Contribution of Mass Elevation Effect to the Altitudinal Distribution of Global Treelines

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Abstract: Alpine treeline, as a prominent ecological boundary between forested mountain slopes and alpine meadow/shrub, is highly complex in altitudinal distribution and sensitive to warming climate. Great efforts have been made to explore their distribution patterns and ecological mechanisms that determine these patterns for more than 100 years, and quite a number of geographical and ecophysiological models have been developed to correlate treeline altitude with latitude or a latitude related temperature. However, on a global scale, all of these models have great difficulties to accurately predict treeline elevation due to the extreme diversity of treeline site conditions. One of the major reasons is that “mass elevation effect” (MEE) has not been quantified globally and related with global treeline elevations although it has been observed and its effect on treeline elevations in the Eurasian continent and Northern Hemisphere recognized. In this study, we collected and compiled a total of 594 treeline sites all over the world from literatures, and explored how MEE affects global

treeline elevation by developing a ternary linear regression model with intra-mountain base elevation (IMBE, as a proxy of MEE), latitude and continentality as independent variables. The results indicated that IMBE, latitude and continentality together could explain 92% of global treeline elevation variability, and that IMBE contributes the most (52.2%), latitude the second (40%) and continentality the least (7.8%) to the altitudinal distribution of global treelines. In the Northern Hemisphere, the three factors’ contributions amount to 50.4%, 45.9% and 3.7% respectively; in the south hemisphere, their contributions are 38.3%, 53%, and 8.7%, respectively. This indicates that MEE, virtually the heating effect of macro-landforms, is actually the most significant factor for the altitudinal distribution of treelines across the globe, and that latitude is relatively more significant for treeline elevation in the Southern Hemisphere probably due to fewer macro-landforms there.

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factor; Continentality; Contribution rate

Introduction

Alpine treeline is an ecological boundary between continuous montane forests to the extreme upper limit of the occurrence of tree species in high mountains. It has been studied for more than 100 years in many disciplines, including geography, biogeography, ecology, climatology, etc. Treeline position has been considered a crucial ecological marker for the lower limit of alpine belts and also a sensitive indicator of climate warming (Troll 1973; Kullman 2007; Rössler et al. 2008).

Treeline elevation has been often associated with latitude or latitude-related temperature, and a number of treeline elevation-latitude models have been developed to determine treeline elevation at regional and global scales (Malyshev 1993; Cogbill et al. 1991; Fang 1995; Körner 1998). However, regional models are only effective regionally and cannot be applied to global scale. For example, according to the Malyshev (1993)'s Ural model, treelines near 30°N should be at 2950 m, but they are actually at 4800-4900 m in the southeast Tibetan Plateau (Schickhoff 2005; Miehe et al. 2007). Körner (1998)'s global model roughly outlines the latitudinal pattern of treeline elevations at a global scale, but cannot accurately predict treeline elevation, because treeline elevation does not have strict correlation with latitude globally. As a matter of fact, treeline elevation can vary greatly at the same latitude, for example, it can rise from 3500 m (Zhong 1983) on the eastern slope of the Gongga Mountains in the eastern periphery of the Tibetan Plateau to 4900 m (Miehe et al. 2007) in Baxoi County in the inner Tibetan Plateau at 30°N with a difference of as large as 1400 m. There is no doubt that some environmental factors unrelated to latitude must have reshaped the altitudinal distribution of global treelines (Körner 1998).

Eco-physiologically, treeline formation and maintenance has been directly related with some isotherms, involving the warmest month air temperature of 10°C (Daubenmire 1954; Grace 1977; Ohsawa 1990), annual biotemperature of 3°C (Holdridge 1947, 1967), warmth index (WI) of 15°C·month (Kira 1945; Ohsawa 1990; Fang et al.

1996), seasonal mean ground temperature of 6.7°C±0.8°C (Körner 1998b; Körner et al. 2004), etc. But it has been found that treeline elevation varies greatly in mountains at similar latitudes (e.g., by 1400 m as mentioned above), implying a great difference in the altitudinal positions of these isotherms. What factors on earth bring about such tremendous difference?

Treeline elevations have been found to ascend from polar to tropical regions, from island to continental inland, and from the periphery to central parts of large mountain massifs (Holtmeier 2009). Many factors interplay to give rise to these patterns of distribution, including zonal factors (latitude, aridity or precipitation), regional factors (macro-landform, relief) and local factors, e.g., slope and aspect, soil, human intervenes, ocean currents, species competition, beetle infestations, invasive pathogens, herbivores, etc. (Holtmeier 2005). Mean annual temperature and seasonal thermal amplitude were ever used to model global altitudinal distribution of treelines (Jobbagy et al. 2000). The two factors, to a great extent, can be reflected with latitude and continentality, respectively. The large thermo-dynamic effects of massive mountains have long been overlooked. At continental and hemispheric scales, it has recently been shown that latitude, continentality and mass elevation effect (MEE) together play a major role in the altitudinal distribution of treelines (Zhao et al. 2014; Han et al. 2012). It means that these three factors, especially MEE, must be taken into account if a global high-accuracy treeline model is to be developed.

The question we now face is that MEE has not been adequately quantified globally. We consider that looking for a proxy for MEE may be a feasible method to quantify MEE at present. The top height or average height of mountains seems to be such a proxy, but treelines may not be very high in some high mountains. For example, the absolute height of Mt. Kilimanjaro is as high as 5895 m above sea level and it is even close to the equator, but the treeline is at about only 3500 m (Hemp 2006), about 1100~1400 m lower than in the interior Tibetan Plateau (Schickhoff 2005). The reason may be that it's a volcanic cone without intra-mountain plateaus or basins, and that mountain slopes are all completely exposed to the free air, so the temperature difference between the mountain

Figure 1 Two treeline examples at 2800-3000 m in the western Tianshan Mts. of Xinjiang (left) and at 4300-4400 m in the Baima Snow Mts. of Yunnan (right) in China.

surface and the free air at the same altitude may be very small. If the mountains are broad and there exist intra-mountain plateaus and basins, such as the interior Tibetan Plateau, treelines are much higher even though they are farther from the equator. In other words, the higher the inner plateaus and basins are, the higher the treeline elevations (Figure 1). Based on this consideration, we consider that IMBE (intra-mountain base elevation) can serve as the proxy of MEE. In this study, we intend to evaluate the significance of MEE for the altitudinal distribution of global treelines by analyzing the contribution of IMBE to global treeline elevations; and to compare the difference in the contribution of MEE between the Northern Hemisphere and Southern Hemisphere.

1 Material and Methods

1.1 Treeline data set

Treeline was defined as ecotone between continuous forest (timberline) and the highest patches of tree species (tree species line) composed of trees of at least 3 m height (Körner et al. 2004). Based on this definition, we collected a data set of treeline sites involving their elevation and geographic coordinates (latitude, longitude) from published literatures. If authors did not explicitly state tree height, but only described ranges of a treeline ecotone, took the middle position of the ecotone as treeline elevation. Treeline data sites were discarded if their elevations, according to

literature descriptions, have been depressed by human disturbance, fire, natural disasters, etc. Moreover, the vertical distance between treeline and mountain summit should be at least 200m so as to minimize the very local climatic effect near the summit on treeline elevation.

Following these criteria, we selected and compiled a total of 594 treeline sites covering almost all the mountains and plateaus globally (Figure 2), from about 130 publications. It is noticeable that most of the treeline sites are in the Northern Hemisphere and only a few in the Southern Hemisphere. This is because there are much more high mountains in the Northern Hemisphere than in the Southern.

1.2 Data set for intra-mountain base elevation

Mountain base elevation (MBE) was commonly defined as the altitude of the basal zone in the previous studies on mountain altitudinal belts (Liu 1981; Zhang et al. 1988). It was generally taken as the average elevation of foothills in isolated mountains in the plain and hilly areas without intra-montane basins or valleys, e.g., Mt. Kilimanjaro (Hemp 2006). For oceanic islands such as Tenerife in the insular Spain, MBE is zero. However, for the immense and towering Tibetan Plateau covering an area of nearly 2.5 million km², there are many local bases, not only in the peripheral plains, but also in the interior basins and valleys (Zhang 1978; Hou 1982). The average height of these basins and valleys was defined as

Figure 2 Distribution of 594 global treeline data sites used in this study.

intra-mountain base elevation (IMBE). Usually, IMBE becomes higher and higher from the peripheral toward the inner plateau, e.g., it is about 3700m in Lhasa, 4300-4500 m in the most parts of the plateau, and 4500-4800 m in its northwest (Zhang et al. 1988). For the isolated mountains, such as Kilimanjaro, due to the lack of intra-montane basins or valleys, IMBE is actually equivalent to MBE. According to these definitions we manually extracted IMBEs for the 594 treeline data sites worldwide based on the topographical data from SRTM 90 m Digital Elevation Data (<http://srtm.csi.cgiar.org/>). The detailed method for calculating IMBE is based on Zhang et al. (2012).

1.3 Climatic variables

Climatic data for monthly mean temperatures at treeline positions were extracted from WorldClim database (Hijmans et al. 2005), which provided interpolated climate surfaces at a spatial resolution of 30 arcs (equivalent to 860m) for 1950-2000 and has been widely used in several macro-ecological studies (Szabo et al. 2009; Casalegno et al. 2010; Kessler et al. 2011). We calculated continentality for each treeline site based on the following Gorczynski's formulas (1922).

Northern Hemisphere:

$$K = 1.7 \times \frac{A}{\sin \Phi} - 20.4 \quad (1)$$

Southern Hemisphere:

$$K = 1.6 \times \frac{A}{\sin \Phi} - 14.4 \quad (2)$$

where K is continentality, Φ is latitude (to avoid the denominator to be zero, take Φ as 10 when $|\Phi| < 10$), and A is the difference of mean temperatures of the warmest and the coldest months.

1.4 Data analyses

We performed a multiple regression analysis with treeline elevation as the dependent variable, and the three variables (latitude, continentality and IMBE) as independent variables. The multiple regression model is as follows:

$$TL(m) = a \times Lat + b \times K + c \times IMBE + d \quad (3)$$

where TL is treeline elevation, Lat latitude, IMBE the proxy of MEE, K continentality; a, b and c are coefficients of independent variables, d is constant term.

Based on this model we calculated the predicted values of treeline elevations and graphed the relationship between predicted and actual treeline elevations with 95% confidence interval globally. Kruskal-Wallis (K-W) test was carried out to test the significance of the independent variables

and the model. A collinearity test based on variance inflation factor (VIF) and tolerance was also conducted to examine the multicollinearity among the independent variables. Supposing that the combined effects of the three independent variables to the altitudinal distribution of treelines is 100%, their respective contribution rates can be figured out based on their standardized coefficients.

2 Results

2.1 Global treeline elevation model

As shown in Figure 3, treeline elevation displays an obvious tendency to lowering with increased latitude from latitude 30°N to latitude 70°N and from latitude 20°S to latitude 60°S; while from 30°N and 20°S to the equator, there is a slight decrease in treeline elevation (Figure 2). The highest treelines do not occur in the equatorial regions but in the subtropics at 30°N and 20°S.

K-W non-parametric test shows that the differences among latitude, continentality, and IMBE are significant with $P < 0.01$. Collinearity statistics shows that there is no multicollinearity among the three independent variables with $VIF < 5$ and tolerance > 0.2 . The multiple regression model developed globally explains 92% of the altitudinal variation of treelines with R^2 as high as 0.92. Unstandardized Coefficients and 95% confidence interval for parameter estimates describe the relationship between treeline elevation and latitude, continentality and IMBE. It reveals that treeline elevation drops for approximately 47m per degree increase of latitude when other parameters keep unchanged; while it is elevated by 80m for 100m increase in IMBE and by 56m for 10 unit increase of continentality (Table 1). The linear regression line and 95% confidence interval shown in Figure 4 reflects the close relationship between the actual and predicted treeline elevation. Standard regression coefficients

indicate that the contributing rate is 52.2% by IMBE, 40% by latitude, and only 7.8% by continentality. This means that IMBE serves as the most significant factor for global treeline elevation distribution.

2.2 Treeline elevation model for the Northern Hemisphere

The model developed for the Northern Hemisphere explains 93% of the altitudinal variation of treelines. K-W test and collinearity statistics all have the same result as for the global

Figure 3 Latitudinal pattern of global treeline elevation distribution (Data from published literatures).

Figure 4 Linear-regressed trend line with 95% predicted interval showing the relationship between actual and predicted treeline elevation of global treelines.

model. Treeline elevation drops by approximately 53 m per degree increase of latitude when other parameters keep unchanged in the Northern Hemisphere; while treeline is elevated by about 74m for 100m increase in IMBE and by 27m for 10 unit increase in continentality (Table 1). The standard regression coefficients reveal that IMBE still has the highest contribution rate of as high as 50.4% with latitude the second (45.9%) and continentality the least (3.7%).

2.3 Treeline elevation model for the Southern Hemisphere

The multiple regression model explains the altitudinal distribution of treelines almost perfectly in the Southern Hemisphere, with R^2 as high as 0.94. K-W test and collinearity statistics all have the same results as for the global model. Treeline elevation drops by approximately 44 m per degree increase of latitude, and increases by 61m for 100m increase of IMBE and by 19 m for 10 unit increase of continentality when other parameters keep unchanged (Table 1). But, unlike the case in the Northern Hemisphere, latitude becomes the leading factor with a contribution rate of 53%, IMBE the second (38.3%) and continentality the least (8.7%).

2.4 Residual analysis

To analyze the prediction accuracy of the

multiple regression models, we calculated the residual between the predicted and actual values of the treeline elevations. According to the results of residual analysis (Figure 5), most of the standardized residuals are distributed around zero in the three cases, and the error term agrees with a normal assumption, which further confirms the validity of the multiple regression models in this study.

3 Discussion and Conclusions

Our study confirms that the altitudinal distributions of treelines at global and hemispherical scales are mainly controlled by the combined effect of IMBE, latitude and continentality. With the three factors, we are able to explain over 90% of the global and hemispherical variability of treeline elevation. That is a great step forward from the result by Jobbagy and Jackson (2000). In their model, almost no high treelines (above 3500m) are included and only 79% of the global variability of treeline elevation is explained. Our model, by contrast, has higher capability of explanation and quite satisfactorily deals with these high treelines. According to our model, the occurrence of high treelines at similar latitudes is closely related to MEE (reflected by IMBE) and continentality, which is very consistent with Schickhoff's (2005) conclusion.

Table 1 Multiple linear regression models of treeline sites. Models include 594 sites globally, 528 for the Northern Hemisphere, 66 for the Southern Hemisphere. Independent variables are IMBE (intra-mountain base elevation), latitude and continentality, dependent variable is treeline elevation

Model		K-W test H/df /Sig.	R^2	C1	C2	CR(%)	P-value	CT/ VIF	95% confidence interval
Globe	Constant			3223			< 0.01		(3060 3387)
	Latitude			-47.1	-0.46	40	< 0.01	0.54 / 1.86	(-50.33 -43.88)
	Continentality	939 / 2 / < 0.01	0.92	5.63	0.09	7.8	< 0.01	0.87 / 1.15	(4 7.27)
	IMBE			0.80	0.60	52.2	< 0.01	0.55 / 1.81	(0.76 0.85)
Northern Hemisphere	Constant			3712			< 0.01		(3529 3895)
	Latitude			-52.78	-0.50	45.9	< 0.01	0.48 / 2.08	(-56.19 -49.36)
	Continentality	831 / 2 / < 0.01	0.93	2.66	0.04	3.7	< 0.01	0.93 / 1.08	(1.04 4.29)
	IMBE			0.74	0.55	50.4	< 0.01	0.50 / 2.01	(0.69 0.78)
Southern Hemisphere	Constant			2713			< 0.01		(2417 3010)
	Latitude			-44.28	-0.61	53	< 0.01	0.66 / 1.52	(-49.53 -39.03)
	Continentality	120 / 2 / < 0.01	0.94	19.33	0.10	8.7	< 0.01	0.79 / 1.27	(6.48 32.19)
	IMBE			0.61	0.44	38.3	< 0.01	0.68 / 1.46	(0.51 0.71)

Notes: CR = Contribution rate; CT/VIF = Collinearity tolerance /variance inflation factor; C1 and C2 refer to Unstandardized coefficients and Standardized coefficients, respectively; IMBE means intra-mountain base elevation.

Figure 5 Standardized residual of the altitudinal distribution of treelines for the globe (a), the Northern Hemisphere (b) and the Southern Hemisphere (c).

Of the three variables we considered (IMBE, latitude and continentality), IMBE contributes most to the altitudinal variation of global treelines meaning that MEE is the most significant factor in modeling global treeline elevation variability. This is in line with our previous studies on the altitudinal distribution of treelines in the northern

hemispherical (Zhao et al. 2014) and southeastern hemispherical (Han et al. 2012). However, it is surprisingly different from what has been expected—temperatures associated with Latitude and continentality should be the major factor for treeline elevation distribution (Wardle 1974; Cogbill et al. 1991; Malyshev 1993; Jobbagy et al. 2000). We consider that MEE has been underestimated as a key factor influencing global treeline distribution patterns. In other words, MEE is a key factor in developing a high-accuracy model for the altitudinal distribution of treelines at a global scale.

The contribution of IMBE to treeline elevation varies greatly between the two hemispheres: 50.4% in the Northern Hemisphere and 38.3% in the southern. This is reasonable, for a number of immense plateaus and mountain ranges are located in the Northern Hemisphere. In the Southern Hemisphere, however, only the Andes range is massive, and it runs roughly north-south coinciding with the latitudinal differentiation of temperature.

The mechanism of MEE has much to do with the heating effect of extensive mountain massifs at the global scale, as global treelines are mainly controlled by temperature (Daubenmire 1954; Jobbagy et al. 2000). High mountain massifs can improve the thermal conditions through the sensible heat transfer associated with elevated heating surface directly (Barry 2008; Holtmeier 2009) and latent heat caused by convective activity and orographic precipitation indirectly (Yeh et al. 1974; Rao et al. 1989). As a result, temperature is higher in the interior of mountain chains or plateaus with high local base elevation than in the free atmosphere above the peripheral low land. For example, monthly mean temperature in the interior Tibetan Plateau is 3.58°C-6.63°C higher than in the eastern Sichuan Basin at 4500 m, according to Yao et al. (2014), which causes treelines to rise by about 500-1000 m in the inner main plateau than in the eastern border areas. At regional and local scales, MEE is also related with continentality (Whitmore 1984; Schickhoff 2005; Holtmeier 2009), species competition (VanSteenis 1961; Hall 1984), availability of soil mineral nutrients (Grubb 1971), and even human disturbances and geomorphologic constraints (Leonelli et al. 2009).

Although our treeline elevation distribution models are of high accuracy, there are still some outliers mainly on oceanic islands. Actual treeline elevations are obviously lower than predicted. The depression of actual treelines on oceanic island mountains may be attributed to many local factors, e.g. temperature inversions by the dry trade-wind belt, immature volcanic soils and other factors (Leuschner 1996), which should be considered in future research of local treeline distribution. Anyhow, the multiple regression model taking latitude, continentality, and IMBE as independent variable is quite robust at global and hemispheric scales.

Besides uplifting treeline, MEE can also put upward snowline (Han et al. 2011), affect continentality (Holtmeier 2009), enrich the biomass of invertebrate (Leakey et al. 1987), reduce the susceptibility of resident species to extrinsic

disturbance, and even improve the stability of ecosystems (Cronk 1997). So its quantification can be expected to have a much wider application. Nevertheless, using IMBE to represent MEE is an expedient measure at the moment. In future study, we will take into account multiple factors, e.g. mountain surface properties, mean altitude, mountain structures, etc. to realize its direct and complete quantification.

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