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Recent treeline dynamics are similar between dry and mesic areas of Nepal, central Himalaya

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Abstract

Aims
We investigated the treeline dynamics of two environmentally contrasting areas in the Nepalese Himalaya to address the following questions: (i) Does the timing of establishment of the current treeline differ between the two study areas, and can area-specific treeline developments be identified? (ii) Do recruitment patterns and height growth indicate recent climate-driven treeline advance, following the general prediction for the central Himalayan region, in the two study areas?

Methods
A dry-climate treeline dominated by *Pinus wallichiana* and a mesic-climate treeline with *Abies spectabilis* were selected for study. In each area, we sampled the size and age structure of the study species along three elevational transects (20-m wide) from the forest line to the tree species line crossing the treeline. We also sampled treeline trees from within and outside transects to reconstruct past treeline establishment dynamics.

Important Findings
Despite differences in moisture regimes, tree species and recent climate trends, our two study areas showed very similar treeline dynamics over the past six decades. In both areas, the recruitment of treeline trees indicates stationary treelines over the past six decades with the current treelines being dominated by trees that were established around 1990. The mesic area has experienced an overall climatic warming trend, and the stationary *Abies* treeline is hypothesized to be regulated by non-climatic factors, notably grazing. The dry area has not experienced warming but increased climatic variability and some very cool summers in the recent decades may explain the stationary to weakly receding *Pinus* treeline, which appears more climatically controlled with decreased recruitment over the past decades and decreased growth towards higher elevations. In both areas, there is a potential for treeline advance, depending on future land use and climate change. Our results highlight the importance of conducting treeline ecotone analyses for several sites or areas, and considering both climatic and non-climatic drivers of the treeline dynamics within each of these areas, for understanding regional treeline dynamics.

Keywords: *Abies spectabilis*, Himalaya, *Pinus wallichiana*, slope aspect, treeline ecotone dynamics

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INTRODUCTION

Treeline ecotones, i.e. arctic or alpine forest-tundra transition zones, are considered highly responsive to climate change (Paulsen *et al.* 2000; Tranquillini 1979). The location of this ecotone generally coincides with the 10°C isotherm of air temperature of the warmest month (Grace *et al.* 2002; Holtmeier 2009; Körner 2003). Hence, temperature is assumed to be a major controlling factor of ecotone dynamics and of forest and tree advance (Grace *et al.* 2002; Körner 2003), which may be mediated through increased regeneration and/or through higher growth of pre-established individuals (Hofgaard *et al.* 2009; Körner and Hoch 2006; Woodall *et al.* 2009). However, the rate and extent of forest and tree advance are not uniform across treeline ecotones (Harsch *et al.* 2009; Holtmeier and Broll 2007) and advancing, stationary and retreating treeline ecotones can occur concomitantly across landscapes within the same region (Aune *et al.* 2011). This suggests that the assumption of regional climatic signals such as growing season temperature as the main driver of treeline structure

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and location may be too simplistic in the context of ecotonal change at local to regional scales (Hofgaard *et al.* 2012; Sveinbjörnsson *et al.* 2002). Tree recruitment and growth across the treeline ecotone have also been shown to be controlled by non-growing season climate conditions, by climate variables other than temperature (Harsch and Bader 2011; Mathisen and Hofgaard 2011), by biotic interactions such as competition and herbivory (Cairns and Moen 2004; Hofgaard *et al.* 2010) and by positive feedbacks (Bekker 2005; Elliott 2011; Malanson *et al.* 2011). Thus, region- and site-specific responses to climate change may result.

The Himalayan region in central Asia is considered to be especially sensitive to climate change (IPCC 2007) with predictions for rapidly advancing treeline ecotones and, as a consequence, altered living conditions for human communities (IPCC 2007; Xu *et al.* 2009). Changing treeline ecotones, both regarding structure and location, have been reported for the greater Himalayan region during recent decades (see Dubey *et al.* 2003; Li *et al.* 2008; Miehe 1982; Shi *et al.* 2008). Advancing pine treelines, e.g. in the western Himalaya, and advancing fir treelines on the Tibetan plateau, have been attributed to climate warming (Dubey *et al.* 2003; Liang *et al.* 2011). However, temperature trends for the past several decades are not characterized by uniform warming across all parts of the greater Himalayan region (IPCC 2007; Shrestha *et al.* 1999). The often stated prediction of a general swift advance of the ecotone in this region can therefore be questioned, and area-specific treeline ecotone trends can be hypothesized as more likely response patterns due to variable climatic trends as well as variable prominence of other climatic and non-climatic drivers.

Central Nepal within the greater Himalaya region is characterized by considerable local variation in climate over short geographical distances due to complex and varied topography and rain-shadow effects of the high mountains. Within this region we selected two climatically contrasting conifer-dominated treeline ecotone areas: a south-facing dry slope dominated by Himalayan blue pine (*Pinus wallichiana* A. B. Jacks.) and a north-facing mesic slope dominated by Himalayan fir (*Abies spectabilis* (D. Don) Spach). These species and moisture-specific ecotones were analysed by means of dendroecological methods to address the following research questions: (i) Does the timing of establishment of the current treeline differ between the two study areas, and can area-specific treeline developments be identified? (ii) Do recruitment patterns and height growth indicate recent climate-driven treeline advance in the two study areas, following the general prediction for the central Himalayan region?

MATERIALS AND METHODS

Study areas

The study areas are located in Ngawal, Manang (28.68°N; 84.00°E) and Lauribinayak, Rasuwa (28.12°N; 85.35°E) in central Nepal (Fig. 1). The Ngawal area (hereafter DRY) is a dry south-facing slope of the upper Manang valley in the trans-Himalayan arid zone in Nepal (Stainton 1972). The Lauribinayak area (hereafter MES) is a mesic north-facing slope in the Langtang valley, which is drained by the Langtang Khola river (a tributary of the Bhotekoshi-Trishuli Gandaki river), near the Tibetan border in Nepal (Ono and Sadakane 1986). The landscape of DRY is characterized by glacial erosion and glacial deposits (Hagen 1969) and that of MES is characterized by rock-fall sediments and glacial fluvial moraines (Heuberger *et al.* 1984). The treeline ecotone in both areas is used by the local people for livestock grazing and medicinal plant collection, and the forest below the ecotone is also used for collection of fuelwood, timber and litter (Miehe 1982; Shrestha and Vetaas 2009). The overall human disturbance pressure appears lower at DRY than at MES, possibly due to more effective implementation of conservation regulations here (K. B. Shrestha, personal observation).

The climate of central Nepal is dominated by the summer Indian monsoon where southerly winds bring heavy rainfall mainly during June to August (Fig. 2a and b). The closest climate stations to the two field areas with temperature and precipitation data are Chame (28.55°N, 84.23°E; 2680 m a.s.l.; ~17 km south-east of DRY, station data since 1978) and Dhunche (28.00°N, 85.30°E; 1982 m a.s.l.; ~25 km south-west of MES, station data since 1999; Fig. 1). The Dhunche climate station does not have reliable long-term climate data, and Kathmandu (27.70°N, 85.37°E; 1336 m a.s.l.; ~44 km south of MES, station data since 1971; Fig. 1) is its closest station with long-term data. The Kathmandu station was therefore used for the temporal comparison.

Comparison between Chame and Dhunche stations is thus limited to the period 1999–2005, and according to the climate station data MES receives much higher annual rainfall than DRY (1610.4 vs. 839.6 mm), and has a more pronounced monsoon rainfall (66.3 vs. 54.6%, respectively, of the annual rainfall) (Fig. 2a and b). The actual rainfall might however differ even more, as DRY probably has lower rainfall than indicated by the data from Chame station, due to the rain-shadow effect of the Annapurna mountain range to the south-east (Anonymous 1995). Snow is common during winter in both study areas and lasts for about 5 months (November to March). December and January are the coldest months in both areas, but while DRY has a relatively long summer season (relatively uniform warm temperatures from April to September); MES has a more pronounced summer season with the highest temperatures in June and July (Fig. 2a and b).

Comparison between Chame and Kathmandu stations is possible for the period 1978–2005. The average annual temperature from Chame shows a weak increasing trend over the past few decades (up to 2005) (Fig. 2e), a trend that is driven by changes in spring temperatures alone (Fig. 2e). The Kathmandu data also show a weak increasing trend for average annual temperature, but here the trend is evident in the winter, spring and summer temperatures (Fig. 2f). Winter and summer temperatures of

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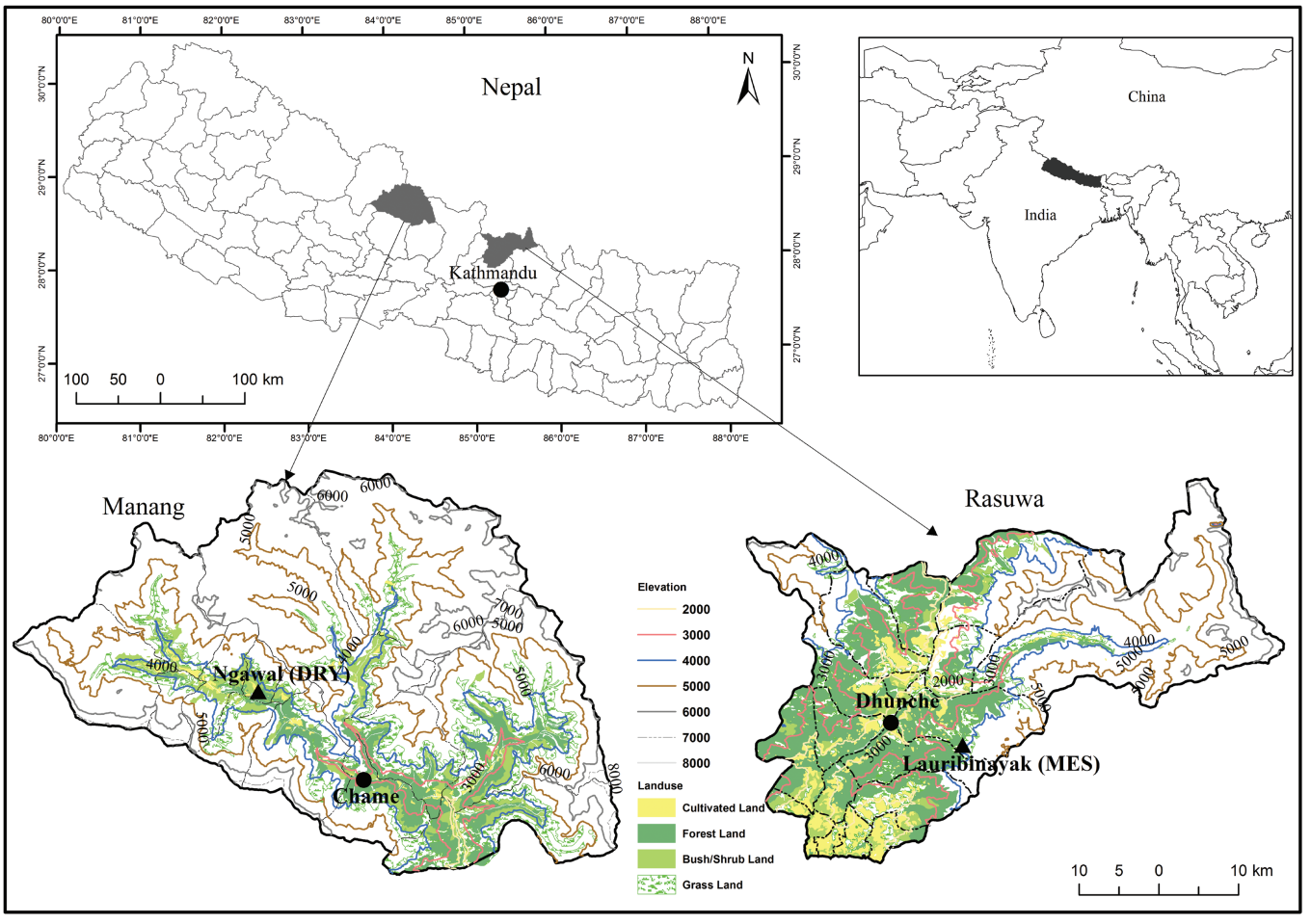

Figure 1: location of the study areas: Ngawal (DRY) in the Manang district and Lauribinayak (MES) in the Rasuwa district in Nepal, central Himalaya. Filled triangle indicates sampling areas and filled circle indicates climate stations.

Chame show increased annual variability after 1998 (Fig. 2e). Precipitation in Chame shows no significant trends over time, while in Kathmandu, summer and annual precipitation show statistically significant increasing trends (Fig. 2d).

The lack of precise climate data for desired locations and the typically relatively short time series from the available climate stations is a common problem in the high-elevation mountain areas of Nepal (Shrestha *et al.* 1999). Thus, to give an overview of the longer term climate trend in the two areas, we present gridded monthly temperature and precipitation data (Climate Research Unit [CRU], TS3.10 at 0.5° spatial resolutions, Mitchell and Jones 2005) for the period 1950–2005 (Fig. 2g–j). In both areas, the gridded average annual temperature shows a significantly increasing trend since ca. 1970 (Fig. 2i and j), and the study period, especially since 2000, is therefore significantly warmer than the normal. Precipitation has remained relatively constant over the normal period (Fig. 2g and h).

Tree species

Himalayan blue pine (*P. wallichiana*) is the dominant tree species in the treeline ecotone at DRY, with *Juniperus indica* as the sub-dominant component. Blue pine generally grows on dry sandy soil and is a light-demanding, drought- and frost-tolerant tree species. The treeline ecotone at MES is dominated by Himalayan fir (*A. spectabilis*), with *Betula utilis* and *Rhododendron campanulatum* as important sub-dominants. Himalayan fir grows on acidic and clay soils on moist shady slopes, and is sensitive to late spring frosts. Most of the seedlings and saplings in both areas were found in association with shrub cover (*J. indica* in DRY and *Rhododendron* spp. in MES) (Fig. 3).

Field sampling

The field investigations were conducted in the summers of 2008 (MES) and 2009 (DRY). Three elevational transects were sampled in each area (Fig. 4). Each transect runs from the forest line (i.e. the uppermost elevations of closed stands of trees >2 m) to the tree species line (i.e. the uppermost tree specimen irrespective of size) crossing the treeline (i.e. the elevation of uppermost tree-sized specimens ≥2 m). The transects were 20-m wide and spanned an elevational range of 250 m (3930–4180 m.a.s.l.) in DRY and 180 m (3770–3950

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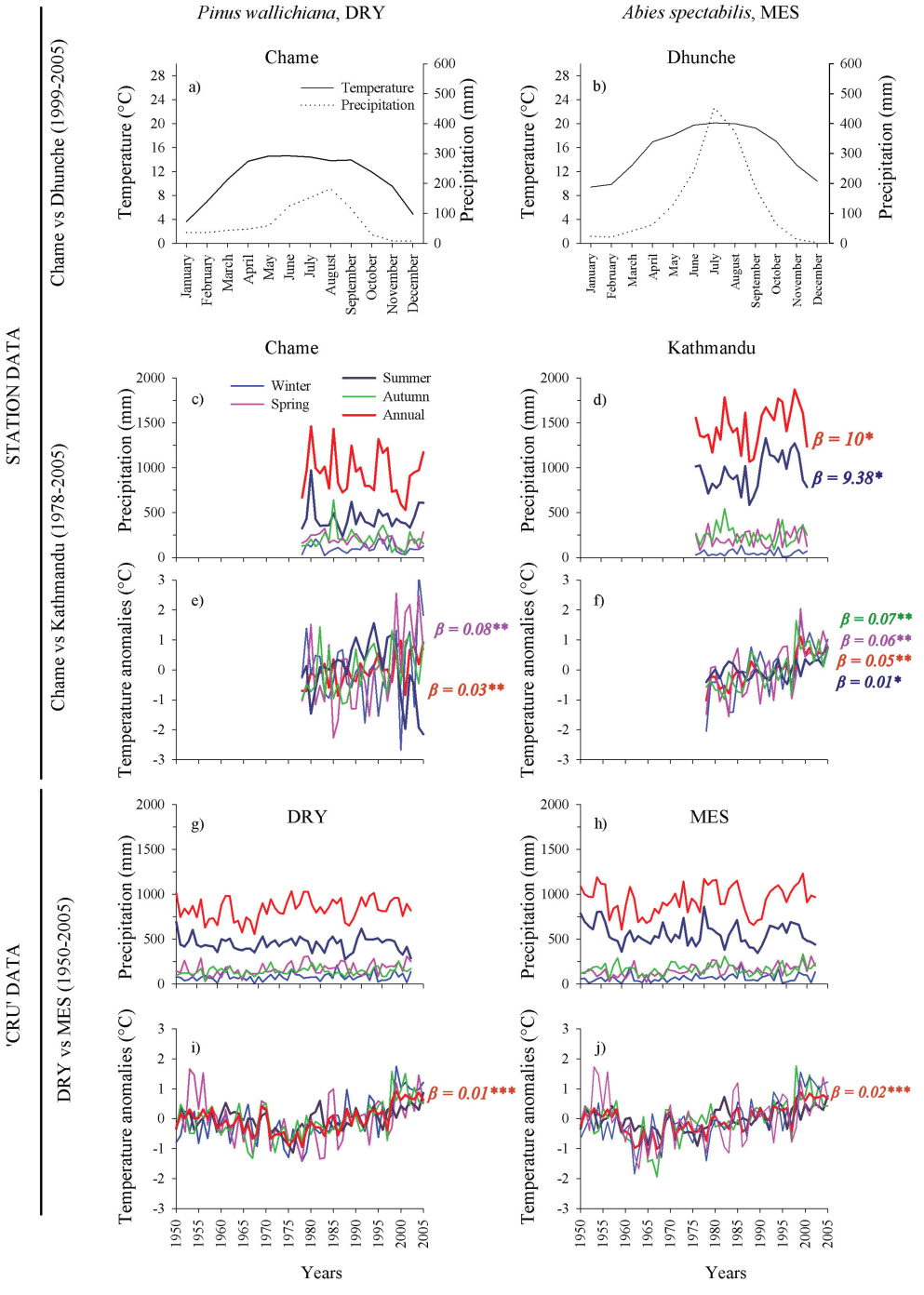

Figure 2: the data from the meteorological stations at Chame and Dhunche (1999–2005) showing monthly average temperatures and total precipitation (**a** and **b**); Chame and Kathmandu (1978–2005) showing seasonal (winter, spring, summer, autumn) and annual total precipitation (**c** and **d**), and mean seasonal and annual temperature anomalies (calculated relative to the mean seasonal and annual temperatures across the entire data series) for Chame and Kathmandu (1978–2005; **e** and **f**). The CRU climate data for the period 1950–2005 showing seasonal (winter, spring, summer, autumn) and annual total precipitation (**g** and **h**), and mean seasonal and annual temperature anomalies (see above) for the same time period (1950–2005; **i** and **j**). β is the slope of the trends. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Legends inside panel 'a' are for 'a and b'; and inside 'c' for 'c–j'.

m.a.s.l.) in MES, giving a total sampling area of 3.2 and 4 ha in the respective study areas. Thus, average distance covered by the transects on the ground was ~533 and ~666 m in DRY and MES, respectively. Geographical coordinates and elevation of all specimen tree species within the sampling areas were recorded by GPS (eTrex Vista Cx; GARMIN). Within

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Figure 3: photos showing (**a**) *Pinus wallichiana* seedlings protected by *Juniperus indica* shrubs in the DRY area and (**b**) *Abies spectabilis* seedlings in *Rhododendron* spp. and *Cassiope fastigiata* dwarf shrubs in the MES area.

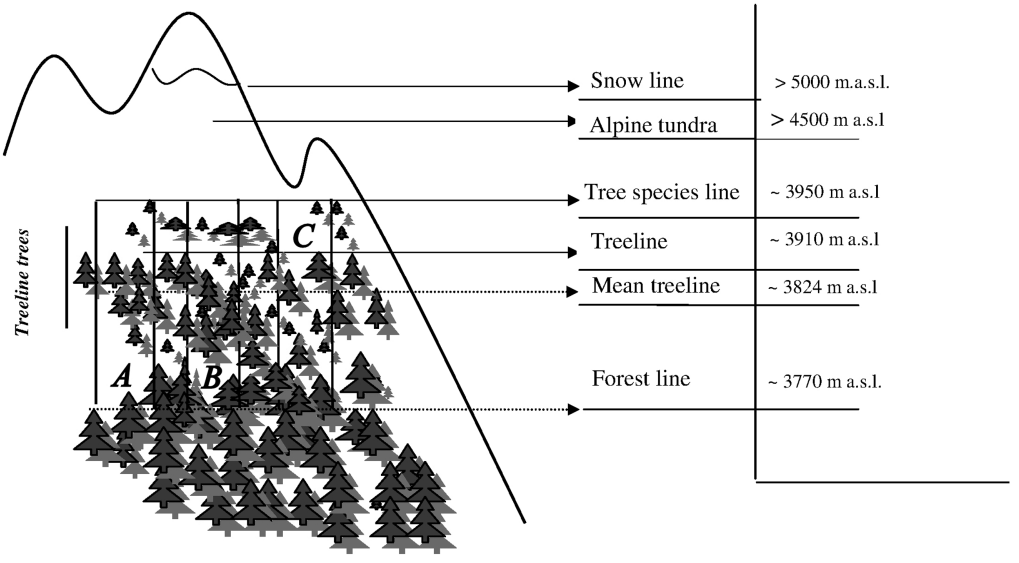

Figure 4: schematic representation of the study design (after Körner and Paulsen 2004; Shrestha 2013) at one of the study areas (MES) showing different components of the treeline ecotone and the alpine tundra and the snow line. A, B and C are the transects.

each transect, all trees (height ≥2 m), saplings (height 0.50–2 m) and seedlings (height <0.50 m) (cf. Wang *et al.* 2006) were sampled for height, DBH (diameter at breast height; when relevant) and age. For the age determination, trees were cored at the base (as close to the ground as possible, referred to as the basal level cores) using a 5-mm increment borer. Due to restrictions on destructive sampling, small pine individuals (seedlings and saplings) were sampled for age by the branch-whorl count method (see below; Puntieri *et al.* 1999), whereas for *Abies*, seedlings and saplings were cut at the base for age determinations. Transect data were pooled per area. Altogether 181 *Pinus* individuals and 163 *Abies* individuals were used in the age structure analysis of DRY and MES, respectively.

Treeline trees

To estimate the establishment period of the current treeline in the two areas, trees were also sampled along the treeline for a horizontal stretch of a minimum of 1.5 km per area (*sensu* Dalen and Hofgaard 2005). This sampling crossed the transects, and thus included any treeline trees from within the transects. The trees were sampled as described above, but were in addition cored at 2 m above ground (referred to as the 2 m cores). The 2-m age determination gives the date when the individuals became treeline trees. In total, 31 *Pinus* and 23 *Abies* treeline trees were sampled in the DRY and MES areas, respectively. The average elevation of these treeline trees per area is termed the 'mean treeline' of the area (see Dalen and Hofgaard 2005).

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Data processing and analysis

All extracted core samples were mounted onto wooden supports. The samples (cores and cut specimens) were kept dry and the rings were made smooth and visible using a scalpel. Zinc ointment was applied to increase the contrast between early and late wood within the annual rings. Age counting was done using a stereo-microscope (×6–40).

Some of the cores had missing rings at the centre due to a failure to hit the piths during coring, or due to butt rot. The numbers of missing rings were estimated by visual inspection. If estimated numbers of missing rings were >5, the sample was discarded. Otherwise, the estimated numbers of missing rings were added to the counted rings. Such corrections were applied to 2.5% of the *Pinus* specimens and 22.5% of the *Abies* specimens. Altogether, 14 trees and 14 saplings of *Abies* and 6 *Pinus* trees were discarded. In the case of *Pinus* saplings and seedlings the accuracy of the branch-whorl count data was tested by using correlation between ages of a subset of cut individuals (17 seedlings and 12 saplings) collected within the transect and the age of the same individuals estimated by the branch-whorl count method. This gave a mean underestimation error of 4.1 ± 0.29 (SE) years which was added to the estimated age of each sapling and seedling.

The vertical growth rate of transect individuals (trees, saplings and seedlings) was calculated by dividing total height by age (cm yr^{-1}). For treeline trees the growth rate to reach tree size was calculated by using the age difference between the base and the 2-m level. Changes in treeline position, using transect data, were analysed by comparing establishment dates for the five uppermost tree individuals per decade (1950–59; 1960–69; 1970–1979; 1980–89; 1990–99) and testing for differences in mean elevation between decades by means of a one-way analysis of variance with a *post-hoc* test (Tukey's honestly significant difference [HSD]; Jason 1996). All analyses were performed using the statistical software R, version 2.11.0 (R Development Core Team 2008).

RESULTS

DRY area

Treeline dynamics

Mean treeline position was located at 4067 m.a.s.l. The treeline tree age estimates at 2 m suggest that the treeline was largely made up of trees that were established around 1990 (Table 1) by individuals that were recruited in the 1970s (1972; based on mean age at the basal level cores; Table 1). On average, the treeline trees from this pine-dominated area had a vertical growth rate of ca. 14 cm yr^{-1} from the time of establishment to the time they reached tree size (2-m height; Table 1). The uppermost tree in the compiled transect data occurred 53 m above the mean treeline (Fig. 5) and the uppermost specimen occurred 60 m above the current treeline. The oldest sampled trees from the transects in this area dated back to the first decade of the 20th century and were growing close to the current forest line elevation (Fig. 5).

The treeline position remained more or less stationary after its establishment, but showed some minor fluctuations between decades. The uppermost trees established during the 1990s occurred at significantly lower elevations than the uppermost trees established during the 1980s ($P < 0.05$), though we detected no significant elevational difference when we compared 1990s establishment to earlier decades (Fig. 6).

Age structure and height growth

The age distribution was dominated by younger age classes, although this pattern was less evident when analysed separately for individuals growing above and below the mean treeline (Fig. 7). The largest age class was 1995–99. The average total number of individuals per hectare for all age classes was 56.6. All height classes (trees, saplings and seedlings) were present both above and below the mean treeline. Height, age and vertical growth rate all decreased with increasing elevation, although the relationship was not statistically significant for age (Fig. 8).

Tree height was significantly correlated with both tree age and DBH, and DBH was significantly correlated with age (Fig. 8). In general, vertical growth rates decreased from larger- to smaller-sized individuals (trees—saplings—seedlings) (Table 2). Vertical growth rates were higher for trees below the mean treeline compared to above (Table 2).

MES area

Treeline dynamics

The mean treeline position was located at 3824 m a.s.l. The treeline tree age estimates at 2 m suggest that the treeline was made up of trees that were established around 1990 (Table 1)

Table 1: characteristics of treeline trees in the DRY and MES study areas (mean values are presented with standard deviations)

Variables	*Pinus wallichiana*, DRY	*Abies spectabilis*, MES
Mean treeline elevation (m.a.s.l.)	4067	3824
Number of trees sampled	31	23
Tree height (m)	3.0 ± 1.3	5.5 ± 3.3
Age at stem base (0 m)	37.3 ± 11.5	29.1 ± 9.0
Age at 2 m	20.3 ± 10.7	14.1 ± 7.6
Years to become 2 m	17.0 ± 7.1	15.0 ± 7.6
Mean vertical growth rate from 0 to 2 m (cm yr^{-1})	14.4 ± 7.3	17.8 ± 11.6

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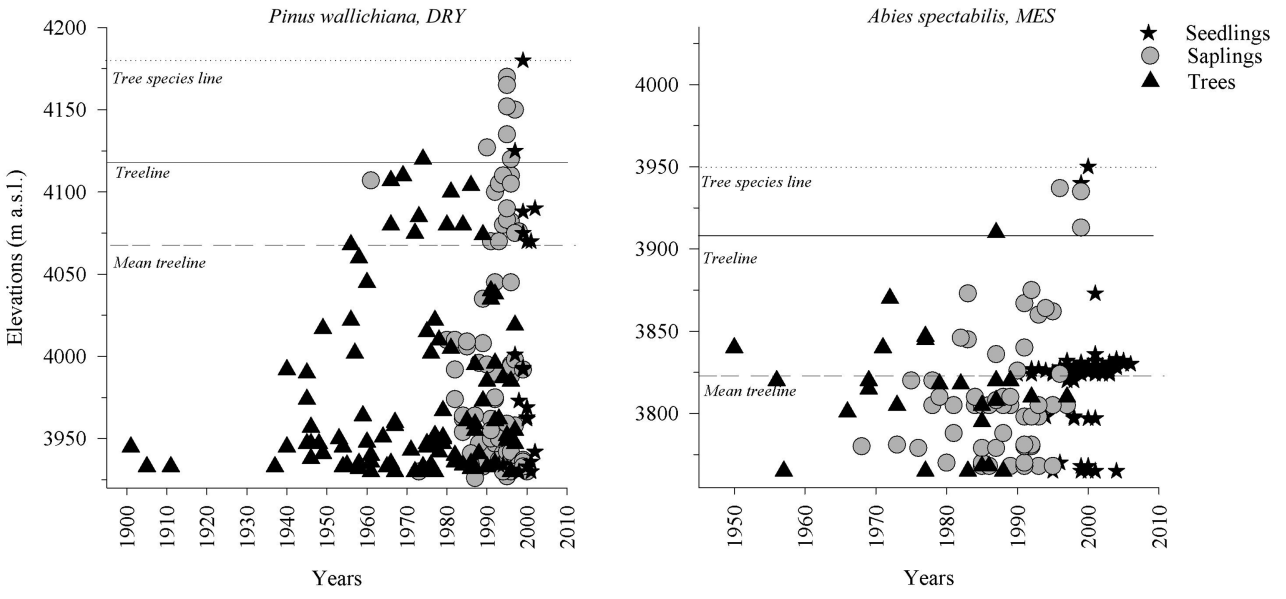

Figure 5: spatio-temporal distribution of tree recruitment within the transects across the alpine treeline ecotones in the DRY and MES study areas. Definitions for tree species line, treeline and mean treeline are given in the text (see Materials and Methods). Filled triangles, grey filled circles and filled stars represent trees, saplings and seedlings, respectively. Note the different scales for *x*- and *y*-axes.

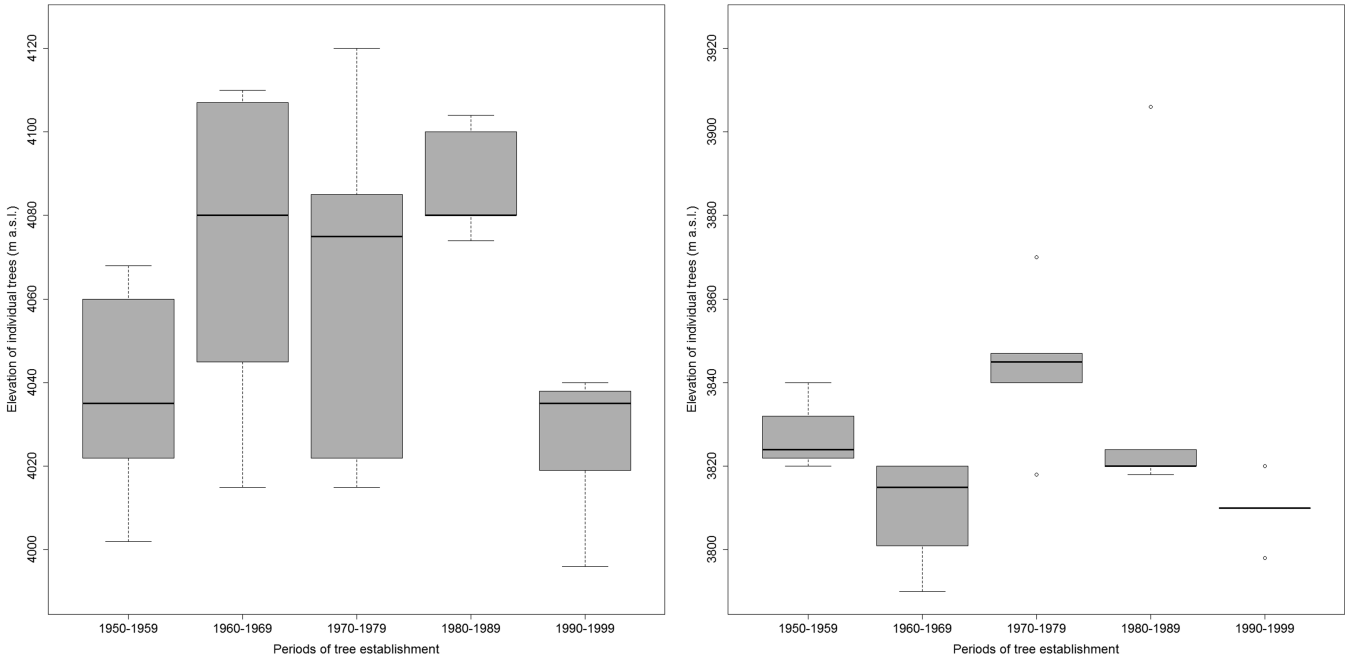

Figure 6: box plots showing decadal variation in the recruitment of treeline trees in the DRY and MES study areas. The five highest elevation trees established in each decade are included in the analyses from each area (transect data). The thick line inside the box indicates the median value, the upper and lower margins the 25th and 75th percentiles, respectively, and the whiskers the value 1.5 times the interquartile range. The circles (MES) outside the whisker indicate outliers. Note the different scales for *y*-axes between panels.

by individuals that were recruited around 1980 (1979, based on mean age at the basal level cores; Table 1). On average, treeline trees from this fir-dominated area had a vertical growth rate of ca. 18 cm yr^{-1} from establishment to tree size (Table 1).

The uppermost tree-sized specimen occurred 86 m above the mean treeline (Fig. 5), and the uppermost specimen, irrespectively of size, occurred 40 m above the current treeline in the transect where it was found. The oldest sampled trees from across the transects dated back to the 1950s, and were found near the current mean treeline elevation (Fig. 5). The treeline position remained more or less stationary since its establishment, but showed

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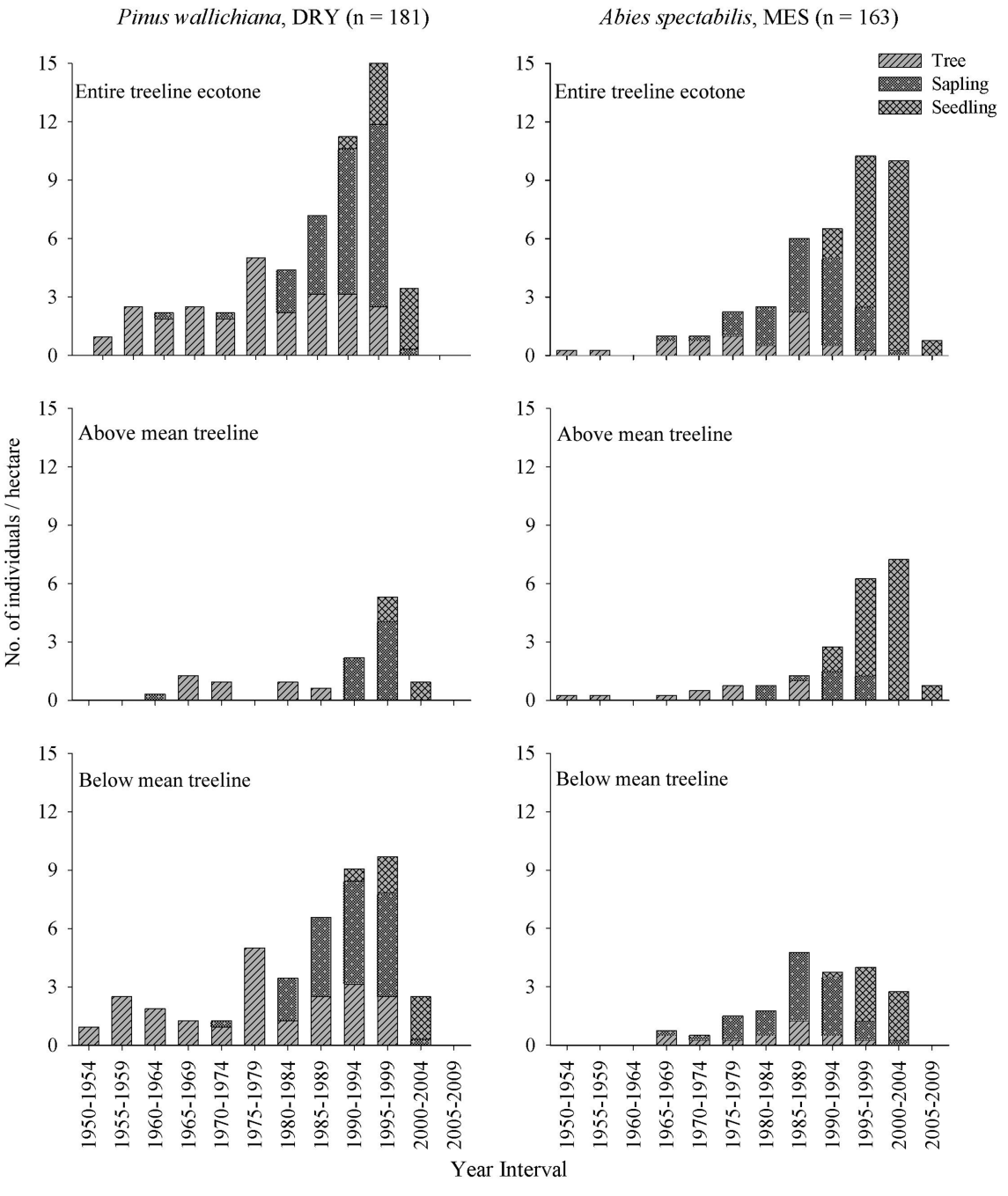

Figure 7: age structure for *Pinus wallichiana* (left) and *Abies spectabilis* (right) trees, saplings and seedlings across the treeline ecotone, and separated into above and below the mean treeline in the DRY and MES study areas.

some minor non-significant fluctuations between decades (Fig. 6).

Age structure and height growth

The age distribution in this area was also dominated by younger age classes, but the pattern was less evident for individuals growing below the mean treeline when analysed separately (Fig. 7). The largest age classes were 1995–99 and 2000–04. Seedlings were particularly abundant above the mean treeline (Fig. 7), and the average total number of individuals per hectare was 40.7. Similar to DRY, all height classes (trees, saplings and seedlings) were present both above and below the mean treeline.

Height, age and vertical growth rate of the trees showed no trend corresponding with the elevation gradient (Fig. 8), but tree height was significantly correlated with both tree age and DBH, and DBH was significantly correlated with age (Fig. 8). In general, vertical growth rates decreased from larger- to

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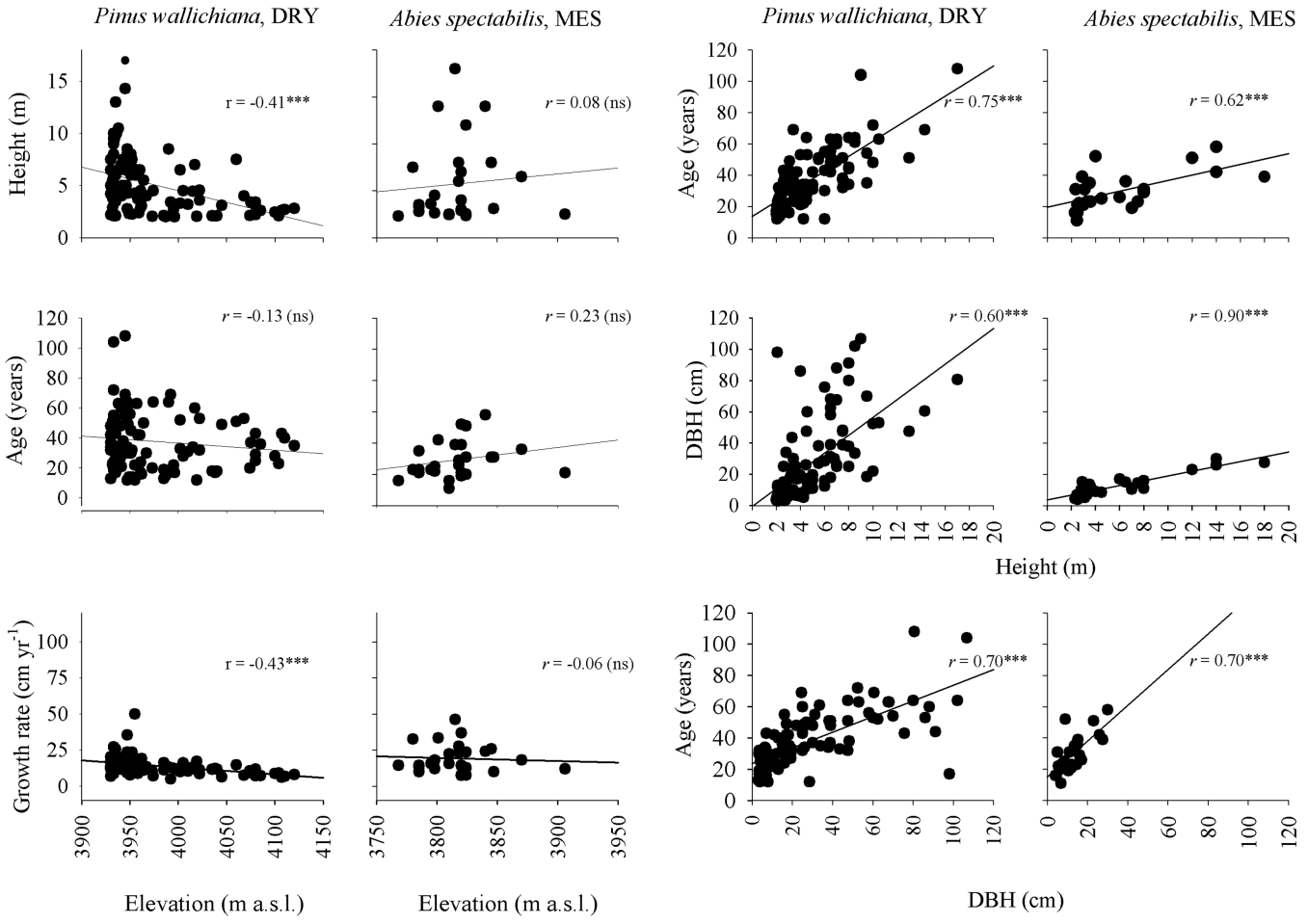

Figure 8: relationships of height, age and vertical growth rate of the trees with elevation in the DRY and MES study areas (left-hand panels). Right-hand panels show inter-correlations between tree parameters (height vs. age; height vs. DBH; DBH vs. age). ns = not significant. ***$P < 0.001$.

Table 2: vertical growth rate (cm yr^{-1}) of trees, saplings and seedlings sampled within transects in the DRY and MES study areas

	Pinus wallichiana, DRY				*Abies spectabilis*, MES			
	Across ecotone	Above mean treeline	Below mean treeline	*t*-test (*P*)	Across ecotone	Above mean treeline	Below mean treeline	*t*-test (*P*)
Trees	14.0 ± 6.2 (96)	8.4 ± 1.6 (12)	14.8 ± 6.2 (84)	$P < 0.001$	19.2 ± 9.9 (26)	16.7 ± 7.1 (8)	20.2 ± 10.9 (18)	ns
Saplings	6.5 ± 1.8 (77)	6.8 ± 1.6 (21)	6.5 ± 2.0 (56)	ns	5.7 ± 2.3 (58)	5.6 ± 1.8 (15)	5.7 ± 2.4 (43)	ns
Seedlings	4.0 ± 1.2 (22)	4.5 ± 1.35 (7)	3.8 ± 1.1 (15)	ns	2.8 ± 1.0 (79)	2.7 ± 1.1 (57)	2.9 ± 0.6 (22)	ns

Numbers of individuals are given in parentheses. Growth rate variations from above and below the mean treeline were tested by a Welch two-sample *t*-test. Mean values are presented with standard deviations (mean ± SD). See Table 1 for elevation of mean treeline. *ns* = not significant.

smaller-sized individuals and were higher for trees below the mean treeline compared to above.

DISCUSSION

Our dendroecological analyses suggest that the investigated treelines have remained approximately stationary over recent decades in contrast to other studies from the greater Himalayan region that report recent treeline advance (Dubey *et al.* 2003; Liang *et al.* 2011). Our analyses also indicate that the current treelines are made up of trees that were established during the same time period, around 1990, in both the dry and mesic environments despite different climate regimes and climatic trends in the two areas. Such contrasting results and climate responses are not unique for the study region (see Aune *et al.* 2011; Harsch *et al.* 2009; Szeicz and Macdonald 1995) and suggest that contrasting climates do not necessarily promote deviating treeline response patterns (Elliott 2012; Lloyd and Fastie 2003).

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Temperature in the greater Himalayan region has shown an overall warming trend during recent decades (IPCC 2007; Mitchell and Jones 2005). The CRU data (see Materials and Methods) for 1950–2005 also suggest a climatic warming trend in the study areas. However, the data available from the nearest climate stations, and validation by means of short-term local climate loggers established at the studied treelines (Shrestha 2013), show that this warming trend is not purely representative of the local climate dynamics in our areas, both in terms of annual trends in seasonal temperature and precipitation patterns, and between-year variability.

Age–structure analyses provide information on temporal variation in the sum outcome of tree recruitment and mortality, and may thus provide insight into species-specific potential for treeline advance (Brubaker 1986; Cullen *et al.* 2001; Wang *et al.* 2006). In the current study, an ecotone-wide analysis of the age structure of both species shows a J-shaped age distribution and overlapping size classes, which taken together indicates that recruitment is balanced by mortality over time (Aune *et al.* 2011; Dalen and Hofgaard 2005; Hett and Loucks 1976; Körner 2003). However, when the data from above and below the mean treeline elevations are analysed separately, size class distribution is variable and the J-shaped pattern mostly disappears. This suggests that recruitment–mortality dynamics vary across the ecotone and should be analysed separately to disentangle population processes operating under different climatic conditions. The J-shaped age structure of the *Abies* population above the current treeline suggests a balanced recruitment–mortality situation with a potential for future treeline advance (Batllori and Gutiérrez 2008). However, close inspection of the data reveals that the seedling density data is influenced by high seedling numbers in a small patch in one transect (shown as a dense seedling patch close to the mean treeline in Fig. 5), and is thus anomalous relative to the whole study area. This seedling patch occurred in a topographic depression (K. B. Shrestha, personal observation) and may reflect a microsite or sheltered environment particularly suitable for germination and survival (Batllori and Gutiérrez 2008; Cullen *et al.* 2001; Peng *et al.* 2012). The low tree and sapling densities throughout the remainder of the MES area suggest that seedling survival and establishment into larger size classes is low.

Harsch and Bader (2011) and Ellenberg (1988) argue that at a climatically driven treeline, trees should become progressively smaller with increasing elevation. The absence of a relationship between elevation and tree height, growth rate, or age thus indicates that the treeline dynamics at the MES area are not climatically driven. This is further supported by the decadal tree recruitment analyses, which show no change in the elevation at which trees establish over time despite a significant warming trend in regional summer temperatures over the past decades. Instead, non-climatic factors are likely to be driving the treeline dynamics, and especially the low recruitment success across the treeline ecotone at this locality. Grazing by ungulate herbivores have been shown to be important determinants of treeline position and tree growth and population structure elsewhere (Cairns *et al.* 2007; Speed *et al.* 2011) and could also be a potentially important factor in the MES area, as young *Abies* individuals have high forage value and may be susceptible to grazing by wild and domestic herbivores, which are abundant at this area (K. B. Shrestha, personal observation). Overall, the treeline in the mesic area provides an example of a stationary treeline despite a regional climatic warming trend.

In the DRY area, there are also indications of a stationary, or even receding, treeline. The elevation at which the uppermost new trees established has declined by >40 m over the past decades and all individuals recruited into the tree size class since 1988 are found below the mean treeline. The growth–elevation relationships indicate that climate is an important factor in the treeline dynamics in this area—the trees found above the mean treeline have significantly reduced height and growth rates relative to those further down (cf. Ellenberg 1988) and numbers of young seedlings are low across the ecotone and especially at high elevations. Decreasing summer temperatures is one potential explanation factor for the dynamics at this treeline, as the summer temperatures have been relatively low during the past decades, despite no significant overall trend over the entire data series. Alternatively, it has been argued that relatively stable temperature conditions over time will tend to provide more consistent and favourable conditions for seed production and establishment than a variable climate (Camarero and Gutierrez 2004; Danby and Hik 2007; Szeicz and Macdonald 1995; Wang *et al.* 2006). Hence, the stationary to recessive treeline development in the dry area could be related to high interannual climatic variability observed in this area over the past decades. Increased climatic variability increases the probability of encountering sub-optimal temperatures. Such climate anomalies are expected to be more harmful at more exposed higher elevations, where the growing season may be very short during especially cold years and severe drought events may occur during low-precipitation anomalies, thus reducing the growth and survival potential of tree recruits (Germino *et al.* 2002; Richardson and Friedland 2009; Shen *et al.* 2014). The high frequency of saplings relative to seedlings in the dry area is indicative of a recently reduced potential for treeline advance and infilling (Mathisen *et al.* 2013), which could be related to the processes discussed above as there has been both relatively low summer temperatures, low precipitation and high climatic variability in the past decade. Overall, the treeline dynamics and population structure in the DRY area suggest a current stationary or receding treeline, possibly driven by increased regional climatic variability, and especially higher frequency of cold summers negatively impacting both recruitment and growth into the tree size class (Elliott and Kipfmueller 2011).

In conclusion, our two study areas in the Nepalese Himalaya differ in climate, environment, tree species and recent seasonal climate trends, yet the treeline dynamics are similar. In both areas, the current treelines established during

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the same period and show stationary or even receding behaviour over the past decades. However, the underlying ecological relationships and population dynamics differ between the two areas. Our results highlight the importance of considering area-specific treeline drivers and responses for making valid regional treeline assessments and predictions. In both of our study areas, seedlings and saplings are found above the current treeline. Height growth of these established saplings and seedlings could therefore, provided that the current growth rate is sustained, result in treeline advance during the next few decades, irrespective of the future recruitment rate (Camarero and Gutierrez 2004; Smith *et al.* 2009).

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REFERENCES

Anonymous (1995) *Iso-Climatic Map of Mean Annual Precipitation*. Kathmandu, Nepal: ICIMOD.

Aune S, Hofgaard A, Söderström L (2011) Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. *Can J For Res* **41**:437–49.

Batllori E, Gutiérrez E (2008) Regional treeline dynamics in response to global change in the Pyrenees. *J Ecol* **96**:1275–88.

Bekker MF (2005) Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. *Arct Antarct Alp Res* **37**:97–107.

Brubaker L (1986) Responses of tree populations to climatic change. *Vegetatio* **67**:119–30.

Cairns DM, Lafon C, Moen J, *et al.* (2007) Influences of animal activity on treeline position and pattern: implications for treeline responses to climate change. *Phys Geog* **28**:419–33.

Cairns DM, Moen J (2004) Herbivory influences treelines. *J Ecol* **92**:1019–24.

Camarero JJ, Gutierrez E (2004) Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Clim Change* **63**:181–200.

Cullen LE, Stewart GH, Duncan RP, *et al.* (2001) Disturbance and climate warming influences on New Zealand Nothofagus treeline population dynamics. *J Ecol* **89**:1061–71.

Dalen L, Hofgaard A (2005) Differential regional treeline dynamics in the Scandes Mountains. *Arct Antarct Alp Res* **37**:284–96.

Danby RK, Hik DS (2007) Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *J Ecol* **95**:352–63.

Dubey B, Yadav RR, Singh J, *et al.* (2003) Upward shift of Himalayan pine in Western Himalaya, India. *Curr Sci* **85**:1135–6.

Ellenberg H (1988) *Vegetation Ecology of Central Europe*. Cambridge: Cambridge University Press.

Elliott GP (2011) Influences of 20th-century warming at the upper tree line contingent on local-scale interactions: evidence from a latitudinal gradient in the Rocky Mountains, USA. *Glob Ecol Biogeogr* **20**:46–57.

Elliott GP (2012) Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, U.S.A. *Ecology* **93**:1614–25.

Elliott GP, Kipfmueller KF (2011) Multiscale influences of climate on upper treeline dynamics in the southern Rocky Mountains, USA: evidence of intraregional variability and bioclimatic thresholds in response to twentieth-century Warming. *Ann Assoc Am Geogr* **101**:1181–203.

Germino MJ, Smith WK, Resor AC (2002) Conifer seedling distribution and survival in an alpine treeline ecotone. *Plant Ecol* **162**:157–68.

Grace J, Berninger F, Nagy L (2002) Impacts of climate change on the tree line. *Ann Bot* **90**:537–44.

Hagen T (1969) *Report on Geological Survey of Nepal*. Zurich, Switzerland: Denkschriften der schweizerischen Naturforschenden Gesellschaft.

Harsch MA, Bader MY (2011) Treeline form – a potential key to understanding treeline dynamics. *Glob Ecol Biogeogr* **20**:582–96.

Harsch MA, Hulme PE, McGlone MS, *et al.* (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol Lett* **12**:1040–9.

Hett JM, Loucks OL (1976) Age structure models of Balsam fir and eastern Hemlock. *J Ecol* **64**:1029–44.

Heuberger H, Masch L, Preuss E, *et al.* (1984) Quaternary landslides and rock fusion in central Nepal and in the Tyrolean Alps. *Mt Res Dev* **4**:345–62.

Hofgaard A, Dalen L, Hytteborn H (2009) Tree recruitment above the treeline and potential for climate-driven treeline change. *J Veg Sci* **20**:1133–44.

Hofgaard A, Harper KA, Golubeva E (2012) The role of the circumarctic forest–tundra ecotone for Arctic biodiversity. *Biodiversity* **13**:174–81.

Hofgaard A, Lokken JO, Dalen L, *et al.* (2010) Comparing warming and grazing effects on birch growth in an alpine environment - a 10-year experiment. *Plant Ecol Divers* **3**:19–27.

Holtmeier FK (2009) *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Germany: Springer.

Holtmeier FK, Broll G (2007) Treeline advance – driving processes and adverse factors. *Landscape Online* **1**:1–32.

IPCC (2007) Climate Change 2007 - The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC.

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Jason C (1996) *Multiple Comparisons: Theory and Methods*. London: Chapman and Hall.

Körner C (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Berlin: Springer-Verlag.

Körner C, Hoch G (2006) A test of treeline theory on a montane permafrost island. *Arct Antarct Alp Res* **38**:113–9.

Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *J Biogeogr* **31**:713–32.

Li MH, Xiao WF, Wang SG, *et al.* (2008) Mobile carbohydrates in Himalayan treeline trees I. Evidence for carbon gain limitation but not for growth limitation. *Tree Physiol* **28**:1287–96.

Liang E, Wang Y, Eckstein D, *et al.* (2011) Little change in the fir treeline position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytol* **190**:760–9.

Lloyd AH, Fastie CL (2003) Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience* **10**:176–85.

Malanson GP, Resler L, Bader M, *et al.* (2011) Mountain treelines: a roadmap for research orientation. *Arct Antarct Alp Res* **43**:167–77.

Mathisen IE, Hofgaard A (2011) Recent height and diameter growth variation in Scots pine (*Pinus sylvestris* L.) along the Arctic margin: the importance of growing season versus non-growing season climate factors. *Plant Ecol Divers* **4**:1–11.

Mathisen IE, Mikheeva A, Tutubalina OV, *et al.* (2013) Fifty years of treeline change in the Khibiny Mountains, Russia: advantages of combined remote sensing and dendroecological approaches. *Appl Veg Sci*: **17**:6–16.

Miehe G (1982) Vegetationsgeographische Untersuchungen im Dhaulagiri-und Annapurna-Himalaya. *Ph.D. Thesis*. Vaduz: Cramer University.

Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int J Climatol* **25**:693–712.

Ono Y, Sadakane A (1986) *Natural Background of the Yak Transhumance in the Langtang Valley, Nepal Himalaya*. Tokyo, Japan: Tokyo Metropolitan University.

Paulsen J, Weber UM, Körner C (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? *Arct Antarct Alp Res* **32**:14–20.

Peng Z, Zhou S, Zhang D-Y (2012) Dispersal and recruitment limitation contribute differently to community assembly. *J Plant Ecol* **5**:89–96.

Puntieri J, Raffaele E, Martinez P, *et al.* (1999) Morphological and architectural features of young ***Nothofagus pumilio*** (Poepp. & Endl.) Krasser (Fagaceae). *Bot J Linn Soc* **130**:395–410.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Richardson AD, Friedland AJ (2009) A review of the theories to explain Arctic and alpine treelines around the world. *J Sust For* **28**:218–42.

Shen W, Zhang L, Liu X, *et al.* (2014) 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 Meteorol* **187**:83–92.

Shi P, Körner C, Hoch G (2008) A test of the growth-limitation theory for alpine treeline formation in evergreen and deciduous taxa of the eastern Himalayas. *Funct Ecol* **22**:213–20.

Shrestha AB, Wake CP, Mayewski PA, *et al.* (1999) Maximum temperature trends in the Himalaya and its vicinity: an analysis based on temperature records from Nepal for the period 1971–94. *J Climate* **12**:2775–86.

Shrestha KB (2013) Treeline and vegetation dynamics in response to environmental changes in Nepal, the Central Himalaya. *Ph.D. Thesis.* Bergen, Norway: University of Bergen.

Shrestha KB, Vetaas OR (2009) The forest ecotone effect on species richness in an arid trans-Himalayan landscape of Nepal. *Folia Geobot* **44**:247–62.

Smith W, Germino M, Johnson D, *et al.* (2009) The altitude of alpine treeline: a bellwether of climate change effects. *Bot Rev* **75**:163–90.

Speed JDM, Austrheim G, Hester AJ, *et al.* (2011) Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *For Ecol Manag* **261**:1344–52.

Stainton JDA (1972) *Forests of Nepal*. London: John Murray.

Sveinbjörnsson B, Hofgaard A, Lloyd A (2002) Natural causes of the tundra-taiga boundary. *Ambio* **12**:23–9.

Szeicz JM, Macdonald GM (1995) Recent white spruce dynamics at the sub-arctic alpine treeline of north-western Canada. *J Ecol* **83**:873–85.

Tranquillini W (1979) *The Physiological Ecology of the Alpine Timberline*. New York: Springer-Verlag.

Wang T, Zhang QB, Ma K (2006) Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. *Glob Ecol Biogeogr* **15**:406–15.

Woodall CW, Oswalt CM, Westfall JA, *et al.* (2009) An indicator of tree migration in forests of the eastern United States. *For Ecol Manag* **257**:1434–44.

Xu J, Grumbine RE, Shrestha A, *et al.* (2009) The melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods. *Conserv Biol* **23**:520–30.

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