Site- and species-specific treeline responses to climatic variability in eastern Nepal Himalaya

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ABSTRACT

Alpine treelines act as bio-indicators and bio-monitors of environmental change impacts in high elevation forests. This dendro-ecological study carried out in treeline ecotones in the Sagarmatha (Mt. Everest) National Park (SNP), eastern Nepal Himalaya, aimed to assess treeline dynamics and to understand the response of treeline forming Abies spectabilis (D. Don, Mirb) and Betula utilis (D. Don) to environmental change. At three treeline sites we placed two to four belt transects (size: 20 m wide, variable length) which bisected the treeline as well as the tree species limit. The results revealed spatio-temporally heterogeneous regeneration with a higher regeneration of A. spectabilis compared to B. utilis. Warm temperatures during summer (JJA) growing seasons combined with sufficient moisture favored the growth of A. spectabilis while moisture stress during spring seasons (MAM) mainly limited the growth of B. utilis. The regeneration of A. spectabilis was favored by high temperatures throughout the year with sufficient moisture. The climatic response of the regeneration of B. utilis was spatiotemporally different and variable. Results predict a changing community structure in the treeline in response to future environmental change. During the past 200 years, A. spectabilis shifted upward by about 0.93 m/yr and B. utilis by 0.42 m/yr, with stabilization during the second half of the 20th century at the majority of the sites. The recent stability in treeline position of both species at most sites indicated that in addition to favorable climate, species-specific competitive abilities during the recruitment phase, recruitment suppression in the Krumholz and dwarf scrub belts, and grazing determine regeneration success and treeline position in the region.

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1. Introduction

Treeline is one of the most highly studied vegetation ecotones in the world because of its sensitivity towards various environmental changes (Holtmeier and Broll, 2005; Holtmeier, 2009; Köner, 2012). As most climatic treelines are shaped due to low temperature limitation (Körner and Paulson, 2004; Köner, 2012), these ecotones respond structurally, positionally, and physiognomically to climate change and, particularly in recent decades, to temperature increase (Holtmeier and Broll, 2005; Harsch et al., 2009; Köner, 2012). However, the response of the treeline to climate change not only varies spatially and temporally but also in relation to treeline form and structure (Holtmeier, 2009; Harsch and Bader, 2011). Many studies have reported changes in the recruitment phases, and in the tree density as well as a shift to the higher altitudes or latitudes in response to long-term climate fluctuation (Harsch et al., 2009; Liang et al., 2011; Kirdyanov et al., 2012; Mamet and Kershaw, 2012; Öberg and Kullman, 2012; Hofgaard et al., 2013; Aakala et al., 2014). The dendroecological approach is very useful to calculate tree establishment and assess the response of forests, including the treeline, to various aspects of environmental perturbations (Fritts and Swetnam, 1989; Wang et al., 2006; Speer, 2010; Köner, 2012).

The Himalaya is a biologically, culturally, and ecologically significant mountain system. However, the region is more sensitive and vulnerable to climate change as the rate of change is more pronounced here compared to other regions (Shrestha et al., 2012; IPCC, 2013; Qi et al., 2013), and its vulnerability is exacerbated by a fragile and young geology. Several imprints of climate change are already observed in diverse sectors (Xu et al., 2009; Shrestha et al., 2012; Bolch et al., 2012; Telwala et al., 2013; Thakuri et al., 2013).

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2. Materials and methods

2.1. Study area and climate

Situated in the northern part of Solukhumbu District in eastern Nepal, SNP (Est. = 1976, Area = 1148 km², Elevation = 2845–8848 masl) is the country’s first national park included in UNESCO’s list of World Natural Heritage Sites in 1979 due to its natural, ecological, and cultural significance (Bhuju et al., 2007). In the north, the Qomolangma National Nature Preserve of Tibet borders the SNP and it extends to the Dudh Kosi River in the south (Gaire et al., 2015). Most of the park area comprises very rugged and steep terrain cut by deep rivers and glaciers. Six vegetation zones, as described for the Nepal Himalaya by Dobremez (1975), exist within the park.

The climate in the SNP region is semi-arid with significant differences between the humid southern valleys, under major influence of the Indian summer monsoon, and the arid northern ones affected by the desiccation effects of the Himalaya range. Precipitation in most of the park is low because it lies in the rain shadow of the Karyalung-Kangtega range. More than 80% of the annual rainfall occurs in the monsoon season (June to September) with heavy snow accumulation during winter (Fig. 1a). Annual precipitation is about 1000 mm in Namche Bazar (3440 m) and it decreases with elevation to approximately 500 mm per year at Pyramid lab (5050 m).
(Fig. 1a, and Thakuri et al., 2014). Despite the fairly short and sparse meteorological records within the area, both a local-based analysis (Salerno et al., 2013) and the global CRU TS3.22 dataset (Harris et al., 2014) extracted using the KNMI climate explorer (Trouet and Oldenborgh, 2013) converge in describing a significant increase in temperature (Fig. 1b), mostly concentrated outside of the monsoon period together with a precipitation weakening (Fig. 1c) during the monsoon season.

2.2. Site-species selection, and data and sample collection

For this study, the treeline is defined as the highest elevation up to where 2 m tall trees can be found and the species limit is defined as the highest position to which seedlings, saplings or trees of the tree species are present (Gaire et al., 2011, 2014, 2015). The timberline is the upper limit of the subalpine forest (with canopy more than 30%).

Fieldwork for this study was carried out during May–June in 2012 and 2013. The treeline was explored in three sites: Dole, Phortse and Pangboche (Fig. 2). The treeline in the area was mostly composed of Abies spectabilis (hereafter only A. spectabilis) and Betula utilis (here after B. utilis) with Sorbus microphylla and R. campanulatum in the understory with some Juniperus and Salix in few places (Gaire et al., 2015). Sorbus and Rhododendron were dominant in the uppermost part of the treeline ecotone while A. spectabilis and B. utilis dominated the lower treeline and timberline regions (Fig. 2b–d). Two to four altitudinal transect plots (20 m wide and 100–190 m long according to the site and treeline position and settings) were marked out at each sites in areas where the treeline ecotones were as natural as possible (Fig. 2a). The plots were oriented vertically with their longer axis parallel to the maximum slope and covered the current species limit and treeline ecotone (Fig. 2b). The transect plots at Dole, Phortse and Pangboche treelines were named as D1 and D2, PH1 and PH2, and P1–P4, respectively. The study was mainly centered on northeast, northwest, and north facing slopes. Individual plants were categorized and enumerated into three height classes: trees (>2 m), saplings (0.5–2 m), and seedlings (<0.5 m) (Wang et al., 2006; Gaire et al., 2011, 2014, 2015).

For every individual, size (diameter at base [DB], diameter at breast height [DBH], and height), growth form, and species were recorded. To calculate the age of tree individuals, one or two cores per tree were collected at the stem base from the A. spectabilis and B. utilis trees. Additional cores were collected from larger trees at breast height to assess growth-climate responses. More than 350 tree cores were collected.

The ages of trees were calculated by tree core analysis, while those of seedlings and saplings of A. spectabilis were estimated by counting the branch whorls and scars left along the main stem (Camarero and Gutiérrez, 2004; Wang et al., 2006; Liang et al., 2011; Gaire et al., 2014). Studies have shown that the whorl count method gives an accurate indication of the age of saplings and seedlings of A. spectabilis (Gaire et al., 2014; Chhetri and Cairns, 2015).

2.3. Population demography, regeneration, and treeline dynamics

The age obtained after crossdating was used for population demographic analysis after the necessary correction for years to core height and years to center of missed pith (Speer, 2010). Such correction was made using age-height and age-diameter regression combined with the fitting of a circle template to the ring curvature at Phortse (f); recent regeneration of Abies spectabilis at the lower reaches of the treeline ecotone at Pangboche (g–h). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
so as to estimate the distance of the core to the center (Camarero and Gutiérrez, 2004; Batllori and Gutiérrez, 2008; Speer, 2010). For B. utilis, a regression analysis model between diameter at base (DB) and age was established (Age = 3.6102 × DB + 2.1; R² = 0.82, n = 65, p < 0.0001) incorporating cores from representative sample trees spanning different DB classes. The ages of all B. utilis individuals from which cores were not taken was estimated based on this model.

The regeneration condition was determined by observing size class distribution (Wangda and Ohsawa, 2006; Körner, 2012; Lv and Zhang, 2012) using a number of seedlings, saplings and trees individuals. Age histograms of the species were produced dividing them into their corresponding calendar year classes (10-year bin). Two sample Kolmogorov-Smirnov tests were carried out to determine the difference in temporal recruitment patterns between different species and sites. Treecline dynamics were analyzed by assessing the spatio-temporal distributions of tree, sapling, and seedling density as well as the elevation-wide age distribution. The upper species limit (treecline) expansion was studied by observing the age of each individual in the entire plot following Camarero and Gutiérrez (2004), Kirdyanov et al. (2012) and Gaire et al. (2014). In order to calculate the rate of treecline/species-limit shift, the maximum elevation of live individuals and the position of the oldest individual within each transect were determined. Then, the treeline or species limit shift rate (m/yr) was calculated by dividing the change in elevation (position) of the species limit by the time elapsed.

2.4. Tree cores analysis and chronology development

Core samples were prepared and analyzed using standard dendrochronological techniques (Fritts, 1976; Cook and Kairiukstis, 1990; Speer, 2010). All cores were air-dried and mounted on grooved sticks, sanded and polished using successively finer grits of sand paper to expose ring details to the cellular level. After carefully examining these samples under the microscope, each ring was counted and dated. Total ring width was measured to the nearest 0.01 mm with a LINTAB® measuring system attached to a PC running TSAP-win software (Rinn, 2003). Crossdating was done using the alignment plotting technique in TSAP and by examining the chronology statistics (Rinn, 2003). Accuracy of crossdating and measurements were further checked using the COFECHA program (Holmes, 1983; Grissino-Mayer, 2001). Out of 5873 rings of B. utilis analyzed, 0.22% rings were missing from the tree ring series. Most of the absent rings were from the years of 2004 and 1999 with one each from 1992 and 1926. As we removed problematic samples, missing rings from the A. spectabilis tree ring series was found to be very rare. Cores that correlated poorly in COFECHA or were very young (less than 50 yrs old) were removed from the final data set prior to chronology development. Tree-ring width chronologies were developed using ARSTAN (Cook, 1985; LDEO, 2015). The standardization using ARSTAN removes both the geometric and other growth trends resulting from tree-to-tree competition and stand dynamics while preserving variability likely related to climate. We performed double detrending for B. utilis, first using a negative exponential curve and then using cubic smoothing splines curves of 20 years. For A. spectabilis, both double and interactive detrendings were tried. Interactive detrending using negative exponential, linear trends or a spline of 20 yrs. preserved more of the common signal. After detrending, individual time series were averaged using a bi-weight robust mean function (Cook, 1985). Chronology quality was estimated using rbar (Briffa, 1995) and expressed population signal statistics (Wigley et al., 1984). After checking for correlation, cores of each species from all sites were pooled together to make a composite chronology for each species.

2.5. Climate influence on tree growth and regeneration

The relationships between the tree-ring width residual chronology of each species and monthly average temperatures and total precipitation were analyzed by correlation functions for the period of 1901–2011 in the CRU gridded dataset TS3.22 and 1961–2011 for instrumental data using DendroClim2002 (Biondi and Waikul, 2004). As climate in the preceding growing season often influences tree growth during the following year (Fritts, 1976), we considered temperatures and precipitation data from June of the previous growth year until October of the current growth year.

To investigate the relationship between regeneration and climate, age data were first summed across five-year intervals to take into account uncertainties in age estimates (Wang et al., 2006; Gaire et al., 2014; Chhetri and Cairns, 2015) and then compared with monthly climate records compiled into five-year averages over the same period. Monthly climatic records (mean temperature and total precipitation) from the CRU gridded dataset (1901–1911) and precipitation data (1961–2011) from Chaurikharka station were used. Climate factors limiting regeneration were identified from simple linear correlation analysis between regeneration and climatic data.

3. Results and discussion

3.1. Population age structure

Population age structures of both species revealed temporal variation in regeneration and mortality rates. In some plots, the recruitment history extends back to the early eighteenth century, but most treeline ecotones experienced recruitment pulses during the early to middle of the 20th century (Fig. 3). The age class distributions of A. spectabilis populations revealed sporadic to continuous regeneration depending on the site. Age class distributions at Pangboche showed a slight peak in regeneration during the 1920s, 1940s and in recent decades (Fig. 3). Young individuals recruited after 1950s dominated the total population of A. spectabilis at Pangboche with 2001–2010 class being the dominant age class. However, the age histories of A. spectabilis at Phortse and Dole only goes back to the 1970s and 1950s, respectively, indicating that the treeline populations of these two sites are formed by very young individuals (Fig. 3).

Similarly, the population age of B. utilis at Pangboche extends to the 1830s having a sporadic age class distribution with a small peak in 1940s (Fig. 3). After that, the regeneration of B. utilis decreases. There were very few young individuals in the total population. The age history of B. utilis at Phortse only goes back to the 1890s. However, the upper treeline (PH1) plot population consisted of individuals all younger than 100 yrs (Fig. 3). The age class distribution at Phortse is slightly unimodal bell shaped with a peak in the 1960s, after which establishment is decreases steadily. The recruitment pattern of B. utilis at Dole is sporadic in nature with no single regeneration peak. Similar young age histories of the treeline forming species are reported from other treeline sites in eastern and western parts of the Nepal Himalaya. In spite of differences in plot level comparison, increased recent regeneration of A. spectabilis at the treeline ecotone is a common finding of treeline research from the Nepal Himalaya (e.g. at Manang (Ghimire and Lekhak, 2007); Manaslu Conservation Area (Gaire et al., 2014); Langtang National Park (Gaire et al., 2011; Schickhoff et al., 2015; Shrestha et al., 2015); Rolwaling Valley, Gaurishankar Conservation Area (Schickhoff et al., 2015); Makalu-Barun National Park (Chhetri and Cairns, 2015); and the Tibetan side of the Everest region (Lv and Zhang, 2012)).
Fig. 3. Age class distribution of *Abies spectabilis* and *Betula utilis* in the treelines of the Sagarmatha National Park, Nepal Himalaya. Here, the normal 10-year age class histograms are first converted into their corresponding calendar year classes, and then shown in calendar years to reveal the temporal distribution of population demography.

3.2. Regeneration and treeline dynamics

*B. utilis* colonized most plots earlier than *A. spectabilis* (Fig. 4a). At most plots and sites, size parameters (age, diameter and height) decreased with increasing elevation. However, there is evidence of site and species-specific regeneration dynamics (Fig. 4a and b). The Kolmogorov-Smirnov test reveals a significant difference in temporal pattern of recruitment between different sites and species ($\alpha = 0.05$). Similarly, there was a significant difference in intra-site (between species) temporal patterns of recruitment for the majority of sites ($\alpha = 0.05$). Rather poor regeneration of *A. spectabilis* is present in the upper part of most of the treeline sites (except Dole) while the opposite was found moving down towards the timberline (Fig. 4b). Poor regeneration of *B. utilis* in the most recent 20–30 years is prevalent at all sites (Fig. 4b). The presence of seedlings and saplings of *A. spectabilis* in the lower reaches of the plots towards timberline or forest line (Fig. 4b) indicates stand densification and infilling of existing treelines. In the treeline ecotones of the Kalchum Lake area of Manaslu Conservation Area (Gaire et al., 2014) and in Makalu-Barun National Park (Chhetri and Cairns, 2015), there was a dominance of seedlings and saplings near the timberline rather than the upper treeline. Shrestha et al. (2015), however, found seedlings abundant above the mean treeline in Langtang National Park. Lv and Zhang (2012) found a significant recruitment of *A. spectabilis* in the last three decades and sporadic recruitment in earlier periods in the treeline of the Tibetan side of the Mt. Everest.

Similar to the observations by Gaire et al. (2014) and Shrestha et al. (2007), *B. utilis* formed an abrupt treeline boundary, where tree individuals formed the upper limit instead of seedlings and saplings. We found almost a stable treeline since the second half of the 20th century with a poor recruitment. In contrast to this work, some studies from the treeline of Nepal (Shrestha et al., 2007; Schickhoff et al., 2015) and the Indian Himalaya (Rai et al., 2012) found good regeneration of *B. utilis*, e.g. in the treeline of Rolwaling Valley, Gaurishankar Conservation Area with seedling establishment of *A. spectabilis*, *B. utilis*, and *Sorbus microphylla* extending far above the upper limit of adult trees (Schickhoff et al., 2015).

At most of the studied sites, there were species- and site-specific shifting patterns with little treeline shifting in more recent years (Table 1). The average rate of upward shifting of *A. spectabilis* was 0.93 m/yr and *B. utilis* 0.42 m/yr, with recent stabilization at the majority of sites. Irrespective of plots, the average rate of treeline shifting of *A. spectabilis* at Pangboche since the 1830s was estimated to be 0.7 m/yr with a stagnant position since the 1970s. There is a very dynamic nature of *A. spectabilis* treeline at Dole with the presence of only seedlings and saplings in the D2 (>160 m long) plot and seedlings and saplings above tree individuals in the D1 plot. The upward shifting of the *B. utilis* treeline since the 1830s at Pangboche was 0.38 m/yr with no upward treeline shifting since the 1950s. The upward shifting at Phortse was slightly greater than at Pangboche; the *B. utilis* treeline at Dole has shifted very little over the past ~200 yrs with almost complete stabilization in recent years (Fig. 4 and Table 1).

Treeline shift in response to climate change, though not uniform and universal, is widely observed throughout the world. The shifting observed in the present study is consistent with other studies in the Himalaya, e.g. *P. wallichiana* in western Himalaya, India (Dubey et al., 2003), *A. spectabilis* and *B. utilis* in Manaslu Conservation Area, Nepal (Gaire et al., 2014), *A. spectabilis* in Barun valley, eastern Nepal (Chhetri and Cairns, 2015). During the last six decades, Shrestha et al. (2015) found the *A. spectabilis* treeline in Langtang and Pine treeline in Manang, central Nepal to be stationary. Available investigations, using remote-sensing and repeat photography data, have reported increasing density as well as an upward shifting of the treeline ecotone in Indian Himalaya (Panigrahy et al., 2010; Bharti et al., 2012; Rawat, 2012; Singh et al., 2012, 2013); however, such
study is lacking in our area. Schickhoff et al. (2015) and Schwab et al. (2015) reported many species limit of the treeline forming species within a treeline ecotone, indicating complexity in assessing the treeline dynamics. Present field based study, focusing mainly on A. spectabilis and B. utilis and not considering Krummholz and shrubby Rhododendron species, found stable treeline in most of the study sites in recent few decades. Therefore, upward treeline shifting with environmental (climate) change in the Himalayas is not a unidirectional response, but it varies depending upon the climatic history of the area involved, site and species included as well as with scale and approach of the analysis. In spite of shifting until mid-20th century, treelines in Tibet and other mountainous regions in China have shifted very little in recent years (Wang et al., 2006; Liang et al., 2011; Gou et al., 2012; Lv and Zhang, 2012). Several studies from mountain systems in Europe and America have also reported an increase in tree density, and shifting of the treeline to higher elevation or latitude in response to global warming (Camarero and Gutiérrez, 2004; Danby and Hik, 2006; Batllori and Gutiérrez, 2008; Kullman and Öberg, 2009; Harsch et al., 2009; Bogart et al., 2011;
Table 1
Trelline or species limit shifting in the treeline ecotones of the Sagarmatha National Park, Nepal Himalaya.

<table>
<thead>
<tr>
<th>Abies spectabilis</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sites</td>
<td>Oldest age (yr)</td>
<td>Youngest age (yr)</td>
</tr>
<tr>
<td>Pangboche</td>
<td>181</td>
<td>50</td>
</tr>
<tr>
<td>Phortse</td>
<td>53</td>
<td>14</td>
</tr>
<tr>
<td>Dole</td>
<td>65</td>
<td>14</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Betula utilis</td>
<td>183</td>
<td>70</td>
</tr>
<tr>
<td>Phortse</td>
<td>126</td>
<td>25</td>
</tr>
<tr>
<td>Dole</td>
<td>271</td>
<td>126</td>
</tr>
<tr>
<td>Average</td>
<td></td>
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Kirdyanov et al., 2012; Mamet and Kershaw, 2012; Kharuk et al., 2013; Hofgaard et al., 2013; Aakala et al., 2014.

3.2. Tree-ring chronologies

Based on ring-width analysis, ring-width site chronologies (one each) for *A. spectabilis* and *B. utilis* were prepared (Fig. 5). The site chronology of *A. spectabilis* extended from 1838 to 2012, and that for *B. utilis* from 1831 to 2012. The chronology statistics (Table 2) show the dendroclimatic potential of these chronologies (Fritts, 1976; Cook and Kairiukstis, 1990; Speer, 2010). The chronologies of the two species were significantly positively correlated ($r = 0.32–0.57$, $p < 0.05$) during the time span covered by CRU data (1901–2011) as well as for the common period covered by most of the tree-ring series (1940–2007), indicating common climatic signals captured by the chronologies. The chronologies of *A. spectabilis* and *B. utilis* did not show a consistent pattern of growth enhancement in the chronology; rather both fluctuate over time. However, some previous studies have reported consistent tree growth in response to recent climate warming in the Himalayas (e.g. Borgaonkar et al., 2011).

3.4. Climatic response of tree growth and regeneration

Trellines show different structural and physiognomic responses to climate change at different spatio-temporal scales (Holtmeier and Broll, 2005; Holtmeier, 2009; Körner, 2012). The sensitivity and response of the treelines to climate change not only varies with local and regional topographical conditions but also with treeline forms (Holtmeier and Broll, 2005; Harsch and Bader, 2011).

Consistent with global and regional patterns of treelines response, the radial growth of *A. spectabilis* growing in the treelines of SNP is limited mainly by low temperatures during the summer (JJA) growing season. There was a significant positive relationship with the average monthly temperature for August ($p < 0.05$) and the average seasonal temperature of the summer (JJA: $p < 0.05$) months (Fig. 6a). The autumn temperature during the pre-growth year also has a positive relationship with the radial growth. The response with the winter temperature may be linked with the processes like winter embolism, freezing stress, winter desiccation, etc. (Pederson et al., 2004; Fan et al., 2009; Körner, 2012; He et al., 2013). The conifers can have a positive carbon gain on warm winter days when their leaves are not frozen (Pederson et al., 2004). In the absence of adequate snow cover, low winter–season temperatures may cause freezing injury and fine roots mortality due to frost penetration, while a deep snow pack in late winter can reduce radial growth rates by maintaining low soil temperatures and delaying initiation of cambial expansion (Pederson et al., 2004; He et al., 2013). Correlations between climate and growth of *A. spectabilis* near the treeline in western (Sano et al., 2005) and central Nepal (Gaire et al., 2011; Kharal et al., 2014) were negative with spring season (MAM) temperature and positive with the same month’s precipitation. Climate systems in the western part of Nepal differ slightly from those in the eastern part and may account for variations in response. Yadav et al. (2004) not only reported significantly negative correlations between ring width chronologies of *A. spectabilis* from treelines in Himachal Pradesh and Uttarakhand, India and long-term pre-monsoon temperature but also a weakening temperature signal in recent years.

In spite of significant positive correlation between the ring-width chronologies of the two species, their climatic response in month-to-month comparison differs (Fig. 6a and b). Differences in temperature and moisture sensitivity between the conifer and broad-leaved tree species may be associated with their contrasting phenology and physiological traits (Pederson et al., 2004; Körner, 2012). The correlation function analysis revealed that there was a significant positive relationship ($p < 0.05$) between the radial growth of *B. utilis* and monthly precipitation during the previous October, current March and May, and with spring season (MAM) precipitation, while a significant ($p < 0.05$) negative relationship with temperature exists for the same season (Fig. 6b). This indicates that radial growth of *B. utilis* at the treeline of SNP was mainly limited by temperature induced moisture stress during the spring season. During spring, temperature increases rapidly and precipitation becomes insufficient to meet evapotranspiration demand. The response we obtained is consistent with other studies carried out in treeline-forming *Betula* species (Bräuning, 2004 Takahashi et al., 2005; Bhattacharyya et al., 2006; Dawadi et al., 2013; Wang et al., 2013; Liang et al., 2014). Reduced pre-monsoon moisture availability is a primary growth-limiting factor for *B. utilis* at many timberline sites (Sagarmatha, Langtang and Manaslu) of the Nepal Himalaya with a high percentage of missing rings or narrow rings coinciding with years that are dry and warm in the pre-monsoon
season (Liang et al., 2014). Bhattacharyya et al. (2006) reported that higher temperatures and less rainfall during pre-monsoon months result in lower tree growth of B. utilis.

The growth response of treeline-forming trees to climate change in the Himalaya is spatiotemporally different, and species-specific (Bhattacharyya and Chaudhary, 2003; Yadav et al., 2004; Sano et al., 2005; Bhattacharyya et al., 2006; Gaire et al., 2011, 2014; Lv and Zhang, 2012; Dawadi et al., 2013; Liang et al., 2014). Studies also report that radial growth of treeline conifers is more responsive to temperature than precipitation (Bräuning, 2004; Sano et al., 2005; Bhattacharyya and Shah, 2009; Borgaonkar et al., 2011; Gaire et al., 2011, 2014; Schickhoff et al., 2015).

In treeline ecotones, the climate conditions that facilitate radial growth may be similar to those conducing to recruitment (Dang et al., 2009; Lv and Zhang, 2012; Zhao et al., 2013), or the processes of recruitment and growth may respond differently to climatic factors (Daniels and Veblen, 2004; Wang et al., 2006). In the present study, the climatic factor that limits or favors radial growth of A. spectabilis and B. utilis were not perfectly same as that for regeneration of the same species, however, differences exist in month-to-month comparisons and site-to-site comparisons (Figs. 6 and 7). The different details in the response among the sites may be associated with the influence of local topographic conditions and/or tree age (Carrer and Urbinati, 2004; Wang et al., 2009; Mérian and Lebourgeois, 2011).

The regeneration-climate relationship is species-specific as well as site-dependent (Fig. 7). The regeneration of A. spectabilis was favored by high temperatures in both winter and summer provided there was no moisture limitation. There is a significant positive relationship (p < 0.01–0.05) between the regeneration of A. spectabilis at Pangboche and monthly average temperature in most of the months and monthly precipitation in March (Fig. 7a). An almost identical response was obtained between the regeneration of A. spectabilis at Dole–Phortse and climate (Fig. 7b). However, month-to-month comparisons exhibit some variations in response between sites that may be associated with variations in topography and other feedback mechanisms. Studies have reported the sensitivity of Abies recruitments with temperature, moisture, and/or drought conditions (Liang et al., 2011; Lv and Zhang, 2012; Gaire et al., 2014). A. spectabilis recruitment was positively correlated with monthly mean air temperature in June and September and with Palmer Drought Severity Index (PDSI) in June at timberline on the Tibetan side of the Everest region (Lv and Zhang, 2012). In the treelines of the Manaslu region, central Nepal, regeneration of A. spectabilis is favored by high temperature throughout the year together with sufficient moisture during the summer season (Gaire et al., 2014). Consistent with our study (Fig. 7a and b), A. georgei var. smithii recruitment in a treeline on the southeastern Tibetan Plateau was sensitive to both summer and winter temperatures with a significant positive correlation (Liang et al., 2011). From a transplant experiment in a treeline ecotone in SE Tibet, Shen et al. (2014) demonstrated that early growing-season freezing events determine the annual mortality of A. georgei seedlings above the treeline.

The regeneration-climate relationship of B. utilis is spatiotemporally differentiated (Fig. 7c–f). Up until 1990s to which time establishment of B. utilis was found, high average monthly temperatures and precipitation during the summer and autumn months favored the regeneration at Pangboche, with a significant positive relationship (p < 0.05) between regeneration and monthly mean temperatures of July to October (Fig. 7d). The lack of recently established seedlings and saplings of B. utilis in treelines weak-
ens the relationship with climate parameters when we consider the entire period covered by CRU climatic data (1901–2011). In contrast to Pangboche, the regeneration at Dole was negatively influenced (p < 0.05) by high monthly mean temperatures in July. In the study area, there is a consistent increasing of temperature and weakening of precipitation, with high intra-annual variability (Salerno et al., 2013). In spite of the warmer climate, moisture stress due to weakening precipitation might limit new seedling and sapling establishment. Schickhoff et al. (2015) found significant positive correlations of seedling and sapling abundance with soil moisture for A. spectabilis, B. utilis, and R. campanulatum, and with soil temperature for A. spectabilis, B. utilis, and Sorbus. Some of the spatial difference and weak regeneration-climate response of B. utilis may be explained by temporal changes in sensitivity, uncertainties in age estimation using regression models, or influences of non-climatic abiotic and biotic factors on regeneration of birch seedlings.

In common with worldwide responses (Körner and Paulsen, 2004; Körner, 2012), temperature is the dominant climatic factors controlling regeneration, growth and dynamics in the studied treelines in the SNP region. Sustained and favorable climatic conditions during establishment, and particularly during recruitment, are crucial for controlling treeline dynamics (Wang et al., 2006; Mamet and Kershaw, 2012) as one poor year is sufficient to kill regeneration established over many favorable years. However, warming temperatures may not necessarily lead to unidirectional changes in treeline position as the direct influence of temperature may be countered by interactions with other factors such as precipitation, cold-induced photo-inhibition, disturbance, or plant–plant interactions (Bekker, 2005; Danby and Hik, 2007; Munier et al., 2012; Speed et al., 2011; Körner, 2012; Schickhoff et al., 2015). In comparison to B. utilis, growth and regeneration of A. spectabilis is more sensitive to temperature than precipitation. The high regeneration of seedlings and saplings of A. spectabilis in the lower reaches of the treeline towards the timberline can be explained by the significant positive relationship between regeneration and climate. We found very few seedlings and saplings of A. spectabilis and B. utilis in the upper reaches of the plots near the tree species limits with recently stabilized treeline position of A. spectabilis at two sites and B. utilis at all sites. Lack of seed dispersal is not limiting for recent treeline

Fig. 6. Correlation (Pearson’s correlation) between radial growth (Ring width residual chronology) of Abies spectabilis and Betula utilis and monthly climate data in the study area of the Sagarmatha National Park, Nepal Himalaya. The horizontal dashed line indicates the 95% significant threshold. The pl to pD indicates June to December of the previous year and J to O indicates months of current year starting from January and ending at October; DJF, MAM and JJA represents the seasonal average climate of winter (December to February), spring (March to May) and summer (June to August), respectively.
shifts; some seedlings and saplings were found to be growing up to several meters above the tree individuals in the present study and in other treeline areas of Nepal Himalaya (Gaire et al., 2011, 2014; Schickhoff et al., 2015; Shrestha et al., 2015).

The regions at and above the treeline are commonly used as summer grazing area in the Himalaya. In addition to weakening precipitation with increasing interannual variability, non-climatic factors such as micro-topography, the competition with dense Krummholz *Rhododendron* trees and shrubs, herbivory, and the competitive ability of treeline forming species might be moderating the beneficial impacts of temperature warming, and ultimately controlling recent seedling establishment and treeline shift (Shrestha et al., 2007, 2015; Munier et al., 2012; Rai et al., 2012; Wang et al., 2012; Zhao et al., 2013; Chhetri and Cairns, 2015; Schickhoff et al., 2015; Schwab et al., 2015). Shrestha et al. (2007) observed that there was a lack of treeline shift of *B. utilis* in trans-Himalaya, Manang due to anthropogenic pressure. Shrestha et al. (2015) suggested that the stationary *A. spectabilis* treeline, even given warming temperatures in the Langtang area, is regulated by non-climatic factors, particularly grazing. Schickhoff et al. (2015) found a negative correlation between the abundance and density of *R. campylanatum* and the recruitment of other tree species, due to competition with the dense foliage of evergreen Rhododendron as well as a probable allelopathic effect. In spite of favorable cli-
mate, the dense Krummholz belt can be an effective barrier for up slope migration of other tree species (Schickhoff et al., 2015; Schwab et al., 2015).

Liang et al. (2014) concluded that birch (B. utilis) treelines of Himalayas are drought-induced alpine timbers lines and that this species is increasingly at risk of survival. We are skeptical of this conclusion. We argue that their categorization of birch treelines was hasty as they mainly sampled at dry sites and did not consider the population demography of the species. Though moisture stress during the spring season affects growth, we (field observation by NP Gaire) found a large number of recently recruiting B. utilis seedlings and saplings above the tree individuals in the treelines of Kanchenjunga Conservation Area, eastern Nepal and fair regeneration at the timberline at other sites in mid- and far-western Nepal. These areas have been experiencing an increasing trend in average annual temperature but no significant trend in annual precipitation with some stations depicting slightly increasing while some decreasing pattern. Comparing with findings of several studies and considering discrepancies in the results, we propose further comprehensive study incorporating, in addition to climatic factors, grazing inclusion-exclusion and transplantation experiments, masting in seed production, testing of growth or carbon limitation in treeline formation for better understanding of the response of treelines and their dynamics to climate change.

4. Conclusions

We assessed treeline dynamics during the past ~200 years in the Sagarmatha National Park, in eastern Nepal Himalaya. The study found the existence of heterogeneous regeneration and tree-line dynamics with recent stable treeline position at most sites. Broadly, warm temperature during the growing season together with sufficient moisture favored the growth of A. spectabilis while moisture stress during the spring season limited the growth of B. utilis. The climatic response of regeneration in the treelines was species-specific as well as site dependent. High winter and summer temperatures favored regeneration of A. spectabilis while the relationship between climatic parameters and regeneration in case of B. utilis was spatio-temporally unstable. In spite of a warming climate, we found poor recent regeneration in the upper reaches of the treeline ecotone. This indicates that along with favorable climate, site dependent abiotic factors, age dependent species-specific competitive abilities with Krummholz and dwarf scrub belts during the recruitment phase, and intensity of grazing will determine future treeline dynamics in the region.

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References


Studies of tree-ring dating and 
more precise dating of ice 
and glacier records have 
shown that 
early Holocene 
climates were 
warmer than today,

but the full extent of these changes and their 
relationship to past 
changes in 
climate is not yet fully understood. 
However, there is 
some evidence for 
periods of 
warmer-than-present 
climates in Central Asia during 
the Holocene, particularly in 
the late Holocene (Veit et al. 2003). 

5.1. Climate and 
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Variation

High-elevation 
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In the Qilian 
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