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An unusually high shrubline on the Tibetan Plateau

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The genus *Juniperus*, composed of about 76 species, has a broad altitudinal distribution over the northern hemisphere (Adams 2014). For instance, some juniper shrub species grow in coastal sites (García-Cervigón et al. 2019), whereas others grow in alpine regions at >5,000 m above sea level [a. s. l.] in the Himalayas (Huang et al. 2019, Lu et al. 2019). In the so-called "Third Pole" region, *Juniperus* species form some of the highest alpine treelines worldwide (ca. 4,900 m a.s.l.) and survive in harsh environments on poor rocky soils (Miehe et al. 2007, Lyu et al. 2019). *Juniperus* trees and shrubs at their upper distributional margins ("treeline" and "shrubline," respectively) likely experience the highest warming rates of all junipers and are recognized as sensitive ecological indicators of responses of land ecosystems to shifting abiotic and biotic conditions (Körner 2012). Accordingly, treelines and shrublines are especially suited for long-term ecological studies, as they are easily relocated over time. However, the upper altitudinal limit of *Juniperus* and its cause(s) remain unknown.

The extreme elevational and topographic variations combine to foster natural landscapes from tropical rainforests to alpine steppes on the Tibetan Plateau. On the inner Tibetan Plateau, the existence of *Juniperus* shrublines, which reach higher elevation than treelines, characterizes altitudinal vegetation boundaries and provides a starting point from which we can forecast how they might change in the near future in response to climate warming (Appendix S1: Table S1).

In August 2016, we discovered an unusually high shrubline of the alpine Wilson juniper (*Juniperus pingii* W.C. Cheng ex Ferré var. *wilsonii* (Rehder) Silba; also known as *Juniperus squamata* Buch.-Ham. ex D.f. Don var. *wilsonii* Rehder) at the upper reaches of the Yarlung Zangbo River on the southern Tibetan Plateau. At our "Saga" site at 5,280 m a.s.l. (29°35'12" N, 84°52'13" E; Fig. 1a–e; Appendix S1: Table S1), an exceptionally high shrubline was located about 380 m above the highest treeline record for the Northern Hemisphere (Lyu et al. 2019), and about 180 m above the world's highest known woodlands dominated by *Polylepis tarapacana* in the Andes, South America (Braun 1997). It was located on the south-facing slope of the mountain, near its 5,760 m a. s. l. peak, and close to the northern and western range margins of Wilson juniper on the Tibetan Plateau. This area has an alpine, semiarid climate with annual precipitation of 263 mm and annual standard pan (20 cm) evaporation of 2,697 mm (Yatagai et al. 2012; evaporation data from Lazi meteorological station at 4,000 m a. s. l. in 1981–2010 period, ca. 270 km from the Saga site). There are 1,265 solar-heating hours from May to September. The mean maximum soil freeze depth is about 28 cm in January at Lazi station. Snow cover is less than 1-cm depth from late October until early May. The mean air and soil (5 cm and 20 cm below the soil surface) temperatures during the growing season (from when the air temperature exceeds 0°C after May until it reaches 0°C again for the first time in autumn) at this shrubline site are estimated to be 3.5 ± 2.2, 7.1 ± 2.9, and 6.6 ± 2.6°C, respectively (Li et al. 2013; data records from an automatic weather station at 5,300 m a. s. l. of Damxung during 2006–2015 period, ca. 600 km from the Saga site). July was the warmest month with mean air temperature of 4.7 ± 1.4°C. The mean air temperature in January was -10.9 ± 3.9°C. Soil moisture at 5 cm below the soil surface increased with elevation from May to September (Appendix S1: Fig. S1). Surviving at such high elevation is a challenge because of cold and dry climatic conditions.

To characterize the natural history and responses to climate of this uniquely high shrubline, we estimated the age and quantified the growth patterns of a random sample of its shrubs. We collected basal discs (diameter range: 20–40 mm) from the largest stems of 14 young and isolated juniper shrub patches growing above

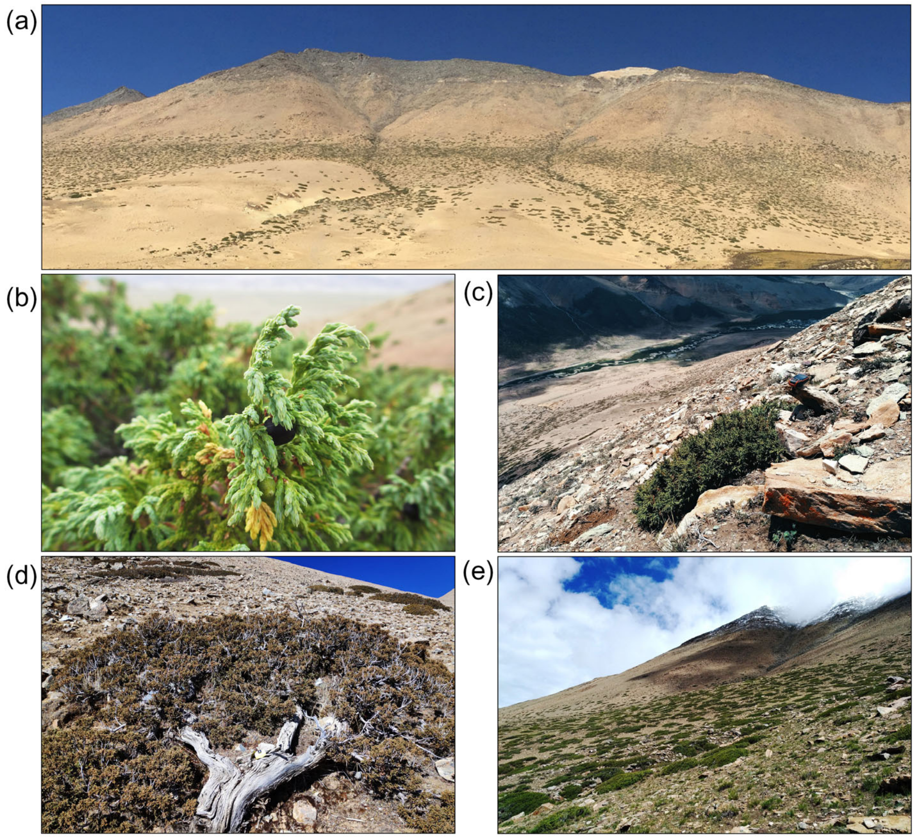

Fig. 1. (a) Wilson juniper shrubline at Saga site. (b) Close-up photo of Wilson juniper shrub with seeds. (c) A prostrate Wilson juniper shrub located at 5,280 m above sea level on the southern Tibetan Plateau. (d) An old prostrate juniper shrub with a basal diameter of 20 cm and a canopy surface of ca. 20 m^2. (e) Wilson juniper shrub population at the study site.

5,250 m a. s. l. A plot survey (size: 30 × 150 m) was also conducted near this shrubline site to estimate the age structure of juniper shrub population (see Appendix S1 for details). Shrub ring-widths were cross dated and measured in the lab using standard dendrochronological methods (Liang et al. 2012). The sampled juniper shrubs were 40–159 yr old, with an average annual radial growth rate of 0.19 ± 0.06 mm/yr (Appendix S1: Table S2, Fig. S2), much lower than average growth rate (0.29 mm/yr) of Wilson junipers found at a lower elevation (4,740 m a.s.l.), a population we studied close to Nam Co Lake on the south-central Tibetan Plateau (30°53’33" N, 90°51’49" E; Liang et al. 2012). Diameters of the oldest juniper shrubs at the Saga shrubline site were 4–5 times larger than the thickest stem we sampled and may be >600 yr old, comparable to millennial juniper shrubs from other extreme sites (e.g., Mediterranean cliffs; Camarero and Ortega-Martínez 2019). Wilson juniper shrubs growing above 5,200 m a. s. l. generally are short (<1 m tall) with a prostrate growth form and dense canopy cover (Fig. 1c). Individual female Wilson juniper shrubs may produce some seeds, but their viability is unknown (Fig. 1b). Some older individuals with thick basal stems may have a canopy surface >20 m^2 (Fig. 1d). Juniper shrub density was low with slow recruitment rate in the most recent five decades (Appendix S1: Fig. S3).

Our observations lead us to hypothesize that radial growth of Wilson juniper at its highest elevation is limited by low temperature and it may take advantage of prostrate growth form to increase heat retention near the soil while avoiding cold air conditions above the boundary layer at such extreme elevation (see Körner 2012). In fact, radial growth of Wilson junipers at the Saga site increased with warmer August air temperatures (r = 0.51, P < 0.01, 1978–2014 period; Fig. 2a). In addition, if juniper shrubs at such high elevations are exposed to free atmosphere conditions, they may not complete the xylogenesis process in the cold conditions during the growing season (mean air temperature = 3.5°C). Soil temperatures during the growing season were more than 3.1°C higher than air temperatures, at least partly highlighting the importance of soil temperature to the juniper shrub growth. Climatic warming

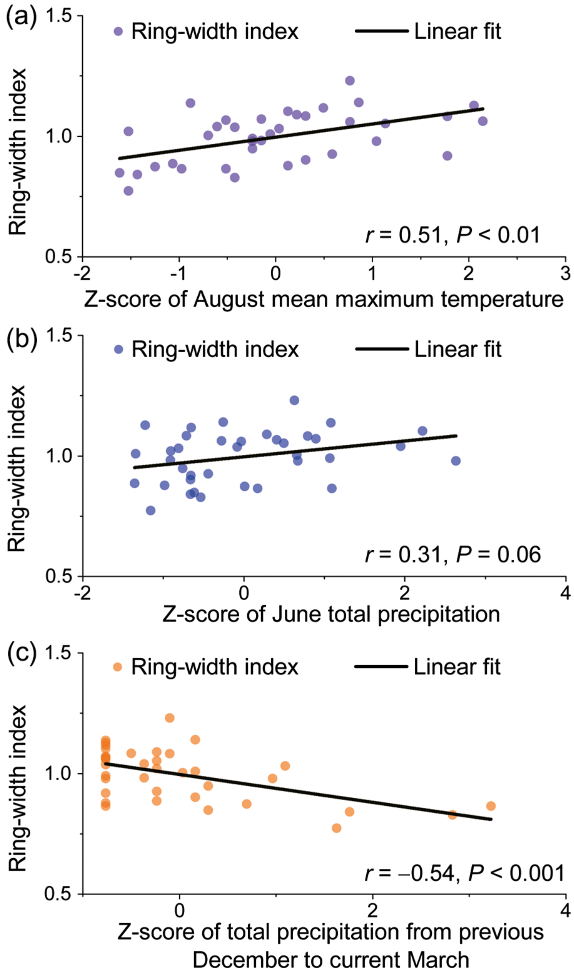

FIG. 2. Linear regressions (time period: 1978–2014) between ring-width indices and *Z*-score of climatic variables ((a) mean maximum air temperature in August, (b) June total precipitation, (c) total precipitation from previous December to current March) influencing radial growth of Wilson juniper shrubs at the shrubline.

in recent decades is likely to further enhance growth of these junipers.

On the Tibetan Plateau, the Saga site is situated near the northern margin (30° N; Yao et al. 2013) of the Indian summer monsoon that brings about 74% of the annual total precipitation from May to September (Yatagai et al. 2012). In the winter season, climate at the Saga site is controlled by westerly winds and shallow, discontinuous snow cover. Interestingly, the growth of Wilson juniper at the shrubline at the Saga site was weakly but positively correlated with June precipitation (r = 0.31, P = 0.06; Fig. 2b). However, juniper growth was strongly reduced by precipitation (falls as snowfall) from December to March prior to ring formation (r = −0.54, P < 0.001; Fig. 2c). We thus hypothesize that increasing aridity towards the interior Tibetan Plateau during the early growing season caused by the fading of the Indian summer monsoon may also determine the altitudinal limit of Wilson juniper. The population at the Saga site has seen few local anthropogenic impacts (e.g., logging, grazing) because of its high elevation and long distance from human settlements. Future studies at this site could further test the hypothesis that the juniper shrubline formation is driven by both low air temperature and combined moisture effects of the Indian summer monsoon and westerly winds at extremely high elevations. Recent studies have suggested that ring widths and oxygen isotopes in juniper shrub rings around the south-central Tibetan Plateau could be used, respectively, as proxies for long-term moisture and temperature (Huang et al. 2019, Lu et al. 2020). By using these climate proxies, we could explore variation in growth of old juniper shrubs growing at different regions and examine long-term associations between shrubline shifts and interactive effects of changes in the Indian summer monsoon and westerly winds. Moreover, the juniper shrubs may have survived during the Last Glacial Maximum (LGM) on the southern Tibetan Plateau, representing high-elevation glacial microrefugia (Opgenoorth et al. 2010). In the future, genetic analyses of juniper shrubs could be used to detect similar refugia in which juniper shrublines persisted after the LGM. These would represent valuable contributions to the natural history of alpine shrublines and illuminate causes of vegetation changes at high elevations during rapid climatic change.

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Supporting Information

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