Has tree density increased at alpine treelines on the eastern Tibetan Plateau?

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Abstract

Treeline densification, along with increased growth rates, is considered a primary manifestation of climate warming at alpine treelines. However, treeline densification has typically been inferred from comparisons of present-day tree density with estimates of former densities inferred from current age structure; the densification has not been verified with long-term monitoring data and thus empirical testing is needed. In this study, a series of plots was established along an altitudinal gradient in a treeline ecotone on the eastern Tibetan Plateau; the plots were then surveyed repeatedly for ten years to analyse spatiotemporal variation in tree regeneration. The densities of Abies fargesii var. faxoniana seedlings and saplings increased from low altitude sites to high altitude sites, before dropping to zero beyond the treeline. The density of fir seedlings at the treeline in 2018 was significantly lower than in 2008. There were no significant differences in the density of saplings, small trees, medium trees, or old-growth trees between 2018 and 2008. As compared to regeneration patterns from 65 years ago, treeline densification represents a spatial phenomenon related to altitude, but not a temporal pattern on the eastern Tibetan Plateau. A more comprehensive understanding of the effects of climate warming on treeline regeneration will require further long-term monitoring and research.

1. Introduction

Alpine treelines represent an obvious forest boundaries that extend from subalpine forests to the uppermost stunted and scattered individuals of forest-forming tree species (Holtmeier 2009). Climate change has stimulated new research into tree regeneration in treeline ecotones and how regeneration may drive observed global treeline shifts (to higher altitudes and latitudes) (Holtmeier and Broll 2020). Temperature is widely considered to be the key factor affecting treeline formation and maintenance. In response to recent climate warming, treelines are expected to advance as a result of forest densification and tree growth acceleration (Kullman 2007, Harsch et al 2009, Liang et al 2011). Although treeline advances have been reported for only 52% of 166 sites surveyed globally (Harsch et al 2009), increases in tree density at the highest elevations were described more frequent than treeline advances, a process was referred to as treeline densification (Camarero and Gutiérrez 2004, Liang et al 2011, Wang et al 2016). However, treeline densification is typically inferred by comparing current tree density with historical densities estimated from the current age structure, not by long-term monitoring. Studies have assumed that mortality is constant for all age classes in order to interpret changes in tree density in the context of tree regeneration dynamics (Camarero and Gutiérrez 2004, Liang et al 2011, Wang et al 2016). However, tree mortality is known to vary with growth stages at the treeline, and regeneration also varies among sites and time periods (Shen et al 2001, Cheng et al 2005, Zhang et al 2008, Liang et al 2011,
Miao et al. 2011). Therefore, treeline densification should be evaluated empirically using long-term monitoring data.

The eastern Tibetan Plateau has the world’s greatest treeline and largest altitudinal range of forest distribution (Miehe et al. 2007, Oppeinboor et al. 2010). In recent decades, climate change on the Tibetan Plateau has led to profound changes in the structure and functioning of local ecosystems (Piao et al. 2019). Climatic data from the eastern Tibetan Plateau reveal significant warming since the 1960s, which has been confirmed using ring-width chronologies from treeline trees and alpine shrubs (Liang et al. 2009). While treeline position changed little after 200 years of warming, fir tree (Abies georgei var. smithii) density has increased over the past 50 years on the eastern Tibetan Plateau (Wang et al. 2016). Fir recruitment is positively correlated with density at treelines (Liang et al. 2011). However, previous tree density was inferred from current age structure of fir population at treelines in these studies, not by long-term monitoring (Camarero and Gutiérrez 2004, Liang et al. 2011, Wang et al. 2016). In fact, Yang et al. (1956) found that fir regeneration increased with altitude, reaching peak levels just below the treeline, before recent climate warming. In addition, fir seedlings and saplings typically undergo a prolonged reduction in numbers, with a variable mortality up to 98% during the first three years (Yang et al. 1979); this suggests that recent treeline densification may be an artifact, neglecting that young individuals disappear over time. Therefore, whether treeline densification is simply a spatial pattern related to altitude or a temporal pattern in response to recent climate warming remains unclear for the eastern Tibetan Plateau.

To date, there have been few monitoring experiments for spatiotemporal variation in tree regeneration at alpine treelines. The objective of this study was to examine the spatiotemporal dynamics of fir regeneration using field investigations along an altitudinal gradient and with repeated monitoring at the treeline. Treeline densification is hypothesized to have both spatial and temporal aspects. Here, fir regeneration was characterized along an altitudinal gradient and regeneration dynamics monitored at the treelines. This study goals were to examine: (1) how regeneration density varies with altitude, and (2) whether regeneration density has increased at treelines over the past ten years (2008–2018).

2. Materials and methods

2.1. Study area and climate data

This study was conducted in the Miyaluo Forest Region (31°24′–31°55′N, 102°35′–103°4′E), located in Li county of Sichuan Province on the eastern Tibetan Plateau, China (figure 1). In the Forest Region, altitude ranges from 2,200 to 5,500 m above sea level and an alpine climate prevails, characterized by cold winters and cool summers. According to the closest meteorological station at Markang (31°54′N, 102°14′E; 2,664 m a.s.l.; about 45 km away from Miyaluo Forest Region), the mean annual precipitation is 788 mm and mean annual temperature 8.75 °C (data from 1954–2019; http://data.cma.cn). The mean monthly temperature ranges from −0.51 °C in January to 16.43 °C in July. Annual, summer, and winter mean temperatures have significantly increased from 1954 to 2019, but there have been no shifts in annual or summer precipitation within this period (figure 2).

Within the study region, forests are distributed in the valleys (ca. 2,600–4,000 m a.s.l.). Minjiang fir (Abies fargesii var. faxoniana) is the dominant tree species, which is distributed between 3,000 m and 4,000 m. Hemlock (Tsuga chimensis) forests occur below 3,000 m and Rhododendron shrubs above 4,000 m. Minjiang fir forests are associated with bamboo (Fargesia spp.) below 3,500 m and Rhododendron spp. above 3,500 m. Minjiang fir seeds can disperse up to 60 m away from parent trees on gentle slopes (Yang et al. 1979), and mast years usually occur every 4–5 years (Yang et al. 1985).

The elevation of the Minjiang fir treeline varies from 3,900 m to 4,000 m a.s.l., depending on local topographical conditions. Diffuse treelines are common on gentle slopes in this region. As wind speeds are generally low, flagged trees or shrubby individuals are usually absent at the treeline. Rhododendron shrubs, ranging in height from of 3–5 m, cover the slopes beyond the treeline.

2.2. Field sampling

In 2008, a 100 m × 100 m square plot was established encompassing 400 quadrats (5 m × 5 m) on a northwest-facing slope, including the treeline ecotone (trees with 2 m height represented the uppermost altitude) (figure 1). The plot was arranged to cover the altitudinal gradient from subalpine forest to alpine shrubland (the ‘x-axis’ was perpendicular to the gradient and the ‘y-axis’ was parallel). The plot ranged from 3,940 m to 4,000 m a.s.l., with a mean slope of 28°. Within the plot, this treeline forest was not locally disturbed by yak (Bos grunniens L.) grazing, logging, or defoliation due to insect outbreaks. Above the treeline, 3–5 m tall Rhododendron shrubs dominated the vegetation, and no stumps or remains of old dead trees were found there. Summer minimum temperatures are the primary constraint on radial growth in adult Minjiang fir individuals at the treeline (Guo et al. 2015).
Measurements were taken each Minjiang fir individual in the 1-ha plot, including diameter at breast height (DBH), basal diameter (tree height < 1.3 m in height), tree height, and the diameter of the tree canopy along the x- and y-axes. Owing to the high abundance of 1–3 years-old seedlings in the 1-ha plot, no measurements were taken. Minjiang fir individuals were sorted into the following age/size classes: young seedlings (1–3 years-old seedlings), older seedlings (height < 30 cm, not including 1–3 years-old seedlings), saplings (≥ 30 cm and < 2 m in height), small trees (height ≥ 2 m and DBH < 5 cm), medium trees (5 cm ≤ DBH < 25 cm), large trees (DBH ≥ 25 cm), and dead trees (DBH > 1 cm, standing dead trees). The location of each Minjiang fir individual (not including young seedlings) within the plot was mapped on the xy-plane. The seedlings and sapling age was non-destructively determined in the field by counting the terminal bud scars along the main stem (Camarero and Gutiérrez 2004, Liang et al 2011). For small trees, medium trees, and large trees, age was estimated from basal cores taken from the main stem with an increment borer. Linear regression was used to characterize the relationship between tree age and DBH; the age of trees with a rotten centre was estimated according to the age-height relationship. In the 1-ha plot, it took trees 25 and 31 years to reach 1.3 m and 2 m in height, respectively (y = 0.09x + 12.98, R² = 0.61; x indicates tree height [cm] and y indicates tree age [a]). All trees in the 1-ha plot in both July 2008 and July 2018 using the methods described above.

Figure 1. Study area and photograph of the treeline on the eastern Tibetan Plateau. The green dots represent 66 of the plots (400–10,000 m²) occurring at the altitudes between 3,200 m and 4,000 m; these plots have been utilized for the past 17 years (2003–2020) to investigate fir tree regeneration in the Miyaluo Forest Region.

Figure 2. Mean annual temperature (a) and annual precipitation (b) in Markang from 1954 to 2019. Red circles, red squares, and red triangles represent the mean annual temperature, mean summer temperature (from June to August), and mean winter temperature (from December to February), respectively. Annual precipitation and summer precipitation are indicated by blue circles and blue squares, respectively.
More than 200 plots (400–10,000 m²) were established in the Miyaluo Forest Region over the past 17 years (2003–2020) to investigate fir regeneration. The altitude of the plots varied from 3,200 m to 4,000 m. In this study, the distributions of seedlings within 66 of the plots spanning an altitudinal gradient were characterized using the same method above.

2.3. Data analysis
The mean densities of young seedlings, older seedlings, saplings, small trees, medium trees, large trees, and dead trees in the 1-ha plot were compared between 2008 and 2018. Among the 400 quadrats (5 m × 5 m), many quadrats were missing individuals from specific size-classes; as a result, all size-classes showed non-normal density distributions. Therefore, a non-parametric method, the Mann-Whitney U test, was used to compare the mean densities of each size-class between 2008 and 2018.

All analyses were conducted using the software package SPSS 22.0 (SPSS Inc., Chicago, IL, USA) at a significance level of \( \alpha = 0.05 \).

3. Results

3.1. Density difference for each size-class between 2008 and 2018
The densities of young seedlings and older seedlings in 2018 were significantly lower than those in 2008 \((p < 0.001)\) (figure 3). In particular, the density of young seedlings declined dramatically from 6,569 stems per ha in 2008 to 244 stems per ha in 2018 (a mortality rate of 96.3%) (figure 3). The densities of older seedlings declined from 5,707 stems per ha in 2008 to 4,082 stems per ha in 2018 (a mortality rate of 28.4%) (figure 3). There were no significant differences in the densities of saplings, small trees, medium trees, and large trees between 2018 and 2008 \((p > 0.05)\). However, the density of dead trees in 2018 was significantly higher than that in 2008 \((p < 0.05)\). The mean annual temperature at the Markang Meteorological Station from 2010 to 2019 (9.29 °C) was significantly higher than that (9.00 °C) from 2000 to 2009 \((p < 0.05)\) (figure 3). Thus, despite the continuous warming in the local area, the density of fir seedlings at the treeline in 2018 was significantly lower than that in 2008.

3.2. Density variation along an altitudinal gradient
With increasing altitude, the densities of both seedlings and saplings first increased, reaching peak values near the treeline, and then dramatically dropped to zero beyond the treeline (figures 4(a), (b)). Thus, seedling and sapling densities were maximized near the treeline on the eastern Tibetan Plateau.
4.1. Treeline densification is a spatial phenomenon

In general, both seed quantity and quality (viability) decrease when approaching the treeline (Holtmeier and Broll 2020). However, in 1955, fir tree (A. georgei) density increased from 700 individuals per hectare at 3,200 m to 23,871 individuals per hectare at 3,800 m; there were 11,231 individuals per hectare at 3,900 m and 5,900 individuals at the treeline (4,000 m) on the eastern Tibetan Plateau (figure 4(b)) (Yang et al 1956). In this study (2008–2018), a similar pattern was found to that in 1955 (figure 4(a)). At low altitudes, fir seedlings usually established in forest gaps with better light availability and low bamboo cover. Bamboo (Fargesia spp.) dramatically restricts fir regeneration, such that very few fir seedlings are found in sites with dense bamboo cover (Taylor and Qin 1988, Taylor et al 1996, Taylor et al 2004, Kang et al 2015). At high altitudes, both canopy closure and tree height decrease, enhancing fir regeneration due to increased light availability (Yang et al 1956). For example, in both the Qinling Mountains and the Shennongjia Mountains, fir tree (A. fargesii) density was much greater at high elevations versus low- and mid-elevations (Dang et al 2010, Dang et al 2013). Therefore, treeline densification is a spatial pattern related to altitude on the eastern Tibetan Plateau.

4.2. The mortality rate of fir seedlings varied over time

After ten years of monitoring, We found that the mortality rate of fir seedlings varied over time. The 1–3 years-old seedlings (young seedlings) were very vulnerable with mortality rates reaching 98%, as a result of sunburn, frost injuries, spring drought, plant diseases, and insect pests. After the first three years, tree mortality dropped to 15% during for the following four to ten years. Some saplings may endure light deficiencies for more than 30 years while awaiting canopy opening. At or below the treeline, numerous saplings grow on the forest floor as a result of better light availability, but only a few individuals will eventually grow to maturity. In this study, the Minjiang fir population showed a reverse J-shape age structure (figure 3), consistent with observed age structures for other fir populations at the treelines on the eastern Tibetan Plateau (Shen et al 2001, Cheng et al 2005, Zhang et al 2008, Liang et al 2011, Miao et al 2011). Common to all those fir forests was an initial high abundance of fir seedlings, followed by dramatic thinning, producing a steady state over time at treelines.

4.3. Steady tree density at treelines over the past 65 years

By assuming a constant mortality rate for fir seedlings, previous studies predicted that tree densification should occur at treelines as the result of global warming (Camarero and Gutiérrez 2004, Liang et al 2011, Wang et al 2016). However, the mortality fir rate of seedlings changes over time; in this study, mortality rates measured 96.3% for the young seedlings and 28.4% for the older ones in our study. Compared to fir recruitment (5,900 stems/ha) observed at the treeline 65 years ago (Yang et al 1956), the similar density (6558 stem/ha) was observed in the treeline plot in 2018. Countless seedlings and saplings died and subsequently disappeared over time at the treeline. Based on repeat censuses in 2008 and 2018, the seedling density at treeline decreased significantly in spite of continuous warming, while other tree size-classes maintained comparatively steady densities. Therefore, treeline densification is a spatial phenomenon related to altitude, and not a temporal shift that has happened over the past 65 years.

Figure 4. Seedling and sapling densities across an altitudinal gradient. (a) Current regeneration pattern of Minjiang fir (young seedlings not included) and (b) regeneration pattern of A. georgei (another fir species on the eastern Tibetan Plateau) in 1955 (young seedlings included) (Yang et al 1956).
5. Conclusions

High-density recruitment at treelines existed 65 years ago. However, as the mortality rate of fir seedlings is very high, few of seedlings successfully grow up into larger trees. Over the past ten years, the number of fir seedlings (both young and older seedlings) declined significantly, but there were no significant differences in the densities of trees from other size classes. Meanwhile, fir recruitment density increased with altitude. Treeline densification is therefore a spatial phenomenon related to altitude rather than a temporal pattern. The effects of climate warming on treeline recruitment require further long-term monitoring and research.

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Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

Conflict of interest statement

The authors declare no conflicts of interest.

Ethics statement

Not applicable.

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