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Warming induced growth decline of Himalayan birch at its lower range edge in a semi-arid region of Trans-Himalaya, central Nepal.

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Abstract

Changes in the position of altitudinal treelines and timberlines are considered useful indicators of climatic changes on tree growth and forest dynamics. We sought to determine if recent warming is driving contrasting growth responses of Himalayan birch, at moist treeline (Lete Lekh) and semi-arid timberline (Chimang Lekh) sites in the Trans-Himalayan zone of central Nepal. We used dendrochronological techniques to measure tree ring width (TRW) and basal area increment (BAI) of birch trees from climatically contrasting but nearby sites. The TRW series were correlated with climate records from nearby meteorological stations, and BAI was compared between populations to explore growth trends over recent decades. We found contrasting precipitation trends between nearby sites such that the wet site (Lete) is getting warmer and wetter, and the dry site (Chimang) is getting warmer and drier in recent decades. The radial growth of birch in both moist and semi arid sites are positively correlated to spring (March-May) rainfall, and negatively

correlated to mean and maximum temperature for the same period. The growth climate analysis indicated that moisture availability in early growing season is crucial for birch growth at these locations. The BAI of birch is declining more rapidly at the dry timberline than at the moist treelines in the recent decades, indicating that climatic warming might negatively impact birch radial growth where warming interacts with increasing spring drought in the region. Our work highlights contrasting growth response of birch to climate change at moist and semi-arid forests indicating that local climatic variation must be accounted for when assessing and forecasting regional patterns of tree growth in topographically complex regions like Trans-Himalaya, in order to make accurate predictions of vegetation responses to climate change.

Keywords: *Betula utilis*; treeline; timberline; ring-width; basal area increment; growth trends

Introduction

Mountains provide habitats for a large portion of the world's biodiversity (Beniston 2003). High mountain species are potentially most threatened under ongoing climate change because of their narrow distribution range, geographical isolation and unique ecological adaptations (Grabherr et al. 1994; La Sorte and Jetz 2010). Besides being susceptible to the impacts of a rapidly changing climate (Xu et al. 2009; Sharma and Tsering 2009; Aryal et al. 2012), mountains also provide valuable locations for the early detection of climatic change and its impacts on ecological and hydrological systems (Beniston 2003; Nogués-Bravo et al. 2007).

Temperature is usually the main limiting factor for tree growth in poleward and high altitude treelines (Körner 2003; Holtmeier & Broll 2007; Harsch et al. 2009). Air and soil temperatures as well as topographic sheltering are important determinants of spatial patterns of tree seedling establishment at high altitude (Greenwood et al. 2014). Trees are, therefore, expected to increase growth and shift poleward and upward with warming temperatures and increased atmospheric CO₂ concentration (Körner 2000; Borgaonkar et al. 2011; Gaire et al. 2014, 2016). However, this expectation only holds true if there are no other factors limiting growth at species distributional limits in these regions. Tree growth in high mountains could also be impaired by increases in temperature, mostly due to warming-induced water deficit (Cook et al. 2003; Sano et al. 2005; Lv and Zhang 2012; Yang et al. 2013; Dawadi et al. 2013; Liang et al. 2014; Qi et al. 2015; Tiwari et al. 2016; Gaire et al. 2016). Furthermore, in topographically complex regions such as the

55 Trans-Himalayan zone of Nepal, rain shadow effects can lead to strong gradients of precipitation and drought stress over
56 short distances, resulting in contrasting local limitations of tree growth and complicating prediction of regional changes
57 (Schickhoff 2005; Schickhoff et al. 2015).

58 Tree ring-width indices have proved to be useful proxies for growth climate interpretation, however, detrended
59 ring-width series retains less ecological and historical information such as forest disturbance, acute growth stress and
60 other low frequency signals (Esper et al. 2002). Hence unstandardized basal area increment (BAI) is often used as a more
61 informative measure of tree growth trends in terms of total biomass production, than ring width measurements alone
62 (Phipps & Whiton 1988; Peñuelas et al. 2011). Climatic warming, increased concentration of atmospheric CO₂ and
63 associated changes to water-use efficiency, are predicted to enhance tree growth across many species and regions
64 (Morison, 1993; Morgan et al. 2004; Norby et al. 2005). However such anticipated positive growth trends have not been
65 observed in many parts of the world (Peñuelas et al. 2011). Rather, tree growth has locally declined, with the potential
66 for increasing levels of mortality due to warming induced drought (Jump et al. 2006; Peñuelas et al. 2007; Allen et al.
67 2010). Hence, quantifying interannual responses of tree growth to local variation in climate is an important approach to
68 understand tree growth patterns and forest productivity (Bunn et al. 2005; Yang et al. 2010) in climate sensitive high
69 elevation forests.

70 Himalayan birch (*Betula utilis*) typically forms the treeline in many parts of Himalaya (Miehe et al. 2015), but
71 its growth across the various climatic zones and complex topography of central Nepal is poorly explored. The treeline is
72 generally considered as the highest elevation at which a single upright tree with height greater than 2 m is found over the
73 landscape (Hofgaard, 1997; Körner, 2003), and alpine timberlines represent the upper limit of closed mountain forest
74 with tree density (trees >5 m tall) of at least 30% coverage (Wardle, 1974; Holtmeier, 2003). Trees typically show
75 contrasting growth responses to warming temperatures at their upper and lower range edges (Peñuelas et al. 2008; Cavin
76 et al. 2016). However, differences in water availability might strongly modify expected responses to temperature.
77 Consequently, we sought to determine the response of birch growth at its upper and lower range edge in high mountain
78 forests which are subject to a contrasting moisture regime. Consequently, we set out to test expectations that the birch
79 treeline should advance in areas with greater water availability (Schickhoff et al. 2015), and retreat in dry sites (Liang et
80 al. 2014) despite general predictions of upward elevational shifts of mountain forest distributions (Harsch et al. 2009).
81 Improving our understanding of local climate variability and its impact on tree growth and forest productivity is of high
82 importance for our ability to predict spatial patterns of forest change and their consequences. Consequently, here we

83 hypothesized that elevated temperatures would have a greater negative impact on tree growth in dry versus wet high
84 altitude sites for *B. utilis*. We used tree ring records of *B. utilis* from contrasting climatic zones in the Trans-Himalayan
85 region to (1) determine the limiting climatic factors for growth of *B. utilis* in moist and dry sites and (2) assess the
86 growth trends of *B. utilis* at its upper and lower range edge with response to ongoing climate change.

87 **Methods**

88 **Study area**

89 This work was conducted at Lete Lekh (28.6° N, 83.58° E, 3650-3900 m asl) and Chimang Lekh (28.75° N,
90 83.7° E, 3000-3300 m asl) of Mustang district in the Trans-Himalayan zone of central Nepal. Lete Lekh is relatively
91 moist area with alpine birch treeline in the north east facing slope, whereas Chimang Lekh is a semi-arid zone with birch
92 timberline in the south–west facing slope. Lete treeline is the upper treeline and the Chimang timberline is the lower
93 range edge of *B. utilis* in the southern part of Mustang District, however, at Chimang, the birch treeline reaches as high
94 as 4000 m asl only in the sheltered north-facing slopes (personal observation). The sites are characterized by a
95 contrasting precipitation regime within a short distance, and lie within the Annapurna Conservation Area (ACA). The
96 Trans-Himalayan zone of central Nepal lies in the rain shadow formed by surrounding high mountains; where runoff
97 water from snow cover is the main source of water (Aryal et al. 2012). The northern part of the Mustang lies in the
98 Trans-Himalayan semi-arid dry zone, further north, the Tibetan type highland forms the driest zone of Nepal
99 (Lomanthang: 200 mm annual rainfall) (Stainton 1972; Schickhoff 2005). The forested areas are thus confined to the
100 southern part of the district covering only about 3.24% of land area (Government of Nepal 2010).

101 **Species**

102 Himalayan birch (*Betula utilis* D. Don) is a moderate-sized (<20 m tall) broadleaved pioneer tree species
103 dominating an extensive area of subalpine forests up to 4500 m elevation, quite close to glaciers on northern slopes of
104 the inner Himalayas (Stainton 1972; Zobel and Singh 1997; TISC 2002; Schickhoff 2005; Miede et al. 2015). This
105 species shows high variation in its local distribution possibly due to the influence of local-scale climate variability and
106 topographic sheltering.

107 **Field sampling**

108 Field sampling was conducted during September-October of 2014 along transects on a topographically uniform area of
109 the treeline at Lete and timberline at Chimang. Tree cores were collected from trees occurring in two treeline transects
110 MT1 and MT2; each of which was 20 m × 120 m (hereafter MT for indicating moist treelines), and the third transect
111 from a single timberline transect of 30 m × 50 m at Chimang (hereafter DT). The treeline sites included the treeline
112 ecotone of *B. utilis* spanning the treeline and timberline.

113 We employed dendrochronological techniques for radial growth measurement and developing ring width
114 chronology of trees. Single, two or three cores were extracted from a tree using a 5.5 mm increment borer. All treeline
115 trees were cored at the base of the tree (< 30 cm), whereas DT trees were cored at breast height level. Tree cores were air
116 dried, mounted on sample holders and sanded using progressively finer sandpaper according to standard methods (Fritts
117 1976). Ring widths were measured at a resolution of 0.01 mm with a LINTAB II measuring system (Rinntech Germany).
118 Statistical analyses were performed using the software R (R Core Team 2015).

119 **Meteorological data**

120 Each study site has a meteorological station nearby (< 4 km), however the wet (Lete) site (28.63° N, 83.6° E, 2384 m
121 asl) does not have temperature data for more than 15 years. The fifteen years mean temperature of Lete was compared
122 with temperature of Thakmarpha station (28.75° N, 83.7° E, 2566 m asl) for the same period and showed high
123 correlation ($r = 0.69$, $n = 15$); hence we used the Thakmarpha (1970-2013 AD) temperature records, and rainfall records
124 of Lete and Chimang separately for growth climate analysis. The meteorological data showed mean annual rainfall of
125 1340 mm at Lete and 393 mm at Thakmarpha with mean annual temperature of 11.17 °C (Fig. 1).

126

127 **Fig. 1** Climate summary of Lete (2384 m asl) and Thakmarpha (2566 m asl) climate station (1970-2013 AD), the white
128 and black bars represent the rainfall at Lete and Thakmarpha respectively.

129 **Growth climate response**

130 Tree ring width (TRW) indices were employed to explore growth response to climate. We adopted visual inspection for
131 cross-dating tree cores (Stokes and Smiley 1968), with statistical tests (sign-test and *t*-test) using the software package
132 TSAP-Win (Rinn 2003). Ring-width measurements were detrended with a negative exponential using ARSTAN

software (Cook 1985). We produced a standard tree ring-width chronology of 107 years using 56 tree cores from 52 trees at MT1, 186 years using 27 tree cores from 23 trees at MT2, and of 122 years using 49 tree cores from 24 trees at DT (Table 1). To maintain a reasonable sample depth, we limit the tree ring width chronology to the period representing a minimum of ten cores for each site (Fig. 4a, b, c). Growth-climate relationships were determined by correlating site standard chronology with monthly climatic variables (total rainfall, mean air temperature) from June of the previous growth year until October of the current growth year (Fritts 1976). Given the previously identified importance of spring season (March-May) moisture sensitivity of birch for high elevation birch populations in the central Himalaya (Dawadi et al. 2013; Liang et al. 2014; Gaire et al. 2016), we also correlated the site chronology with mean climate for the March-May period.

Basal area index (BAI) chronology

BAI is commonly used to assessing tree and stand growth since it allows accurate quantification of tree productivity (Rubino and McCarthy 2000; Peñuelas et al. 2011). The BAI sigmoidal growth model is an appropriate means for detecting changes in tree growth avoiding detrending and standardizing employed in calculation of RWI (Phipps & Whiton 1988; Esper et al. 2002; Salzer et al. 2009). Here we used individual tree BAI to produce mean unstandardized BAI series across all trees at each site for each year.

Ring width was converted into tree BAI according to the following standard formula:

$$BAI = \pi (R_n^2 - R_{n-1}^2),$$

where ‘ R ’ is the radius of the tree and ‘ n ’ is the year of tree ring formation. The BAI chronology was produced using the `bai.out` function in the `dplR` package in R as some tree cores had missed pith and almost every core had intact bark (R Core Team 2015). We produced BAI series from each site from the period which has at least 10 trees to represent the site population, and to avoid idiosyncrasies at the individual tree level. We analyzed the trend of BAI series at each site for the time period of 1990-2014 AD, that represented the growth trend after the growth release phase, thereby avoiding periods of juvenile growth that are likely to be substantially determined by competitive interactions rather than climate (Jump et al. 2006).

157 Results

158 Climatic trends

159 Mustang (Lete and Thakmarpha) showed significant warming with a consistent increase of mean and maximum annual
 160 temperature during recent decades but without any trend in minimum temperatures (Fig. 2). The moist site (Lete) showed
 161 a significant increase in annual rainfall and a stable trend of spring season (March-May) rainfall, whereas the dry site
 162 (Thakmarpha) showed no rainfall trend. Hence, considering the overall balance of temperature trends and total rainfall,
 163 the moist site (MT) is getting wetter and warmer whereas the dry site (DT) is getting drier and warmer in the recent
 164 decades (Fig. 2, 3a, b). The amount and duration of snow cover is an important determinant of soil moisture in high
 165 mountains in Himalayas (Müller et al. 2016). While we do not have direct measurements of snow cover at each study
 166 site, local people report substantial decrease in snow fall around Chimang (Tiwari, 2015 personal communication).

167 **Fig. 2** Annual temperature trend of Thakmarpha (Mustang); maximum temperature (T_{max}), mean temperature (T_{mean})
 168 and minimum temperature (T_{min}).

169 **Fig. 3** Rainfall trend; total annual rainfall and total spring season (March-May) rainfall; (a) MT, (b) DT

170 Ring-width chronology and growth climate response

171 We produced three well-replicated tree ring with chronologies of *Betula utilis*, from the moist treeline sites, and semi-
 172 arid timberline site. The location of sampling sites and chronology statistics are summarised in Table 1.

173 **Table 1**

174 Tree-ring chronology summary statistics.

Sampled location	Elevation range (m asl)	Chronology (years)	Mean series Length	No of cores (trees)	Mean sensitivity	EPS	All series Rbar	1 st order AC
Moist Treeline (MT1)	3650-3900	186	73	27 (23)	0.382	0.907	0.226	0.062
Moist Treeline (MT2)	3700-3900	107	65	56 (52)	0.324	0.954	0.415	0.026
Timberline Dry (DT)	3000-3300	122	79	49 (24)	0.360	0.968	0.315	0.001

(EPS: Expressed population signal, AC: Autocorrelation)

Fig. 4 Tree ring-width standard chronology of *B. utilis*; (a) MT1, (b) MT2, (c) DT.

The growth climate analysis of *B. utilis* revealed a significant positive relationship ($p < 0.05$) between the ring width series and monthly rainfall during spring season (March-May) both at moist treeline (MT1, MT2) and dry timberline (DT) (Fig. 5d,e,f). At least one month during spring season, showed significant positive correlation ($p < 0.05$) of total rainfall with ring width indices in each site. Previous year's summer rainfall was found to have a stronger positive impact on tree radial growth at DT, while this effect was observed more weakly at MT1 and MT2. A significant negative relationship ($p < 0.05$) between radial growth and mean temperature (T_{mean}) for the spring season was observed at both treeline sites (MT1 and MT2), although this relationship was weaker at DT. T_{mean} of October also showed a significant negative relationship with radial growth ($p < 0.05$) at MT1 and DT (Fig. 5a,c). Further, the minimum temperature (T_{min}) showed stronger negative correlation in early growing season (Feb-May) at MT2, which was weaker at MT1 and DT. However, the maximum temperature (T_{max}) showed stronger negative correlation to ring-width indices at DT in comparison to MT1 and MT2. Overall, while similarities in response are clear, we also found a contrasting response of radial growth to monthly climate among sites.

Fig. 5 Correlation coefficients of tree ring width indices, with total monthly maximum (T_{max}), mean (T_{mean}) and minimum temperature (T_{min}); MT1(a), MT2(b), DT(c), and total monthly rainfall; MT1(d), MT2(e), DT(f); of June in the previous year to October of the current year, spring season and annual climate, dashed horizontal lines indicate significant correlation at 95% confidence limit for a two-tailed test.

Temporal pattern of radial growth

BAI chronology at MT1 (1933-2014) and MT2 (1935-2014 AD) indicated a rapid increase followed by relatively stable (MT1) and weakly declining (MT2) trend in recent years, whereas at DT, BAI (1912-2014 AD) increased steadily at the beginning and declined abruptly in recent decades. BAI at DT showed a statistically significant declining trend, while that of MT1 and MT2 was without statistically significant trend for the same period (1990-2014 AD) as indicated by linear regression (Fig. 6,7).

Fig. 6 Basal area increment (BAI) chronology of *B. utilis* at moist treeline; MT1(a), MT2(b), dry timberline DT(c),

200 **Fig. 7** BAI trend during 1990-2014 AD at MT1(a), MT2(b) and DT(c), solid lines are the regression line and the shaded
201 lines represent the 95% confidence interval.

202 **Discussion**

203 **Climatic trends**

204 Climate data for the study regions at Mustang showed a consistent warming both at MT and DT, and high spatial
205 variability in rainfall, as reported in Eastern Himalayas (Sharma et al. 2000; Shrestha et al. 2012). The moist region of
206 Lete is getting wetter and warmer with increasing rainfall, whereas the semi-arid region of Thakmarpha is getting drier
207 and warmer with very low and stable rainfall over recent decades. Such diverging trends of temperature and precipitation
208 might have significant impacts on plant growth and forest productivity, given that the rapidly increasing maximum
209 temperature enhances evapotranspiration and will negatively impact soil moisture availability in the drier spring season (
210 Schickhoff et al. 2015). The increasing rainfall at Lete and almost stable rainfall at Thakmarpha is contrary to the
211 enhanced frequency of winter and pre-monsoon drought reported from western Nepal (Wang et al. 2013). While the
212 climatic trend of the Trans- Himalayan region (Mustang) showed the typical regional pattern of a rapid increase in
213 maximum temperature and almost stable trend in minimum temperature, local precipitation trends show more variability.
214 A consistent trend of increasing average rainfall was reported in the central Himalayas except the Northern Triangle
215 temperate forest ecoregion (Shrestha et al. 2012), irrespective of decreasing precipitation trends in Western Himalayas
216 (Kumar and Jain 2009). This contrast limits broad generalizations of climate trends and vegetation responses in the
217 region (Schickhoff 2005; Miede et al. 2015; Tiwari et al. 2016). We emphasize that the climate of the interior of the
218 topographically complex Trans-Himalayan region is highly spatially variable and regionally complex so that
219 extrapolation of future precipitation trends and forest responses for the region could be misleading.

220 **Ring-width chronology and growth climate response**

221 Our results demonstrated that the radial growth of *B. utilis* was mainly limited by temperature induced moisture
222 stress during the spring season both at treeline (MT) and timberline (DT), irrespective of substantial differences in total
223 rainfall between sites. The spring season rainfall and maximum temperature were relatively more important than mean
224 temperature in the dry timberline site (DT). Our findings are in agreement with the moisture sensitivity of birch reported
225 from the upper timberline in central Himalaya (Dawadi et al. 2013; Liang et al. 2014; Gaire et al. 2016), and for *Abies*

226 *spectabilis* from the semi-arid treeline in the Trans-Himalayan zone (Tiwari et al. 2016). However, tree growth at high
227 altitudes and latitudes was also reported to have been favored by high summer temperature (Barber et al. 2004; Chen et
228 al. 2011). In our results, the temperature sensitivity of birch at MT was seen in the negative correlation with mean
229 temperature (*Tmean*) of early spring (Feb-March), which was less strong at DT.

230 Our results revealed that spring season precipitation was more important for radial growth at DT in comparison
231 with MT, this could be because of higher temperature and increased competition between trees at DT and also due to
232 precipitation deficit in that area, in comparison to sparse trees and higher precipitation at MT, as has been reported in
233 various studies in Himalaya and Tibet (Lv and Zhang 2012; Qi et al. 2015; Tiwari et al. 2016). Spring season climate is
234 critical for *B. utilis* in the Himalayan highlands as shoot, leaf and floral buds begin to sprout during April (Bisht et al.
235 2014), and warmer springs can contribute to elevated frost damage and reduced water availability, with consequent
236 negative impacts on tree growth (Körner 2003). The early growing season (Feb-May) mean temperature (*Tmean*)
237 sensitivity in the treeline sites could be associated with snow pack accumulation, as most of the precipitation during this
238 time falls in the form of snow. The timing and duration of snow accumulation are important factors in the treeline where
239 early warming (increase of *Tmean*) of growing season (Feb-March) could facilitate budding and shoot formation (Bisht
240 et al. 2014) and radial growth by snow melt (Vaganov et al. 1999; Bekker 2005). However, there is a chance of heat
241 induced water deficit during the spring season and any such drought exposure could affect growth and seedling
242 establishment at treelines, and may even cause retreating of treeline (Liang et al. 2014).

243 Here, we reported more or less similar climate growth response at MT1, MT2 and DT, although the strength of
244 the correlation differed. Tree radial growth showed a stronger negative response to maximum temperature (*Tmax*) at DT
245 (Fig. 5), implying that projected warming will negatively impact future growth as drought stress intensifies at DT, given
246 consistent warming and low precipitation in the region (Fig. 1,2,3). In the Himalayan region, moisture stress during
247 spring season (March-May) was found to limit the radial growth of *B. utilis* even at the treeline (Gaire et al. 2016). Some
248 studies in the Himalaya also reported radial growth of *A. spectabilis* to be temperature sensitive (Bräuning 2004;
249 Borgeonkar et al. 2011; Gaire et al. 2014) and they explained a negative relationship between spring climate and radial
250 growth as threshold effects of moisture or temperature. Further, they emphasized heat induced water deficit associated
251 with high velocity of wind and increased evapotranspiration, to have negative influence on tree growth (Cook et al. 2003;
252 Gaire et al. 2014). We infer that the precipitation seasonality is highly important for systems with a short growing season
253 in higher altitude, with a shorter time for plants to compensate for a dry period, and especially so when the season is also

254 characterized by high temperature (Spence et al. 2015). However we also emphasize here that, although the rainfall is
255 increasing in the moist region like Lete Lekh, and it is stable in the semi-arid region like Chimang, if precipitation is
256 increasingly falling as rainfall rather than snow, soil water recharge from snow could further decline. Hence even where
257 overall precipitation is increased, the site might even be drier in the summer since water from rain flows away quickly
258 while the water from snowmelt seeps gradually into the soil over a longer period (Müller et al. 2016). Consequently,
259 accurate characterisation of snow fall is desirable to help understand if weaker spring precipitation and continuous
260 warming will drive further decline of birch radial growth and vitality in the semi-arid region of Mustang.

261 **Temporal pattern of radial growth**

262 In mature forest stands, age-related trends of BAI are generally positive. BAI may continue to increase in healthy stands
263 (LeBlanc 1992; Duchesne et al. 2003), or stabilize (LeBlanc et al. 1992), but it does not show a decreasing trend until
264 trees begin to senesce or unless trees are subject to significant growth stress (LeBlanc 1992; Weiner & Thomas 2001;
265 Duchesne et al. 2003, Jump et al. 2006). Our results showed that the BAI of birch at MT1 and MT2 typically followed a
266 sigmoidal pattern as it increased rapidly from young to middle age and remained almost stable during period of middle
267 and older age as described by Spiecker et al. (1996) and Weiner and Thomas (2001). We report abruptly decreasing BAI
268 of birch trees in the semi arid timberline (DT) over recent decades in comparison to that of relatively moist treeline
269 (MT). The negative influence of warm-day conditions (T_{max}) to radial growth also indicated that the semi-arid high
270 mountain biota is experiencing temperature induced drought stress (Fig. 5c,f). This finding emphasises that tree growth
271 and productivity in the semi-arid high mountains might further decline under the projected warming scenario (IPCC
272 2013). The contrasting growth trend of birch at moist treeline and semi-arid timberline sites showed the strong influence
273 of precipitation associated with increasing warm-day conditions. The decrease of BAI at DT should be interpreted with
274 some caution, however, because of lower canopy exposure at DT than MT, and potentially higher competition between
275 trees in this semi-arid zone. In contrast, MT is characterized by comparatively less competition and a more open canopy
276 (Spiecker et al. 1996), which might contribute to increasing/stable BAI at MT. Furthermore, nutrient availability, soil
277 quality, and topographic exposure also play important roles in modifying local growth patterns of birch forests in the
278 region (Müller et al. 2016). Nonetheless, given the growth-climate relationships identified, we believe that structural
279 differences and potential localized site quality variation between the treelines do not adequately explain BAI decline at

DT, since this site would be expected to show lower BAI with lower individual tree resource availability but not declining BAI over time.

Consequently, we interpret our results as demonstrating that declining BAI at the semi-arid site is an early signal of growth decline at DT over the recent decades, due to increasing drought stress. Although growth climate analysis revealed DT to be more sensitive to precipitation than temperature, we emphasize that the increasing temperature in the future (IPCC, 2013) would further intensify any temperature induced drought stress in the region. *B. utilis* is an important early successional species in the Himalayan treelines (Shrestha et al. 2007) and therefore a highly significant species in terms of forest ecosystems in the Himalayan highlands, declining growth in this species might alter competitive relationships and hence future forest composition at the lower range edge in the semi-arid forest of Chimang Lekh.

Conclusion

The spatial variability of climate in the interior of high mountain regions like the Himalayas is high due to interactions of complex topography and rain shadow effects. Although climate warming is generally expected to have an ameliorating influence on plant growth at high elevation, leading to upward elevational shifts of tree species, the positive influence of increasing temperature is not always universal in such regions. Strong gradients of precipitation over a short distances result in high altitude forests showing varying sensitivity to temperature and moisture. We find that spring precipitation and temperature is critical for radial growth of Himalayan birch, yet precipitation is more important than temperature at drier sites. Birch radial growth declined significantly at the dry site investigated here, where the rainfall trend is almost stable despite increasing temperatures over the recent decades. No such growth decline is seen in the wet site, where moisture availability remains adequate. Decreasing birch radial growth at its lower range edge demonstrates the negative influence of increasing temperatures in contrast with the moist upper treeline. Our results highlight the strongly spatially variable response of Himalayan birch to elevated temperatures and changing precipitation patterns in the region and can refine our understanding of likely responses of mountain forests to climate change.

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311 **References**

- 312 Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears
 313 DD, Hogg EH (Ted), Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW,
 314 Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging
 315 climate change risks for forests. *Forest Ecology and Management* 259:660–684. doi:
 316 10.1016/j.foreco.2009.09.001
- 317 Aryal A, Hipkins JJW, Raubeinhimer D, Brunton D (2012) Distribution and diet of brown bear in Annapurna
 318 Conservation Area, Nepal. *Ursus* 23:231–236.
- 319 Barber VA, Juday GP, Finney BP, Wilmking M (2004) Reconstruction of summer temperatures in interior Alaska from
 320 tree-ring proxies: evidence for changing synoptic climate regimes. *Climatic Change* 63: 91–120.
- 321 Bekker MF (2005) Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier
 322 National Park, Montana, U.S.A. *Arctic Antarctic and Alpine Research*. 37(1): 97–107. doi:10.1657/1523-
 323 0430(2005)037[0097:PFBTEA] 2.0.CO;2.
- 324 Beniston M (2003) Climatic changes in mountain regions: a review of possible impacts. *Climatic change* 59: 5-31.
- 325 Bhattacharyya A, Shah SK, Chaudhary V (2006) Would tree ring data of *Betula utilis* be potential for the analysis of
 326 Himalayan glacial fluctuations? *Current Science* 9, 754e761.
- 327 Bhattarai S, Chaudhary RP, Quave SL, Taylor RSL (2010) The use of medicinal plants in the Trans-Himalayan arid zone
 328 of Mustang district, Nepal. *Journal of Ethnobiology and Ethnomedicine* 6:14. doi:10.1186/1746-4269-6-14.
- 329 Bisht VK, Kuniyal CP, Bhandari AK, Nautiyal BP, Prasad P (2014) Phenology of plants in relation to ambient
 330 environment in a subalpine forest of Uttarakhand, western Himalaya. *Physiology and molecular biology of plants* :
 331 an international journal of functional plant biology 20:399–403. doi: 10.1007/s12298-014-0238-2

332 Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*
 333 320:1444–1449

334 Borgeonkar HP, Sikder AB, Ram S (2011) High altitude forest sensitivity to the recent warming: A tree-ring analysis of
 335 conifers from Western Himalaya, India. *Quaternary International* 236:158–166. doi: 10.1016/j.quaint.2010.01.016

336 Bräuning A (2004) Tree-ring studies in the Dolpo-Himalaya (western Nepal). *Proceedings of the*
 337 *DENDROSYMPOSIUM 2003* 2:8–12.

338 Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, Shiyatov SG, Vaganov EA, Grudd H, Cowie J (1998)
 339 Trees tell of past climates: But are they speaking less clearly today? [and Discussion]. *Philosophical Transactions:*
 340 *Biological Sciences* 353: 65–73.

341 Bunn AG, Graumlich LJ, Urban DL (2005) Trends in twentieth-century tree growth at high elevations in the Sierra
 342 Nevada and White Mountains, USA. *Holocene* 15: 481–488.

343 Cavin L, Jump AS (2016) Highest drought sensitivity and lowest resistance to growth suppression are found in the range
 344 core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Global Change Biology*. doi: 10.1111/gcb.13366

345 Chen L, Wu S, Pan T (2011) Variability of climate-growth relationships along an elevation gradient in the Changbai
 346 Mountain, northeastern China. *Trees* 25: 1133–1139.

347 Cherubini P, Dobbertin M, Innes JL (1998) Potential sampling bias in long-term forest growth trends reconstructed from
 348 tree-rings: A case study from the Italian Alps. *Forest Ecology and Management* 109: 103–118.

349 Cook ER (1985) A time-series analysis approach to tree-ring standardization. Ph.D Dissertation. The University of
 350 Arizona Press, Tucson.

351 Cook ER, Krusic PJ, Jones PD (2003) Dendroclimatic signals in long tree-ring chronologies from the Himalayas of
 352 Nepal. *International Journal of Climatology* 23, 707e732.

353 Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, Jones CD, Luke CM (2013) Sensitivity of tropical
 354 carbon to climate change constrained by carbon dioxide variability. *Nature* 494:341–345

355 Dai A (2011) Drought under global warming: A review. *Wiley Interdisciplinary Reviews: Climate Change* 2:45–65. doi:
 356 10.1002/wcc.81

357 Dai AG (2013) Increasing drought under global warming in observations and models. *Nature Climate Change* 3:52–58.
 358 doi: 10.1038/nclimate1633

359 Dawadi B, Liang E, Tian L, Devkota LP, Yao T (2013) Pre-monsoon precipitation signal in tree rings of timberline

360 *Betula utilis* in the central Himalayas. *Quaternary International* 283:72–77. doi: 10.1016/j.quaint.2012.05.039
 361 Duchesne L, Ouimet R, Morneau C (2003) Assessment of sugar maple health based on basal area growth pattern.
 362 *Canadian Journal of Forest Research* 33, 2074–2080.
 363 Esper J, Cook E, Schweingruber F (2002) Low-frequency signals in long tree-ring chronologies for reconstructing past
 364 temperature variability. *Science*, 295, 2250–2253.
 365 Fritts HC (1976) (Reprint, 2001) *Tree rings and climate*, Caldwell, New Jersey: The Blackburn Press.
 366 Gaire NP, Koirala M, Bhuju DR, Borgaonkar HP (2014) Treeline dynamics with climate change at the central Nepal
 367 Himalaya. *Climate of the Past* 10:1277–1290. doi: 10.5194/cp-10-1277-2014
 368 Gaire NP, Koirala M, Bhuju DR, Carrer M (2016) Site- and species-specific treeline responses to climatic variability in
 369 eastern Nepal Himalaya. *Dendrochronologia* 1–13. doi: 10.1016/j.dendro.2016.03.001
 370 Government of Nepal (2010) Mustang District profile. District Statistical Office, Government of Nepal, Mustang District,
 371 Nepal, p 87.
 372 Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature* 369: 448.
 373 Greenwood S, Chen JC, Chen CT, Jump AS (2014) Strong topographic sheltering effects lead to spatially complex
 374 treeline advance and increased forest density in a subtropical mountain region. *Global Change Biology* 20:3756–
 375 3766. doi: 10.1111/gcb.12710
 376 Harsch M a., Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline
 377 response to climate warming. *Ecology Letters* 12:1040–1049. doi: 10.1111/j.1461-0248.2009.01355.x
 378 Hofgaard A (1997) Inter-relationships between treeline position, species diversity, land use and climate change in the
 379 central scandes mountains of Norway. *Global Ecology and Biogeography Letters* 6, 419–429.
 380 doi:10.2307/2997351
 381 Holtmeier FK (2003) *Mountain timberlines: ecology, patchiness and dynamics*. Dordrecht, Germany: Kluwer Academic
 382 Publishers.
 383 Holtmeier FK, Broll G (2007) Treeline advance - driving processes and adverse factors. *Landscape Online* 1:1–33. doi:
 384 10.3097/LO.200701
 385 IPCC (2013) Summary for policymakers. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels
 386 A, Xia Y, Bex V, Midgley PM (eds) *Climate Change 2013: The physical science basis*. Contribution of Working

Group I to the Fifth Assessment Report of the Intergovernmental Panel on climate change. Cambridge University Press, Cambridge, pp 3–32.

Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology* 12:2163–2174. doi: 10.1111/j.1365-2486.2006.01250.x

Körner C (2000) Biosphere response to CO₂ enrichment. *Ecological Applications* 10: 1590-1619.

Körner C (2003) *Alpine plant life: functional plant ecology of high mountain ecosystems*. Berlin, Germany: Springer.

Kumar V, Jain SK (2009) Trends in seasonal and annual rainfall and rainy days in Kashmir valley in the last century. *Quaternary International* 211: 64–69.

La Sorte FA, Jetz W (2010) Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences* 277: 3401-3410.

LeBlanc DC, Nicholas NS, Zedaker SM (1992) Prevalence of individual-tree growth decline in red spruce populations of the southern Appalachian Mountains. *Canadian Journal of Forest Research*, 22, 905–914.

Liang E, Dawadi B, Pederson N, Eckstein D (2014) Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature? *Ecology* 95:140307191613003. doi: 10.1890/13-1904.1

Lv LX, Zhang Q Bin (2012) Asynchronous recruitment history of *Abies spectabilis* along an altitudinal gradient in the Mt. Everest region. *Journal of Plant Ecology* 5:147–156. doi: 10.1093/jpe/rtr016

Mäenpää E, Skre O, Malila E, Partanen R, Wielgolaski FE, Laine K (2001) Carbon economy in birch-dominated ecosystem species in northern Fennoscandia. In: Wielgolaski FE (ed) *Nordic Mountain Birch Ecosystems*. MAB Series vol 27. The Parthenon Publishing Group, N. Y. – London, pp 93-114

McCabe GJ, Wolock DM (2015) Increasing Northern Hemisphere water deficit. *Climatic Change* 132:237–249. doi: 10.1007/s10584-015-1419-x

Miehe S, Miehe G, Miehe S, Böhner J, Bäumler R, Ghimire SK, Bhattarai K, Chaudhary RP, Subedi M (2015) 16. Vegetation Ecology. In book: *Nepal: an introduction to the natural history, ecology and human environment in the Himalayas – A companion to the Flora of Nepal*, Edition: 1st, Chapter: 16, Publisher: The Royal Botanical Garden Edinburgh, Editors: G. Miehe & C.A. Pendry, pp.385-472

Monserud RA, Sterba H (1996) A basal area increment model for individual trees growing in even-and uneven-aged forest stands in Austria. *Forest Ecology and Management* 80: 57–80.

414 Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD,
 415 Niklaus PA, Nippert JB, Nowak RS, Parton WJ, Polley HW, Shaw MR (2004) Water relations in grassland and
 416 desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*, 140, 11–25.
 417 Morison JIL (1993) Response of plants to CO₂ under water limited conditions. *Vegetatio*, 104, 193–209.
 418 Müller M, Schwab N, Schickhoff U, Böhner J, Scholten T (2016) Soil temperature and soil moisture patterns in a
 419 Himalayan alpine treeline ecotone. 48:501–521. doi: 10.1657/AAAR0016-004
 420 Nogués-Bravo D, Araújo MB, Errea MP, Martínez-Rica JP (2007) Exposure of global mountain systems to climate
 421 warming during the 21st century. *Global Environmental Change* 17: 420–42.
 422 Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJP,
 423 Ceulemans R, De Angelis P, Finzi AC, Karnosky DF, Kubiske ME, Lukac M, Pregitzer KS, Scarascia-Mugnozza
 424 GE, Schlesinger WH, Oren O (2005) Forest response to elevated CO₂ is conserved across a broad range of
 425 productivity. *Proceedings of the National Academy of Sciences USA*, 102, 18052–18056.
 426 Peñuelas J, Ogaya R, Boada M, Jump AS (2007) Migration, invasion and decline: changes in recruitment and forest
 427 structure in a warming-linked biome shift in Catalonia (NE Spain). *Ecography*, 30, 830–838.
 428 Peñuelas J, Hunt JM, Ogaya R, Jump AS (2008) Twentieth Century changes of tree-ring $\delta^{13}C$ at the southern range-edge
 429 of *Fagus sylvatica*: Increasing water-use efficiency does not avoid the growth decline induced by warming at low
 430 altitudes. *Global Change Biology* 14:1076–1088. doi: 10.1111/j.1365-2486.2008.01563.x
 431 Peñuelas J, Canadell JG, Ogaya R (2011) Increased water-use efficiency during the 20th Century did not translate into
 432 enhanced tree growth. *Global Ecology and Biogeography* 20:597–608. doi: 10.1111/j.1466-8238.2010.00608.x
 433 Phipps RL, Whiton JC (1988) Decline in long-term growth trends of white oak. *Canadian Journal of Forestry Research*,
 434 18, 24–32.
 435 Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA & Solomon AM (1992) A global biome model based on
 436 plant physiology and dominance, soil properties and climate. *Journal of Biogeography* 19: 117–134.
 437 Qi Z, Liu H, Wu X, Hao Q (2015) Climate-driven speedup of alpine treeline forest growth in the Tianshan Mountains,
 438 Northwestern China. *Global Change Biology* 21:816–826. doi: 10.1111/gcb.12703
 439 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for
 440 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

441 Rinn F (2003) TSAP-Win: Time Series Analysis and Presentation for Dendrochronology and Related Applications.
 442 Version 0.55 User reference. Heidelberg, Germany (<http://www.rimatech.com>).

443 Rubino DL, McCarthy BC (2000) Dendroclimatological analysis of white oak (*Quercus alba* L., Fagaceae) from an old-
 444 growth forest of southeastern Ohio, USA. *Journal of the Torrey Botanical Society* 127: 240-250.

445 Sala OE, Parton WJ, Joyce LA & Lauenroth WK (1988) Primary production of the central grassland region of the
 446 United-States. *Ecology* 69: 40–45.

447 Sano M, Furuta F, Kobayashi O, Sweda T (2005) Temperature variations since the mid-18th century for western Nepal,
 448 as reconstructed from tree-ring width and density of *Abies spectabilis*. *Dendrochronologia* 23, 83e92.

449 Salzer MW, Hughes MK., Bunnb AG, Kipfmüller KF (2009) Recent unprecedented tree-ring growth in bristlecone pine
 450 at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences of the United*
 451 *States of America* 106, 20348–20353.

452 Schickhoff U (2005) The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and
 453 ecological aspects, in: *Mountain ecosystems: studies in treeline ecology*, edited by: Broll, G. and Keplin, B.,
 454 Springer, Berlin, Germany, 275–354.

455 Schickhoff U, Bobrowski M, Böhner J, Bürzle B, Chaudhary RP, Gerlitz L, Heyken H, Lange J, Müller M, Scholten T,
 456 Schwab N, Wedegärtner R (2015) Do Himalayan treelines respond to recent climate change? An evaluation of
 457 sensitivity indicators. *Earth System Dynamics* 6:245–265. doi: 10.5194/esd-6-245-2015

458 Sharma E, Tsering K (2009) Climate change in the Himalayas: The vulnerability of biodiversity. *Sustainable Mountain*
 459 *Development* 55: 10–12.

460 Sharma K, Moore B, Vorosmarty C (2000) Anthropogenic, climatic, and hydrologic trends in the Koshi basin, Himalaya.
 461 *Climatic Change* 47: 141–165.

462 Shrestha AB, Wake CP, Mayewski PA, Dibb JE (1999) Maximum temperature trends in the Himalaya and its vicinity:
 463 An analysis based on temperature records from Nepal for the period 1971–94. *Journal of Climatology* 12: 2775–
 464 2786.

465 Shrestha AB, Wake CP, Dibb JE, Mayewski PA (2000) Precipitation fluctuations in the Nepal Himalaya and its vicinity
 466 and relationship with some large scale climatological parameters. *International Journal of Climatology* 20: 317–
 467 327.

468 Shrestha BB, Ghimire B, Lekhak HD, Jha PK (2007) Regeneration of Treeline Birch (*Betula utilis* D. Don) Forest in a

469 Trans-Himalayan Dry Valley in Central Nepal. *Mountain Research and Development* 27:259–267. doi:
 470 10.1659/mrdd.0784

471 Shrestha UB, Gautam S, Bawa KS (2012) Widespread climate change in the Himalayas and associated changes in local
 472 ecosystems. *PloS one* 7:1–10. doi: 10.1371/journal.pone.0036741

473 Spence LA, Liancourt P, Boldgiv B, Petraitis PS, Casper BB (2015) Short-term manipulation of precipitation in
 474 Mongolian steppe shows vegetation influenced more by timing than amount of rainfall. *Journal of Vegetation*
 475 *Science* 1–10. doi: 10.1111/jvs.12349

476 Spiecker H, Mielikaeinen K, Kohl M, Skovsgaard P (eds) (1996) Growth trends in European forests: Studies from 12
 477 countries. Research Report, European Forest Institute No. 5. Springer. Berlin, Germany.

478 Stainton JDA (1972) *Forests of Nepal*. New York

479 Stokes MA, Smiley TL (1968) *An Introduction to Tree-Ring Dating*. The University of Chicago Press, Chicago. 63 p.

480 TISC (Tree Improvement and Silviculture Component) (2002) *Forest and Vegetation Types of Nepal*. TISC Document
 481 Series 105. Kathmandu, Nepal: Department of Forest.

482 Tiwari A, Fan Z-X, Jump AS, Li S-F, Zhou Z-K (2016) Gradual expansion of moisture sensitive *Abies spectabilis* forest
 483 in the Trans-Himalayan zone of central Nepal associated with climate change. *Dendrochronologia* 1–10. doi:
 484 10.1016/j.dendro.2016.01.006

485 Tsering K (2003) Constructing future climate scenarios of Bhutan. In Project report on climate change vulnerability and
 486 adaptation study for rice production in Bhutan; Climate change studies in Bhutan, Ministry of Agriculture,
 487 Bhutan.

488 Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH and Silkin PP (1999) Influence of snowfall and melt
 489 timing on tree growth in subarctic Eurasia. *Nature* 400(6740): 149–151. doi:10.1038/22087.

490 Voelker SL, Muzika R, Guyette RP, Stambaugh MC (2006) Historical CO₂ growth enhancement declines with age in
 491 *Quercus* and *Pinus*. *Ecological Monographs* 76: 549-564.

492 Wang SY, Yoon JH, Gillies RR, Cho C (2013) What caused the winter drought in western nepal during recent years?
 493 *Journal of Climate* 26:8241–8256. doi: 10.1175/JCLI-D-12-00800.1

494 Wardle P (1974) Alpine timberlines. In: lives JD, Barry RG (eds) *Arctic alp environments*. Methuen, London, pp 371–
 495 402.

496 Weiner J, Thomas SC (2001) The nature of tree growth and the age-related decline in forest productivity. *Oikos* 94: 374-
 497 376.

498 Xu J, Grumbine RE, Shrestha A, Eriksson M, Yang X, Wang Y, Wilkes A (2009) The melting Himalayas: Cascading
 499 effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology* 23:520–530. doi:
 500 10.1111/j.1523-1739.2009.01237.x

501 Yang B, Kang XC, Liu JJ, Brauning A, Qin C (2010) Annual temperature history in Southwest Tibet during the last 400
 502 years recorded by tree rings. *International Journal of Climatology* 30: 962–971.

503 Yang B, He M, Melvin TM, Zhao Y, Briffa KR (2013) Climate control on tree growth at the upper and lower treelines: a
 504 case study in the Qilian Mountains, Tibetan Plateau. *PLoS ONE* 8(7):e69065

505 Zhang Q, Zhang Y, Peng S, Yirdaw E, Wu N (2009) Spatial structure of alpine trees in mountain baima xueshan on the
 506 southeast tibetan plateau. *Silva Fennica* 43:197–208.

507 Zobel DB, Singh SP (1997) Himalayan forests and ecological generalizations. *BioScience* 47:735–745.

508