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Heterogeneous Responses of Alpine Treelines to Climate Warming across the Tibetan Plateau

Yafeng Wang [1,*], Daihan Li [1], Ping Ren [2], Shalik Ram Sigdel [3,4] and Jesús Julio Camarero [5]

[1] College of Biology and the Environment, Nanjing Forestry University, Nanjing 210037, China; lidaihan1@163.com
[2] College of Life Sciences, Anhui Normal University, Wuhu 241000, China; renping@ahnu.edu.cn
[3] State Key Laboratory of Tibetan Plateau Earth System, Resources and Environment (TPESRE), Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China; srsigdel@itpcas.ac.cn
[4] Institute of Fundamental Research and Studies, Kathmandu 44600, Nepal
[5] Instituto Pirenaico de Ecología (IPE-CSIC), 50059 Zaragoza, Spain; jjcamarero@ipe.csic.es
* Correspondence: wangyf@njfu.edu.cn

Abstract: The Tibetan Plateau hosts a continuous distribution of alpine treelines from the Qilian Mountains to the Hengduan Mountains and the Himalaya Mountains. However, not much is known about the broadscale alpine treeline dynamics and their responses to climate warming across the Tibetan Plateau. Herein, we collected a total of 59 treeline sites across different forest regions of the Tibetan Plateau and the related field data (i.e., upward advance magnitude, tree recruitment and height growth), expansion potential (i.e., elevational difference between the current treeline and the tree species line (EP)) and vegetation TI (an index of species interactions) from the published references. Site characteristics (e.g., elevation, slope and aspect) and the related environmental factors were used to analyze the relationships between treeline shifts and environmental variables. Despite increases in the recruitment and growth of trees at most treeline sites, alpine treeline positions showed heterogeneous responses to climate warming. Most treelines advanced over the last century, while some treelines showed long-term stability. EP was significantly and positively linked to the summer warming rate and treeline shifts, suggesting that the position of current tree species line is of crucial importance in evaluating treeline dynamics under climate change. In addition, warming-induced treeline advances were modulated by plant–plant interactions. Overall, this study highlighted the heterogeneous responses of regional-scale alpine treelines to climate warming on the Tibetan Plateau.

Keywords: treeline; recruitment; tree growth; climate warming; Tibetan Plateau

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1. Introduction

High-elevation forests usually show heterogeneous responses to climate change [1,2]. Such a finding is particularly relevant for alpine treelines, which have fluctuations that are heterogeneous and subject to a series of abiotic and biotic factors [3–5]. Elucidating both the trend and heterogeneity in treeline changes under climate warming contributed to a better understanding of the patterns of treeline changes [6–10].

The responses of alpine treelines to climate vary with the study scales. At the global scale, alpine treeline positions generally follow a common temperature isotherm [11]. In addition to climatic limitations, treeline positions at regional scales are subjected to multiple non-temperature variables (e.g., moisture, biotic interactions and topography) [5,12,13]. Accordingly, climate warming is expected to cause spatially inhomogeneous variations in the structure and position of treelines at the local, landscape and regional scales [6]. To date, a growing body of treeline studies have focused primarily on global, continental, landscape, and local scales [6,14–16]; however, at regional scales, how alpine treelines respond to climate change remains unclear.

The Tibetan Plateau hosts the Northern Hemisphere's highest alpine treelines [17,18], providing an ideal place to investigate relationships between alpine treelines and environmental variables from local to regional scales. Despite a similar warming trend across the plateau, local-scale and regional treeline studies have shown heterogeneous patterns of tree recruitment and treeline shift rates [5,10,19–24]. However, spatiotemporal patterns of alpine treelines at regional scales covering diverse tree species and different climatic zones on the Tibetan Plateau have yet to be evaluated.

This study aimed to (1) quantify the spatiotemporal dynamics of alpine treelines at regional scales on the Tibetan Plateau; (2) reveal the linkages between treeline shifts over the last century and the associated environmental variables across the Tibetan Plateau; (3) elucidate the possible mechanism underlying treeline changes on the Tibetan Plateau. Previous treeline studies have found that the coupling of treeline position and temperature is mediated by non-thermal factors across the Tibetan Plateau [25–27]; thus, we hypothesized that treeline dynamics on the Tibetan Plateau would be heterogeneous under climate warming. Based on previous treeline work [5], we also hypothesized that warming-induced treeline advance is negatively regulated by species interactions but positively driven by the indicator associated with key ecological processes of treeline ecotone (e.g., recruitment and growth) [24,25].

2. Materials and Methods

2.1. Study Region and Climate

The study region covered several natural treeline sites across the Tibetan Plateau (hereafter, TP) (Figure 1). This region is also known as the roof of the world and the Asian water tower. The eastern regions are mainly influenced by the South Indian monsoon during summer, while mid-latitude westerlies mainly influenced the winter season in the western regions [28]. The climate on the TP is featured by strong solar radiation, a large diurnal temperature range and low temperature [29]. Mean air temperature for the coldest month was in a range of −15 to −10 °C, with lower than 10 °C for the warmest month [29]. Mean annual precipitation varied from ca. 300 to more than 2000 mm across the TP [15,17,30]. Mean wind speed is usually $\leq$3 m·s^{-1} at treelines of the TP [31].

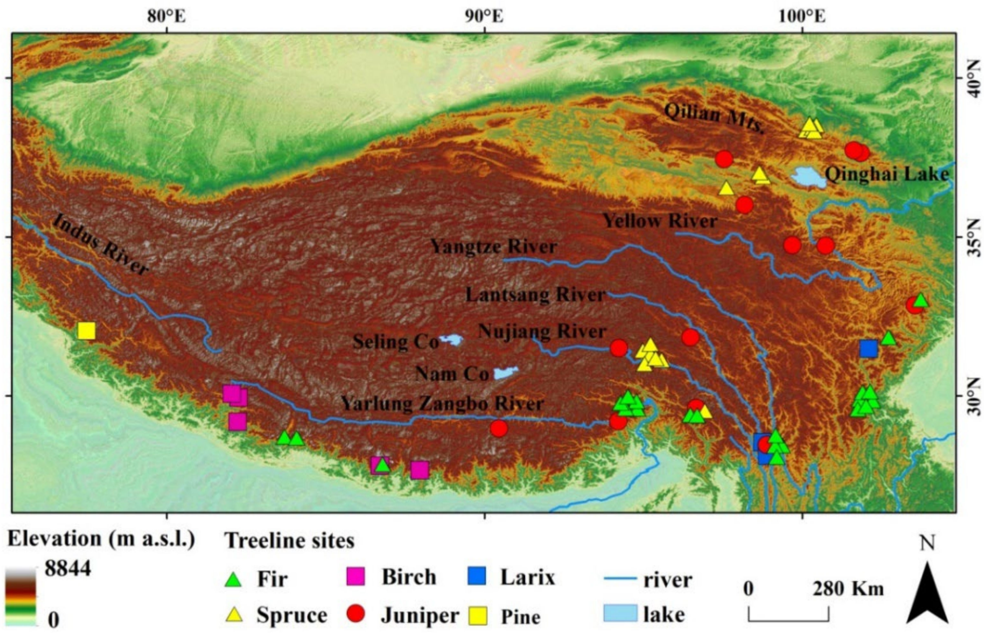

Figure 1. Locations of alpine treeline sites and tree genera (see the tree species in Table S1) forming the treelines across the TP.

2.2. Tree Species and Treeline Ecotone

Treeline ecotone refers to the transition zone from the timberline (altitudinal limit of dense forests) to the tree species line [4]. A treeline is identified by the presence of upright trees of higher than 2 m at the highest altitude, while a tree species line is determined by the uppermost elevation of tree seedlings (individuals with height $\leq$ 0.50 m) [11,15]. The subalpine forests on the Tibetan Plateau are made up of a diverse set of tree species. The natural treelines in the Himalayas are compounded by Himalayan birch (*Betula utilis*), Himalayan fir (*Abies spectabilis*) and Himalayan pine (*Pinus wallichiana*) [10,32]. In the central south of the TP, *Sabina tibetica* Kom. is the dominant tree species at treelines [18]. In the southeastern and eastern TP, one juniper species (*Sabina saltuaria*) and four fir species (i.e., *Abies georgei* var. *smithii*, *Abies georgei* Orr, *Abies fabri* and *Abies faxoniana*) or larch (i.e., *Larix potaninii* var. *macrocarpa*) form the primitive treelines on the sunny and shady slopes, respectively [5,19,33–37]. In the northeastern TP, spruce (*Picea likiangensis* var. *balfouriana*, *Picea crassifolia* Kom.) and juniper (*Juniperus przewalskii* Kom.) grow on the sunny and shady slopes, respectively [29,38–40]. Previous treeline studies did not find significant impacts of tree species (e.g., spruce vs. fir) on the treeline shifts of the TP [5]; therefore, we did not explore the linkages of tree species to treeline shifts in this study.

2.3. Data Collection

Several field-based treeline studies have been conducted over the past 20 years across the TP and Himalayas [5,10,20,21,33,41–45]. In view of this background, field data (particularly height growth, tree recruitment and treeline shift rates) and their associated site conditions (i.e., slope, aspect, elevation, disturbance regimes and vegetation cover) at 59 treeline sites were extracted from the published literature (Table S1). Treeline shift data covered the period from 1901 to 2017. Previous treeline studies did find the spatial autocorrelation among treeline sites [6,14]; therefore, we assume that it did not affect our results. Climatic variables near each treeline site (Tables S1 and S2) were extracted from the CRU (Climate Research Unit) TS4.01 database (resolution: 0.5° $\times$ 0.5°) [46]. Based on the CRU data, it was found that elevation of treeline position was closely linked to seasonal temperature changes [25]; thus, the CRU data were considered as a reliable climatic data source in the study of linkages between treeline shifts and climate on the TP. Changes in CAT, CWT and CST were from the slope of the linear regression of the CRU temperature data. Mean annual, summer and winter precipitation values at all of the sites were 677 $\pm$ 297, 397 $\pm$ 184 and 25 $\pm$ 24 mm, respectively. Tree growth at the treelines of the TP is usually linked to summer mean minimum temperature [38,39]; thus, we postulated that tree recruitment at the treeline and treeline shifts are driven by summer warming.

Given that biotic interactions could modulate treeline responses to climate change [5], vegetation thickness index (TI) (mean plant height $\times$ cover) at and beyond current treeline boundaries can be used to indicate the interspecific interactions at treeline ecotones [5]. Based on the field data or description in the published literature (see Table S1), the thickness index (TI) was calculated for each treeline site. Note that TI is calculated from the mean cover and height of the dominant ground vegetation (e.g., shrub and grass) across the treeline ecotone at each site [5]. Previous treeline studies showed that the value of TI is inversely related to the magnitude of the treeline advance [5]. A higher TI value implies stronger interspecific competition that may counteract the effects of warming on tree establishment, whereas low vegetation cover may facilitate treeline advance [5].

Tree seedlings above the current treelines are likely to advance under ongoing climate warming [47]. Based on the current treeline position and recruitment conditions above the treeline, the elevational differences between the current treeline and the tree species line was defined as the expansion potential index (hereafter, EP), which involves several key ecological processes (i.e., seed conditions, tree recruitment and growth) [4,48]. EP was measured at the current time for all the study sites. We assumed that the value of EP remained relatively constant under climate change, so the EP measured at the current time can be linked to treeline shifts. In addition, definitions of the biotic variables and explicit hypothesis as well as some terminologies are presented in Table S3.

2.4. Data Analysis

Using a data set of 59 treeline sites located on the TP, we analyzed the trend of variations in elevation position, tree recruitment and height growth of alpine treelines. The mean maximum tree height at the treeline was approximately 10 m [14]; thus, the upslope advance of 10 m served as a rapid movement criterion over the last century for global treelines [14,15]. Following these previous treeline studies, an upslope shift of >10 m was defined as a rapidly advancing treeline. We also defined the other two types of treelines based on their dynamics and upslope shift (slow advance: >0 and $\leq$10 m; stability: 0 m). Herein, treeline shift data of the TP over the last century were grouped into three types: rapid advance (>10 m in elevation), slow advance (>0 and $\leq$10 m) and stability (0 m). Similarly, tree recruitment patterns were divided into two classes: increase in recruitment and insufficient recruitment. The increase in tree recruitment means an increase in tree seedlings (height $\leq$ 0.5 m) or saplings (0.5 m < height < 2 m) with time, whereas the insufficient recruitment means a lack of tree seedlings and saplings with time. Here, we defined treeline as the uppermost elevation of trees ($\geq$2 m) [49]. According to different height-growth rates, tree ages corresponding to 2 m at the treeline were categorized into three classes: A (15–30 years), B (31–50 years) and C (>50 years). Following previous treeline studies [15,49], we postulated that seedlings took the same amount of time to reach 2 m under past and current climatic conditions. Based on the above classification, for all of the treeline sites, percentages of the different types of treeline shift, recruitment and height growth data were calculated. The number of sites for the three classes of treeline shift data (i.e., rapid advance, slow advance and stability) was divided by the total number of treeline sites (n = 59) so we could obtain the percentage for the three classes of treeline shifts. Similarly, the number of sites for the two classes of tree recruitment (i.e., increased and insufficient recruitment) was divided by the total number of treeline sites (n = 59) so we could obtain the percentage for the two classes of tree recruitment. The number of sites for the three classes of height growth data (i.e., A, B and C) was divided by the total number of treeline sites (n = 59) so we could obtain the percentage for the three classes of height growth data.

Based on the geographic distributions of the treelines, the TP was grouped into eight subareas: Hengduan Mountains (HD), Chuangxi region (CX), Linzhi region (LZ), Changdu-Naqu region (CDN), Yushu region (YS), Haixi-Hainan region (HXN), Qilian Mountains (QL) and Himalaya Mountains (HM) (Table S1). The minimum and maximum values of the treeline shift data were extracted for each subarea across the TP, respectively. We calculated Pearson correlation coefficients between treeline shift rates over the last century and site factors. The associated site factors included changes in annual, summer and winter mean minimum temperature over the past 100 years (i.e., CAT, CST and CWT); annual, summer and winter precipitation (i.e., AP, SP and WP); slope, aspect, northness (sin (aspect) $\times$ cos (slope)), disturbance regime (0, absence of disturbance; 0.5, low intensity of disturbance; 1, high intensity of disturbance), tree recruitment (binary variable: 1, 0), height growth rate, vegetation thickness index (TI) and expansion potential of treeline (EP). Tree recruitment conditions at the treeline were set as a binary variable (1, 0). At each treeline site, the increase in recruitment was indicated by 1, while the insufficient recruitment was indicated by 0. The height growth rate was obtained by the field data of previous treeline studies. For instance, a seedling took approximately 30 years to reach a height of 2 m in the LZ region; thus, the height growth rate could be obtained [15]. Treeline advance during the last century was potentially driven by six predictor variables: height growth rate (HGR); tree recruitment (RE); vegetation TI; EP; changes in annual, summer and winter mean minimum temperature (i.e., CAT, CWT and CST); annual, summer and winter precipitation (i.e., AP, SP and WP) over the last century. Seasonal temperature variables (i.e., CAT, CWT and CST) were correlated with each other. Likewise, seasonal precipitation (i.e., AP, SP and WP) may also be autocorrelated with each other. In addition, biotic variables (i.e., HGR, RE, TI and EP) could be autocorrelated with each other. To avoid the correlations among potential predictor variables, partial correlations were calculated between them and treeline shifts by controlling other potentially correlated variables. The partial correlation correlations were calculated using R software and the "ggm" package [50,51]. Linear mixed-effects models (LMMs) were applied to explore the effects of different predictor variables on the TP treeline shifts. All significant ($p < 0.05$) factors revealed by the partial correlation analysis were used in the LMMs. Climatic factors were set as fixed effects in the LMMs. Given that treeline shifts vary among regions or subareas, subarea was set as a random effect to explain the nonindependence of data within subareas. The Akaike Information Criterion (AIC) and the explained variance by fixed (R^2m, marginal R^2) and fixed plus random effects (R^2c, conditional R^2) were used to show the fitness and performance of the LMMs. The LMMs were performed using the "nlme" package and R software [52].

Structural equation models (SEMs) were used to explore the complex multivariate linkages among the related variables using a form of path analysis [53]. The overall goodness of fit of the SEMs was evaluated using a chi-square test (P) in the selected SEM. If the p-value > 0.05, the model would be reliable for the reproduction of the hypothesized causal network [53,54]. In addition, we selected the model with the fewest explanatory variables and the minimum Akaike Information Criterion (AIC) [54]. In this study, all the significant variables shown by the partial correlation analysis were used in the SEMs, whereas insignificant variables shown by the partial correlation analysis were not included in the SEMs.

3. Results

Rapid advancing treelines across the TP were recorded at 50.8% of the sites over the past century, while slowly advancing and stable treelines accounted for 16.9% and 32.2% of the study sites, respectively (Figure 2a). Increased and insufficient tree recruitments at treelines were found at 73% and 27% of the study sites, respectively (Figure 2b). The percentages for the three types (i.e., A: 15–30 years; B: 31–50 years; C: >50 years) of tree height growth data were 67.8% (A), 16.9% (B) and 15.3% (C), respectively. The upward advance of treelines occurred at 73% of the study sites (Figure 2a). Increased tree recruitment was observed at 73% of the study sites (Figure 2b). A rapid height growth rate appeared at 67.8% of the study sites (Figure 2c).

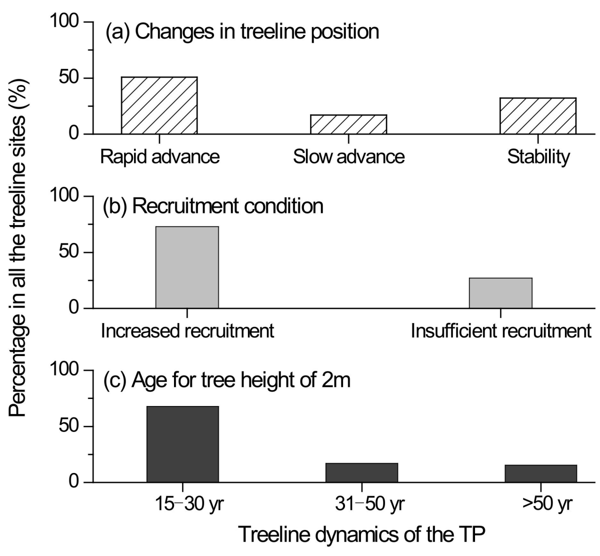

Figure 2. Frequency of treeline sites in the TP showing different treeline advances (**a**); recruitment changes (**b**); height growth rates (**c**).

The minimum upward magnitude of treeline advance for most subareas on the TP was 0 m, except for the HM region with a minimum magnitude of 5.5 m (Figure 2). The maximum upward magnitude of treeline advance for different subareas of the TP varied from 9.1 m in the LZ region to 124 m in the Himalayan Mountains (Figure 2). Box plots showed that the overall and mean magnitude of treeline advance varied among the different subareas (Figure 3). The frequency of treeline advance magnitude at a 10 m interval also showed the large variability of the treeline advance (Figure 3).

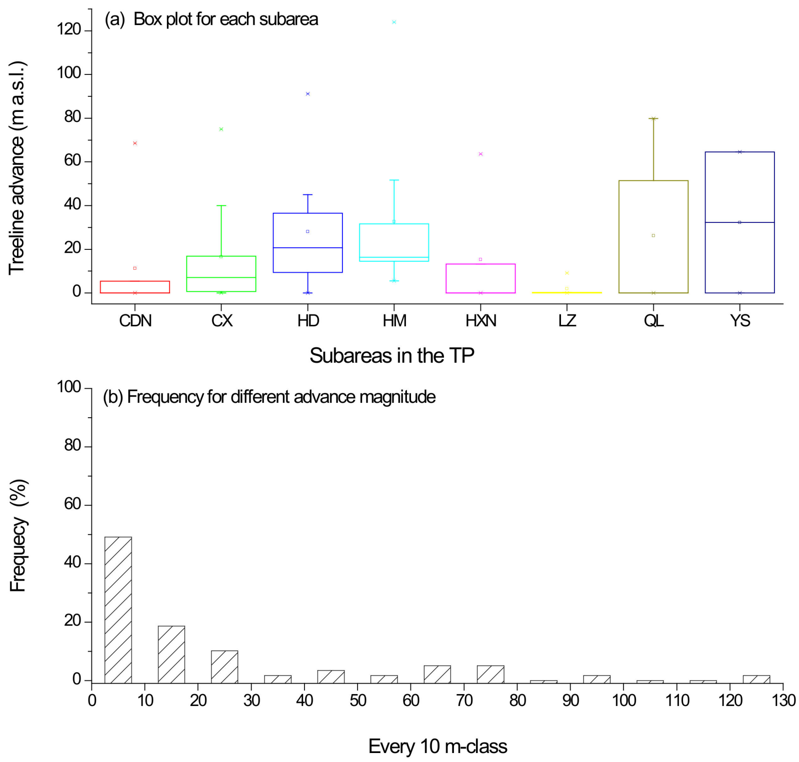

Figure 3. Box plots of treeline advance over the past century for different subareas (**a**) and the frequency of different advance magnitudes (10 m class) (**b**) on the TP. The eight subareas include Hengduan Mountains (HD), Chuangxi region (CX), Linzhi region (LZ), Changdu-Naqu region (CDN), Yushu region (YS), Haixi-Hainan region (HXN), Qilian Mountains (QL) and Himalaya Mountains (HM).

Expansion potential index (EP), changes in summer mean minimum temperature (CST) and height growth rate were significantly associated with treeline shift magnitude (EP: r = 0.54; CST: r = 0.49; height growth rate: r = 0.42; in all cases: $p < 0.001$) (Table 1). Recruitment and vegetation TI were also significantly associated with treeline shift magnitude (recruitment: r = 0.39; vegetation TI: r = −0.34; in all cases: $p < 0.01$) (Table 1). Other site variables (i.e., annual, summer and winter precipitation; changes in annual and winter mean minimum temperature; slope, aspect, northness and disturbance regime) were not significantly related to treeline shift magnitude ($p > 0.05$ in all cases) (Table 1). In short, EP and CST were the two variables most closely linked to treeline shifts.

Partial correlations between CST and treeline shifts were positively related when controlling for CAT and CWT (r = 0.49, $p < 0.001$; Table 2). Partial correlations between EP and treeline shifts were also positively correlated when controlling for RE, HGR and TI (r = 0.41, $p < 0.001$; Table 2). Partial correlations between RE and treeline shifts were, again, positively correlated when controlling for HGR, TI and EP (r = 0.31, $p < 0.05$; Table 2). Partial correlations between TI and treeline shifts were negatively correlated when controlling for RE, HGR and EP (r = −0.41, $p < 0.001$; Table 2). Therefore, the following variables EP, CST and TI had significant impacts on treeline shifts.

Table 1. Correlation coefficients between several variables and magnitude of treeline advance over the last century for study sites located on the TP ($n = 59$). Climatic variables included changes in annual, summer and winter mean minimum temperature (i.e., CAT, CWT and CST) and annual, summer and winter precipitation (i.e., AP, SP and WP) over the last century. EP denotes expansion potential (i.e., elevational difference of current treeline and tree species line). A composite topographic index "northness" that equals sin (aspect) × cos (slope) was also used in the analysis. Correlation significance: ** $p < 0.01$; *** $p < 0.001$.

Variable	Correlation (r)
Recruitment	0.39 **
Height growth rate	0.42 **
CAT	0.09
CST	0.49 ***
CWT	0.14
AP	−0.17
SP	−0.12
WP	0.24
Northness	0.16
Slope	0.06
Aspect	−0.11
Vegetation TI	−0.34 **
Disturbance regime	0.13
EP	0.54 ***

Table 2. Partial correlations between predictor variables and treeline shifts. The potential predictor variables included changes in annual, summer and winter mean minimum temperature (i.e., CAT, CWT and CST) and annual, summer and winter precipitation (i.e., AP, SP and WP) over the last century; height growth rate (HGR), tree recruitment (RE), vegetation TI (TI) and expansion potential (EP). Partial correlation significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Variables	Partial Correlations with Treeline Shifts	Controlled Variables
CST	0.49 ***	CAT, CWT
CAT	−0.10	CST, CWT
CWT	−0.08	CAT, CST
AP	−0.19	SP, WP
SP	0.172	AP, WP
WP	0.29	AP, SP
RE	0.31 *	HGR, TI, EP
HGR	0.08	RE, TI, EP
TI	−0.41 **	RE, HGR, EP
EP	0.41 **	RE, HGR, TI

The results of the LMMs showed that the fixed effects with five variables (i.e., CST, EP, TI, RE and HGR) explained 57.7% of the variance of treeline shifts in the TP, whereas the random effect associated with subarea explained 9.2% of the variance (Table 3). LMMs further showed that the fixed effects with three variables (i.e., CST, EP, TI and RE) explained 56.6% of the variance of treeline shifts in the TP, whereas the random effect associated with subarea explained 6.4% of the variance of treeline shifts in the TP. In other LMMs (variables for fixed effects: $n \leq 3$), the fixed effects explained 29.3–47.4% of the variance of treeline shifts in the TP, while the random effect associated with subarea explained 0–7.2% of the variance of treeline shifts in the TP.

As mentioned above, only three predictor variables (i.e., EP, CST and TI) showed significant effects on treeline shifts when considering correlations among predictors; thus, we used these three variables to establish the SEM. The results of the SEM showed that changes in summer warming (CST) had a positive effect on both the EP and treeline advance (Figure 4). TI (vegetation interactions) negatively affected treeline advance. EP had a positive effect on treeline advance. Coincidentally, the goodness fit of the SEM had a good performance (p = 0.08, AIC = 29.06).

Table 3. Summary of the fitted linear mixed-effects models (LMEs) fitted to treeline data on the Tibetan Plateau. The predictor variables included changes in summer mean minimum temperature (CST), height growth rate (HGR), tree recruitment (RE) and vegetation TI (TI). The subarea was set as the random factor in the LME model. R^2m and R^2c denote the marginal R^2 for fixed effects and the conditional R^2 for the fixed and random effects, respectively. Significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Fixed Effects$^{\text{significance level}}$	AIC	R^2m (%)	R^2c (%)
CST ** + EP * + TI ** + RE ** + HGR	493.4	57.7	66.9
CST ** + EP * + TI ** + RE **	503.8	56.6	63.0
CST * + EP ** + TI	521.0	39.7	40.1
CST ** + EP ** + RE **	515.5	47.4	54.6
CST ** + EP **	526.9	36.8	38.4
CST *** + TI	526.3	29.3	30.6
CST *** + RE **	518.7	36.5	36.5
CST *** + HGR ***	512.8	37.4	37.4

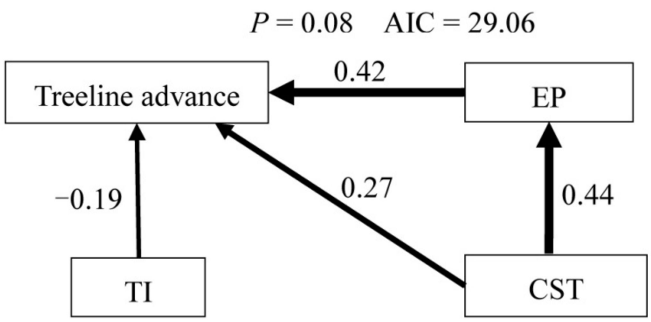

Figure 4. Structural equation model showing the direct and indirect effects of three key predictor variables (i.e., CST, EP and TI) on treeline advance of TP. The importance of the predictor variables is indicated by the width of the arrow lines.

4. Discussion

Environmental conditions within the treeline ecotone are highly heterogeneous and very complex across space [55–57]. In particular, the coupling of treeline elevation and temperature is mediated by a series of non-thermal variables [15,22,26]. As a consequence, previous treeline reviews reveal the spatially heterogeneous responses of alpine treelines to climate warming [6,14]. Our results also elucidate the considerable variability in the magnitude of alpine treeline shifts across the TP. The results of the LMMs further showed that subarea as the random effect could explain 9.2% of the variance of treeline shifts in the TP, suggesting that local and regional differences should be carefully considered when exploring the broadscale drivers of treeline shifts [6,10,53]. This result confirmed our first hypothesis, namely that treeline dynamics on the Tibetan Plateau would be heterogeneous under climate warming. This result is comparable to the treeline studies conducted in different regions outside the TP. For instance, the maximum upslope magnitudes of alpine treelines in the Qinling Mountains, the Changbai Mountains and Taiwan of China are lower than the TP [7,9,58]. In addition, large heterogeneity in treeline migrations has been reported in Central Asia, Europe and America [59–61]. Given this aforementioned background, the TP can be used as a good model to investigate the treeline dynamics under global change.

Our results showed that the upward advance of treeline position (67.7%), the increase in tree recruitment (73%) and the rapid growth rate (67.8%) occurred at the majority of treeline sites. This result suggests that the increase in tree recruitment and accelerated tree growth appear within the treeline ecotones on the TP. On the one hand, tree recruitment and growth may benefit from climate warming due to the growth limitations at treelines [62,63]. In fact, multiple approaches have evidenced the increase in tree density and growth at treelines globally when the non-thermal factors are not limiting [13,64–67].

Tree establishment processes at and above the treeline are the key aspects that drive the treeline structure and its position [68,69]. Theoretically, several ecological processes of trees (e.g., seed dispersal, tree recruitment, survival and growth) at the treeline could affect the advance rates of alpine treelines [70]. Due to the lack of seed data at most treeline sites, we could not directly evaluate the impacts of seed condition on treeline shifts of the TP. Nevertheless, field observations and experiments of previous treeline studies found that seed condition (seed quality and dispersal) did not constitute a limitation for treeline advance on the southeastern TP [36,71]. In such cases, we suppose that it also holds true for this study. In this context, tree recruitment and subsequent growth are the prerequisites to the upward shifts of alpine treelines. Indeed, our results show that these two variables can exert significant positive influences on the treeline shifts of the TP. By contrast, the species interactions indicated by the vegetation TI was reverse associated with treeline shifts across the TP, being consistent with previous treeline studies on the TP [5]. In addition, the EP involving the key ecological processes motioned above (seed condition, tree recruitment and growth) was found to be the most important factor related to treeline shifts on the TP.

The results of the SEMs reveal the different impacts of three key predictor variables (i.e., summer warming, TI and EP) on the treeline advance of the TP. Specifically, climate warming during the summer season had a positive effect on EP, indicating that the alleviation of cold stress under a warmer climate may promote the expansion potential by increasing the recruitment and growth of treeline trees. Seed production usually increases with warming, thereby more seeds can be dispersed to the potential safe microsites above the treeline [72]. EP and TI have positive and negative effects on treeline shifts, respectively. Presumably, climate warming may be favorable for several key ecological processes (e.g., abundant seeds, increased recruitment and growth of trees) [64,73] and would lead to the upslope shifts of alpine treeline. The positive associations between EP and treeline advance also suggest that the tree species line' position has important implications for evaluating treeline dynamics under climate change. As demonstrated by previous treeline studies, plant–plant competition would impede warming-induced treeline advance [5,26,74]. Furthermore, climate warming has an indirectly positive effect on treeline shifts, suggesting that other factors (e.g., soil nutrient conditions) than the above predictors might be improved under climate warming, thereby contributing to upslope shifts of alpine treelines [75]. Therefore, our second hypothesis was also supported; namely that warming-induced treeline advance is negatively regulated by species interactions but positively driven by the indicator associated with key ecological processes of treeline ecotone (e.g., recruitment and growth).

Upslope advances of alpine treelines have important implications for carbon uptake and related services (e.g., plant biodiversity and biogeochemical cycles) provided by mountainous ecosystems [76]. Recent studies also found that the alpine treeline ecotone can provide potential refugia for some threatened plant species [77]. Tree encroachment within the treeline ecotone may lead to a shift in species' relative abundances and functional diversity, possibly affecting alpine community assembly patterns [78]. Therefore, the possible implications of alpine treeline changes for the Tibetan Plateau ecosystems are worth special attention.

5. Conclusions

This study revealed the heterogeneous responses of broadscale alpine treelines to climate warming across the TP. Thus, the spatial heterogeneity of treeline response was not only observed at global and hemispheric scales but also at regional scales. Increased recruitment and growth of trees were detected at most treeline sites of the TP. The new indicator EP was closely related to tree recruitment and growth and, thus, can be used in alpine treeline studies. Climate warming would enhance the expansion potential of treeline trees, therefore leading to the upslope shift of alpine treelines on the TP. The close linkages between EP and treeline advance indicate that the position of current tree species line is of great importance in evaluating treeline shifts under climate change. However, plant–plant interactions regulate the warming-induced treeline shifts on the TP. Field monitoring data and controlled experiments are urgently needed to reveal the dynamics of the key ecological processes (e.g., seed condition, growth and recruitment of seedlings and saplings) beyond the treelines and their driving mechanisms.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13050788/s1, Table S1. Basic information for the alpine treeline sites located in the TP. Table S2. Location of CRU 0.5° gridded data near the study treeline sites. Table S3. Definitions of the biotic variables and three terminologies used in this study.

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References

1. Fadrique, B.; Báez, S.; Duque, Á.; Malizia, A.; Blundo, C.; Carilla, J.; Osinaga-Acosta, O.; Malizia, L.; Silman, M.; Farfán-Ríos, W.; et al. Widespread but heterogeneous responses of Andean forests to climate change. *Nature* **2018**, *564*, 207–212. [CrossRef] [PubMed]
2. Gao, S.; Liang, E.; Liu, R.; Babst, F.; Camarero, J.J.; Fu, Y.; Pioa, S.; Rossi, S.; Shen, M.; Wang, T.; et al. An earlier start of the thermal growing season enhances tree growth in cold humid areas but not in dry areas. *Nat. Ecol. Evol.* **2022**, *6*, 397–404. [CrossRef] [PubMed]
3. Beloiu, M.; Poursanidis, D.; Tsakirakis, A.; Chrysoulakis, N.; Hoffmann, S.; Lymberakis, P.; Barnias, A.; Kienle, D.; Beierkuhnlein, C. No treeline shift despite climate change over the last 70 Years. *For. Ecosyst.* **2022**, *9*, 100002. [CrossRef]
4. Holtmeier, F.K. *Mountain Timberlines: Ecology, Patchiness and Dynamics*; Springer: Berlin, Germany, 2009.
5. Liang, E.; Wang, Y.; Piao, S.; Lu, X.; Camarero, J.J.; Zhu, H.; Zhu, L.; Ellison, A.M.; Ciais, P.; Peñuelas, J. Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 4380–4385. [CrossRef]
6. Lu, X.; Liang, E.; Wang, Y.; Babst, F.; Camarero, J.J. Mountain treelines climb slowly despite rapid climate warming. *Glob. Ecol. Biogeogr.* **2021**, *30*, 305–315. [CrossRef]
7. Du, H.; Liu, J.; Li, M.H.; Büntgen, U.; Yang, Y.; Wang, L.; Wu, Z.; He, H.S. Warming-induced upward migration of the alpine treeline in the Changbai Mountains, Northeast China. *Glob. Change Biol.* **2018**, *24*, 1256–1266. [CrossRef]
8. Elliott, G.P. 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. Change Biol.* **2011**, *20*, 46–57. [CrossRef]
9. Greenwood, S.; Chen, J.C.; Chen, C.T.; Jump, A.S. Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. *Glob. Change Biol.* **2014**, *20*, 3756–3766. [CrossRef]
10. Sigdel, S.R.; Wang, Y.; Camarero, J.J.; Zhu, H.; Liang, E.; Peñuelas, J. Moisture-mediated responsiveness of treeline shifts to global warming in the Himalayas. *Glob. Change Biol.* **2018**, *24*, 5549–5559. [CrossRef]
11. Körner, C.; Paulsen, J. A world-wide study of high altitude treeline temperatures. *J. Biogeogr.* **2004**, *31*, 713–732. [CrossRef]
12. Macias-Fauria, M.; Johnson, E.A. Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 8117–8122. [CrossRef] [PubMed]
13. Camarero, J.J.; Gazol, A.; Sánchez-Salguero, R.; Fajardo, A.; McIntire, E.J.B.; Gutiérrez, E.; Batllori, E.; Boudreau, S.; Carrer, M.; Diez, J.; et al. Global fading of the temperature-growth coupling at alpine and polar treelines. *Glob. Change Biol.* **2021**, *27*, 1879–1889. [CrossRef] [PubMed]
14. Harsch, M.A.; Hulme, P.E.; McGlone, M.S.; Duncan, R.P. Are treelines advancing? a global meta-analysis of treeline response to climate warming. *Ecol. Lett.* **2009**, *12*, 1040–1049. [CrossRef] [PubMed]
15. Liang, E.; Wang, Y.; Eckstein, D.; Luo, T. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytol.* **2011**, *190*, 760–769. [CrossRef]
16. Lett, S.; Dorrepaal, E. Global drivers of tree seedling establishment at alpine treelines in a changing Climate. *Funct. Ecol.* **2018**, *32*, 1666–1680. [CrossRef]

17. Lyu, L.; Zhang, Q.-B.; Pellatt, M.G.; Büntgen, U.; Li, M.H.; Cherubini, P. Drought limitation on tree growth at the northern hemisphere's highest tree line. *Dendrochronologia* **2019**, *53*, 40–47. [CrossRef]
18. Miehe, G.; Miehe, S.; Vogel, J.; Co, S.; Duo, L. Highest Treeline in the northern hemisphere found in southern Tibet. *Mt. Res. Dev.* **2007**, *27*, 169–173. [CrossRef]
19. Cui, J.; Qin, J.; Sun, H. Population spatial dynamics of *Larix potaninii* in alpine treeline ecotone in the eastern margin of the Tibetan Plateau, China. *Forests* **2017**, *8*, 356. [CrossRef]
20. Gou, X.; Zhang, F.; Deng, Y.; Ettl, G.J.; Yang, M.; Gao, L.; Fang, K. Patterns and dynamics of tree-line response to climate change in the Eastern Qilian Mountains, Northwestern China. *Dendrochronologia* **2012**, *30*, 121–126. [CrossRef]
21. Lyu, L.; Zhang, Q.-B.; Deng, X.; Mäkinen, H. Fine-scale distribution of treeline trees and the nurse plant facilitation on the eastern Tibetan Plateau. *Ecol. Indic.* **2016**, *66*, 251–258. [CrossRef]
22. Wang, Y.; Mao, Q.; Ren, P.; Sigdel, S.R. Opposite tree-tree interactions jointly drive the natural fir treeline population on the southeastern Tibetan Plateau. *Forests* **2021**, *12*, 1417. [CrossRef]
23. Zhang, F.; Chen, Q.; Gou, X.; Du, M.; Wang, F.; Zhang, J. Climatic control on the growth and regeneration of Juniperus Przewalskii at alpine treeline in the eastern Qilian Mountains, northwest China. *Trees* **2021**, *35*, 1085–1097. [CrossRef]
24. Wang, Y.; Sylvester, S.P.; Lu, X.; Dawadi, B.; Sigdel, S.R.; Liang, E.; Julio Camarero, J. The stability of spruce treelines on the eastern Tibetan Plateau over the last century is explained by pastoral disturbance. *For. Ecol. Manag.* **2019**, *442*, 34–45. [CrossRef]
25. Wang, Y.; Liang, E.; Sigdel, S.R.; Liu, B.; Camarero, J.J. The coupling of treeline elevation and temperature is mediated by non-thermal factors on the Tibetan Plateau. *Forests* **2017**, *8*, 109. [CrossRef]
26. Sigdel, S.R.; Liang, E.; Wang, Y.; Dawadi, B.; Camarero, J.J. Tree-to-tree interactions slow down Himalayan treeline shifts as inferred from tree spatial patterns. *J. Biogeogr.* **2020**, *47*, 1816–1826. [CrossRef]
27. Naudiyal, N.; Wang, J.; Ning, W.; Gaire, N.P.; Peili, S.; Yanqiang, W.; Jiali, H.; Ning, S. Potential distribution of *Abies*, *Picea*, and *Juniperus* species in the sub-alpine forest of Minjiang headwater region under current and future climate scenarios and its implications on ecosystem services supply. *Ecol. Indic.* **2021**, *121*, 107131. [CrossRef]
28. Yao, T.; Thompson, L.; Yang, W.; Yu, W.; Gao, Y.; Guo, X.; Yang, X.; Duan, K.; Zhao, H.; Xu, B.; et al. Different glacier status with atmospheric circulations in Tibetan Plateau and surroundings. *Nat. Clim. Change* **2012**, *2*, 663–667. [CrossRef]
29. Zheng, D. *A Study on the Ecogeographic Regional System of China*; Chinese Business Press: Beijing, China, 2008.
30. Fu, T.; Liang, E.; Lu, X.; Gao, S.; Zhang, L.; Zhu, H.; Rossi, S.; Julio Camarero, J.J. Tree growth responses and resilience after the 1950-Zayu-Medog earthquake, southeast Tibetan Plateau. *Dendrochronologia* **2020**, *62*, 125724. [CrossRef]
31. Liu, B.; Liang, E.; Zhu, L. Microclimatic conditions for *Juniperus saltuaria* treeline in the Sygera Mountains, southeastern Tibetan Plateau. *Mt. Res. Dev.* **2011**, *31*, 45–53. [CrossRef]
32. Dubey, B.; Yadav, R.R.; Singh, J.; Chaturvedi, R. Upward shift of Himalayan pine in Western Himalaya, India. *Curr. Sci.* **2003**, *85*, 1135–1136.
33. Baker, B.B.; Moseley, R.K. Advancing treeline and retreating glaciers: Implications for conservation in Yunnan, China. *Arct. Antarct. Alp. Res.* **2007**, *39*, 200–209. [CrossRef]
34. Miao, N.; Liu, S.; Yu, H.; Shi, Z.; Moermond, T.; Liu, Y. Spatial analysis of remnant tree effects in a secondary Abies-Betula forest on the eastern edge of the Qinghai-Tibetan Plateau, China. *For. Ecol. Manag.* **2014**, *313*, 104–111. [CrossRef]
35. Ran, F.; Liang, Y.; Yang, Y.; Yang, Y.; Wang, X. Spatial-temporal dynamics of an *Abies fabri* population near the alpine treeline in the Yajiageng area of Gongga Mountains, China. *Acta Ecol. Sin.* **2014**, *34*, 6872–6878. [CrossRef]
36. Wang, Y.; Case, B.; Lu, X.; Ellison, A.M.; Peñuelas, J.; Zhu, H.; Liang, E.; Camarero, J.J. Fire facilitates warming-induced upward shifts of alpine treelines by altering interspecific interactions. *Trees* **2019**, *33*, 1051–1061. [CrossRef]
37. Zhang, Q.; Zhang, Y.; Luo, P.; Wang, Q.; Wu, N. Ecological characteristics of a *Sabina saltuaria* population at timberline on the south facing slope of Baima Snow mountain, southwest China. Chinese. *J. Plant Ecol.* **2007**, *31*, 857–864. [CrossRef]
38. Liang, E.; Shao, X.; Qin, N. Tree-ring based summer temperature reconstruction for the source region of the Yangtze River on the Tibetan Plateau. *Glob. Planet. Change* **2008**, *61*, 313–320. [CrossRef]
39. Zhu, H.; Shao, X.; Yin, Z.; Xu, P.; Xu, Y.; Tian, H. August temperature variability in the southeastern Tibetan Plateau since AD 1385 inferred from tree rings. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2011**, *305*, 84–92. [CrossRef]
40. Liu, X.; Zeng, X.; Leavitt, S.W.; Wang, W.; An, W.; Xu, G.; Sun, W.; Wang, Y.; Qin, D.; Ren, J. A 400-year tree-ring $\delta^{18}O$ chronology for the southeastern Tibetan Plateau: Implications for inferring variations of the regional hydroclimate. *Glob. Planet. Change* **2013**, *104*, 23–33. [CrossRef]
41. Cheng, W.; Luo, P.; Wu, N. Ecological characteristics of Minjiang fir (Abies faxoniana Rehd et Wild) population near timberline on upper Min River. Chin. *J. Appl. Environ. Biol.* **2005**, *11*, 300–303. [CrossRef]
42. Shao, X.; Huang, L.; Liu, H.; Liang, E.; Fang, X.; Wang, L. Precipitation changes recorded in tree ring over the last 1000 years in the Delingha region of Qinghai province. *Sci. China Ser. D Earth Sci.* **2004**, *34*, 145–153. [CrossRef]
43. Zhu, H.; Zheng, Y.; Shao, X.; Liu, X.; Xu, Y.; Liang, E. Millennial temperature reconstruction based on tree-ring widths of Qilian juniper from Wulan, Qinghai Province. *China Sci. Bull.* **2008**, *53*, 3914–3920. [CrossRef]
44. Fang, K.; Gou, X.; Chen, F.; Peng, J.; D'Arrigo, R.; Wright, W.; Li, M.H. Response of regional tree-line forests to climate change: Evidence from the northeastern Tibetan Plateau. *Trees* **2009**, *23*, 1321–1329. [CrossRef]
45. Shi, C.; Shen, M.; Wu, X.; Cheng, X.; Li, X.; Fan, T.; Li, Z.; Zhang, Y.; Fan, Z.; Shi, F.; et al. Growth response of alpine treeline forests to a warmer and drier climate on the southeastern Tibetan Plateau. *Agric. For. Meteorol.* **2019**, *264*, 73–79. [CrossRef]

46. Harris, I.; Jones, P.D.; Osborn, T.J.; Lister, D.H. Updated high-resolution grids of monthly climatic observations–the CRU TS3. 10 Dataset. *Int. J. Climatol.* **2014**, *34*, 623–642. [CrossRef]
47. Hofgaard, A.; Dalen, L.; Hytteborn, H. Tree recruitment above the treeline and potential for climate-driven treeline change. *J. Veg. Sci.* **2009**, *20*, 1133–1144. [CrossRef]
48. Körner, C. *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*; Springer: Basel, Switzerland, 2012.
49. Camarero, J.J.; Gutiérrez, E. Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the Spanish Pyrenees. *Clim. Change* **2004**, *63*, 181–200. [CrossRef]
50. R Development Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2022. Available online: http://www.r-project.org (accessed on 15 April 2022).
51. Sadeghi, K.; Marchetti, G.M. Graphical markov models with mixed graphs. *R J.* **2012**, *4*, 65–73. [CrossRef]
52. Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D.; Heisterkamp, S.; Willigen, B.V.; Ranke, J. nlme: Linear and nonlinear mixed effects models. *UTC* **2022**, *3*, 25.
53. Wang, Y.; Liang, E.; Lu, X.; Camarero, J.J.; Babst, F.; Shen, M.; Peñuelas, J. Warming-induced shrubline advance stalled by moisture limitation on the Tibetan Plateau. *Ecography* **2021**, *44*, 1631–1641. [CrossRef]
54. Lefcheck, J.S. PiecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **2016**, *7*, 573–579. [CrossRef]
55. Shi, H.; Zhou, Q.; He, R.; Zhang, Q.; Dang, H. Climate warming will widen the lagging gap of global treeline shift relative to densification. *Agri. For. Meteorol.* **2022**, *313*, 108917. [CrossRef]
56. Batllori, E.; Camarero, J.J.; Ninot, J.M.; Gutiérrez, E. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. *Glob. Ecol. Biogeogr.* **2009**, *18*, 460–472. [CrossRef]
57. Camarero, J.J.; Gutiérrez, E.; Fortin, M.J. Spatial patterns of plant richness across treeline ecotones in the Pyrenees reveal different locations for richness and tree cover boundaries. *Glob. Ecol. Biogeogr.* **2006**, *15*, 182–191. [CrossRef]
58. Resler, L.M. Geomorphic controls of spatial pattern and process at alpine treeline. *Prof. Geogr.* **2006**, *58*, 124–138. [CrossRef]
59. Shi, H.; Zhou, Q.; Xie, F.; He, N.; He, R.; Zhang, K.; Zhang, Q.; Dang, H. Disparity in elevational shifts of upper species limits in response to recent climate warming in the Qinling Mountains, North-central China. *Sci. Total Environ.* **2020**, *706*, 135718. [CrossRef]
60. Gazol, A.; Moiseev, P.; Camarero, J.J. Changes in plant taxonomic and functional diversity patterns following treeline advances in the South Urals. *Plant Ecol. Divers.* **2017**, *10*, 283–292. [CrossRef]
61. Kullman, L. A review and analysis of factual change on the max rise of the Swedish Scandes treeline, in relation to climate change over the past 100 years. *J. Ecol. Nat. Res.* **2018**, *2*, 8. [CrossRef]
62. Moret, P.; Muriel, P.; Jaramillo, R.; Dangles, O. Humboldt's tableau physique revisited. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 12889–12894. [CrossRef]
63. Li, X.; Liang, E.; Gričar, J.; Rossi, S.; Čufar, K.; Ellison, A.M. Critical minimum temperature limits xylogenesis and maintains treelines on the southeastern Tibetan Plateau. *Sci. Bull.* **2017**, *62*, 804–812. [CrossRef]
64. Liang, E.; Wang, Y.; Xu, Y.; Liu, B.; Shao, X. Growth variation in *Abies georgei* var. *smithii* along altitudinal gradients in the Sygera Mountains, southeastern Tibetan Plateau. *Trees* **2010**, *24*, 363–373. [CrossRef]
65. Wang, Y.; Pederson, N.; Ellison, A.M.; Buckley, H.L.; Case, B.S.; Liang, E.; Camarero, J.J. Increased stem density and competition may diminish the positive effects of warming at alpine treeline. *Ecology* **2016**, *97*, 1668–1679. [CrossRef] [PubMed]
66. Bailey, S.N.; Elliott, G.P.; Schliep, E.M. Seasonal temperature-moisture interactions limit seedling establishment at upper treeline in the Southern Rockies. *Ecosphere* **2021**, *12*, e03568. [CrossRef]
67. Zheng, L.; Shi, P.; Zhou, T.; Hou, G.; Song, M.; Yu, F. Tree regeneration patterns on contrasting slopes at treeline ecotones in eastern Tibet. *Forests* **2021**, *12*, 1605. [CrossRef]
68. Lu, X.; Camarero, J.J.; Liang, E. Threshold responses of juniper tree growth and regeneration to climate warming and drought stress at alpine treeline. *Trees* **2021**, *35*, 1081–1083. [CrossRef]
69. Schickhoff, U.; Bobrowski, M.; Böhner, J.; Bürzle, B.; Chaudhary, R.P.; Gerlitz, L.; Heyken, H.; Lange, J.; Müller, M.; Scholten, T.; et al. Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators. *Earth Syst. Dyn.* **2015**, *6*, 245–265. [CrossRef]
70. Holtmeier, F.K.; Broll, G. Treeline advance-driving processes and adverse factors. *Landsc. Online* **2007**, *1*, 1–33. [CrossRef]
71. Shen, W.; Zhang, L.; Guo, Y.; Luo, T. Causes for treeline stability under climate warming: Evidence from seed and seedling transplant experiments in southeast Tibet. *For. Ecol. Manag.* **2018**, *408*, 45–53. [CrossRef]
72. Körner, C. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*; Springer: Berlin, Germany, 2003.
73. Johnson, J.S.; Gaddis, K.D.; Cairns, D.M.; Krutovsky, K.V. Seed dispersal at alpine treeline: An assessment of seed movement within the alpine treeline ecotone. *Ecosphere* **2017**, *8*, e01649. [CrossRef]
74. Zhang, J.; Li, X.; Ren, P.; Leavitt, S.W.; Rossi, S.; Liang, E. Terminal bud size, spring and summer temperatures regulate the timing of height-growth cessation of Smith fir on the southeastern Tibetan Plateau. *Agric. For. Meteorol.* **2022**, *316*, 108883. [CrossRef]
75. Neuschulz, E.L.; Merges, D.; Bollmann, K.; Gugerli, F.; Böhning-Gaese, K. Biotic interactions and seed deposition rather than abiotic factors determine recruitment at elevational range limits of an alpine tree. *J. Ecol.* **2018**, *106*, 948–959. [CrossRef]

76. Chapin, F.S.; Shaver, G.R.; Giblin, A.E.; Nadelhoffer, K.J.; Laundre, J.A. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* **1995**, *76*, 694–711. [CrossRef]
77. Greenwood, S.; Jump, A.S. Consequences of treline shifts for the diveristy and function of high altitude ecosystems. *Arct. Antarct. Alp. Res.* **2014**, *46*, 829–840. [CrossRef]
78. Maher, C.T.; Millar, C.I.; Affleck, D.L.R.; Keane, R.E.; Sala, A.; Tobalske, C.; Larson, A.J.; Nelson, C.R. Alpine treeline ecotones are potential refugia for a montane pine species threatened by bark beetle outbreaks. *Ecol. Appl.* **2021**, *31*, e02274. [CrossRef] [PubMed]