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# The Mass Elevation Effect of the Central Andes and Its Implications for the Southern Hemisphere's Highest Treeline

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One of the highest treelines in the world is at 4810 m above sea level on the Sajama Volcano in the central Andes. The climatological cause of that exceptionally high treeline position is still unclear. Although it has been suggested that the

mass elevation effect (MEE) explains the upward shift of treelines in the Altiplano region, the magnitude of MEE has not yet been quantified for that region. This paper defines MEE as the air temperature difference in summer at the same elevation between the inner mountains/plateaus (Altiplano) and the free atmosphere above the adjacent lowlands of the Andean Cordillera. The Altiplano air temperature was obtained from the Global Historical Climatology Network-Monthly temperature database, and the air temperature above the adjacent lowlands was interpolated based on the National Center for Environmental

Prediction/National Center for Atmospheric Research Reanalysis 1 data set. We analyzed the mean air temperature differences for January, July, and the warm months from October to April. The air temperature was mostly higher on the Altiplano than over the neighboring lowlands at the same altitude. The air temperature difference increased from the outer Andean east-facing slope to the interior of the Altiplano in summer, and it increased from high latitudes to low latitudes in winter. The mean air temperature in the Altiplano in summer is approximately 5 K higher than it is above the adjacent lowlands at the same mean elevation, averaging about 3700 m above sea level. This upward shift of isotherms in the inner part of the Cordillera enables the treeline to climb to 4810 m, with shrub-size trees reaching even higher. Therefore, the MEE explains the occurrence of one of the world's highest treelines in the central Andes.

**Keywords:** Mass elevation effect; central Andes; treeline; heating effect; air temperature.

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## Introduction

The high-elevation treeline is one of the most obvious land cover demarcations and represents the transition from trees to shrubs or other low-stature alpine vegetation (Körner 2012; Paulsen and Körner 2014). The prevailing hypothesis regarding the cause of treeline formation is that heat deficiency limits tree growth at high elevations from an ecophysiological perspective, which is based on notable similarities in various temperature parameters at treelines worldwide (Körner and Paulsen 2004; Hoch and Körner 2009; Harsch and Bader 2011).

Treelines exhibit striking differences as well as similarities (Harsch and Bader 2011; Malanson et al 2011). A conspicuous example is that one of the highest treelines in the world is 4810 m above sea level on the Sajama Volcano in the central Andes, with shrub-size individuals up to 5100 m, extending more than 700 m higher than on the outer Andean east-facing slope (Jordan 1980; Kessler

1995; Hoch and Körner 2005; Bader et al 2007; Kessler et al 2007, 2014). This may result from the so-called mass elevation effect (MEE) or *Massenerhebungseffekt*, first introduced by Quervain in 1904 to account for the observed tendency of temperature-related parameters such as treeline and snowline to occur at higher elevations in the central Alps than in the outer margins (Quervain 1904). MEE has also been reported in many other regions of the world (Hall 1984; Holtmeier 2009; Han et al 2011).

MEE is mainly explained as the upslope movement of isotherms from front ranges into central ranges of larger mountain systems (Quervain 1904; Ellenberg 1963; Körner 2012). According to Richter (2000) and Barry (2008), there are 3 components of MEE: (1) continentality with a predominance of air mass advection, (2) mountains where convection is dominant, and (3) windward blocking with lee-side foehn. Types 1 and 3 were found in the central Andes. The first type is mainly related to cloud formation and precipitation (Fliri 1975; Witmer et al 1986; Holtmeier 2009; Körner 2012). As air masses move upslope, clouds are

formed and precipitation is enhanced on the outer slope of a mountain. In comparison, in the central parts of the mountain area, there are fewer clouds, lower precipitation, and more hours of sunshine (Körner 2012). The elevated plateau surfaces receive more radiation, and serve as a heating surface absorbing solar radiation and transferring the heat to the atmosphere, which can cause the air above an elevated plateau to be warmer than the adjacent air at the same elevation above lowlands in summer (Flohn 1953; Yeh and Chang 1974; Rao and Erdogan 1989; Barry 2008). The third type is the most widely occurring one. An increasing height of the crest of mountains leads to screening of the leeward escarpments, and the climatic features on the outer windward slope are different from those on the leeward slope (Richter 2000).

Although it has been suggested that MEE can explain the upward shift of treelines, the magnitude of MEE has not been well quantified. Recently, it has been confirmed that the monthly mean air temperature in the interior of the Tibetan Plateau is approximately 2–7°C higher than in the surrounding mountains and adjacent lowland areas at the same latitude and altitude, which contributes to the rise of treelines to 4600–4700 m (Yao and Zhang 2015), with some junipers at elevations up to 4900 m on a few sunny slopes (Miehe et al 2007). However, the magnitude of MEE in the central Andes and the extent of warming in this region relative to the surrounding areas remain unknown. Thus, this paper attempts to quantify MEE by comparing air temperatures in the central Andes with those above the adjacent lowlands at the same altitude and to discuss the implications of MEE for the occurrence of one of the highest treelines in the world, which occurs in the central Andes.

## Study area

The study area is located between latitudes 13–27°S and longitudes 60–75°W. This mainly corresponds to the central Andes (Figure 1), the widest part of the mountain range, with a width of about 200–700 km, which splits into an eastern and a western range between 15 and 22°S, encompassing a large plateau, the Altiplano, with an average elevation of 3500–4000 m (Vuille 1999). The Altiplano is defined as internally drained basins with moderate relief (Lamb and Hoke 1997; McQuarrie et al. 2005). At 18.1°S, where the highest treeline is located, from west to east 5 main geological zones can be distinguished: the Western Cordillera, the Altiplano, the Eastern Cordillera, the sub-Andean zone (the frontal, most active portion of the Andean fold-thrust belt), and the plain (lowlands) (McQuarrie et al 2005) (Figure 2). In this paper, the outer slope of the Andes mainly corresponds to the east-facing slope of the Eastern Cordillera and the sub-Andean zone area. In the austral summer, easterly winds prevail in the middle and upper troposphere over the Altiplano, resulting in a reduction in westward transport of moisture (Vuille 1999).

## Methods

### Data sources and interpolation

We obtained air temperature data for the central Andes from the Global Historical Climatology Network-Monthly temperature data set (<http://www.ncdc.noaa.gov/ghcnml/>), which has the most explicit quality control of available data sets (Peterson and Vose 1997; Peterson et al 1998; Hijmans et al 2005; Pepin and Seidel 2005). In order to make a reasonable comparison, all available mean monthly temperatures from this data set between 1980 and 2010 were used to maintain consistency with the temperature data for the air outside of the Andes.

Air temperature data for outside the Andes were obtained from the National Center for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) Reanalysis 1 data set (<http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.html>), which has comprehensive coverage with few missing data (Kistler et al 2001). It is a combination of air data, including radiosonde and satellite data, with model output. Air temperatures are recorded on a 2.5° latitude–longitude grid, at 17 pressure levels (Pepin and Seidel 2005).

To get the temperature of the air outside the mountain ( $T_{\text{air\_out}}$ ) at a given altitude  $h$ , vertical interpolation was done based on a linear lapse rate between the 2 nearest pressure levels, using the following equation:

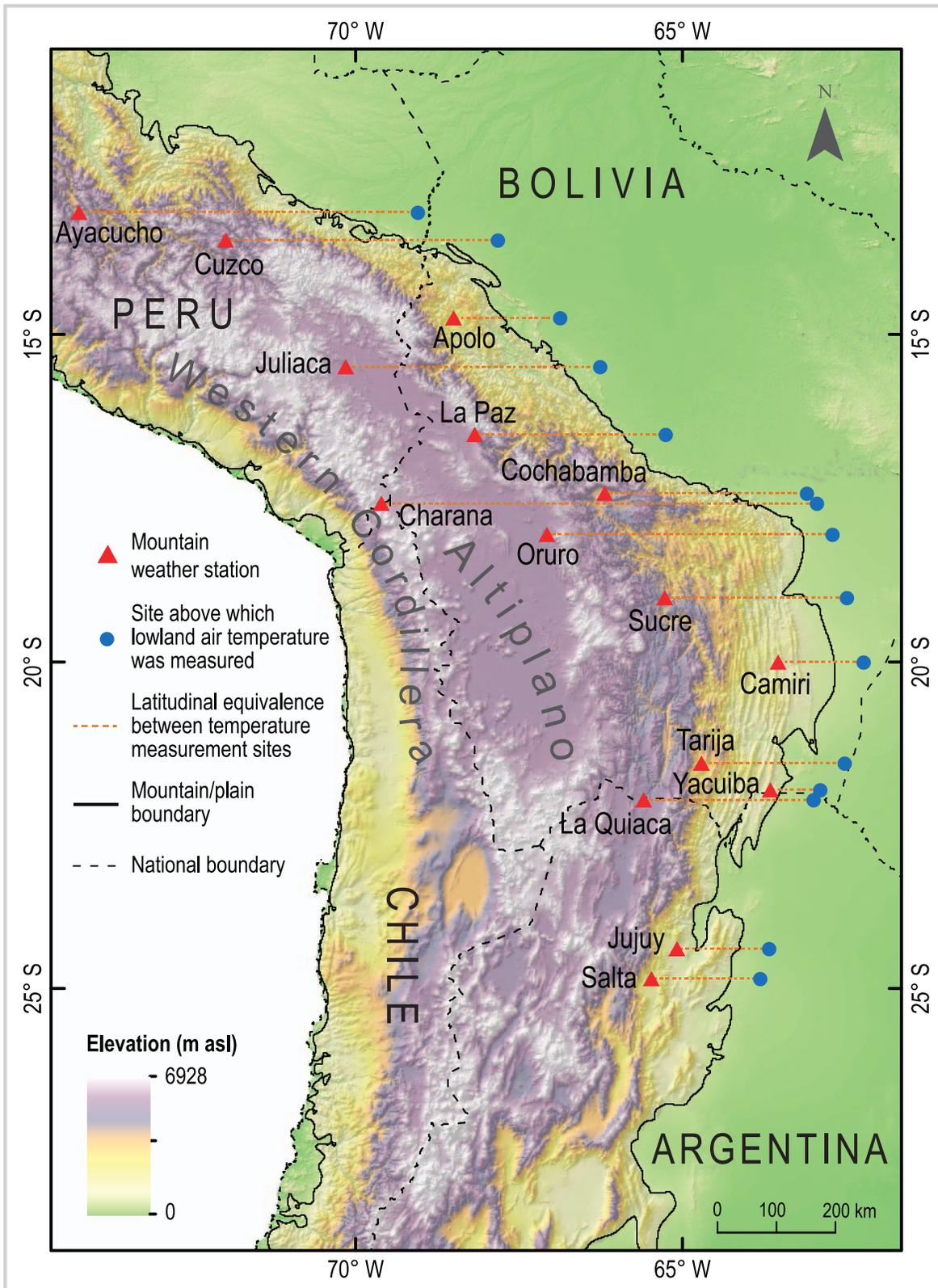
$$T_{\text{air\_out}} = T_n - (h - H_n) / (H_m - h) (T_n - T_m) \quad (1)$$

where  $H_m$  and  $H_n$  ( $H_n < H_m$ ) are the heights of the 2 nearest pressure levels, and  $T_m$  and  $T_n$  are air temperatures at  $H_m$  and  $H_n$  pressure levels, respectively. This method assumes a linear temperature lapse, which is usually appropriate at altitudes well above the surface (Pepin and Losleben 2002).

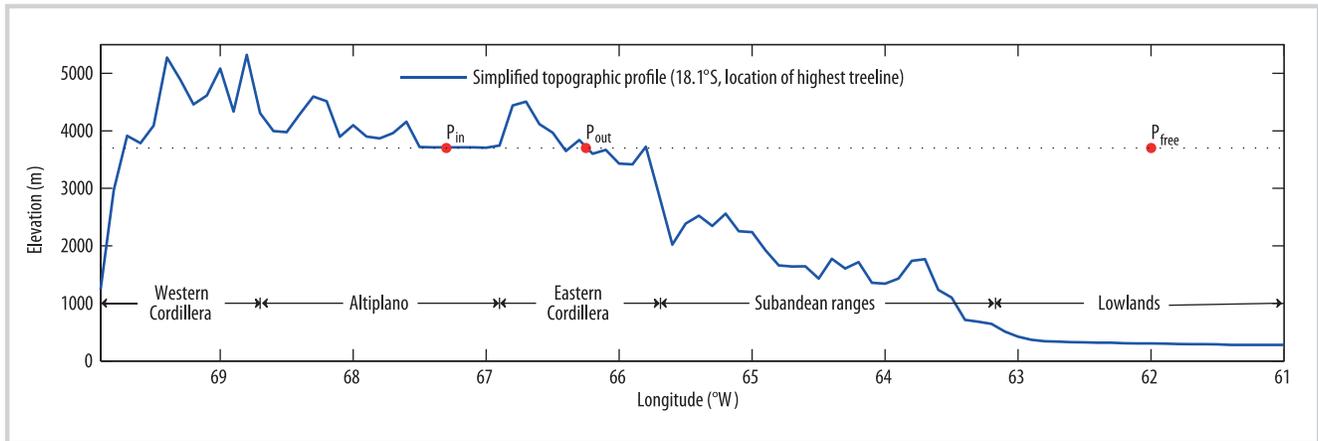
The Shuttle Radar Topography Mission (SRTM) 90-m-resolution digital elevation model (DEM) data, which were produced by the National Aeronautics and Space Administration Jet Propulsion Laboratory (<http://srtm.csi.cgiar.org/>), were downloaded. These topography data were used to separate mountains from plains, with 500-m elevation as the cutoff. We converted the reclassified DEM to polygons, and merged the small polygons into a large one using ArcGIS. We also smoothed the border of the polygon that was regarded as the mountain–plain boundary (Figure 1).

To illustrate MEE on the treelines in the central Andes, we collected treeline data from 4 published journal articles, including positions, elevations, and environmental information. The treelines were located both on the outer slope of the Cordillera and in the Altiplano.

**FIGURE 1** Locations of mountain stations in the central Andes and air sites above the adjacent eastern lowlands at the same elevations. (Map by Wenhui He)



**FIGURE 2** Model of MEE in the central Andes.  $P_{out}$  and  $P_{in}$  are on the outer slope of the Cordillera and the Altiplano, respectively.  $P_{free}$  is in the free atmosphere above the adjacent lowlands. All 3 points are at the same latitude and elevation. The simplified topographic profile is based on the SRTM DEM data, which were resampled to  $0.05 \times 0.05^\circ$  resolution and extracted at 90 points from 61 to 70°W at  $0.1^\circ$  intervals.



### Conceptual model

We used a conceptual model to describe MEE in the central Andes (Figure 2) containing 3 locations at the same latitude and elevation (or altitude for  $P_{free}$ )— $P_{out}$  and  $P_{in}$ , on the outer slopes of the eastern Cordillera and the Altiplano, respectively, and  $P_{free}$  in the free atmosphere above the adjacent lowlands.  $P_{out}$  and  $P_{in}$  could be expected to be warmer in summer than  $P_{free}$  because of the higher number of sunshine hours and the heating effect. Nevertheless, because the air at  $P_{out}$  is well mixed with the cold air at  $P_{free}$ , its temperature could be lower than that at  $P_{in}$ . One of the consequences of air temperature difference between  $P_{out}$  and  $P_{in}$  is that treelines are higher on the Altiplano than on the outer slope.

However, meteorological observation stations in the mountains are scarce, and it is difficult to find 2 stations in a mountain area with the same elevation and latitude to quantify the extent of MEE on the mountain. One solution is comparing the air temperature at  $P_{in}$  with that at  $P_{free}$  instead of with that at  $P_{out}$ . Moreover, because of the complex and multiscale characteristics of mountain terrains, it is difficult to provide a convincing distinction between the inner and outer parts of a mountain. Hence, we compared the air at both  $P_{out}$  and  $P_{in}$  with  $P_{free}$ , and we introduced a new parameter, *distance*—defined as the horizontal distance from the mountain–plain boundary to  $P_{out}$  or  $P_{in}$  for convenience—instead of identifying the inner plateau and the outer slope of a mountain.

### Calculations

We calculated the temperature difference between air at stations in the Andes and air at the same altitude over the neighboring lowlands to quantify the extent of MEE in the central Andes. We calculated the mean air temperature difference over 12 months, focusing on the difference between January and July, the warmest and coldest

months, respectively. We also calculated and analyzed the average difference in the warm months from October to April, which roughly correspond to the growing season. We selected locations 50 km from the mountain–plain boundary on the outside of the mountain for comparison, because we found that the variation in air temperature over lowlands within 200 km of the mountains' eastern boundary is less than  $1.5^\circ\text{C}$  at different pressure levels. We analyzed the relationship between the air temperature difference and the elevation, latitude, and *distance* of the location. We calculated air temperature over the neighboring lowlands at the same altitude as the maximum elevation of the treeline and compared treeline temperature data from previous studies with our calculations.

### Results

In this discussion, temperatures are presented in  $^\circ\text{C}$  and temperature differences in K, to avoid confusion between them, as is the custom in bioclimatology and applied physics (Hoch and Körner 2005). One K is equivalent to  $1^\circ\text{C}$ . Three key findings are summarized below.

#### Air temperature in the mountains versus over neighboring lowlands

Air temperature in the Andes was mostly higher than air temperature at the same altitude over the neighboring lowlands. Of 15 points of temperature difference in January, 12 (80%) were positive (Table 1). At 3 stations, the temperature difference was negative, but the absolute difference was less than 2 K. Temperature difference in January varied greatly, from  $-1.8$  to  $7.1$  K. The mean air temperature difference during the warm months between sites in the Andes and over the neighboring lowlands at the same altitude was similar to the difference in January.

**TABLE 1** Mountain stations that provided the data used in this study.

| Station name | Elevation (m) | Latitude (°S) | Distance (km) <sup>a)</sup> | Temperature difference (K) |      |             |
|--------------|---------------|---------------|-----------------------------|----------------------------|------|-------------|
|              |               |               |                             | January <sup>b)</sup>      | July | Warm months |
| Ayacucho     | 2749          | 13.13         | 402.0                       | 7.1                        | 7.1  | 7.5         |
| Cuzco        | 3249          | 13.55         | 269.6                       | 3.7                        | 2.6  | 4.1         |
| Apolo        | 1415          | 14.73         | 78.4                        | 3.1                        | 2.1  | 2.8         |
| Juliaca      | 3827          | 15.48         | 339.4                       | 6.1                        | 4.8  | 6.7         |
| La Paz       | 4038          | 16.52         | 232.9                       | 5.0                        | 3.4  | 5.3         |
| Cochabamba   | 2548          | 17.42         | 192.7                       | 6.0                        | 3.8  | 6.4         |
| Charana      | 4054          | 17.58         | 568.1                       | 5.9                        | 0.4  | 4.9         |
| Oruro        | 3702          | 18.05         | 394.9                       | 6.1                        | 0.9  | 6.0         |
| Sucre        | 2903          | 19.02         | 215.7                       | 4.4                        | 3.7  | 4.5         |
| Camiri       | 798           | 20.00         | 85.0                        | 0.6                        | -1.0 | 0.6         |
| Tarija       | 1854          | 21.55         | 121.0                       | 2.2                        | 0.2  | 2.3         |
| Yacuiba      | 645           | 21.95         | 15.9                        | -1.4                       | -4.7 | -1.9        |
| La Quiaca    | 3459          | 22.10         | 200.4                       | 4.4                        | -0.7 | 4.4         |
| Jujuy        | 905           | 24.38         | 86.3                        | -1.6                       | -5.3 | -1.9        |
| Salta        | 1221          | 24.85         | 116.7                       | -1.8                       | -5.3 | -2.0        |

<sup>a)</sup>Distance = horizontal distance from the position in the central Andes to the mountain–plain boundary.

<sup>b)</sup>January is the warmest month; July is the coldest month; mean values are given for the warm months (October–April), which constitute the growing season.

The same pattern held true in July, the cold month, when of 15 points of temperature difference, 10 (~67%) were positive (Table 1). The highest positive value (7.1 K) was recorded at the Ayacucho station. The largest negative July difference was -5.3 K, at the Jujuy and Salta stations. The largest difference between the July and January difference values, 5.5 K, occurred at the Charana station (Figure 3). The difference between July and January difference values at the Ayacucho station was small, and the values of both were positive (Figure 3). The difference between absolute July and January difference values at the Camiri station was the smallest except for the Ayacucho station, and the air temperature was close to that over the neighboring lowlands at the same elevation throughout the year (Figure 3).

#### Air temperature difference trends by season

Air temperature difference increased from the outer Andean east-facing slope to the Altiplano in summer, and increased from high latitude to low latitude in winter. In January, the temperature difference showed more significant correlation with elevation than with latitude and *distance*, with the coefficient of determination  $R_2 = 0.72$  (Figure 4). At stations lower than 1000 m, January's absolute difference was less than 2 K. In

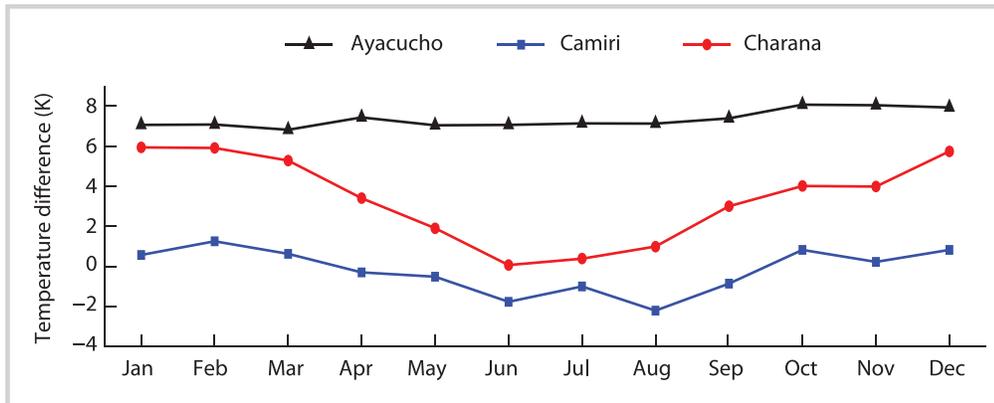
comparison, January temperature differences at stations above 3700 m were more than 5 K. All the high-elevation stations lie in the Altiplano. January temperature differences at the stations in the Altiplano (*distance* > 300 km) were more than 5 K, whereas the mean of the absolute January temperature differences at the stations near the mountain–plain boundary (*distance* < 150 km) was only 1.8 K. The mean air temperature differences for the warm months were more closely related to latitude than to *distance*.

In July, the correlation between temperature difference and latitude was obvious ( $R_2 = 0.76$ ). Air temperature values at the stations north of 20°S were higher than those over the neighboring lowlands at the same altitude. All 3 of the largest negative July temperature differences at the Yacuiba, Jujuy, and Salta stations occurred south of 20°S and below 1500 m. July temperature difference had no obvious correlation with *distance* ( $R_2 = 0.29$ ).

#### Air temperature at treelines versus over neighboring lowlands

At the Sajama Volcano in the Altiplano, the mean soil temperature at -10 cm under trees has been reported as  $5.4 \pm 0.1^\circ\text{C}$  in the growing season (Hoch and Körner

**FIGURE 3** Air temperature differences between stations in the central Andes and air sites over the neighboring lowlands throughout the year.



2005). The growing season mean shaded soil temperature at  $-10$  cm is virtually identical to seasonal mean treeline air temperature (Körner 2012; Green and Stein 2015). Air temperature outside the Cordillera ( $18^{\circ}07'S$ ,  $62^{\circ}41'W$ , at an altitude of 4810 m, above lowlands) was  $0^{\circ}C$  in January,  $-2.3^{\circ}C$  in July, and  $-0.3^{\circ}C$  in warm months at the same latitude and altitude (Table 2). There is about 5 K air temperature difference between altitude at treeline and over neighboring lowlands in January.

In comparison, the treeline elevation at Keara on the outer Andean east-facing slope is only 3300 m, and the air temperature 150 cm above the soil surface has been reported as  $7.0 \pm 2.1^{\circ}C$  in September (Bader et al 2007). Air temperature outside the mountain ( $14^{\circ}42'S$ ,  $66^{\circ}55'W$ , at an altitude of 3300 m above the lowlands) was  $8.2^{\circ}C$  in January,  $6.4^{\circ}C$  in July, and  $8.0^{\circ}C$  in warm months at the same latitude and altitude. Because of the low latitude, the air temperature outside the mountain varied little through the whole year, and the value ( $7.0^{\circ}C$  in September) was close to the air temperature at treeline site in September.

However, the treeline elevation at Chumbre Chulumani in the humid Eastern Cordillera of Bolivia is 4050 m (Hertel and Wesche 2008). The temperature of the air outside the mountain ( $17^{\circ}16'S$ ,  $63^{\circ}28'W$ , at an altitude of 4050 m, above the lowlands) was  $4.2^{\circ}C$  in January, and  $3.9^{\circ}C$  in the warm months as a whole, which was not in the range of mean warmest-month temperatures of  $6$ – $13^{\circ}C$  and mean growing-season temperature of  $5.5$ – $7.5^{\circ}C$  for treelines worldwide (Ohsawa 1990; Malyshev 1993; Körner 1998, 2012; Körner and Paulsen 2004).

## Discussion

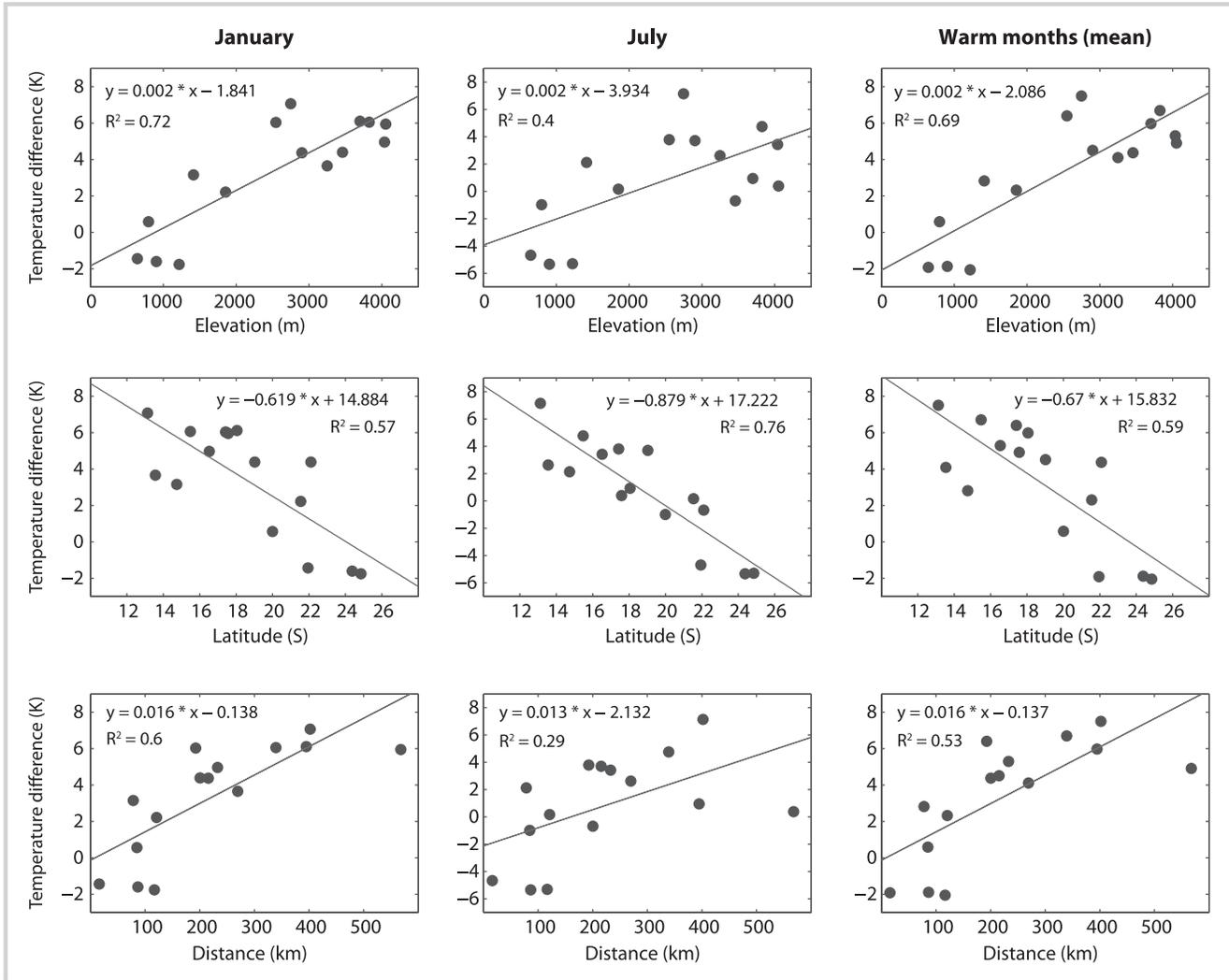
This is the first study to quantify the extent of MEE in the central Andes. Our results showed that air temperature in the Andes was mostly higher than that over the neighboring lowlands at the same altitude in warm months. It confirmed the conclusions of Quervain (1904), Ellenberg (1963), and Körner (2012) that isotherms move

upslope from the outer slope into central ranges of larger mountain systems, which enables temperature-related phenomena such as treelines to reach higher elevations.

In our study, temperature differences in January and in the warm months in general were closely correlated to the elevation of the central Andes. Nevertheless, the temperature difference obtained along altitudinal gradients reflected the combined regional peculiarities and general elevation phenomena (Körner 2007). In fact, the term “mass elevation” in MEE refers to the mean elevation of a mountain massif, which can be understood as the mean elevation of an inner plateau (Holtmeier 2009). Our result showed that all difference values for January at the stations in the Altiplano at about 3700 m above sea level were more than 5 K, which reflected the influence of the average terrain elevation. The difference in January difference values at these high-elevation stations was about 1 K, which may have been caused by the regional peculiarities, and further research is needed to confirm this corollary. Our results were also close to the mean maximum air temperature difference of 6.6 K found for the dry and humid slopes of the eastern cordilleras (Kessler et al 2014).

Our study also showed that temperature difference in January had a link to latitude. It is well known that solar and net radiation and temperature broadly decrease with increasing latitude (Barry 2008), and under similar mass elevation, mountains at lower latitudes would receive more solar and net radiation, which was considered to be one of the factors causing MEE (Cantlon 1953; Barry 2008; Yao and Zhang 2015). The low latitude of the Ayacucho station might help explain why the January temperature difference was as large as 7.1 K there. Meanwhile, the influence of latitude is apparent in the relative importance of seasonal and diurnal climatic rhythms, and seasonal changes of solar radiation and day length are basically small in low latitudes (Barry 2008). Accordingly, it was not surprising that the difference between January and July temperature differences at the (low-latitude) Ayacucho station was small.

**FIGURE 4** Air temperature differences between stations in the central Andes and air sites over the neighboring lowlands, plotted against elevation, latitude, and horizontal distance from the mountain–plain boundary to the position in the mountain area. Solid black lines represent best linear fittings.



Temperature difference in January was also shown to be associated with *distance*, which might relate to the distribution of the stations. Most of these stations, except Charana, are in the eastern part of the central Andes from the outer Andean east-facing slope to the eastern Altiplano. *Distance* reflects not only the rising elevation from the outer Andean east-facing slope to the eastern Altiplano but also the spatial variation of precipitation. Aridity increases with *distance*, and thus solar radiation received by the elevated surface also increases (Garreaud 2009). Moreover, the greater the *distance*, the less mixture exists between air in the Andes and air from outside the mountains. These variations along *distance* could lead to the spatial variation of temperature difference in January. These climate characteristics in the eastern part of the central Andes fit the features of the first type of 3 components of MEE in meteorology, where strong continentality results from the predominance of air mass

advection (Richter 2000; Barry 2008). However, the western part of the central Andes is considered to be dominated by the third type, where windward blocking gives rise to lee-side foehn effects. It has been reported that at 4000 m, the Altiplano and Western Cordillera are 1–4 K warmer than the outer slopes (Lauer 1982; Kessler et al 2007).

Our results showed that there is a large air temperature difference (5 K) between the highest treeline location and the air over the neighboring lowlands at the same altitude in warm months, which is significant to enable the treeline to climb to 4810 m (Hoch and Körner 2005). We also noticed that air temperature at the highest treeline was close to that outside the mountain in July. Based on this, we inferred that air temperature in warm months rather than in cold months may be the key determinant of the highest treeline in the Altiplano. This inference was consistent with the point of view that

**TABLE 2** Treeline data from the central Andes and the air temperature outside the mountain at same altitude with treeline site.

| Study area        | Location           | Elevation | Reference              | Temperature (°C) outside the mountain |      |             |
|-------------------|--------------------|-----------|------------------------|---------------------------------------|------|-------------|
|                   |                    |           |                        | January <sup>a)</sup>                 | July | Warm months |
| Keara             | 14°42'S<br>69°05'W | 3300 m    | Bader et al 2007       | 8.2                                   | 6.4  | 8.0         |
| Chumbre Chulumani | 17°16'S<br>65°44'W | 4050 m    | Hertel and Wesche 2008 | 4.2                                   | 2.8  | 3.9         |
| Nevado Sajama     | 18°07'S<br>68°57'W | 4810 m    | Hoch and Körner 2005   | 0.0                                   | -2.4 | -0.3        |
| Cerro Granada     | 22°32'S<br>66°35'W | 4750 m    | Morales et al 2004     | 0.5                                   | -3.4 | -0.3        |

<sup>a)</sup>January is the warmest month; July is the coldest month; mean values are given for the warm months (October–April), which constitute the growing season.

freezing low temperature extremes were not considered as the decisive factor for treeline formation except in some highly localized places (Körner 1998; Körner and Paulsen 2004). *Polylepis tarapacana*, the dominant species at the highest treeline in the central Andes, is considered frost tolerant (Rada et al 2001).

Air temperature at the treeline site at Chumbre Chulumani, on the outer slope of the Andes, was close to that outside the mountain, which was not in the mean temperature ranges for worldwide treelines in warm months. One explanation is that *Polylepis* treeline forests may grow under lower temperatures than the global mean for high-elevation treeline forests (Kessler and Hohnwald 1998; Hertel and Wesche 2008; Kessler et al 2014). Another explanation is that there might be a difference between air temperatures at the Chumbre Chulumani treeline and outside the mountain. In fact, unlike the smooth western flank of the central Andes, there is rough topography on the eastern flank (Isacks 1988; Allmendinger et al 1997). Due to the complex and multiscale terrain characteristics, the eastern outer slope of the Andes could be also divided into the outer windward slope and inner leeward slope. There would be air temperature difference at different locations on the eastern outer slope of the Andes at the same latitude and altitude, with the upper limits of different tree species increasing from the outer slope of the outer slope to the inner slope of the outer slope and to the inner plateau, as has been shown for subtropical northwestern Argentina

(Morales et al. 2004). More field measurements or experiments are needed to verify these causal hypotheses.

Air temperature outside the mountain was almost identical to that at treelines at Keara in the outer Andean east-facing slope in January, where there was little MEE. MEE was also low at stations near the mountain–plain boundary (<150 km). However, there were still some absolute temperature differences (<2 K) at these locations. Two possible reasons may explain this difference. First, air temperatures outside the mountain were calculated by interpolation from the NCEP/NCAR temperature data set, which is relatively coarse compared with the data measured at the weather stations. Second, there is likely some turbulence in the lowest layer of the atmosphere, the surface layer, when air masses pass over the mountain surface, which is influenced by surface roughness and atmospheric stability (Hunt et al 1991; Geernaert 2003).

## Conclusion

In summer, air temperature at the same elevation (about 3700 m above sea level) and latitude increases from the eastern outer slope to the Altiplano, with a mean difference of about 5 K. This enables the treeline to climb to 4810 m and higher in the Altiplano. Therefore, MEE contributes greatly to the occurrence of the Southern Hemisphere's highest treeline in the Andes.

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Colorado, USA ([http://www.esrl.noaa.gov/psd/data/gridded/data.ncep\\_reanalysis.html](http://www.esrl.noaa.gov/psd/data/gridded/data.ncep_reanalysis.html)). We would like to thank the editors, Michael Kessler, and another anonymous reviewer for very helpful suggestions that improved the manuscript.

## REFERENCES

- Allmendinger RW, Jordan TE, Kay SM, Isacks BL.** 1997. The evolution of the Altiplano-Puna plateau of the Central Andes. *Annual Review of Earth and Planetary Sciences* 25(1):139–174.
- Bader MY, Rietkerk M, Bregt AK.** 2007. Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic, Antarctic, and Alpine Research* 39(3):353–364.
- Barry RG.** 2008. *Mountain Weather and Climate*. Boulder, CO: University of Colorado.
- Cantlon JE.** 1953. Vegetation and microclimates on north and south slopes of Cushtunk Mountain, New Jersey. *Ecological Monographs* 23(3):241–270.
- Ellenberg H.** 1963. *Vegetation Mitteleuropas mit den Alpen in kausaler, dynamischer und historischer Sicht*. Stuttgart, Germany: Ulmer.
- Fliri F.** 1975. *Das Klima der Alpen im Raume von Tirol (Monographien zur Landeskunde Tirols 1)*. Innsbruck, Austria: Universitätsverlag Wagner.
- Flohn H.** 1953. Hochgebirge und allgemeine Zirkulation. II. Gebirge als Wärmequellen. *Archiv für Meteorologie, Geophysik und Bioklimatologie A* 5: 265–279.
- Garreaud R.** 2009. The Andes climate and weather. *Advances in Geosciences* 22:3–11.
- Geernaert G.** 2003. Surface layer. *Encyclopedia of Atmospheric Sciences*. Amsterdam, Netherlands: Elsevier, pp 305–311.
- Green K, Stein JA.** 2015. Modeling the thermal zones and biodiversity on the high mountains of Meganesia: The importance of local differences. *Arctic, Antarctic, and Alpine Research* 47(4):671–680.
- Hall JB.** 1984. *Juniperus excelsa* in Africa: A biogeographical study of an Afrotropical tree. *Journal of Biogeography* 11:47–61.
- Han F, Zhang B, Yao Y, Zhu Y, Pang Y.** 2011. Mass elevation effect and its contribution to the altitude of snowline in the Tibetan Plateau and surrounding areas. *Arctic, Antarctic, and Alpine Research* 43(2):207–212.
- Harsch MA, Bader MY.** 2011. Treeline form—a potential key to understanding treeline dynamics. *Global Ecology and Biogeography* 20(4):582–596.
- Hertel D, Wesche K.** 2008. Tropical moist *Polylepis* stands at the treeline in East Bolivia: The effect of elevation on stand microclimate, above- and below-ground structure, and regeneration. *Trees* 22(3):303–315.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A.** 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25(15):1965–1978.
- Hoch G, Körner C.** 2005. Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. *Functional Ecology* 19(6):941–951.
- Hoch G, Körner C.** 2009. Growth and carbon relations of tree line forming conifers at constant vs. variable low temperatures. *Journal of Ecology* 97(1): 57–66.
- Holtmeier FK.** 2009. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Heidelberg, Germany: Springer.
- Hunt J, Tampieri F, Weng W, Carruthers D.** 1991. Air flow and turbulence over complex terrain: A colloquium and a computational workshop. *Journal of Fluid Mechanics* 227:667–688.
- Isacks BL.** 1988. Uplift of the central Andean plateau and bending of the Bolivian orocline. *Journal of Geophysical Research: Solid Earth* 93(B4): 3211–3231.
- Jordan E.** 1980. Das durch Wärmemangel und Trockenheit begrenzte Auftreten von *Polylepis* am Sajama Boliviens mit dem höchstem *Polylepis*gebüschvorkommen der Erde. *Deutscher Geographentag* 42:303–305.
- Kessler M.** 1995. The genus *Polylepis* (Rosaceae) in Bolivia. *Candollea* 50(1): 131–171.
- Kessler M, Böhner J, Kluge J.** 2007. Modelling tree height to assess climatic conditions at tree lines in the Bolivian Andes. *Ecological Modelling* 207(2): 223–233.
- Kessler M, Hohnwald S.** 1998. Bodentemperaturen innerhalb und ausserhalb bewaldeter und unbewaldeter Blockhalden in den bolivianischen Hochanden: Ein Test der Hypothese von Walter und Medina (1969) [Soil temperatures inside and outside forested and treeless boulder slopes in the Bolivian High Andes. A test of the hypothesis of Walter and Medina (1969)]. *Erdkunde* 52: 54–62.
- Kessler M, Toivonen JM, Sylvester SP, Kluge J, Hertel D.** 2014. Elevational patterns of *Polylepis* tree height (Rosaceae) in the high Andes of Peru: Role of human impact and climatic conditions. *Frontiers in Plant Science* 5:194.
- Kistler R, Collins W, Saha S, White G, Woollen J, Kalnay E, Chelliah M, Ebisuzaki W, Kanamitsu M, Kousky V.** 2001. The NCEP-NCAR 50-year reanalysis: Monthly means CD-ROM and documentation. *Bulletin of the American Meteorological Society* 82(2):247–267.
- Körner C.** 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115(4):445–459.
- Körner C.** 2007. The use of “altitude” in ecological research. *TRENDS in Ecology and Evolution* 22(11):569–574.
- Körner C.** 2012. *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Basel, Switzerland: Springer.
- Körner C, Paulsen J.** 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31(5):713–732.
- Lamb S, Hoke L.** 1997. Origin of the high plateau in the Central Andes, Bolivia, South America. *Tectonics* 16(4):623–649.
- Lauer W.** 1982. Zur Ökologiklimatologie der Kallawaya-Region (Bolivien) [On the eco-climatology of the Kallawaya-region (Bolivia)]. *Erdkunde* 36(4):223–247.
- Malanson GP, Resler LM, Bader MY, Holtmeier F-K, Butler DR, Weiss DJ, Daniels LD, Fagre DB.** 2011. Mountain treelines: A roadmap for research orientation. *Arctic, Antarctic, and Alpine Research* 43(2):167–177.
- Malyshev L.** 1993. Levels of the upper forest boundary in northern Asia. *Plant Ecology* 109(2):175–186.
- McQuarrie N, Horton BK, Zandt G, Beck S, DeCelles PG.** 2005. Lithospheric evolution of the Andean fold-thrust belt, Bolivia, and the origin of the central Andean plateau. *Tectonophysics* 399(1):15–37.
- Miehe G, Miehe S, Vogel J, Co S, La D.** 2007. Highest treeline in the northern hemisphere found in southern Tibet. *Mountain Research and Development* 27(2):169–173.
- Morales MS, Villalba R, Grau HR, Paolini L.** 2004. Rainfall-controlled tree growth in high-elevation subtropical treelines. *Ecology* 85(11):3080–3089.
- Ohswawa M.** 1990. An interpretation of latitudinal patterns of forest limits in south and east Asian mountains. *Journal of Ecology* 78(2): 326–339.
- Paulsen J, Körner C.** 2014. A climate-based model to predict potential treeline position around the globe. *Alpine Botany* 124(1):1–12.
- Pepin N, Losleben M.** 2002. Climate change in the Colorado Rocky Mountains: Free air versus surface temperature trends. *International Journal of Climatology* 22(3):311–329.
- Pepin N, Seidel DJ.** 2005. A global comparison of surface and free-air temperatures at high elevations. *Journal of Geophysical Research: Atmospheres* 110:D03104.
- Peterson TC, Vose R, Schmoyer R, Razuvaev V.** 1998. Global Historical Climatology Network (GHCN) quality control of monthly temperature data. *International Journal of Climatology* 18(11):1169–1179.
- Peterson TC, Vose RS.** 1997. An overview of the Global Historical Climatology Network temperature database. *Bulletin of the American Meteorological Society* 78(12):2837–2849.
- Quervain A de.** 1904. Die Hebung der atmosphärischen Isothermen in der Schweizer Alpen und ihre Beziehung zu deren Höhengrenzen. *Gerlands Beiträge zur Geophysik* 6:481–533.
- Rada F, García-Núñez C, Boero C, Gallardo M, Hilal M, Gonzalez J, Prado F, Liberman-Cruz M, Azocar A.** 2001. Low-temperature resistance in *Polylepis tarapacana*, a tree growing at the highest altitudes in the world. *Plant, Cell & Environment* 24(3):377–381.
- Rao GV, Erdogan S.** 1989. The atmospheric heat source over the Bolivian plateau for a mean January. *Boundary-Layer Meteorology* 46(1): 13–33.
- Richter M.** 2000. A hypothetical framework for testing phytodiversity in mountainous regions: The influence of airstreams and hygrothermic conditions. *Phytocoenologia* 30(3–4):519–541.
- Vuille M.** 1999. Atmospheric circulation over the Bolivian Altiplano during dry and wet periods and extreme phases of the Southern Oscillation. *International Journal of Climatology* 19:1579–1600.
- Witmer U, Filliger P, Kunz S, Küng P.** 1986. *Erfassung, Bearbeitung und Kartierung von Schneedaten in der Schweiz*. Bern, Switzerland: Geographisches Institut der Universität Bern.
- Yao Y, Zhang B.** 2015. The mass elevation effect of the Tibetan Plateau and its implications for Alpine treelines. *International Journal of Climatology* 35(8): 1833–1846.
- Yeh TC, Chang CC.** 1974. Preliminary experimental simulation on heating effect of Tibetan Plateau on general circulation over eastern Asia in summer. *Scientia Sinica* 17(3):397–420.