, *Quatern. Int.* 236, 158-166, 2011.
- Bräuning, A.: Tree-ring studies in the Dolpo-Himalaya (western Nepal), *TRACE - Tree Rings in Archaeol. Climatol. Ecol.* 2, 8-12, 2004.
- Bräuning, A.: Tree-ring evidence of “Little Ice Age” glacier advances in southern Tibet, *The Holocene* 16, 1-12, 2006.

- Bräuning, A. and Mantwill, B.: Summer temperature and summer monsoon history on the Tibetan plateau during the last 400 years recorded by tree rings, *Geophys. Res. Lett.* 31, L24205, doi:10.1029/2004GL020793, 2004.
- Bräuning, A. and Griesinger, J.: Late Holocene variations in monsoon intensity in the Tibetan-Himalayan region - evidence from tree rings, *J. Geol. Soc. India* 68, 485-493, 2006.
- Camarero J.J. and Gutiérrez, E.: Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the Spanish Pyrenees, *Clim. Change* 63, 181-200, 2004.
- Case, B.S. and Duncan, R.P.: A novel framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline position, *Ecography* 37, 838-851, 2014.
- Chaudhary, V. and Bhattacharyya, A.: Tree ring analysis of *Larix griffithiana* from the Eastern Himalayas in the reconstruction of past temperature, *Curr. Sci.* 79, 1712-1715, 2000.
- Chou, S.C., Huang, C.H., Hsu, T.W., Wu, C.C. and Chou, C.H.: Allelopathic potential of *Rhododendron formosanum* Hemsl in Taiwan, *Allelopathy J.* 25, 73-92, 2010.
- Cook, E.R., Krusic, P.J. and Jones, P.D.: Dendroclimatic signals in long tree-ring chronologies from the Himalayas of Nepal, *Int. J. Climatol.* 23, 707-732, 2003.
- Cook, E.R., Anchukaitis, K.J., Buckley, B.M., D'Arrigo, R.D., Jacoby, G.C. and Wright, W.E.: Asian monsoon failure and megadrought during the last millennium, *Science* 328, 486-489, 2010.
- Dalen, L. and Hofgaard, A.: Differential regional treeline dynamics in the Scandes Mountains, Arct., Antarct., *Alp. Res.* 37, 284-296, 2005.
- Danby, R.K.: Monitoring forest-tundra ecotones at multiple scales, *Geogr. Compass* 5, 623-640, 2011.
- Danby, R.K. and Hik, D.S.: Variability, contingency and rapid change in recent subarctic alpine treeline dynamics, *J. Ecol.* 95, 352-363, 2007.
- Daniels, L.D. and Veblen, T.T.: Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia, *Ecology* 85, 1284-1296, 2004.
- Dawadi, B., Liang, E., Tian, L., Devkota, L.P. and Yao, T.: Pre-monsoon precipitation signal in tree rings of timberline *Betula utilis* in the central Himalayas, *Quatern. Int.* 283, 72-77, 2013.
- Dolezal, J., Altman, J., Vetrova, V.P. and Hara, T.: Linking two centuries of tree growth and glacier dynamics with climate changes in Kamchatka, *Clim. Change* 124, 207-220, 2014.
- Duan, K., Yao, T. and Thompson, L.G.: Response of monsoon precipitation in the Himalayas to global warming, *J. Geophys. Res. Atmosph.* (1984–2012) 111, 2006.
- Dubey, B., Yadav, R.R., Singh, J. and Chaturvedi, R.: Upward shift of Himalayan pine in western Himalaya, India, *Curr. Sci.* 85, 1135-1136, 2003.
- Dulamsuren, C., Hauck, M. and Leuschner, C.: Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia, *Global Change Biol.* 16, 3024-3035, 2010.
- Dullinger, S., Dirnböck, T. and Grabherr, G.: Modelling climate-change driven treeline shifts: Relative effects of temperature increase, dispersal and invisibility, *J. Ecol.* 92, 241-252, 2004.
- Dutta, P.K., Dutta, B.K., Das, A.K. and Sundriyal, R.C.: Alpine timberline research gap in Himalaya: A literature review, *Ind. For.* 140, 419-427, 2014.

- Elith, J., Kearney, M., and Phillips, S.: The art of modelling range-shifting species, *Methods Ecol. Evol.* 1, 330-342, 2010.
- Elliott, G.P.: Influences of 20<sup>th</sup> century warming at the upper tree line contingent on local-scale interactions: Evidence from a latitudinal gradient in the Rocky Mountains, USA, *Global Ecol. Biogeogr.* 20, 46-57, 2011.
- Engler, R., Randin, C. F., Thuiller, W. et al.: 21st century climate change threatens mountain flora unequally across Europe, *Global Change Biol.* 17, 2330-2341, 2011.
- Esper, J., Schweingruber, F.H. and Winiger, M.: 1.300 years of climate history for western central Asia inferred from tree-rings, *The Holocene* 12, 267-277, 2002.
- Esper, J., Frank, D., Wilson, R., Büntgen, U. and Treydte, K.: Uniform growth trends among central Asian low- and high-elevation juniper tree sites, *Trees* 21, 141-150, 2007.
- Fagre, D.B.: Introduction: Understanding the importance of alpine treeline ecotones in mountain ecosystems. In: Butler, D.R., Malanson, G.P., Walsh, S.J. and Fagre, D.B. (eds.): *The Changing Alpine Treeline: The Example of Glacier National Park*, pp. 1-9, Elsevier, Amsterdam, 2009.
- Fajardo, A. and McIntire, E.J.: Reversal of multicentury tree growth improvements and loss of synchrony at mountain tree lines point to changes in key drivers. *J. Ecol.* 100, 782-794, 2012.
- Fan, Z.X., Bräuning, A., Yang, B. and Cao, K.F.: Tree ring density-based summer temperature reconstruction for the central Hengduan Mountains in southern China, *Global Planet. Change* 65, 1-11, 2009.
- Flohn, H.: *Contributions to a Meteorology of the Tibetan Highlands*, Atmospheric Sciences Paper 130, Fort Collins, 1968.
- Gaire, N.P., Dhakal, Y.R., Lekhak, H.C., Bhujju, D.R. and Shah, S.K.: Dynamics of *Abies spectabilis* in relation to climate change at the treeline ecotone in Langtang National Park, Nepal *J. Sci. Technol.* 12, 220-229, 2011.
- Gaire, N.P., Koirala, M., Bhujju, D.R. and Borgaonkar, H.P.: Treeline dynamics with climate change at the central Nepal Himalaya, *Clim. Past* 10, 1277-1290, 2014.
- Gairola, S., Rawal, R.S. and Todaria, N.P.: Forest vegetation patterns along an altitudinal gradient in sub-alpine zone of west Himalaya, India, *Afr. J. Plant Sci.* 2, 42-48, 2008.
- Gehrig-Fasel, J., Guisan, A. and Zimmermann, N.E.: Tree line shifts in the Swiss Alps: Climate change or land abandonment? *J. Veg. Sci.* 18, 571-582, 2007.
- Gerlitz, L.: Using fuzzyfied regression trees for statistical downscaling and regionalization of near surface temperatures in complex terrain, *Theor. Appl. Climatol.*, accepted, 2014.
- Gerlitz, L., Conrad, O., Thomas, A. and Böhner, J.: Warming patterns over the Tibetan Plateau and adjacent lowlands derived from elevation- and bias-corrected ERA-Interim data, *Clim. Res.* 58, 235-246, 2014.
- Germino, M.J., Smith, W.K. and Resor, A.C.: Conifer seedling distribution and survival in an alpine-treeline ecotone, *Plant Ecol.* 162, 157-168, 2002.
- Ghimire, B.K. and Lekhak, H.D.: Regeneration of *Abies spectabilis* (D. Don) Mirb. in subalpine forest of upper Manang, north-central Nepal. In: Chaudhary, R.P., Aase, T.H., Vetaas, O. and Subedi, B.P. (eds.): *Local Effects of Global Changes in the Himalayas: Manang, Nepal*, pp. 139-149, Tribhuvan Univ., Nepal, Univ. of Bergen, Norway, 2007.

- Ghimire, B.K., Mainali, K.P., Lekhak, H.D., Chaudhary, R.P. and Ghimeray, A.: Regeneration of *Pinus wallichiana* A.B. Jackson in a trans-Himalayan dry valley of north-central Nepal, *Himal. J. Sci.* 6, 19-26, 2010.
- Gieger, T. and Leuschner, C.: Altitudinal change in needle water relations of *Pinus canariensis* and possible evidence of a drought-induced alpine timberline on Mt. Teide, Tenerife, *Flora* 199, 100-109, 2004.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J.L., Coldea, G., Dick, J., Erschbamer, B., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. and Grabherr, G.: Continent-wide response of mountain vegetation to climate change, *Nature Clim. Change* 2, 111-115, 2012.
- Grabherr, G., Gottfried, M. and Pauli, H.: Climate change impacts in alpine environments, *Geogr. Compass* 4, 1133-1153, 2010.
- Grace, J., Berninger, F. and Nagy, L.: Impacts of climate change on the tree line, *Ann. Bot.* 90, 537-544, 2002.
- Gratzer, G. and Rai, P.B.: Density dependent mortality versus spatial segregation in early life stages of *Abies densa* and *Rhododendron hodgsonii* in central Bhutan, *For. Ecol. Manag.* 192, 143-159, 2004.
- Gratzer, G., Rai, P.B. and Schieler, K.: Structure and regeneration dynamics of *Abies densa* forests in central Bhutan, *Centralbl. ges. Forstwes.* 119, 279-287, 2002.
- Graumlich, L.J., Waggoner, L.A. and Bunn, A.G.: Detecting global change at Alpine treeline: Coupling paleoecology with contemporary studies. In: Huber, U.M., Bugmann, H.K.M. and Reasoner, M.A. (eds.): *Global Change and Mountain Regions. An Overview of Current Knowledge*, pp. 501-508. Springer, Dordrecht, 2005.
- Harsch, M.A. and Bader, M.Y.: Treeline form – a potential key to understanding treeline dynamics, *Global Ecol. Biogeogr.* 20, 582-596, 2011.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. and Duncan, R.P.: Are treelines advancing? A global meta-analysis of treeline response to climate warming, *Ecol. Lett.* 12, 1040-1049, 2009.
- He, M., Yang, B. and Bräuning, A.: Tree growth–climate relationships of *Juniperus tibetica* along an altitudinal gradient on the southern Tibetan Plateau, *Trees* 27, 429-439, 2013.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A.: Very high resolution interpolated climate surfaces for global land areas, *Int. J. Climatol.* 25, 1965-1978, 2005.
- Hoch, G. and Körner, C.: Global patterns of mobile carbon stores in trees at the high-elevation tree line, *Global Ecol. Biogeogr.* 21, 861-871, 2012.
- Hoch, G., Popp, M. and Körner, C.: Altitudinal increase in mobile carbon pools in *Pinus cembra* suggests sink limitation in growth at the Swiss treeline, *Oikos* 98, 361-374, 2002.
- Hofgaard, A., Dalen, L. and Hytteborn, H.: Tree recruitment above the treeline and potential for climate-driven treeline change, *J. Veg. Sci.* 20, 1133-1144, 2009.
- Holtmeier, F.K.: *Mountain Timberlines. Ecology, Patchiness, and Dynamics*, Springer, Dordrecht, 2009.
- Holtmeier, F.K. and Broll, G.: Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales, *Global Ecol. Biogeogr.* 14, 395-410, 2005.

- Holtmeier, F.K. and Broll, G.: Treeline advance – driving processes and adverse factors, *Landscape Online* 1, 1-21, 2007.
- Holtmeier, F.K. and Broll, G.: Altitudinal and polar treelines in the northern hemisphere – causes and response to climate change, *Polarforschung* 79, 139-153, 2009.
- Holtmeier, F.K. and Broll, G.: Landform influences on treeline patchiness and dynamics in a changing climate, *Phys. Geogr.* 33, 403-437, 2012.
- Jain, S.K., Kumar, V. and Saharia, M.: Analysis of rainfall and temperature trends in northeast India, *Int. J. Climatol.* 33, 968–978, 2013.
- Kabeya, D.: Differentiating between the adverse effects of nutrient-limitation and direct-cold-limitation on tree growth at high altitudes, *Arct., Antarct., Alp. Res.* 42, 430-437, 2010.
- Kharuk, V.I., Ranson, K.J., Im, S.T. and Vdovin, A.S.: Spatial distribution and temporal dynamics of high-elevation forest stands in southern Siberia, *Global Ecol. Biogeogr.* 19, 822-830, 2010.
- Kohler, T., Giger, M., Hurni, H., Ott, C., Wiesmann, U., Wymann von Dach, S. and Maselli, D.: Mountains and climate change: A global concern, *Mt. Res. Dev.* 30, 53-55, 2010.
- Körner, C.: A re-assessment of high elevation treeline positions and their explanation, *Oecologia* 115, 445-459, 1998.
- Körner, C.: *Alpine Treelines. Functional Ecology of the High Elevation Tree Limits*, Springer, Basel, 2012a.
- Körner, C.: Treelines will be understood, once the functional difference between a tree and a shrub is, *Ambio* 41, 197-206, 2012b.
- Körner, C. and Paulsen, J.: A world-wide study of high altitude treeline temperatures, *J. Biogeogr.* 31, 713-732, 2004.
- Kullman, L.: Tree-limits and montane forests in the Swedish Scandes: Sensitive biomonitors of climate change and variability, *Ambio* 27, 312-321, 1998.
- Kullman, L.: Tree-limit rise and recent warming: A geoecological case study from the Swedish Scandes, *Norsk Geogr. Tidsskr.* 54, 49-59, 2000.
- Kullman, L.: Treeline population monitoring of *Pinus sylvestris* in the Swedish Scandes 1973-2005: Implications for treeline theory and climate change ecology, *J. Ecol.* 95, 41-52, 2007.
- Kullman, L.: Thermophilic tree species reinvade subalpine Sweden – early responses to anomalous late Holocene climate warming, *Arct., Antarct., Alp. Res.* 40, 104-110, 2008.
- Kullman, L. and Öberg, L.: Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: A landscape ecological perspective, *J. Ecol.* 97, 415-429, 2009.
- Kumar, P.: Assessment of impact of climate change on Rhododendrons in Sikkim Himalayas using Maxent modelling: limitations and challenges, *Biodiv. Conserv.* 21, 1251-1266, 2012.
- Laurance, W.F., Carolina Useche, D., Shoo, L.P., Herzog, S.K., Kessler, M., Escobar, F., Brehm, G., Axmacher, J.C., Chen, I.C., Gámez, L.A., Hietz, P., Fiedler, K., Pyrcz, T., Wolf, J., Merkord, C.L., Cardelus, C., Marshall, A.R., Ah-Peng, C., Aplet, G.H., Arizmendi, M.C., Baker, W.J., Barone, J., Brühl, C.A., Bussmann, R.W., Cicuzza, D., Eilu, G., Favila, M.E., Hemp, A., Hemp, C., Homeier, J., Hurtado, J., Jankowski, J., Kattán, G., Kluge, J., Krömer, T., Lees, D.C., Lehnert, M., Longino, J.T., Lovett, J., Martin, P.H., Patterson, B.D., Pearson, R.G., Peh, K.S.H., Richardson, B., Richardson, M., Samways, M.J., Senbeta, F., Smith, T.B., Utteridge, T.M.A., Watkins, J.E., Wilson, R., Williams,



- S.E. and Thomas, C.D.: Global warming, elevational ranges and the vulnerability of tropical biota, *Biol. Conserv.* 144, 548-557, 2011.
- Lescop-Sinclair, K. and Payette, S.: Recent advance of the arctic treeline along the eastern coast of Hudson Bay, *J. Ecol.* 83, 929-936, 1995.
- Liang, E., Shao, X.M. and Xu, Y.: Tree-ring evidence of recent abnormal warming on the southeast Tibetan Plateau, *Theor. Appl. Climatol.* 98, 9-18, 2009.
- Liang, E., Wang, Y., Xu, Y., Liu, B. and Shao, X.: Growth variations of *Abies georgei* var. *smithii* along altitudinal gradients in the Sygera Mts., southeastern Tibetan Plateau, *Trees* 24, 363-373, 2010.
- Liang, E., Wang, Y., Eckstein, D. and Luo, T.: Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming, *New Phytol.* 190, 760-769, 2011.
- Liang, E., Dawadi, B., Pederson, N. and Eckstein, D.: Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature? *Ecology* 95, 2453-2465, 2014.
- Liu, B., Li, Y., Eckstein, D., Zhu, L., Dawadi, B. and Liang, E.: Has an extended growing season any effect on the radial growth of Smith fir at the timberline on the southeastern Tibetan Plateau? *Trees* 27, 441-446, 2013.
- Liu, J., Qin, C. and Kang, S.: Growth response of *Sabina tibetica* to climate factors along an elevation gradient in South Tibet, *Dendrochronologia* 31, 255-265, 2013.
- Liu, X. and Chen, B.: Climatic warming in the Tibetan Plateau during recent decades, *International J. Climatol.* 20, 1729-1742, 2000.
- Lloyd, A.H.: Ecological histories from Alaskan tree lines provide insight into future change, *Ecology* 86, 1687-1695, 2005.
- Lloyd, A.H. and Fastie, C.L.: Spatial and temporal variability in the growth and climate response of treeline trees in Alaska, *Clim. Change* 52, 481-509, 2002.
- Lv, L.X. and Zhang, Q.B.: Asynchronous recruitment history of *Abies spectabilis* along an altitudinal gradient in the Mt. Everest region, *J. Plant Ecol.* 5, 147-156, 2012.
- MacDonald, G.M., Velichko, A.A. and Gattaulin, V.N.: Holocene treeline history and climate change across northern Eurasia, *Quatern. Res.* 53, 302-311, 2000.
- Maher, E.L. and Germino, M.J.: Microsite differentiation among conifer species during seedling establishment at alpine treeline, *Ecoscience* 13, 334-341, 2006.
- Malanson, G.P., Butler, D.R., Fagre, D.B., Walsh, S.J., Tomback, D.F., Daniels, L.D., Resler, L.M., Smith, W.K., Weiss, D.J., Peterson, D.L., Bunn, A.G., Hiemstra, C.A., Liptzin, D., Bourgeron, P.S., Shen, Z. and Millar, C.I.: Alpine treeline of western North America: Linking organism-to-landscape dynamics *Phys. Geogr.* 28, 378-396, 2007.
- Malanson, G.P., Resler, L.M., Bader, M.Y., Holtmeier, F.K., Butler, D.R., Weiss, D.J., Daniels, L.D. and Fagre, D.B.: Mountain treelines: a roadmap for research orientation, *Arct., Antarct., Alp. Res.* 43, 167-177, 2011.
- Maussion, F., Scherer, D., Mölg, T., Collier, E., Curio, J. and Finkelburg, R.: Precipitation seasonality and variability over the Tibetan Plateau as resolved by the High Asia reanalysis, *J. Clim.* 27, 1910-1927, 2013.
- Miehe, G.: *Langtang Himal. Flora und Vegetation als Klimazeiger und -zeugen im Himalaya. A prodromus of the vegetation ecology of the Himalayas*, Diss. Bot. 158, Berlin-Stuttgart, 1990.

- Miehe, G.: Alpine vegetation types of the central Himalaya. In: Wielgolaski, F.E. (ed.): Polar and Alpine Tundra. Ecosystems of the World 3, pp. 161-184, Elsevier, Amsterdam, 1997.
- Miehe, G.: Himalaya. In: Burga, C.A., Klötzli, F. and Grabherr, G. (eds.): Gebirge der Erde. Landschaft, Klima, Pflanzenwelt, pp. 325-359, Ulmer, Stuttgart, 2004.
- Miehe, G. and Miehe, S.: Comparative high mountain research on the treeline ecotone under human impact, *Erdkunde* 54, 34-50, 2000.
- Miehe, G., Miehe, S., Vogel, J., Co, S. and La, D.: Highest treeline in the northern hemisphere found in southern Tibet, *Mount. Res. Developm.* 27, 169-173, 2007.
- Moiseev, P.A., Bartysh, A.A. and Nagimov, Z.Y.: Climate changes and tree stand dynamics at the upper limit of their growth in the North Ural Mountains, *Russ. J. Ecol.* 41, 486-497, 2010.
- Munier, A., Hermanutz, L., Jacobs, J.D. & Lewis, K.: The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: Implications for treeline advance with climate warming, *Plant Ecol.* 210, 19-30, 2010.
- Naidu, C.V., Durgalakshmi, K., Muni Krishna, K., Ramalingeswara Rao, S., Satyanarayana, G.C., Lakshminarayana, P. and Malleswara Rao, L.: Is summer monsoon rainfall decreasing over India in the global warming era? *J. Geophys. Res.* 114:D24108, doi: 10.1029/2008JD011288, 2009.
- Negi, P.S.: Climate change, alpine treeline dynamics and associated terminology: focus on northwestern Indian Himalaya, *Trop. Ecol.* 53, 371-374, 2012.
- Ohse, B., Jansen, F., and Wilmking, M.: Do limiting factors at Alaskan treelines shift with climatic regimes? *Environ. Res. Lett.* 7, 015505 doi:10.1088/1748-9326/7/1/015505, 2012.
- Panigrahy, S., Anitha, D., Kimothi, M.M. & Singh, S.P.: Timberline change detection using topographic map and satellite imagery, *Trop. Ecol.* 51, 87-91, 2010.
- Pant, G.B., Rupa Kumar, K. and Yamashita, K.: Climatic response of *Cedrus deodara* tree-ring parameters from two sites in the western Himalaya, *Can. J. For. Res.* 30, 1127-1135, 2000.
- Paulsen, J. and Körner, C.: A climate-based model to predict potential treeline position around the globe, *Alp. Bot.* 124, 1-12, 2014.
- Paulsen, J., Weber, U.M. and Körner, C.: Tree growth near treeline: Abrupt or gradual reduction with altitude? *Arct., Antarct., Alp. Res.* 32, 14-20, 2000.
- Phillips, S.J., Anderson, R.P., Schapire, R.E.: Maximum entropy modeling of species geographic distributions, *Ecol. Model.* 190, 231-259, 2006.
- Qi, Z., Liu, H., Wu, X. and Hao, Q.: Climate-driven speedup of alpine treeline forest growth in the Tianshan Mountains, northwestern China, *Global Change Biol.* 21, 816-826, 2015.
- Rai, I.D., Bharti, R.R., Adhikari, B.S. and Rawat, G.S.: Structure and functioning of timberline vegetation in the western Himalaya: A case study. In: Wu, N., Rawat, G.S., Joshi, S., Ismail, M. and Sharma, E. (eds.): High-Altitude Rangelands and their Interfaces in the Hindu Kush Himalayas, pp. 91-107, ICIMOD, Kathmandu, 2013.
- Ram, S. and Borgaonkar, H.P.: Growth response of conifer trees from high altitude region of western Himalaya, *Curr. Sci.* 105, 225-231, 2013.
- Ram, S. and Borgaonkar, H.P.: Tree-ring analysis over western Himalaya and its long-term association with vapor pressure and potential evapotranspiration, *Dendrochronologia* 32, 32-38, 2014.

- Rawal, R.S. and Pangtey, Y.P.S.: High altitude forests with special reference to timber line in Kumaun, central Himalaya. In: Pangtey, Y.P.S. and Rawal, R.S. (eds.): High Altitudes of the Himalaya. Biogeography, Ecology & Conservation, pp. 353-399, Gyanodaya Prakashan, Nainital, 1994.
- Rawat, D.S.: Monitoring ecosystem boundaries in the Himalaya through an 'eye in the sky', *Curr. Sci.* 102, 1352-1354, 2012.
- Reasoner, M. A., and Tinner, W.: Holocene treeline fluctuations. In: Encyclopedia of Paleoclimatology and Ancient Environments, edited by Gornitz, V., Springer, Dordrecht, 442-446, 2009.
- Ren, Q.S., Yang, X.L., Cui, G.F., Wang, J.S., Huang, Y., Wei, X.H. and Li, Q.L.: Smith fir population structure and dynamics in the timberline ecotone of the Sejila Mountain, Tibet, China, *Acta Ecol. Sinica* 27, 2669-2677, 2007.
- Rössler, O., Bräuning, A. and Löffler, J.: Dynamics and driving forces of treeline fluctuation and regeneration in central Norway during the past decades, *Erdkunde* 62, 117-128, 2008.
- Rolland, C., Petitcolas, V. and Michalet, R.: Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750, *Trees* 13, 40-53, 1998.
- Romatschke, U., Medina, S. and Houze, R.A.: Regional, seasonal, and diurnal variations of extreme convection in the South Asian region, *J. Clim.* 23, 419–439, 2010.
- Roush, W., Munroe, J.S. and Fagre, D.B.: Development of a spatial analysis method using ground-based repeat photography to detect changes in the alpine treeline ecotone, Glacier National Park, Montana, U.S.A., *Arct., Antarct., Alp. Res.* 39, 297-308, 2007.
- Salzer, M.W., Hughes, M.K., Bunn, A.G. and Kipfmueller, K.F.: Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes, *Proc. Nat. Acad. Sc.* 106, 20348-20353, 2009.
- Sano, M., Furuta, F., Kobayashi, O. and Sweda, T.: Temperature variations since the mid-18th century for western Nepal, as reconstructed from tree-ring width and density of *Abies spectabilis*, *Dendrochronologia* 23, 83–92, 2005.
- Schickhoff, U.: Himalayan forest-cover changes in historical perspective. A case study in the Kaghan Valley, northern Pakistan, *Mount. Res. Developm.* 15, 3-18, 1995.
- Schickhoff, U.: Persistence and dynamics of long-lived forest stands in the Karakorum under the influence of climate and man. In: Miehe, G. and Zhang, Y. (eds.): Environmental Changes in High Asia. Proceedings of an International Symposium at the University of Marburg, *Marburger Geogr. Schr.* 135, 250-264, 2000.
- Schickhoff, U.: Die Degradierung der Gebirgswälder Nordpakistans. Faktoren, Prozesse und Wirkungszusammenhänge in einem regionalen Mensch-Umwelt-System, *Erdwiss. Forsch.* 41, Steiner Verlag, Stuttgart, 2002.
- Schickhoff, U.: The upper timberline in the Himalayas, Hindu Kush and Karakorum: A review of geographical and ecological aspects. In: Broll, G. and Keplin, B. (eds.): Mountain Ecosystems. Studies in Treeline Ecology, pp. 275-354, Springer, Berlin-Heidelberg, 2005.
- Schickhoff, U.: Dynamics of mountain ecosystems. In: Millington, A., Blumler, M. and Schickhoff, U. (eds.): Handbook of Biogeography, pp. 313-337, Sage Publ., London, 2011.

- Schmidt-Vogt, D.: High Altitude Forests in the Jugal Himal (Eastern Central Nepal). Forest Types and Human Impact. Geocol. Res. 6, Steiner Verlag, Stuttgart, 1990.
- Shen, W., Zhang, L., Liu, X. and Luo, T.: Seed-based treeline seedlings are vulnerable to freezing events in the early growing season under a warmer climate: Evidence from a reciprocal transplant experiment in the Sergyemla Mountains, southeast Tibet, Agric. For. Meteor. 187, 83-92, 2014.
- Shrestha, A.B., Wake, C.P., Mayewski, P.A. and Dibb, J.E.: Maximum temperature trends in the Himalaya and its vicinity: An analysis based on temperature records from Nepal for the period 1971-94, J. Clim. 12, 2775–2786, 1999.
- Shrestha, B.B., Ghimire, B., Lekhak, H.D. and Jha, P.K.: Regeneration of tree line birch (*Betula utilis* D.Don) forest in trans-Himalayan dry valley in central Nepal, Mt. Res. Dev. 27, 259-267, 2007.
- Shrestha, K.B.: Treeline and vegetation dynamics in response to environmental changes in Nepal, the central Himalaya. PhD Diss., Univ. of Bergen, Norway, 2013.
- Shrestha, U.B., Gautam, S. and Bawa, K.S.: Widespread climate change in the Himalayas and associated changes in local ecosystems, PLoS ONE 7, e36741, doi:10.1371/journal.pone.0036741, 2012.
- Singh, C.P., Panigrahy, S., Thapliyal, A., Kimothi, M.M., Soni, P. and Parihar, J.S.: Monitoring the alpine treeline shift in parts of the Indian Himalayas using remote sensing, Curr. Sci. 102, 559-562, 2012.
- Singh, C.P., Panigrahy, S., Parihar, J.S. and Dharaiya, N.: Modeling environmental niche of Himalayan birch and remote sensing based vicarious validation, Trop. Ecol. 54, 321-329, 2013.
- Singh, J., Park, W.K. and Yadav, R.R.: Tree-ring-based hydrological records for western Himalaya, India, since AD 1560, Clim. Dyn. 26, 295-303, 2006.
- Singh, J., and Yadav, R.R.: Tree-ring indications of recent glacier fluctuations in Gangotri, western Himalaya, India, Curr. Sci. 79, 1598-1601, 2000.
- Singh, J. and Yadav, R.R.: Spring precipitation variations over the western Himalaya, India, since A.D. 1731 as deduced from tree rings, J. Geophys. Res. 110, D01110, doi:10.1029/2004JD004855, 2005.
- Singh, J. and Yadav, R.R.: February–June temperature variability in western Himalaya, India, since AD 1455, Quatern. Int. 349, 98–104, 2014.
- Singh, J.S. and Singh, S.P.: Forests of Himalaya, Gyanodaya Prakashan, Nainital, 1992.
- Slatyer, R.O. and Noble, I.R.: Dynamics of montane treelines. In: di Castri, F. and Hansen, A.J. (eds.): Landscape Boundaries. Consequences for Biotic Diversity and Ecological Flows, pp. 346-359, Springer, New York, 1992.
- Smith, W.K., Germino, M.J., Hancock, T.E. and Johnson, D.M.: Another perspective on altitudinal limits of alpine timberlines, Tree Physiol. 23, 1101-1112, 2003.
- Smith, W.K., Germino, M.J., Johnson, D.M. and Reinhardt, K.: The altitude of alpine treeline: a bellwether of climate change effects, Bot. Rev. 75, 163-190, 2009.
- Telwala, Y., Brook, B.W., Manish, K. and Pandit, M.K.: Climate-induced elevational range shifts and increase in plant species richness in a Himalayan biodiversity epicentre, PLoS ONE 8, e57103, doi:10.1371/journal.pone.0057103, 2013.
- Theurillat, J.P. and Guisan, A.: Potential impacts of climate change on vegetation in the European Alps: A review, Clim. Change 50, 77-109, 2001.
- Tinner, W. & Theurillat, J.P.: Uppermost limit, extent, and fluctuations of the timberline and treeline ecocline in the Swiss Central Alps during the past 11,500 years, Arct., Antarct., Alp. Res. 35, 158-169, 2003.

- Villalba, R., Boninsegna, J.A., Veblen, T.T., Schmelter, A. and Rubulis, S.: Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia, *Clim. Change* 36, 425-454, 1997.
- Vittoz, P., Rulence, B., Largey, T. and Freléchoux, F.: Effects of climate and land-use change on the establishment and growth of Cembran Pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the central Swiss Alps, *Arct., Antarct., Alp. Res.* 40, 225-232, 2008.
- Wallentin, G., Tappeiner, U., Strobl, J. and Tasser, E.: Understanding alpine tree line dynamics: An individual-based model, *Ecol. Model.* 218, 235-246, 2008.
- Wang, S.Y., Yoon, J.H., Gillies, R.R. and Cho, C.: What caused the winter drought in western Nepal during recent years? *J. Clim.* 26, 8241–8256, 2013.
- Wang, T., Zhang, Q.B. and Ma, K.P.: Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China, *Global Ecol. Biogeogr.* 15, 406-415, 2006.
- Wang, Y., Camarero, J.J., Luo, T. and Liang, E.: Spatial patterns of Smith fir alpine treelines on the south-eastern Tibetan Plateau support that contingent local conditions drive recent treeline patterns, *Plant Ecol. Div.* 5, 311-321, 2012.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M. and Stephens, P.R.: Niche conservatism as an emerging principle in ecology and conservation biology, *Ecol. Lett.* 13, 1310-1324, 2010.
- Wieser, G.: Limitation by an insufficient carbon assimilation and allocation. In: Wieser, G. and Tausz, M. (eds.): *Trees at Their Upper Limit. Treeline Limitation at the Alpine Timberline*, pp. 79-129, Springer, Dordrecht, 2007.
- Wieser, G.: Lessons from the timberline ecotone in the Central Tyrolean Alps: A review. *Plant Ecol. Div.* 5, 127-139, 2012.
- Wong, M.H., Duan, C., Long, Y., Luo, Y. and Xie, G.: How will the distribution and size of subalpine *Abies georgei* forest respond to climate change? A study in Northwest Yunnan, China, *Phys. Geogr.* 31, 319–335, 2010.
- Xu, J., Grumbine, R.E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y. and Wilkes, A.: The melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods, *Conserv. Biol.* 23, 520-530, 2009.
- Yadav, R.R. and Singh, J.: Tree-ring analysis of *Taxus baccata* from the western Himalaya, India, and its dendroclimatic potential, *Tree-Ring Res.* 58, 23-29, 2002.
- Yadav, R.R., Bräuning, A. and Singh, J.: Tree ring inferred summer temperature variations over the last millennium in western Himalaya, India, *Clim. Dyn.* 36, 1545-1554, 2011.
- Yadav, R.R., Park, W.K. and Bhattacharyya, A.: Dendroclimatic reconstruction of April-May temperature fluctuations in the western Himalaya of India since A.D. 1968, *Quatern. Res.* 48, 187-191, 1997.
- Yadav, R.R., Park, W.K. and Bhattacharyya, A.: Spring-temperature variations in western Himalaya, India, as reconstructed from tree-rings: AD 1390-1987, *The Holocene* 9, 85-90, 1999.
- Yadav, R.R., Singh, J., Dubey, B. and Chaturvedi, R.: Varying strength of relationship between temperature and growth of high level fir at marginal ecosystems in western Himalaya, India, *Curr. Sci.* 86, 1152–1156, 2004.
- Yadav, R.R., Singh, J., Dubey, B. and Misra, K.G.: A 1584-year ring width chronology of juniper from Lahul, Himachal Pradesh: Prospects of developing millennia-long climate records, *Curr. Sci.* 90, 1122-1126, 2006.

- Yao, Y. and Zhang, B.: The mass elevation effect of the Tibetan Plateau and its implications for alpine treelines. *Int. J. Climatol.* 34, DOI: 10.1002/joc.4123, 2014.
- Zhang, Y., Shao, X. and Wilmking, M.: Dynamic relationships between *Picea crassifolia* growth and climate at upper treeline in the Qilian Mts., Northeast Tibetan Plateau, China, *Dendrochronologia* 29, 185-199, 2011.
- Zhu, H.F., Shao, X.M., Yin, Z.Y., Xu, P., Xu, Y. and Tian, H.: August temperature variability in the southeastern Tibetan Plateau since AD 1385 inferred from tree rings, *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 305, 84-92, 2011.
- Zurbriggen, N., Hättenschwiler, S., Frei, E.S., Hagedorn, F. and Bebi, P.: Performance of germinating tree seedlings below and above treeline in the Swiss Alps, *Plant Ecol.* 214, 385-396, 2013.

Figure captions:

Tab. 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

Tab. 2: Cumulative numbers of seedlings/saplings (N/ha<sup>-1</sup>) of *Betula utilis*, *Abies spectabilis*, *Rhododendron campanulatum*, and *Sorbus microphylla* in the treeline ecotone in Langtang Valley according to altitude and size classes (dbh = diameter at breast height)

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

Fig. 2: Altitudinal zonation of a near-natural north-facing treeline in the central Himalaya: Upper subalpine forests of *Abies spectabilis* and *Betula utilis* (leaves still unfolded) give way to *Rhododendron campanulatum* krummholz at c. 4000 m, Rolwaling, Nepal (Schickhoff, 2013-04-15)

Fig. 3: South-facing treeline with *Pinus wallichiana* and *Juniperus indica* at c. 4100 m, Manang, Nepal (Schickhoff, 2013-09-21)

Fig. 4: Seasonal temperature trends [°C/decade] 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)

Fig. 5: Anthropogenic treeline in Manang, Nepal, showing an abrupt transition to alpine grazing lands (Schickhoff, 2013-09-24)

Fig. 6: Climatic treeline (3900-4000 m) on a north-facing slope in Rolwaling, Nepal (Schwab, 2014-09-18)

Fig. 7: *Abies spectabilis* sapling at 4200 m in *Rhododendron anthopogon* dwarf scrub heath, Rolwaling, Nepal, c. 200 m above treeline (Schickhoff, 2013-08-20)

Fig. 8: 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)

Fig. 9: Spearman rank correlations between seedling/sapling abundance and soil temperature and soil moisture in the treeline ecotone in Rolwaling Valley

Fig. 10: 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)

Fig. 11: Tall saplings of *Betula utilis* (c. 2 m) growing 100-150 m above the current treeline in Langtang, Nepal (Schickhoff, 2010-07-21)

Fig. 12: Potential range shift of *Betula utilis* under novel climate conditions in AD 2070, based on ecological niche modelling