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How does the stand structure of treeline-forming species shape the treeline ecotone in different regions of the Nepal Himalayas?

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Abstract: Stand structure dynamics are considered as major happenings in any forest as a response to environmental changes. However, this important topic is underrepresented in the treeline studies in the Nepal Himalayas. We aimed to investigate site- as well as species-specific changes in morphometric features (basal diameter, crown cover, density, and height) along the elevational gradient across treeline ecotones in response to recent environmental changes. The stand structure characteristics of *Abies spectabilis*, *Pinus wallichiana*, and *Betula utilis* across the treeline ecotone of three study sites in Eastern (Barun), Central (Manang), and Western (Dhorpatan) Nepal were analyzed to elucidate structural heterogeneities. Altogether, eight transects (20 m × (60–250 m)) across the treeline ecotone were established. Trees of all life forms, trees (> 2 m), saplings (0.5–2 m), and seedlings (< 0.5 m), within each transect were enumerated and sampled for the morphometric features and age. Site-specific and species-specific stand structure dynamics were found. The rate of basal area increment was higher in Barun, but the Manang treeline, despite profound regeneration in recent years, had a low annual basal area increment. Moreover, the altitudinal distribution of age and morphometry were not consistent among those ecotones. Furthermore, intra-specific competition was not significant. The site-specific stand structure dynamics explain why treelines do not respond uniformly to increasing temperature. It invokes, in further studies, the incorporation of the tree's morphometric adaptation traits, phenotypic plasticity, and interactions between species genotype and the environment.

Keywords: Climate change; Morphometry; Nepal Himalayas; Stand structure; Treeline; Tree-rings

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Introduction

The treeline (uppermost elevation of an individual tree, > 2 m height) ecotone is a transition zone (Cairns and Malanson 1998; Moen et al. 2008) starting from the forest line (uppermost elevation of a closed stand with at least 30% cover in a forest area of at least 500 m^2 (Holtmeier 2009; Chhetri and Cairns 2015; Liang et al. 2016; Tiwari et al. 2017a) to the tree species line (upper elevation of treeline-forming species in any life form). It is considered a temperature limited ecotone (Gosz and Sharpe 1989; Körner 1998), especially the root zone temperature during the growing season (Holtmeier and Broll 2020). This conspicuous transitional zone is highly responsive to environmental changes (Körner and Kullman 1998; Moen et al. 2008; Körner 2012). Environmental conditions become progressively harsher upslope with decreasing temperature, increased wind speed, long-standing snow cover, and several other factors unfavorable for life processes (e.g., germination, survival, growth, and regeneration) of the treeline-forming species (Körner 2003; Schickhoff 2005). Besides temperature, topography governed non-climatic, edaphic, and moisture limiting factors (Cairns and Malanson 1998), altered disturbance regimes (Liang et al. 2016) (such as abiotic disturbances (Moen et al. 2008), and biotic interactions like competition or facilitation (Cairns and Moen 2004; Moen et al. 2008; Sigdel et al. 2020) and herbivory (Cairns and Moen 2004; Moen et al. 2008)) also influence treeline ecotone structure and processes. The treeline ecotone responds to environmental change by changing the growth-forms (Cairns and Malanson 1998; Devi et al. 2008; Harsch et al. 2009; Holtmeier 2009; Hagedorn et al. 2014), demographic conditions (e.g. recruitment, mortality) (Camarero and Gutiérrez 2004; Moen et al. 2008; Schickhoff et al. 2015; Schwab et al. 2017), spatial patterns (Sigdel et al. 2020), and ecotone position (Cairns and Moen 2004; Camarero and Gutiérrez 2004; Devi et al. 2008; Harsch et al. 2009; Gaire et al. 2014; Chhetri and Cairns 2015; Shrestha et al. 2015a; Crofts and Brown 2020).

Treeline ecotones in the Himalayas show uniqueness in position, physiognomy, and species composition (Schickhoff 2005; Chhetri and Cairns 2015; Schickhoff et al. 2015; Shrestha et al. 2015a; Sigdel et al. 2018a, 2020). The variation in tree physiognomies and the significance of patterns, formations, locations, and dynamics of the treelines in response to environmental change are worth studying. The treeline physiognomies are determined by morphometric variations, spatial presence of individuals or patches of trees, and availability of distinctive tree growth forms. As seedling growth and mortality rate depend critically on the climatic conditions, physiognomy renders different pictures of treeline dynamics under different climatic influences (Holtmeier 2009).

The difference in physiognomy results in the difference in treeline dynamics (Martínez et al. 2011). Transition in the morphometric characteristics (such as basal diameter, crown cover, density, and height) depend on a subtle balance between mortality and tree growth across the ecotone space (Wiegand et al. 2006; Martínez et al. 2011). For example, smaller upright trees and deformed krummholz grow towards the upper limit of the ecotone due to the severity of stressors (insufficient temperature and strong wind velocity), and competition with the neighboring individual trees (Körner 1998; Harsch and Bader 2011). Vertical tree growth rate (shoot elongation) is higher at the lower elevation levels as compared to the higher elevation levels (Takahashi and Yoshida 2009; Shrestha et al. 2015b). Changes in tree growth forms are crucial to understanding the effect of climate on treeline populations (Lavoie and Payette 1992). Several studies have reported that treeline shift occurs when the tree density changes in response to global warming (Szeicz and MacDonald 1995; Camarero and Gutiérrez 2004; Gaire et al. 2014; Suwal et al. 2016; Tiwari et al. 2017a). However, some studies have also considered that the spatial variation in tree growth forms and tree sizes (Weisberg and Baker 1995), competition, and the facilitative interactions among close neighboring plants along abiotic stress gradients (Bertness and Callaway 1994; Venn and Morgan 2009; Liang et al. 2016; Sigdel et al. 2020) are some of the main controlling factors for spatial patterns and treeline dynamics. Furthermore, micro-environmental heterogeneity and land-use changes also affect the vegetation structure in treeline ecotones (Batllori and Gutiérrez 2008; Batllori et al. 2009).

Most of the treeline studies from the Nepal Himalayas have focused on the recruitment pattern (Gaire et al. 2014; Chhetri and Cairns 2015; Shrestha et al. 2015a; Tiwari et al. 2017b; Chhetri and Cairns 2018; Sigdel et al. 2018a), tree radial growth (Shrestha et al. 2015b; Chhetri and Cairns 2016; Sigdel et al. 2018b; Gaire et al. 2020), and treeline position (Gaire et al. 2014; Suwal et al. 2016; Chhetri et al. 2017) in response to climate change. There is a site- and species-specific recruitment pattern and treeline dynamics in the Nepal Himalayas (Gaire et al. 2014, 2017; Tiwari and Jha 2018). For example, poor regeneration (Chhetri and Cairns 2015, 2018; Shrestha et al. 2015a; Gaire et al. 2017) and higher recruitment (Suwal et al. 2016; Gaire et al. 2017; Tiwari et al. 2017b), stable treeline (Gaire et al. 2014, 2017; Schickhoff et al. 2015; Shrestha et al. 2015a), and advancing treeline (Gaire et al. 2014; Suwal et al. 2016; Tiwari et al. 2017b; Sigdel et al. 2018a), recent growth decline (Tiwari et al. 2017b; Aryal et al. 2020), and increased growth (Gaire et al. 2020) indicate inconsistencies in spatiotemporal patterns, process, and dynamics. The variations indicate the complexity of treeline processes and forest functioning governed by climatic factors, site- and species-specific traits, and possibly physiognomy. However, studies on the changes in stand stature or morphometric features of the treeline ecotone in response to climate change have not yet been carried out in these areas. Changes in the growth form can modify the microenvironment, which can ultimately influence the recruitment process (Camarero and Gutiérrez 1999). Crown cover changes bring differences in soil temperature during the growing season and may limit recruitment (Liang et al. 2016). The morphometric features of the treeline can also help to explain the reasons for the non-uniform response of the treelines to the changing climate and reflect the relative importance of the tree's adaptive strategies and mechanisms along environmental gradients (Meng et al. 2009).

This study elucidates how the treeline dynamics of treeline forming species have been affected by the changes in morphometric characteristics in the treeline ecotone of different regions of the Nepal Himalayas, in the different lines with current and hitherto treeline studies focusing on treeline dynamics and tree ring analysis. Morphometric analysis was assumed to help answer several questions concerning the change in the role of high-mountain tree stands as a carbon sink during their dynamics (Moiseev et al. 2016).

The study was carried out in treeline ecotones from three different regions harboring three treeline-forming species (*Abies spectabilis*, *Betula utilis*, and *Pinus wallichiana*) to investigate: i) how the morphometric features (e.g., basal diameter, crown cover, density, and height) change along the elevational gradient across treeline ecotones, ii) whether these morphometric changes are site-specific or species-specific, and iii) how the basal area increment varies with species and areas.

1 Materials and Methods

1.1 Study area

Studies were carried out in the treeline ecotone sites formed by *Abies spectabilis* (Yangle, Barun), *Pinus wallichiana* (Ngawal, Manang), and *Betula utilis* (Rugakharka, Dhorpatan), representing the eastern, central, and western regions of the Nepal Himalayas (Figure 1). Yangle (27.75° N; 87.15° E; 3900–4000 m above sea level (asl)), situated in Barun Valley is traversed by Barun Khola, a tributary of the Arun river that constitutes a major part of Makalu Barun National Park (MBNP). The valley lies within the subtropical Asian monsoon zone, characterized by considerable summer rainfall between June and September (Chhetri and Cairns 2016). Ngawal (28.65° N; 84.10° E; 3900–4025 m asl) is the south-facing site in Manang valley, a trans-Himalayan arid region in Annapurna Conservation Area (ACA). Manang receives around 840 mm annual rainfall (Shrestha et al. 2015a) as the south-west monsoon fails to cross the high mountains of the Annapurna range. Rugakharka (28.55° N; 83.17° E; 3550–3900 m asl) is located in the eastern part of Dhorpatan Hunting Reserve (DHR). The climate of DHR varies from its low elevation (subtropical) to high elevation levels (alpine). Monthly average temperature (Barun: 3.55°C, Manang: 5.24°C, Dhorpatan: 6.34°C) and precipitation (Barun: 1367 mm, Manang: 851 mm, Dhorpatan: 1206 mm) trends of the three study sites (average of grids in Barun: 27.25°–27.75° N, 86.75°–87.25° E and 27.75°–28.25° N, 86.75°–87.25° E; Manang: 28.5°–29.0° N and 84.0°–84.5° E, Dhorpatan: 28.0°–28.5° N, 83.0°–83.5° E and 28.5°–29.0° N, 83.0°–83.5° E) according to long-term (1901–2019) climatic research unit (CRU TS v4.04) data (Harris et al. 2020) are presented in Figures 2a and 2b. Clear trends (increasing or decreasing) were not observed in the precipitation data. However, increasing trends were observed for

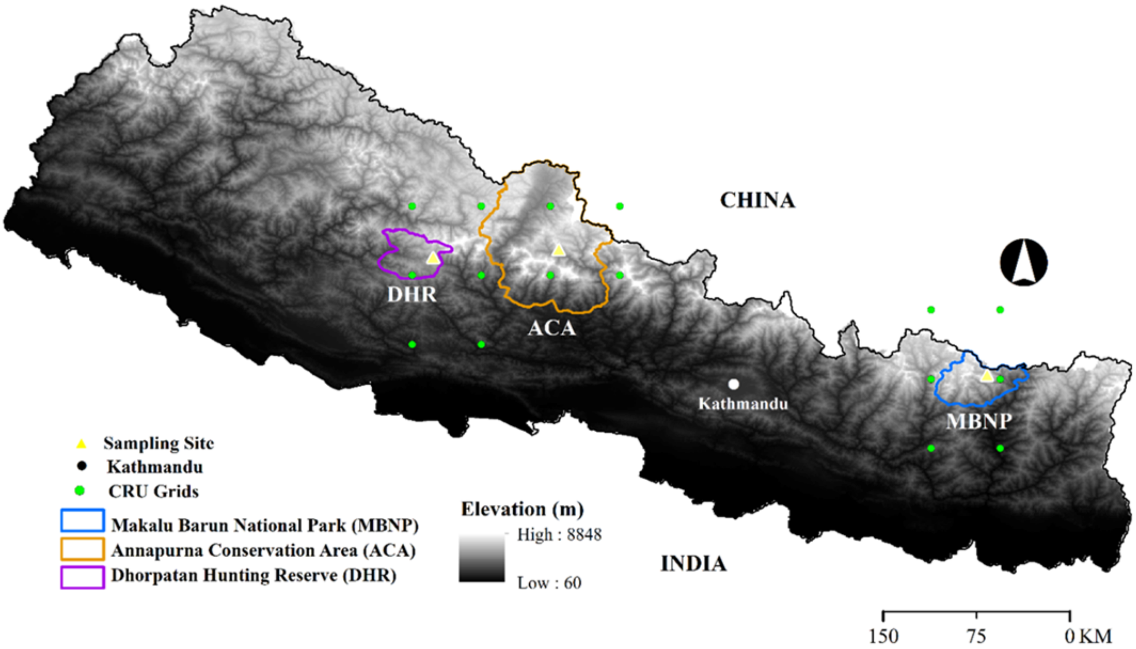

Figure 1 A map showing the three study sites (MBNP – Makalu Barun National Park, eastern Nepal; ACA – Annapurna Conservation Area, central Nepal; and DHR – Dhorpatan Hunting Reserve, western Nepal). Green dots are grids for Climatic Research Unit (CRU) climate data.

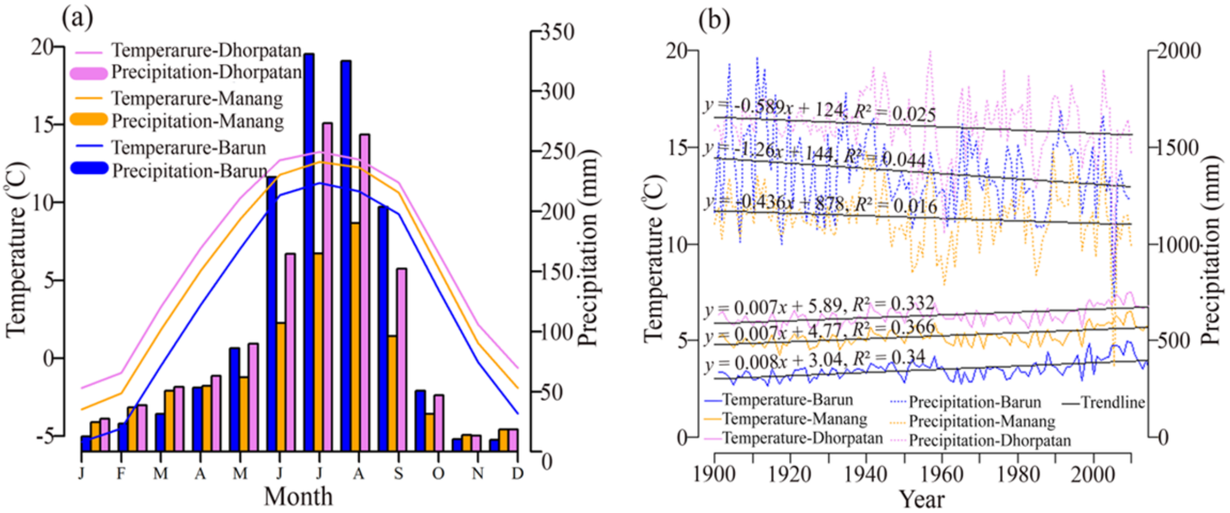

Figure 2 Average monthly (a) and average annual (b) temperature and precipitation in the study sites (Barun, Manang, and Dhorpatan). Data Source: Climatic Research Unit (CRU) (Harris et al. 2020).

the annual temperatures in all the sites, particularly after 1960 (Figure 2b).

1.2 Tree species

Abies spectabilis (Himalayan silver fir), *P. wallichiana* (Himalayan blue pine), and *B. utilis* (Himalayan birch) were studied as representative treeline-forming species from the sub-alpine forests of Barun, Manang, and Dhorpatan, respectively. These three tree species (*A. spectabilis, P. wallichiana*, and *B. utilis*) are the dominant treeline forming species in the ecotone at their respective sites (Chhetri et al. 2017). *Abies spectabilis* is a tall, pyramidal, evergreen tree species, which dominates sub-alpine forests of the central Himalayas at an elevation of 2700–4200 m asl in Nepal (Chhetri and Cairns 2015). Trees of this species are characterized by low branches with dense foliage. *Abies spectabilis* is the dominant treeline-forming tree in Barun with a dense thicket of understory *Rhododendron campanulatum* growing profusely in the ecotone. *Pinus wallichiana* is the dominant tree species in the Manang treeline ecotone with scant *Juniperus indica* and prostrate *J. squamata*. *Pinus wallichiana* is an evergreen conifer found at an elevation of 1800–4200 m asl (Ghimire et al. 2010). This Himalayan pine (*P. wallichiana)* is primarily confined to the dry central and western regions of Nepal. Local people use this species as an important source of timber and fuel (Ghimire et al. 2010). *Betula utilis* is a moderately sized (< 20 m tall), broadleaved, pioneer tree species native to the Himalayas and is found at an elevation of 2700–4500 m asl (Tiwari et al. 2017b). The species is dominant among the broadleaved tree species in the sub-alpine region of the Himalayas and localized in the moist and shady areas, where snow remains until the end of spring and sometimes even in summer (Shrestha et al. 2007).

1.3 Field sampling

Transects (three in Barun and Manang; two in Dhorpatan) were laid down from the forest line up to the tree species line, crossing the treeline in each study site (Table 1). All the tree species within the transects were enumerated and classified into three height classes: trees (> 2 m), saplings (0.5–2 m), and seedlings (< 0.5 m) (Wang et al. 2006; Kullman 2007). Forest line, treeline, and tree species line were determined by following the method used by Chhetri and Cairns (2015) and Shrestha et al. (2015a). Basal diameter (BD) and diameter at breast height (DBH at 1.37 m above ground level) of each tree were measured. The height of the trees was measured using a clinometer. Seedling and sapling heights were measured with a wooden scale. Crown cover was measured using a wooden scale and measuring tape. The crown diameter was measured twice for each sampling unit. The first measurement was along the widest crown and another measurement was taken at a right angle to the first, and both were averaged for the crown diameter (Krajicek et al. 1961). Elevation and geographical coordinates for each tree species individual were recorded using a handheld GPS, the accuracy of which was ensured with a nearby reference point in Dhorpatan.

Tree cores (Barun - 48, Manang – 88, Dhorpatan - 36) were collected from the base of the tree for age determination. There were 31 (17 trees), and 18 (12 trees) tree cores collected from Manang, and Dhorpatan for basal area estimation. To reduce the error with the reaction wood effect in basal area estimations, the cores were taken along the contour, i.e., trees were bored at a right angle to the slope (Lebourgeois 2000). The age of sapling and seedlings was determined by the branch whorl and scar count methods (Aune et al. 2011).

1.4 Stand competition and growth conditions

All three treeline ecotones sites had mono-dominant treeline forming species. Stand-level crowding of these species (in terms of density, basal area, and crown coverage) can provide some indication of intraspecific interaction. It is assumed that stands of a higher density, higher basal area and higher coverage of crown may have higher competition which in turn influences tree growth dynamics and may indicate the stand growth and productivity. Within-stand competition is explained by variables such as stand density/individual or tree density, total basal area

Table 1 Site characteristics of Barun (eastern Nepal), Manang (central Nepal), and Dhorpatan (western Nepal)

Characteristic parameters	Study sites / Species		
	Barun *Abies spectabilis*	Manang *Pinus wallichiana*	Dhorpatan *Betula utilis*
Number of plots	3	3	2
Transect size (m × m)	20 × (60-140)	20 × 250	20 × 120
Treeline ecotone (m asl)	3950-4100	3910-4180	3870-3905
Aspect	South	South	North
Average slope (°)	30-35	30-35	35-40
Number of tree cores collected at base	48	88	36
Number of tree cores collected at breast height	-	31 (17 trees)	18 (12 trees)

per hectare, quadratic mean diameter, stand density index (Shaw 2006), and crown competition factors (Krajicek et al. 1961).

1.4.1 Stand stocking

Reineke's Stand Density Index (SDI) is a relative measure of competition in forest stands and indicates the crowding in forest stands by comparing the availability of space for growth per tree with the growing space available to trees of the same size from the species in some reference conditions (Shaw 2006). This index uses the stand's quadratic mean diameter (which is the measure of average tree diameter per tree basal area) calculated from the total basal area of the stand divided by the total number of trees (Curtis and Marshal 2000). SDI was calculated using the formula (Shaw 2006):

$$SDI = TPHa\left(\frac{Dq}{25.4}\right)^{1.605}, \quad (1)$$

where, TPHa = trees per hectare, Dq = Quadratic mean diameter (cm) and

$$Dq = \sqrt{\frac{BA}{k \times n}}, \quad (2)$$

where, BA = total stand basal area in m², k = a constant whose value is 0.0000785 when the basal area is in a square meter, Dq is in cm, n = number of trees (Curtis and Marshal 2000).

Crown competition factor (CCF) is another measure of stand density to compare the availability of growing space per tree with the vertical projection of the average growing space (average crown) of an open-grown tree with the same diameter at breast height, calculated as (Krajicek et al. 1961):

$$\text{CCF} = \text{Total MCA/Area in acres}, \quad (3)$$

where MCA (Maximum Crown Area is the maximum area (percentage of an acre) that could be occupied by the crown of a tree. CCF is the percentage of crown coverage in the stand. So, 100 CCF means a closed crown with greater competition.

1.4.2 Basal area increment (BAI)

Basal area increment (BAI) is calculated to estimate the trends in tree growth (annual growth rates) among the species and sites. For this purpose, 35 (35 trees), 31 (17 trees), and 18 (12 trees) tree cores were used from Barun, Manang, and Dhorpatan, respectively. Climate-growth relationships from the core samples from these forest stands have already been analyzed (see Shrestha et al. 2015b; Chhetri and Cairns 2016; Bista and Chhetri 2020). The collected tree radii were used to analyze the retrospective basal area increment in those stands. After measurements of tree ring width using a Velmex measuring system, with 0.001 mm precision, a visual cross-dating approach was used using spaghetti and segment plots of the individual ring-width series produced by using 'dplR' (Bunn 2008) in R software (Version 3.6.1, R Core Team 2019) to calculate the accuracy of tree age determinations from tree-ring cores. Because BAI is more closely related to tree biomass increment and net productivity (Motta and Nola 2001; Popa et al. 2017), the ring width measurements were then converted into BAI for quantifying tree growth. This transformation was made to facilitate the assessment of how different tree species from the corresponding study sites respond differently to climate change. This metric shows growth trends independent of tree age, which is biologically significant (Marqués et al. 2016). The formula used for calculating BAI is as follows:

$$BAI = \pi(R_t^2 - R_{t-1}^2), \quad (4)$$

where, R is tree radius, and t is the year of tree ring formation (Biondi and Qeadan 2008).

1.5 Data analysis

Linear regression analysis was used to establish the relationship between morphometric characteristics (age, height, basal diameter, and crown cover) and elevation (R software - Version 3.6.1, R Core Team 2019). A nonparametric Mann-Whitney U-test was performed for the above-mentioned tree characteristics of the three different species (*A. spectabilis*, *P. wallichiana*, and *B. utilis*) representing the three study sites (Camarero and Gutiérrez 1999).

2 Results

2.1 Treeline ecotone characteristics

The oldest trees in Barun, Manang, and Dhorpatan were established in 1790, 1900, and 1910, respectively. The *A. spectabilis* treeline at

Barun was found to be the oldest in all the three study sites and has remained stable since 1925. *Pinus wallichiana* and *B. utilis* treelines at Manang and Dhorpatan were advancing until around 1950 and started to decline afterwards. Saplings were most abundant in Manang, whereas seedlings were equally abundant in all the sites (Figure 3).

The *P. wallichiana* treeline in Manang was in the highest elevation amongst the three ecotones. The elevation of the forest line was highest in Barun (Table 1). *Abies spectabilis* from Barun had the highest number of total individuals and number of trees. The mean age was nearly similar in all three sites. The average crown cover and height were highest in Manang and lowest in Barun. Mean basal diameter was highest in Manang and lowest in Dhorpatan (Table 2).

2.2 Stature change along an elevation gradient

Abies spectabilis tree age increased with

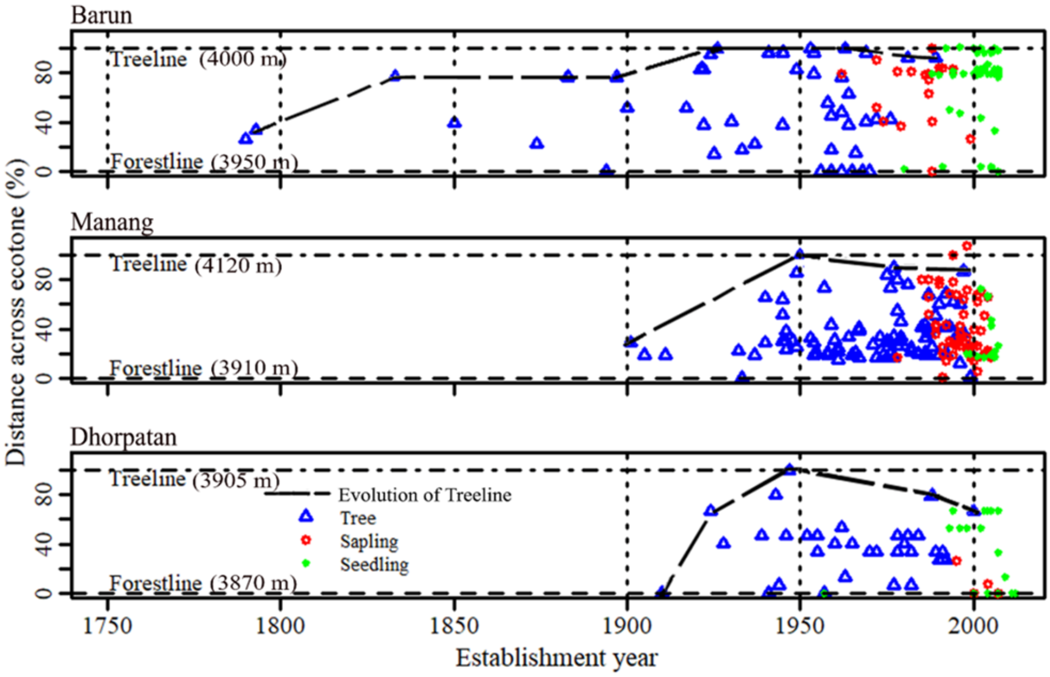

Figure 3 Treeline structure, establishment pattern, and evolution in Barun, Manang, and Dhorpatan. The distance across ecotone (%) was calculated by using following equation (Chhetri and Cairns 2015): $\frac{Elevation\ of\ individual\ (m\ asl) - Forestline\ elevation\ (m\ asl)}{Treeline\ elevation\ (m\ asl) - Forestline\ elevation\ (m\ asl)}$. For example, 50% in y-axis for Barun corresponds to a tree with an elevation of 3975 m in the ecotone with forest line at 3950 m and treeline at 4000 m.

Table 2 Measured and calculated structural characteristics of the studied treeline ecotones

Characteristic parameters	Study sites / Species		
	Barun *Abies spectabilis*	Manang *Pinus wallichiana*	Dhorpatan *Betula utilis*
Mean treeline (m asl)	4000	4120	3905
Mean forest line (m asl)	3950	3910	3870
Density (Individuals/ha)	752.50	104.00	387.50
Tree density (No. of trees/ha)	139.00	58.00	141.60
Mean age (years ± SE)	28.00 ± 2.40	26.00 ± 1.70	31.00 ± 2.00
Mean height (m ± SE)	0.90 ± 11.00	3.80 ± 0.55	3.01 ± 0.29
Mean basal diameter (cm ± SE)	21.19 ± 1.90	23.96 ± 2.40	16.88 ± 2.10
Quadratic mean diameter (cm)	65.48	37.93	25.22
Basal area (cm²/ha)	758654.10	117442.00	62400.38
Stand density index (SDI)	1074.31	110.38	69.19
Mean crown cover (m² ± SE)	5.10 ± 0.65	12.00 ± 1.57	11.96 ± 4.11
Crown competition factor (CCF)	21.05	11.60	9.88

elevation in Barun. Even though the correlation is weaker, the trend was statistically significant (Figure 4). There was no significant trend (decreasing or increasing) observed with respect to elevation in the other two study sites – Manang and Dhorpatan. Height increased with increasing elevation in Barun (significantly). In contrast, tree height significantly decreased in Manang. However, the relationship was not significant in Dhorpatan. Basal diameter decreased with increasing elevation in Manang, although the relationship was not significant. The relationships were not clear in Barun and Dhorpatan as well. Crown cover was found to decrease with increasing elevation in all the study sites, although the association was statistically significant only for *A. spectabilis* in Barun (Figure 4).

2.3 Stature difference among study sites and species

Non-parametric Mann Whitney tests suggest that the height and crown cover vary significantly among the study sites or species. There was no significant difference in age structure between Barun (*A. spectabilis*) and Manang (*P. wallichiana*), but between Barun (*A. spectabilis*) and Dhorpatan (*B. utilis*), the difference was significant. The difference in basal diameter among study sites was not significant (Table 3) even though the variables like quadratic mean diameter and basal area per hectare varied among the sites (Table 2).

2.4 Basal area increment (BAI) and competition indices

BAI showed varied growth patterns in the three treeline forming species. All three species showed multiple growth plateaus and peaks. *Abies spectabilis* was found to have a high growth rate compared to *P. wallichiana* and *B. utilis*. The BAI of *A. spectabilis* exhibited an increasing growth trend over the study period. BAI of *P. wallichiana* exhibited increased growth rates coinciding with the establishment surge in the 1970s. Similarly, it showed a positive growth rate of *B. utilis* after 1990 (Figure 5).

Having a comparatively higher basal area per hectare, the quadratic mean diameter was larger (65.5 cm) in trees in Barun than in Manang (37.9 cm) and Dhorpatan (25.2 cm) (Table 2). The stand density index showed higher stocking in Barun (SDI = 1074.3) compared to Manang (SDI = 110.38)

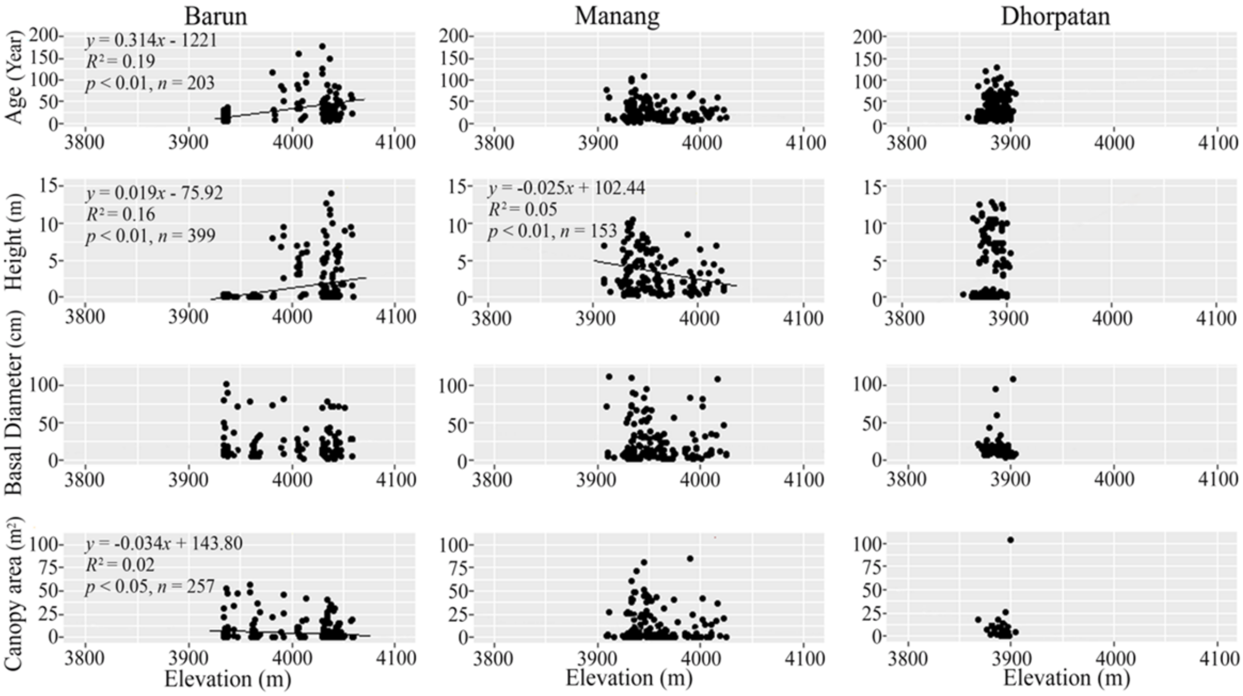

Figure 4 Relationships between stand characteristics (Age, Height, BD - Basal Diameter, Crown Cover) and elevations in Barun, Manang, and Dhorpatan. Only the significant associations have been explained with trend lines.

Table 3 Mann Whitney Test and Z-score value (the numbers in bold indicate significance at $p < 0.01$)

	Abies spectabilis				*Pinus wallichiana*			
	Age	Height	BD	Crown cover	Age	Height	BD	Crown cover
Pinus wallichiana	-1.4	**-13.9**	-1.3	**-6.3**	-	-	-	-
Betula utilis	**-3.2**	**-9.1**	0.1	**-4.5**	1.6	**-5.1**	-0.9	-0.9

Note: BD - Basal Diameter.

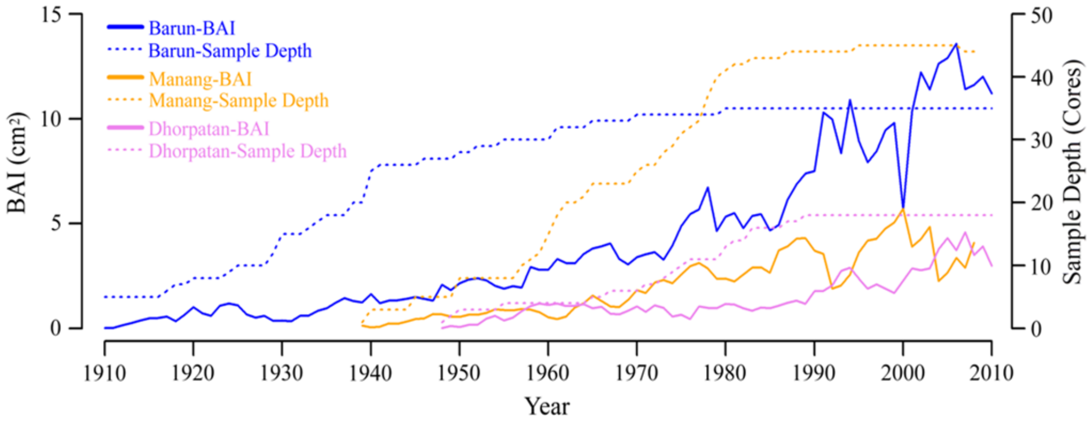

Figure 5 Basal Area Increment (BAI) trend in the three study sites (Barun, Manang, and Dhorpatan). Solid lines indicate BAI, dashed lines indicate the number of trees to estimate the BAI. Blue, Yellow and Pink colors represent Barun, Manang, and Dhorpatan, respectively.

and Dhorpatan (SDI = 69.19). The SDI implies, for example, in Dhorpatan, that only 69 birch individuals with a DBH of 25.4 cm in a hectare were estimated, whereas in Barun, 1074 trees of a 25.4 cm DBH were estimated per hectare. Within-stand competition was therefore higher in Barun. In terms of crown competition, CCF showed low crown coverage in all the ecotones.

3 Discussion

Worldwide, treelines are not ubiquitously responding to climate change, due to multiple factors controlling the treeline (Holtmeier 2009). Complex interactions between external mechanical forces (Körner 2012), genotype (Johnson et al. 2017), environmental changes (Hagedorn et al. 2014), and plant developmental history, shape plant morphology (Hou et al. 2011). Hence, physiological or morphological adaptation of a tree species explains the impact of climate on tree growth survival and reproduction at the treeline ecotone (Hou et al. 2011). On the other hand, these morphometric changes result in a modification in canopy depth, cover, and gap dynamics thereby altering essentials like light interception, atmospheric exchange process, nutrient, and water absorption (Hou et al. 2011). This suggests that stand structure of treeline-forming species shapes the treeline ecotone and ultimately how the treeline will respond to climate change.

3.1 Treeline ecotone characteristics

In general, height pattern and growth forms in the treeline are adaptive features against thermic constraints (Körner 1998; Camarero and Gutiérrez 2001). The diffused form of treeline ecotone was found at Barun and Manang, formed by *A. spectabilis* and *P. wallichiana*, respectively, indicating that the treelines are controlled by the climate (Chhetri and Cairns 2015; Shrestha et al. 2015a). In contrast, the *B. utilis* treeline ecotone at Dhorpatan appeared narrower and abrupt (Chhetri and Cairns 2018), which suggests sharp environmental heterogeneities, local phenomena, and disturbances (Camarero and Gutiérrez 2001). There is always a browsing and trampling risk for young individual trees (Cairns and Moen 2004). The presence of a minimal number of young individuals in Dhorpatan (Figure 3) further supports this argument (Chhetri and Cairns 2018). This means only a few individuals of seedlings and saplings could achieve the tree stages.

The smaller value of stand age at Barun compared to Manang and Dhorpatan might also be attributed to the higher number of young individuals. The reverse J-shaped age structure of *A. spectabilis* in Barun indicated good regeneration in the undisturbed area (Chhetri and Cairns 2015) with a very high frequency of seedlings although evidence suggests a higher juvenile mortality. At the Manang treeline ecotone, younger age classes dominated the age distribution (Shrestha et al. 2015a) with a higher proportion of juveniles clustering at the lower elevation. The age structure in Dhorpatan showed the occurrence of seedlings and saplings of *B. utilis* below the forest line but very poor regeneration in the open area above the forest line where spatial analysis revealed poor clustering (Chhetri and Cairns 2018). These age structure analyses suggest that stand age is a species-specific characteristic governed by local phenomena in different areas. Polychromy (multi stems) was prevalent at Manang (*P. wallichiana*) and Dhorpatan (*B. utilis*). Traumatic reiteration (shoot emergence from trunk or branch; Légère and Payette 1981) results from winter injuries and herbivory. At the marginal limit of tree growth, the polychromy may be the response of winter stress such as wind abrasion, snow and ice damage, and winter desiccation (Devi et al. 2008, Hagedorn et al. 2014) inducing the decline of apical meristematic dominance so that branches or whorls develop into clusters of new trees (Légère and Payette 1981). Polychromy is therefore an adaptive feature developed in treeline trees for combating harsh environmental conditions. Disturbances are assumed to be the likely cause of polychromy because there were less frequent multi-stemmed younger trees. In ameliorated conditions, prevalence of polychromy decreases (Devi et al. 2008). In the current study though, it is difficult to disentangle the synchronicity of climatic favorability and disturbance releases. Considering current regeneration, if factors like shrub cover, human disturbances, and topography were not a hinderance, the *A. spectabilis* treeline at Barun may advance in the future (Chhetri and Cairns 2015). However, it is less likely that treeline advance will be triggered with the current rate of increasing temperatures in Manang and Dhorpatan with poor regeneration in and above treeline (Shrestha et al. 2015a; Chhetri and Cairns 2018).

3.2 Change in stature along an elevational gradient

Quite different morphometric features were observed among the studied sites and species. In the ecotone of thermal and wind constraints, trees develop physiological and mechanical adaptive strategies in crown architecture, branching pattern, or in stunted height (Körner 2012). This suggests that species in the treeline ecotone environment invest more in morphometric growth or for making stature more adaptive than in generating new individuals. Having argued on morphometry, a point to consider is that allometric relationships in tree size (i.e. basal diameter, crown, and height parameters) of conifers are different from those of angiosperms (Carnicer et al. 2013).

Variation in tree morphometry in the study sites indicates that multiple factors determine treeline positions. Physiognomy, besides climatic factors, is influenced by shrubs (Chhetri and Cairns 2015), ground vegetation, and anthropogenic activities (Shrestha et al. 2015a; Chhetri et al. 2017). For example, in the Barun treeline, dense *R. campanulatum* shrub layers hinder seed dispersal and germination upslope resulting in lower density and basal area (Chhetri and Cairns 2015). In contrast, in Manang, the *J. squamata* thicket provides a nurturing facility for seedling establishment to densification in the upward elevational ranges in the treeline (Shrestha et al. 2015a). In Dhorpatan, herbivory pressure seems to suppress recruitment upslope and elevational changes in morphometry (Chhetri and Cairns 2018). So even under warming climatic scenarios, these controlling factors can mask the climatic favorability in the ecotone.

3.3 Difference in stature among study sites and species

Species or site-specific treeline responses to climate change were observed. Earlier studies from these study sites reported that the treeline response to global warming is site dependent. Chhetri and Cairns (2015) found the treelines in Barun to be infilling, whereas, Shrestha et al. (2015a), and Chhetri and Cairns (2018) have identified the treelines of Manang and Dhorpatan as stationary. These studies have further suggested that the historical and current state of stand structure will control how the treeline will respond to an increase in temperatures in the future. However, controlling factors at the treeline are very complex (Malanson et al. 2007; Holtmeier 2009). Variations in stand structure might be the reason for site-specific responses to the temperature increase (Camarero et al. 2017). Moreover, various biotic and abiotic variables play a role in explaining the spatial patterns, besides the temperature limitation. For example, tree to tree interactions, either competition or facilitation (Wang et al. 2006; Sigdel et al. 2018a, 2020) also mask the climatic influence. Low temperature, winter snow, *inter alia,* may be the prime controlling factors of morphometric variation and recruitment constraints along elevational gradients. The presence and density of other cohabitant species that have competitive or facilitative roles, soil properties, seed dispersal strategies, *inter alia*, compound and complicate the understanding of engineers of stand morphometry. For example, *R. campanulatum* and *B. utilis* have anemochory seed dispersal patterns whereas zoochory is found in *A. spectabilis* and *P. wallichiana* (Schwab et al. 2017). The nature of dispersal also has a role in shaping morphometry and results in species-specific responses to climate change. Thus, it is essential to incorporate site-specific factors other than climate (specifically for those related to stand structure) for accurate projections of future treeline dynamics (Camarero et al. 2017).

3.4 Basal area increment (BAI) and competition

Basal area increment showed growth trends in all three study sites. There was an increase in growth and yield production in Barun and Dhorpatan, as signaled by the significant increase in BAI in *A. spectabilis* (Barun) and *B. utilis* (Dhorpatan), despite the treeline being stable. The increase might be attributed to the increasing trends of winter temperature in the area in recent decades. CRU long term climate data analysis indicates that the temperature, especially the winter minimum, is increasing in these sites (Figure 2b) which may result in a longer growing season. Dendroclimatological studies have shown a strong relationship between the growing season temperature and precipitation and radial growth (Malanson et al. 2007; Shrestha et al. 2015b; Shrestha et al. 2017). The studies from central and south European subalpine areas (Motta and Nola 2001; Vittoz et al. 2008; Popa et al. 2017) have also reported similar results. Several studies from the central Himalayas (Dawadi et al. 2013; Liang et al. 2014) have emphasized the role of pre-monsoon precipitation on tree growth at the treeline. Higher temperatures in spring exacerbate moisture stress and limit growth (Sigdel et al. 2018b). Thus, the role of the pre-monsoon climate on BAI and treeline dynamics of these study sites will need to be investigated.

Stand structure and composition also drive stand dynamics and tree growth, and the same morphometric trait can have varying contributions depending upon site conditions (Hou et al. 2011). For example, higher crown cover reduces the light interception and thus induces less photosynthesis. At higher elevations (since height growth is not a successful strategy in lower atmospheric temperatures; Wright et al. 2018), trees have a tendency towards dwarfing and horizontal branching. Therefore, the lower BAI response of the *P. wallichiana* from Manang might be related to its polymorphism and lateral branching. Bernoulli and Körner (1999) found an increased branch to stem ratio in pine species with decreasing height along increasing elevation at a treeline in the Swiss Alps. Approaching the upper limit of tree growth, the carbon allocation strategy, particularly of pines, is such that investment in autotrophic structures (especially branching and leaves) increases progressively with respect to heterotrophic structures (Bernoulli and Körner 1999). Most of the trees growing in the treeline in Manang are multi-stemmed. This might indicate that these trees are investing more energy in multiple stems and branching (Légère and Payette 1981) and have a lower basal area increment.

Inter- and intraspecific interactions also have substantial roles in determining growth patterns (Venn and Morgan 2009; Liang et al. 2016; Sigdel et al. 2020). Nurse effects and habitat amelioration by close neighbors buffer harsh environmental conditions and the relative importance of facilitation rather than competition increases with abiotic stress gradients (Bertness and Callaway 1994; Sigdel et al. 2020). However, competitive effects may nullify this facilitation especially in the early life stages (Venn and Morgan 2009). Different climatic variables alter the tree's response and sensitivity to competition (Carnicer et al. 2013). For example, reduced moisture and increased temperature can enhance a tree's sensitivity to competition in drought-frequent Mediterranean forests (Carnicer et al. 2013). However, competition factors also mask the effects of climate on growth. The response of trees to climatic favorability or adversity, thus, can be modulated by the extent of competition in the stand. For example, Wright et al. (2018) found high temperature resulting in reduced growth in a white spruce stand with a higher basal area but increased growth in less crowded stands. In the current study, site specific interactions (competition and facilitation) and intraspecific competition were considerably less, as depicted by density, crown coverage factor, basal area, or quadratic mean diameter (Table 2). Dense shrub thickets of *R. campanulatum* appear to control treeline advance in Barun (outcompeting fir for regeneration) similar to what Liang et al. (2016) found in the treeline on the Tibetan Plateau, where the interspecific interactions have considerably outweighed the treeline's dynamic response to climate warming. A considerable number of pine seedlings and saplings were observed in the bushes of *J. squamata,* facilitating their establishment above the treeline in Manang. Intraspecific interactions generally have a positive feedback in harsh environments (Bertness and Callaway 1994). Sigdel et al. (2020) evidenced the positive intraspecific interactions from the central Himalayan treeline where drought stress-induced clustering at the upper limits of the treeline weakened the responsiveness of the treeline to climate. However, competitive effects may nullify this facilitation, especially in the early life stages (Venn and Morgan 2009). According to the stress-gradient hypothesis, ameliorated abiotic stress conditions can shift the facilitative interactions into competition, as argued by Wang et al. (2016) on the basis of a study on treelines in the southeastern Tibetan Plateau, where increased tree density negatively affected vertical growth as well as recruitment. In Dhorpatan though, low densities of scattered individuals did not employ such interactions. Without knowledge on substrate, edaphic conditions, many other ecophysiological traits, and the retrospective disturbances, it is difficult to discern the discrepancy in growth patterns.

4 Conclusions

Our study suggests that stand structure dynamics is site-specific as well as species-specific. Site-specific stand structure dynamics explain the non-unanimous response of treelines to the increase in temperature and disturbances. Species-specific stand structure dynamics explain the possible differences in species response to future climate. In the absence of controlling factors (shrub cover, human disturbance, and topography), the *A. spectabilis* treeline at Barun may advance in the future, following the increasing temperature trend, while *P. wallichiana* (Manang) and *B. utilis* (Dhorpatan) treelines will remain stable for the immediate future.

In conclusion, warming may have a disproportionate effect on treeline ecotones in different regions of the Nepal Himalayas. Disturbances have apparently compounded the climatic response. While a site-specific environment influences a tree's specific morpho-physiological traits, treeline response to warming also depends on the species composition, stand structure, and biotic interaction. Currently, intraspecific interaction (among scattered individuals with low density) is lower in all ecotones, and the basal area is increasing. But increasing climatic favorability and the evident stand densification (baring Dhorpatan) will enhance biotic interaction, which in turn has the potential to impact growth. Ecotone structure in Dhorpatan suggests that it will remain as such unless grazing pressure (at least) is released. An important caveat for the current study is that the stands were mono-dominant and a comparative study would have been better and reasonable. Future studies focusing on stand structure together with recruitment patterns, BAI climate response, phenotypic plasticity, and inter-and intraspecific interactions will help understand the patterns of treeline dynamics in the Nepal Himalayas.

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