forests

MDPI

Article

The Coupling of Treeline Elevation and Temperature is Mediated by Non-Thermal Factors on the Tibetan Plateau

Yafeng Wang [1,*], Eryuan Liang [2], Shalik Ram Sigdel [2], Bo Liu [3] and J. Julio Camarero [4]

1 College of Biology and the Environment, Nanjing Forestry University, Nanjing 210037, China
2 Key Laboratory of Alpine Ecology and Biodiversity, Chinese Academy of Science, Beijing 100101, China; liangey@itpcas.ac.cn (E.L.); srsigdel@itpcas.ac.cn (S.R.S.)
3 College of Urban and Environmental Sciences, Northwest University, Xi'an 710127, China; liubo@nwu.edu.cn
4 Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50080 Zaragoza, Spain; jjcamarero@ipe.csic.es
* Correspondence: wangyf@njfu.edu.cn; Tel.: +86-25-8542-7210

Academic Editor: Constance Millar
Received: 21 December 2016; Accepted: 31 March 2017; Published: 5 April 2017

Abstract: Little is known about the relationships between treeline elevation and climate at regional and local scales. It is compelling to fill this research gap with data from the Tibetan Plateau where some of the highest alpine treelines in the world are found. This research question partially results from the lack of in situ temperature data at treeline sites. Herein, treeline variables (e.g., elevation, topography, tree species) and temperature data were collected from published investigations performed during this decade on the Tibetan Plateau. Temperature conditions near treeline sites were estimated using global databases and these estimates were corrected by using in situ air temperature measurements. Correlation analyses and generalized linear models were used to evaluate the effects of different variables on treeline elevation including thermal (growing-season air temperatures) and non-thermal (latitude, longitude, elevation, tree species, precipitation, radiation) factors. The commonality analysis model was applied to explore how several variables (July mean temperature, elevation of mountain peak, latitude) were related to treeline elevation. July mean temperature was the most significant predictor of treeline elevation, explaining 55% of the variance in treeline elevation across the Tibetan Plateau, whereas latitude, tree species, and mountain elevation (mass-elevation effect) explained 30% of the variance in treeline elevation. After considering the multicollinearity among predictors, July mean temperature (largely due to the influence of minimum temperature) still showed the strongest association with treeline elevation. We conclude that the coupling of treeline elevation and July temperature at a regional scale is modulated by non-thermal factors probably acting at local scales. Our results contribute towards explaining the decoupling between climate warming and treeline dynamics.

Keywords: air temperature; climate warming; mass-elevation effect; tree species; treeline ecotone

1. Introduction

One of the most striking biogeographic findings in the recent decades is that alpine treelines occur at the elevation where seasonal mean temperature is around 6.4 °C (see [1]). Due to such surprising similarity across forest biomes, temperature during the vegetative period is considered the key factor driving the treeline elevation worldwide [2]. However, treeline studies at the regional and local scales are needed to give further support to this idea, because often few treeline sites represent some biomes which could affect the validity of this global pattern [1]. For instance, in Mediterranean or some temperate biomes, drought, in addition to low temperatures, constrains tree growth and determines the treeline elevation [3–5]. In addition, based on new data from New Zealand and Chile, it was found that southern temperate treelines are driven by similar thermal thresholds as are northern treelines, thus refuting the postulated taxon-specific limitation hypothesis and confirming that southern treelines are not climatically depressed [6]. Therefore, more reliable climate data must be recorded in situ to determine the treeline thermal thresholds at regional and local scales.

The relationships between treeline elevation and thermal factors remain little explored in some remote areas such as the Tibetan Plateau, where studies on treeline elevations and local thermal conditions are still rare (but see [7–9]). Furthermore, little information is available about the impacts of non-temperature factors on treeline dynamics, even though climate warming and treeline dynamics often appear decoupled. This suggests that treeline shifts are partly determined by non-thermal variables including lagged treeline responses to climate, biotic interactions, or geomorphic constraints (e.g., [10–14]).

The world's highest alpine treelines are found on the Tibetan Plateau [15]. The diverse climatic types, the different tree species, and the low disturbance intensity of remote treeline sites on the Tibetan Plateau make this region an ideal place for treeline studies [12,16–19]. Unfortunately, in situ temperature data are only available at few treeline sites on the Tibetan Plateau, resulting from its remoteness, poor access, and the harsh climatic conditions prevailing in these sites throughout the year [8,9].

Despite a lack of in situ microclimatic data, a series of treeline studies have been carried out recently on the different mountains of the Tibetan Plateau (e.g., [12,17,20–24]). A previous study evidenced that monthly climatic information provided by a global climate data base with about 1-km^2 spatial resolution (WorldClim–Global Climate Data, see more details in [25]) can be downscaled to treeline climate at local scales [25]. Such easy-to-access meteorological data and treeline inventory data provide an excellent opportunity to explore the relationships between treeline elevation and climatic variables on the Tibetan Plateau.

This study aims: (1) to explore the relationships between treeline elevation and environmental variables at regional to local scales across the Tibetan Plateau; and (2) to assess the roles played by thermal and non-thermal variables on treeline elevation. Because tree growth and recruitment at treelines on the Tibetan Plateau is generally linked to July temperature [7,12], we hypothesize that July temperature is the major driver of treeline elevation on the Tibetan Plateau. Considering the complex treeline responses to climate and other environmental factors [12], we also hypothesize that the links between treeline elevation and site temperature are modulated by non-thermal factors.

2. Materials and Methods

2.1. Study Area and Climate

The study area is located on the Tibetan Plateau, covering around 250 million km^2, with longitude and latitude ranging 73° E–104° E and 26° N–40° N, respectively [26]. The elevation (1200–7694 m) increases from the southeastern to the northwestern Tibetan Plateau. The western, eastern, and southern Tibetan Plateau regions are influenced by the westerlies, and East Asian and Indian monsoons, respectively [27]. It includes humid, sub-humid, semiarid, and arid climatic zones [26], resulting from different impacts of atmospheric circulation in Asia. Cold and continental climate conditions dominate over the Tibetan Plateau. January (mean temperature of −15–10 °C) and July (around 10 °C) are the coldest and warmest months, respectively [26].

2.2. Study Sites and Environmental Factors

Basic information of each study site is shown in Table A1 of Appendix A. Most treeline sites were obtained from previous studies [12,18,28]. Some sites were investigated by our team in the past three years. Other treeline studies were obtained from literatures published in the last decade [15,21,23,24,29,30]. All the treeline studies followed the treeline definition proposed by [10]. Specifically, treeline was defined as the maximum elevation of living trees with stems at least 2 m high [10]. A total of 57 treeline sites spanning different climatic zones and forest regions were used in this study (Figure 1).

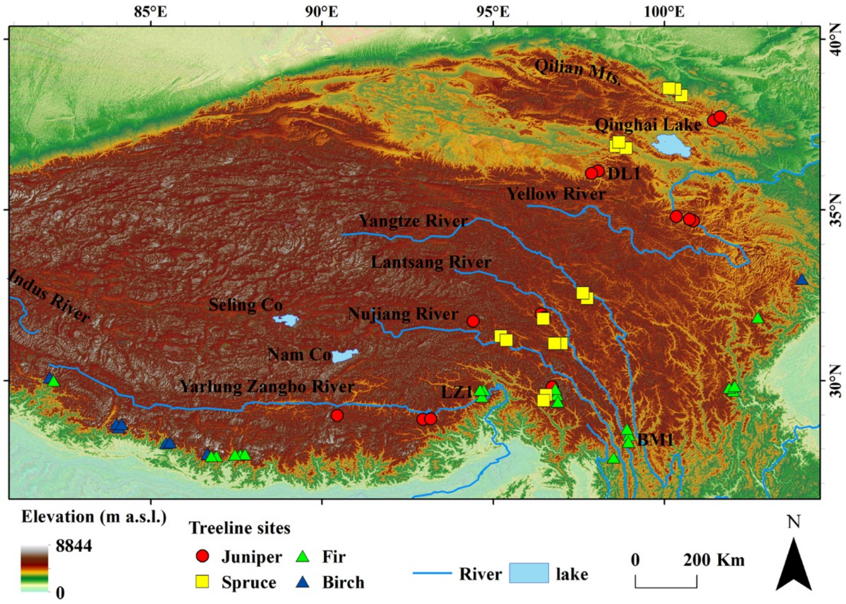

Figure 1. Map showing the geographical location of treeline sites and the four different tree species forming the treelines on the Tibetan Plateau. The site codes (DL1, LZ1, BM1) indicate the location of sites with in situ climate data taken near treeline sites.

Several variables were considered for each site: treeline elevation, the geographical location (latitude and longitude), the aspect and mean slope of the treeline site, and tree species forming the treeline. A composite topographic index "Eastness" that equals sin (aspect) $\times$ sin (slope) was also used in the analyses. The thickness index of short vegetation including shrubs or grasses (hereafter TI) was defined as the plant height $\times$ cover beyond the treeline in following [12]. The TI was used to evaluate the strength of species interactions, since denser shrublands above treeline can reduce tree establishment and slow down upward treeline shift [11]. The elevation of the closest mountain peak at each site was extracted from Google Earth version 7.1 (Google, Santa Clara County, CA, USA), and it was used to indicate the mass-elevation effect, involving the phenomenon that higher mountains always have higher treelines and snowlines [31]. The aspect and slope information were available for most sites, while for other sites the topographic information was extracted from a Digital Elevation Model of the Tibetan Plateau (spatial resolution: 90 m). Monthly temperatures (maximum, minimum, and mean temperature), precipitation, and altitude data (spatial resolution: 1 km^2) were downloaded from the Worldclim climate data base. The treeline sites were added to the temperature map using the ArcMap 10.2 software (Esri, RedLands, CA, USA). Using "Spatial Analyst Tools" in the ArcToolbox, the temperature and precipitation information were extracted from the climatic map for each site. Radiation data was downloaded from the gridded Climatic Research Unit (CRU) dataset (spatial resolution ca. 50 km^2) [32]. The elevation of the worldclim data grid cells for each site (hereafter A) was compared to treeline elevation based on field investigation (hereafter B). Based on the standard adiabatic lapse rate (0.6 °C/100 m) and the elevational difference between A and B (-529 m $\leq$ A $-$ B $\leq$ 264 m), we can downscale the data to the location of the treeline sites. Then, surface solar radiation (SSR) at each site was derived from radiation map in the ArcMap 10.2. Lastly, continentality of each treeline site was calculated using the [33] index (K), as $K = (1.7 \times A/\sin \xi) - 20.4$, where K is continentality, ξ is latitude, and A is the difference between the mean temperatures of the warmest and coldest months [33].

It is evident that treeline site and related variables mostly interact at local scales. Since these treeline sites are located in different mountains of the Tibetan Plateau, we can draw the conclusion at the regional scale. In fact, this argument is frequently used in biogeography (e.g., [7,12,23]).

2.3. Data Analysis

2.3.1. Correlation Analysis

The Pearson correlation coefficients between treeline elevation and the biotic/abiotic factors were calculated for the compiled treeline dataset. These factors included latitude and longitude of treeline site, mountain peak corresponding to each treeline site, slope and aspect of the treeline site, TI, continentality, and radiation. Monthly mean, maximum, and minimum temperatures and monthly precipitations were correlated to treeline elevations, but only the most significant temperature/precipitation factors were presented.

2.3.2. Relative Contribution of Environmental Factors to Treeline Elevation

The above site factors and the other two interactive thermal variables (July temperature × elevation of mountain peak, July temperature × latitude) were used in the models. Generalized linear models were employed to evaluate the relative impacts of each predictor variable on treeline elevation. We calculated the variance explained by each predictor variable using R software system [34] and the package relaimpo, which evaluates the relative importance of predictors in linear models [35]. Based on the "successive sweep method", we determined whether growing season temperature was a significant predictor of treeline elevation.

To avoid the multicollinearity among predictor variables [36], a commonality analysis model was applied to disentangle the pure effect of thermal factors (July mean temperature, elevation of mountain peak, latitude) from their joint effects on treeline elevation (see also examples in [37]). If July mean temperature had the strongest influence on treeline elevation, it should drive the treeline elevation despite the presence of multicollinearity among predictors.

2.3.3. Comparison between Temperatures Extracted from Worldclim Data and Reference Values

Since tree growth at treelines on the Tibetan Plateau is generally correlated with July temperature [34], we expect that July temperature drives the treeline elevation on the Tibetan Plateau. For all the treeline sites, July temperatures derived from the Worldclim dataset were compared and related to other climatic data sources (in situ climate data, CRU 0.5°-gridded data, and interpolated data). Note that CRU 0.5°-gridded data was interpolated to the nearest location for the treeline site based on the lapse rate of 0.6 °C/100 m. If the mean difference between the temperature data is less than 0.5 °C and they are significantly correlated, the July temperature extracted from Worldclim dataset reflects the true climate that treeline trees experience.

3. Results

3.1. Relationships between Treeline Elevation and Environmental Factors

Latitude, elevation of mountain peak, and July mean/minimum temperature were significantly correlated with treeline elevation on the Tibetan Plateau (latitude: $r = -0.45$; elevation of mountain peak: $r = 0.47$; July mean temperature: $r = -0.51$; July minimum temperature: $r = -0.48$; in all cases: $n = 57$, $p < 0.001$) (Table 1). Precipitation in May and July maximum temperature were also significantly associated with treeline elevation, albeit showing a negative correlation (precipitation: $r = -0.31$, $p = 0.03$; temperature: $r = -0.32$, $p = 0.03$; $n = 57$; see Table 1). Other factors, including longitude, aspect, slope, Eastness, TI, and continentality, were not significantly associated with treeline elevation (in all cases: $p > 0.05$; see Table 2). In short, July mean temperature was the variable most closely related to treeline elevation across the Tibetan Plateau followed by mountain elevation.

Table 1. Pearson correlation coefficients obtained by relating treeline elevation and different variables for sites located in the Tibetan Plateau (n = 57 treelines).

Variable	Correlation (r)	p Value
Latitude	−0.45	<0.001
Longitude	−0.19	0.13
Elevation of mountain peak	0.47	<0.001
Aspect	−0.09	0.50
Slope	0.01	0.79
Eastness	−0.18	0.19
Vegetation thickness index	−0.13	0.40
July mean temperature	−0.51	<0.001
July minimum temperature	−0.48	<0.001
July maximum temperature	−0.32	0.03
May precipitation	−0.31	0.03
Continentality	−0.24	0.08
Surface solar radiation	−0.26	0.05

The variables included latitude and longitude of treeline, elevation of mountain peak, aspect and slope of the treeline, vegetation thickness index, July mean/minimum/maximum temperature, May precipitation, continentality index, and surface solar radiation. A composite topographic index "Eastness" that equals sin (aspect) × sin (slope) was also used in the analysis. Underlined correlations represent the three most important predictors of treeline elevation.

Table 2. Comparison between the July mean temperatures extracted from the Worldclim global climate dataset (see more details in [25]) and the reference values obtained from in situ climatic observations. Sites' characteristics are described with more detail in the references (first column).

Reference	Study Area (Site Code)	July Mean Temperature Extracted from Worldclim Data (°C)	Reference Value (°C)	Source of Climate Data	Period of Climate Data
Unpublished data	Dulan, northeastern TP (DL1)	8.5	8.2	In situ data	2013
[8]	Nyingchi, southeastern TP (LZ1)	8.5	8.2	In situ data	2007–2009
[38]	Deqin, southeastern TP (BM1)	7.9	7.4	In situ data	1981–1984

3.2. Comparison between July Mean Temperatures Extracted from Worldclim Data and Reference Values

At three treeline sites, July mean temperatures extracted from the Worldclim database were similar to the reference values obtained from in situ climatic data (Table 2). Specifically, in situ temperature data taken at treeline sites showed deviations lower than 0.5 °C from the temperature data extracted (Table 2). When considering all the treeline sites, July mean temperatures extracted from the Worldclim database was significantly correlated with the reference values obtained from other climatic data sources, including in situ measurements ($r = 0.88$, $p < 0.0001$, $n = 57$). Likewise, reference values at treelines, derived from interpolated data or CRU gridded data, deviated 0.14 ± 0.63 °C from temperature data extracted from the Worldclim database.

3.3. Predicting Treeline Elevation

A generalized linear model that included the selected variables (tree species forming the treeline, latitude and longitude of treeline site, aspect and slope, TI, elevation of mountain peak, radiation, July mean temperature and May precipitation at treelines, continentality index) explained 85.7% of the variance in treeline elevation across the Tibetan Plateau (Table 3). However, only three predictors (July mean temperature, latitude, and tree species forming the treeline) explained 72.4% of the variance in treeline elevation (Table 3). Furthermore, two predictors (July mean temperature and latitude) explained 44.4% of the variance in treeline elevation (Table 3). In either model, July temperature alone accounted for over half of the variance in treeline elevation (Table 3). Therefore, even though latitude, species forming the treeline, and elevation of mountain peak significantly influenced treeline elevation, July mean temperature was the main predictor of treeline elevation.

As demonstrated by the commonality analysis (Figure 2), the model including three thermal factors explained 44.7% of the variance of treeline elevation. In the model, the pure effect of July mean temperature, latitude, and elevation of mountain peak explained 18.1%, 8.5%, and 0.33% variance of treeline elevation, respectively. The joint effects of other variables explained very small amounts of the variance of treeline elevation. To sum up, July mean temperature was the most important predictor of treeline elevation when considering the multicollinearity among predictors.

Table 3. Relative importance of predictors of treeline elevation across the Tibetan Plateau and variance explained (R^2) by generalized linear models.

Predictors of Treeline Elevation											R^2 (%)
Species *	Lat **	Lon	MP *	Aspect	Slope	TI	MeanT_7 ***	Pre_5	Con	SSR	85.7
Species *	Lat **	Lon	MP *		Eastness	TI	MeanT_7 ***	Pre_5	Con	SSR	79.1
Species *	Lat **		MP				MeanT_7 ***				72.6
Species *	Lat **						MeanT_7 ***				72.4
Species *			MP **				MeanT_7 ***				54.9
	Lat **		MP *				MeanT_7 ***				44.7
			MP **				MeanT_7 ***	MeanT_7 × MT			48.4
			MP **				MeanT_7 ***				36.2
	Lat **		MP *				MeanT_7 ***	MeanT_7 × Lat ***			44.8
	Lat **		MP *				MeanT_7 ***				44.8
	Lat ***						MeanT_7 ***	MeanT_7 × Lat			44.5
	Lat **						MeanT_7 ***				44.4

All the models include as predictors: tree species forming the treeline (Species), latitude and longitude of treeline (Lat, Lon), elevation of mountain peak for the treeline (MP), mean slope of treeline ecotone (Slope), aspect of treeline ecotone (Aspect), a composite topographic index "Eastness" that equals sin(aspect) × sin(slope), thickness index (TI) as a surrogate of species interactions, July mean temperature (MeanT_7), precipitation in May (Pre_5), continentality (Con), and surface solar radiation (SSR). The significance of variables is indicated by different asterisks (*, **, and *** indicate $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively).

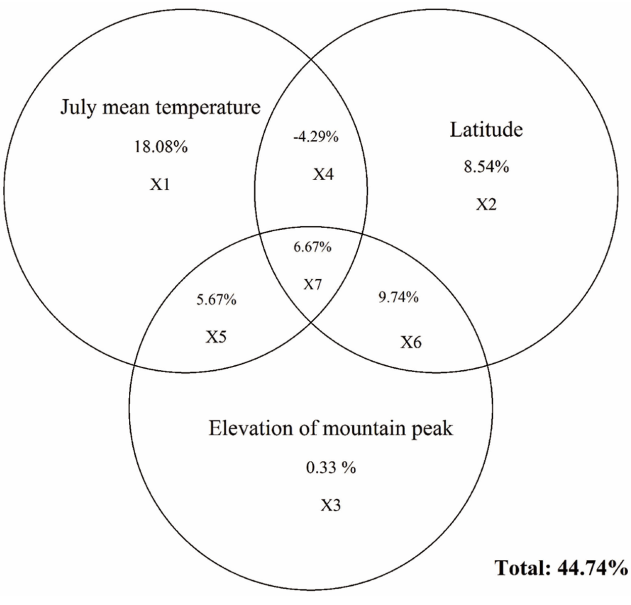

Figure 2. Variation of treeline elevation explained by the commonality analysis for the evaluated variables. The commonality analysis led to seven fractions of explained variations for the response variable: pure effect of July mean temperature (X1); pure effect of latitude (X2); pure effect of the elevation of mountain peak (X3); joint effects of X1 and X2 (X4), X1 and X3 (X5), X2 and X3 (X6), three groups of predictors (X7). The corresponding percentage values represent the explained variance of each fraction.

4. Discussion

The Tibetan Plateau is characterized by cold and continental climate conditions [26]. There is growing evidence that tree growth at treeline is mainly limited by summer temperatures in this region [16,21,22,39–47], thereby suggesting a coupling of thermal conditions and treeline dynamics. In some sites and species, moisture availability also constrains tree growth at treelines [4,48]. Furthermore, regardless of non-thermal factors, elevation of treelines on the different parts of Tibetan Plateau has shifted upwards during the past century, indicating that shifts of treeline elevation are largely warming-driven, albeit species interactions slow warming-induced upward shift rate [12]. Thus, it seems reasonable to argue that treeline elevations on the Tibetan Plateau are closely tied to temperatures.

In this study, July mean temperatures at all treeline sites, derived from the Worldclim data, were consistent with the values obtained from other climatic data sources (e.g., in situ climate data). In fact, the feasibility of this method has also been evidenced at a global scale [25]. We should keep in mind that the influence of July mean temperatures is strongly associated with July minimum temperature. Therefore, our results can be reliably used to estimate treeline temperatures across the Tibetan Plateau. We further found that July mean temperature was the most important driver of treeline elevation on the Tibetan Plateau. When considering the multicollinearity among predictor variables, July mean temperature still had the strongest influence on treeline elevation. These results confirmed our first hypothesis, namely that July temperature is the major driver of treeline elevation on the Tibetan Plateau. However, due to the coarse temporal resolution of Worldclim data [25], we cannot precisely calculate the seasonal temperature threshold that drives treeline elevation on the Tibetan Plateau. Nevertheless, our result has important implications for current ecological studies on the Tibetan Plateau, where elevational shifts of tree species forming the uppermost treeline are largely temperature controlled [12,16,49,50].

Based on results of [25], treeline elevation along the Himalayan Mountains was mainly related to mean temperature in the growing season [25]. However, very few treeline sites located in other mountains of the Tibetan Plateau were included in the analysis of [25]. Using the method they proposed, we found the similar result that treeline elevations in the Tibetan Plateau were primarily driven by July mean temperature.

Latitude has a significant negative effect on treeline elevation on the Tibetan Plateau. This result is in line with the results from other parts of the world [1,51]. However, latitude is not a precise predictor of treeline elevation, since it is a variable indirectly affecting local-scale temperature but also radiation (see also [1]). This is supported by a previous study showing that treeline elevations on the southeastern Tibetan Plateau range between 4300 to 4900 m at similar latitude [18]. Based on the results of generalized linear models, July mean temperature rather than latitude was the most significant predictor of treeline elevation, suggesting that latitude plays a secondary and indirect role in driving treeline elevation in comparison with July mean temperature.

In high mountains, slopes can be heated by the enhanced irradiation and reduced evaporative cooling [52]. This causes isotherms to shift to higher elevations in the center of high mountain massifs, and so do vegetation boundaries such as alpine treelines [1]. Intriguingly, there is evidence that higher elevations of mountain peaks are associated with higher snowlines and treelines, which is the so-called mass elevation effect [53]. In this study, the elevation of mountain peaks was positively associated with treeline elevation, which is consistent with global models of treeline elevation driven by seasonal temperatures [25]. Presumably, the mass elevation effect is tightly linked to temperature regime at the local scale, which ultimately determines the treeline elevation [53,54]. Nevertheless, the detailed mechanism of the mass elevation effect on treeline dynamics merits further exploration [53,54].

Tree species have a considerable effect on treeline elevation (e.g., [55]). For instance, Juniper treelines can reach elevations of 4500–4900 m a.s.l. on the southeastern Tibetan Plateau, whereas fir and spruce treeline elevations are usually located at 4300–4500 m [12,15]. By contrast, the elevation of birch treelines is less than 4100 m in the Himalayas [4]. In this study, tree species also reached different treeline elevations on the Tibetan Plateau which may be attributed to their different traits (e.g., growth and phenology thresholds, vulnerability to freezing damage, evergreen and deciduous leaf habit, vegetative vs. sexual reproduction, recruitment limitation), which have far-reaching influence on treeline responses to climate at local and landscape scales (e.g., [24,56]).

Together with the aforementioned results, the non-thermal factors played important roles in controlling treeline elevation on the Tibetan Plateau. Indeed, all the assessed predictors explained 86% of the variance in treeline elevation on the Tibetan Plateau, whereas growing-season thermal factors explained 55% of the variance. Therefore, our second hypothesis was also supported; namely that links between treeline elevation and site temperature are modulated by non-thermal factors. Such findings have far-reaching implications, since they allow for the speculation that treelines would not respond to climate warming by showing rapid or widespread upward shifts. Alternatively, treeline inertia [57,58] characterized by treeline stasis, lagged responses to climate warming, or even treeline-climate decoupling are expected based on the presented data. If climate warming triggers rapid changes in these ecotones, this may be better reflected in other variables than treeline elevation, for example tree density [10]. In such cases, temperature-based predictions of treeline dynamics might underestimate the impacts of non-thermal factors, but overestimate the sensitivity and reaction time of treeline position to thermal factors [59].

5. Conclusions

We found that July temperature was the most important predictor of treeline elevation on the Tibetan Plateau. Other variables such as latitude, the mass-elevation effect, and tree species were also related to treeline elevation. As the world's highest plateau, the Tibetan Plateau hosts many treeline types which can be used to monitor the effects of climate warming on mountain forest ecosystems. The presented research indicates that thermal factors mainly determine treeline elevation at regional to local scales, but that other non-thermal factors such as tree species also affect treeline elevation. Further studies should combine both sources of information to understand how treeline dynamics will respond to climate warming across the Tibetan Plateau.

Acknowledgments: This work was funded by the National Natural Science Foundation of China (41661144040, 41525001, and 41301207), the International Partnership Program of Chinese Academy of Sciences (131C11KYSB20160061), and the project supported by Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD).

Author Contributions: Y.W., E.L. and J.J.C. designed the research. Y.W. and S.S.R. did the field work. Y.W., B.L. and J.J.C. analyzed the data. Y.W., E.L. and J.J.C. wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Basic information for the treeline sites located in the Tibetan Plateau.

Site Code	Elevation (m a.s.l.)	Aspect	Slope (°)	Tree Species	Treeline Form	Study Region
QL1	3098	N	8	Spruce	diffuse	Qilian Mts
QL2	3386	N	33	Spruce	diffuse	Qilian Mts
QL3	3496	NE	37	Spruce	diffuse	Qilian Mts
QL4	3580	S	31	Juniper	abrupt	Qilian Mts
QL5	3700	S	32	Juniper	abrupt	Qilian Mts
DL1	4186	S	18	Juniper	abrupt	Dulan
DL2	4079	S	39	Juniper	abrupt	Dulan
WL1	3877	NW	27	Spruce	diffuse	Wulan
WL2	3847	NE	32	Spruce	diffuse	Wulan
WL3	3887	NE	24	Spruce	diffuse	Wulan
MQ1	3845	SE	12	Juniper	abrupt	Maqu
MQ2	3877	SE	13	Juniper	abrupt	Maqu
MQ3	3845	SE	20	Juniper	abrupt	Maqu
PW	3240	N	41	Birch	diffuse	Pingwu
DZ1	4195	N	28	Spruce	diffuse	Yushu

Table A1. *Cont.*

Site Code	Elevation (m a.s.l.)	Aspect	Slope (°)	Tree Species	Treeline Form	Study Region
DZ2	4279	N	21	Spruce	diffuse	Yushu
AB	3968	NW	32	Fir	diffuse	Aba
BZ1	4462	S	26	Juniper	abrupt	Yushu
BZ2	4501	S	33	Juniper	abrupt	Yushu
BZ3	4370	N	26	Spruce	abrupt	Yushu
CD1	4308	NE	30	Spruce	diffuse	Changdu
CD2	4472	NW	38	Spruce	diffuse	Changdu
CD3	4436	NE	40	Spruce	diffuse	Changdu
CD4	4460	E	30	Spruce	diffuse	Changdu
CD5	4900	W	28	Juniper	abrupt	Changdu
LZ1	4390	N	10	Fir	Diffuse	Nyingchi
LZ2	4387	N	9	Fir	diffuse	Nyingchi
LZ3	4370	N	15	Fir	diffuse	Nyingchi
MD1	4095	N	30	Spruce	diffuse	Maduo
MD2	4116	N	30	Spruce	diffuse	Maduo
RW1	4471	NE	30	Fir	diffuse	Ranwu
RW2	4448	NE	33	Fir	diffuse	Ranwu
RW3	4478	NW	27	Fir	diffuse	Ranwu
BM1	4397	N	15	Fir	diffuse	Deqin
BM2	4398	N	22	Fir	diffuse	Deqin
BM3	4428	NE	26	Fir	diffuse	Deqin
GG1	3647	SW	42	Fir	diffuse	Gongga Mts
GG2	3641	SW	37	Fir	diffuse	Gongga Mts
GG3	3802	SE	31	Fir	diffuse	Gongga Mts
GLG	3800	N	34	Fir	diffuse	Gaoligong Mts
DJ1	3920	N	19	Fir	diffuse	Rikaze
DJ2	3700	N	20	Fir	diffuse	Rikaze
DJ3	3410	NW	21	Fir	diffuse	Rikaze
LKZ	4647	SW	39	Juniper	abrupt	Shannan
SX	4585	SW	38	Juniper	abrupt	Naqu
LX1	4406	SW	28	Juniper	abrupt	Langxian
LX2	4378	SE	32	Juniper	abrupt	Langxian
LT1	4031	NE	30	Birch	diffuse	Himalayan Mts
LT2	4067	N	35	Birch	diffuse	Himalayan Mts
EV1	4098	N	26	Fir	diffuse	Himalayan Mts
EV2	4049	N	24	Fir	diffuse	Himalayan Mts
MN1	4086	W	33	Birch	diffuse	Himalayan Mts
MN2	4145	N	31	Birch	diffuse	Himalayan Mts
MN3	4095	NW	7	Birch	diffuse	Himalayan Mts
HUM1	4023	NW	31	Birch	diffuse	Himalayan Mts
HUM2	3990	N	22	Fir	diffuse	Himalayan Mts
SKB1	4150	NE	8	Birch	diffuse	Himalayan Mts

a.s.l., above sea level.

References

1. Körner, C. *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*; Springer: Basel, Switzerland, 2012.
2. Körner, C.; Paulsen, J. A world-wide study of high altitude treeline temperatures. *J. Biogeogr.* **2004**, *31*, 713–732. [CrossRef]
3. Liu, H.; Tang, Z.; Dai, J.; Tang, Y.; Cui, H. Larch timberline and its development in North China. *Mt. Res. Dev.* **2002**, *22*, 359–367. [CrossRef]
4. Liang, E.; Dawadi, B.; Pederson, N.; Eckstein, D. Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature? *Ecology* **2014**, *95*, 2453–2465. [CrossRef]
5. Piper, F.I.; Viñegla, B.; Linares, J.C.; Camarero, J.J.; Cavieres, L.A.; Fajardo, A. Mediterranean and temperate treelines are controlled by different environmental drivers. *J. Ecol.* **2016**, *104*, 691–702. [CrossRef]
6. Cieraad, E.; Mcglone, M.S.; Huntley, B. Southern Hemisphere temperature tree lines are not climatically depressed. *J. Biogeogr.* **2014**, *41*, 1456–1466. [CrossRef]
7. Shi, P.; Körner, C.; Hock, G. A test of the growth-limitation theory for alpine treeline formation in evergreen and deciduous taxa of the eastern Himalayas. *Funct. Ecol.* **2008**, *22*, 213–220. [CrossRef]

8. Liu, B.; Liang, E.; Zhu, L. Microclimatic conditions for *Junipers saltuaria* treeline in the Sygera Mountains, southeastern Tibetan Plateau. *Mt. Res. Dev.* **2011**, *31*, 45–53. [CrossRef]
9. Liu, X.; Luo, T. Spatial temporal variability of soil temperature and moisture across two contrasting timberline ectotones in the Sergyemla Mountains, southeast Tibet. *Arct. Antarct. Alp. Res.* **2011**, *43*, 229–238. [CrossRef]
10. Camarero, J.J.; Gutiérrez, E. Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the Spanish Pyrenees. *Clim. Chang.* **2004**, *63*, 181–200. [CrossRef]
11. 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**, *20*, 8117–8122. [CrossRef] [PubMed]
12. 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] [PubMed]
13. Holtmeier, F.K.; Broll, G. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Glob. Ecol. Biogeogr.* **2005**, *14*, 395–410. [CrossRef]
14. Harsch, M.A.; Bader, M.Y. Treeline form—A potential key to understanding treeline dynamics. *Glob. Ecol. Biogeogr.* **2011**, *20*, 582–596. [CrossRef]
15. 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]
16. Fang, K.; Gou, X.; Chen, F.; Peng, J.; D'Arrigo, R.; Wright, W.; Li, M. Response of regional treeline forests to climate change: Evidence from the northeastern Tibetan Plateau. *Trees* **2009**, *23*, 1321–1329. [CrossRef]
17. He, J.; Luo, T.; Xu, Y. Characteristics of ecoclimate at Smith fir timberline in the Segyemal Mountains, southeast Tibetan Plateau. *Acta Ecol. Sin.* **2009**, *29*, 37–46.
18. Liang, E.; Wang, Y.; Eckstein, D.; Luo, T. Little change in the fir treeline positon on the southeastern Tibetan Plateau after 200 years of warming. *New Phytol.* **2011**, *190*, 760–769. [CrossRef] [PubMed]
19. Lyu, L.; Zhang, Q.; Deng, X.; Mäkinen, H. Fine-sale distribution of treeline trees and the nurse plant facilitation on the eastern Tibetan Plateau. *Ecol. Indic.* **2016**, *66*, 251–258. [CrossRef]
20. Ren, Q.; Yang, X.; Cui, G.; Wang, J.; Huang, Y.; Wei, X.; Li, Q. Smith fir population structure and dynamic in the timberline ecotone of the Sejila Mountain, Tibet, China. *Acta Ecol. Sin.* **2007**, *27*, 2669–2677. [CrossRef]
21. Lv, L.; Zhang, Q. Asynchronous recruitment history of Abies spectabilis along an altitudinal gradient in the Mt. Everest region. *J. Plant Ecol.* **2012**, *5*, 147–156. [CrossRef]
22. Gou, X.; Zhang, F.; Deng, Y.; Ettl, G.J.; Yang, M.; Gao, L.; Fang, K. Patterns and dynamics of tree-line responses to climate change in the eastern Qilian Mountains, northwestern China. *Dendrochronologia* **2012**, *30*, 121–126. [CrossRef]
23. Ran, F.; Liang, Y.; Yang, Y.; Yang, Y.; Wang, G. 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.
24. Wang, B.; Chen, T.; Xu, G.; Liu, H.; Wang, W.; Wu, G.; Zhang, Y. Alpine timberline population dynamics under climate change: A comparison between Qilian juniper and Qinghai spruce tree species in the middle Qilian Mountains of northeast Tibetan Plateau. *Boreas* **2016**, *45*, 411–422. [CrossRef]
25. Paulsen, J.; Körner, C. A climate-based model to predict potential treeline position around the globe. *Alpine Bot.* **2014**, *124*, 1–12. [CrossRef]
26. Zheng, D. *A Study on the Ecogeographic Regional System of China*; Chinese Business Press: Beijing, China, 2008.
27. 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. Chang.* **2012**, *2*, 663–667. [CrossRef]
28. Lu, X.; Huang, R.; Wang, Y.; Sigdel, S.R.; Dawadi, B.; Liang, E.; Camarero, J.J. Summer temperature drives radial growth of alpine shrub willows on the northeastern Tibetan Plateau. *Arct. Antarct. Alp. Res.* **2016**, *48*, 461–468. [CrossRef]
29. Lv, L. Timberline Dynamics and Its Response to Climate Change on the Tibetan Plateau. Doctor Thesis, Institute of Botany, Chinese Academy of Sciences, Beijing, China, 2011.
30. Xu, Z.; Hu, T.; Zhang, Y. Effects of experimental warming on phenology, growth and gas exchange of treeline birch (*Betula utilis*) samplings, Eastern Tibetan Plateau, China. *Eur. J. For. Res.* **2012**, *131*, 811–819. [CrossRef]
31. Zhao, F.; Zhang, B.; Yu, P.; Pang, Y.; Yao, Y. A study of the contribution of mass elevation effect to the altitudinal distribution of timberline in the Northern Hemisphere. *J. Geogr. Sci.* **2014**, *24*, 226–236. [CrossRef]

32. 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]
33. Gorczynski, L. The calculation of the degree of continentality. *Mon. Weather Rev.* **1922**, *50*, 369–370. [CrossRef]
34. R Development Core Team. R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna). 2015. Available online: http://www.r-project.org (accessed on 25 November 2016).
35. Grömping, U. Relative importance for linear regression in R: The Package relaimpo. *J. Stat. Softw.* **2006**, *17*, 1–27. [CrossRef]
36. Ray-Mukherjee, J.; Nimon, K.; Mukherjee, S.; Morris, D.W.; Slotow, R.; Hamer, M. Using commonality analysis in multiple regressions: A tool to decompose regression effects in the face of multicollinearity. *Methods Ecol. Evol.* **2014**, *5*, 320–328. [CrossRef]
37. Huang, R.; Zhu, H.; Liu, X.; Liang, E.; Grießinger, J.; Wu, G.; Li, X.; Bräuning, A. Does increasing intrinsic water use efficiency (iWUE) stimulate tree growth at natural alpine timberline on the southeastern Tibetan Plateau? *Glob. Planet. Chang.* **2017**, *148*, 217–226. [CrossRef]
38. Li, W.; Zhang, Y. *Vertical Climates in the Hengduan Mountains and their Impact on Forest Distribution*; China Meteorological Press: Beijing, China, 2010.
39. 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]
40. Liu, X.; Qin, D.; Shao, X.; Chen, T.; Ren, J. Temperature variations recovered from tree-rings in the middle Qilian Mountain over the last millennium. *Sci. China Ser. D* **2005**, *48*, 521–529. [CrossRef]
41. 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. Chang.* **2008**, *61*, 313–320. [CrossRef]
42. Liang, E.; Shao, X.; Xu, Y. Tree-ring evidence of recent abnormal warming on the southeast Tibetan Plateau. *Theor. Appl. Climatol.* **2009**, *98*, 9–18. [CrossRef]
43. Zhu, H.; Zhang, 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. *Chin. Sci. Bull.* **2008**, *53*, 3914–3920. [CrossRef]
44. Li, X.; Liang, E.; Gričar, J.; Prislan, P.; Rossi, S.; Čufar, K. Age dependence of xylogenesis and its climatic sensitivity in Smith fir on the south-eastern Tibetan Plateau. *Tree Physiol.* **2013**, *33*, 48–56. [CrossRef] [PubMed]
45. Li, X.; Rossi, S.; Liang, E.; Camarero, J.J. Temperature threshold for the onset of xylogenesis in alpine shrubs on the Tibetan Plateau. *Trees* **2016**, *30*, 2091–2099. [CrossRef]
46. Asad, F.; Zhu, H.; Zhang, H.; Liang, E.; Muhammad, S.; Farhan, S.B.; Hussain, I.; Wazir, M.A.; Ahmed, M.; Esper, J. Are Karakoram temperatures out of phase compared to hemispheric trends? *Clim. Dyn.* **2016**. [CrossRef]
47. Liu, B.; Wang, Y.; Zhu, H.; Liang, E.; Camarero, J.J. Topography and age mediate the growth responses of Smith fir to climate warming in the southeastern Tibetan Plateau. *Int. J. Climatol.* **2016**, *60*, 1577–1587. [CrossRef] [PubMed]
48. Schickhoff, U. The upper timberline in the Himalayas, Hindu Kush and the Karakorum: A review of geographical and ecological aspects. In *Mountain Ecosystems: Studies in Treeline Ecology*; Broll, G., Keplin, B., Eds.; Springer: Berlin, Germany, 2005.
49. Zhu, H.; Shao, X.; Yin, Z.; Xu, Y.; Tian, H. August temperature variability in the southeastern Tibetan Plateau since AD 1385 inferred from tree rings. *Palaeogeogr. Palaeoclimatol. Palaeocol.* **2011**, *305*, 84–92. [CrossRef]
50. Shen, M.; Piao, S.; Dorji, T.; Liu, Q.; Cong, N.; Chen, X.; An, S.; Wang, S.; Wang, T.; Zhang, G. Plant phenological responses to climate change on the Tibetan Plateau: Research status and challenges. *Natl. Sci. Rev.* **2015**, *2*, 454–467. [CrossRef]
51. Case, B.S.; Duncan, R.P. A novel framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline position. *Ecography* **2014**, *37*, 1–14. [CrossRef]
52. Zhang, B.; Yao, Y. *Studies on Mass Elevation Effect*; China Environmental Science Press: Beijing, China, 2015.
53. Yao, Y.; Zhang, B. The mass elevation effect of the Tibetan Plateau and its implications for Alpine treelines. *Int. J. Climatol.* **2015**, *35*, 1833–1846. [CrossRef]
54. Zhao, F.; Zhang, B.; Zhang, S.; Qi, W.; He, W.; Wang, J.; Yao, Y. Contribution of mass elevation effect to the altitudinal distribution of global treelines. *J. Mt. Sci.* **2015**, *12*, 289–297. [CrossRef]

55. Shen, W.; Zhang, L.; Liu, X.; Luo, T. Seed-based treeline seedlings are vulnerable to freezing events in the early growing season under a warmer climate: Evidence from a reciprocal transplant experiment in the Sergyemal Mountains, southeast Tibet. *Agric. For. Meteorol.* **2014**, *187*, 83–92. [CrossRef]
56. Rehm, E.M.; Feeley, K.J. Seedling transplants reveal species-specific responses to high-elevation tropical treeline trees to climate change. *Oecologia* **2016**, *181*, 1–10. [CrossRef] [PubMed]
57. Kullman, L. One century of treeline change and stability—Experiences from the Swedish Scandes. *Landsc. Online* **2010**, *17*, 1–31. [CrossRef]
58. Camarero, J.J.; García-Ruiz, J.M.; Sangüesa-Barreda, G.; Galván, J.D.; Alla, A.Q.; Sanjuán, Y.; Beguería, S.; Gutiérrez, E. Recent and intense dynamics in a formerly static treeline. *Arct. Antarct. Alp. Res.* **2015**, *47*, 773–783. [CrossRef]
59. Zhu, K.; Woodall, C.W.; Clark, J. Failure to migrate: Lack of tree range expansion in response to climate change. *Glob. Chang. Biol.* **2012**, *18*, 1042–1052. [CrossRef]