An ancient forest on the move: range shifts in bristlecone pines

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ABSTRACT

Recent changes in global climate are causing many species to shift their ranges towards higher elevations. The rate at which species can shift their ranges may determine whether or not they will be able to persist in light of such rapid environmental change. In this study, we examined the effect of elevation on recruitment, mortality, and intraspecific competition in Great Basin bristlecone pines (Pinus longaeva, BC), a long-lived subalpine species whose upper limit is often at the alpine treeline. We measured recruitment, mortality, and neighbor abundance at ten predominantly BC groves across an elevational gradient in the White Mountains of California. We found proportionally more small BC and fewer large and dead BC at higher elevations, indicating recruitment increased and mortality decreased at higher elevation. Larger trees had fewer small and medium neighbors which suggests intraspecific competition may limit recruitment. Overall, increasing recruitment of Great Basin bristlecone pines at higher elevations may signal an expanding climatic range.

Keywords: bristlecone pine, treeline shift, recruitment, competition, White Mountain

INTRODUCTION

Climate change poses a major threat to global biodiversity, but may especially impact range restricted species (Dirnböck 2011, Dullinger et. al 2012). Species living within small ranges will be disproportionately vulnerable to extinction (Ohlemüller et al. 2008), and the range of many endemic flora are projected to be significantly reduced or fragmented within the century (Loarie et al. 2008). Variation in abiotic factors including slope, aspect, substrate, and temperature have been shown to impact plant recruitment (Harsch 2009, Kullman 2006). Treelines around the world are shifting upslope (Kelly and Goulden 2008, Harsch 2009, Kullman 2006, Feeley 2010, Beckage et. al 2008) and high elevation treeline encroachment poses a threat to endemic alpine species (Dirnböck 2011, Dullinger 2004).

Some evidence shows treeline shifts are more dependent on tree density than temperature (Camarero 2004). However, in
high-altitude regions with temperature-limited treelines, warming periods allow recruitment of seedlings at higher elevation (LaMarche and Stockton 1974). When climate cools again, recruitment may be limited to lower elevations, and the treeline recedes downslope. This is especially evident in Great Basin bristlecone pines (Pinus longaeva, hereafter referred to as BC). Historically, during periods of warmer climate, BC has recruited at higher elevations, but when climate cooled, the treeline receded downslope (LaMarche 1973). However, it is unclear if this trend is currently present.

Bristlecone pines, found in subalpine regions, are the oldest non-clonal living organisms in the world. Bristlecone pines grow very slowly due to temperature and moisture limitation (Brunstein and Yamaguchi 2018) and thrive at high elevation due to minimal competition for resources within an already limited environment (Schlenz 2008). Because of their longevity, tree ring analysis of BC can provide thousands of years of climatic history on moisture availability, disturbances, and temperature variation (Salzer et. al 2014, LaMarche and Stockton 1974, Feng and Epstein 1994, Salzer and Hughes 2007). This makes them an ideal organism for understanding the effects of current climate change. As average annual temperatures increase, BC recruitment may increase at higher elevations, expanding their range upwards. However, if competition for resources is a determining factor in upper range expansion, neighboring BC abundance may inhibit recruitment. The stand structure of a grove may provide data on BC recruitment and distribution over past climatic conditions.

In this study, we assessed BC demography by examining the abundance of varying size classes at different elevations, using size as a proxy for relative age. We expected greater recruitment at high elevations. Additionally, we expected to find greater mortality at lower elevations as changing climatic conditions may create a more inhospitable habitat. We also expected that larger BC trees would hinder neighbor recruitment because they are better competitors for limited resources than small trees.

**METHODS**

*2.1 Study Area*

We conducted research in the subalpine coniferous forests in the White Mountains of California. We surveyed a total of ten study sites at elevations ranging between 2,900 and 3,500 meters; sites chosen represented most of the elevational range encompassing BC (Figure 1). Study sites were dominated by BC, but also had Limber pine (P. flexilis) present. Soil substrate varied among sites, but was predominantly a mix of dolomite, quartzite, and granite.

*2.2 Research Design*

In order to study the effect of elevation on BC recruitment and mortality, we measured the abundance of three different size classes across ten mountain slopes at varying elevations. Each study site represented one tree grove, which we defined as an area of land less than 400 m in length consisting of a lower and upper treeline. We determined the lower and upper treeline by the presence of BC clusters containing at least three BC greater
than 3 m in height within 10 m of each other (Smithers et al. 2018). In order to assess size distribution, we sampled within a 50 x 14 m belt transect at lower, middle, and upper elevations within a grove. The middle transect was located halfway between the lower and upper treeline. At each sample transect, we recorded the number of dead trees and the number of BC, categorized by size. Dead trees were characterized by absence of green needles. Size classes were determined as follows: small trees were less than 3 m in height; medium trees were greater than 3 m in height with a circumference of less than 65 cm; large trees were taller than 3 m and had a circumference greater than 65 cm.

To test for intraspecific competition that may affect BC recruitment across varying elevations, we surveyed BC neighbor abundance around focal trees. A focal large tree was measured at 35 m intervals between the lower and upper tree line at each site. We recorded neighbors present within a 7 m radius of the focal BC, categorized to the same size classes as above. We also recorded DBH as a proxy for tree age (Brown and Schoettle 2008). Slope, aspect, and elevation were recorded to account for any environmental variation that may also affect recruitment and size class distribution. A total of 69 replicate focal trees were surveyed over a period of four days.

2.3 Statistical Analysis

All statistical analyses were conducted using JMP statistical software v.14. We used a MANOVA to test the effect of treeline position (lower, middle, or upper) on all four size class proportions. We used linear regression models to test for relationships between elevation and the proportions of small, medium, and large trees out of the total living trees. We also used a linear regression model to test the correlation between small BC neighbor abundance and elevation. We used a multivariate model to test the effect of slope, aspect, elevation, distance from lower treeline, and their interaction on small BC abundance over total BC. To test for a correlation between DBH and elevation, a linear regression model was used. It was also used to test for the correlation of DBH and BC neighbor abundance, separated by size class.
RESULTS

3.1 Bristlecone Recruitment and Mortality

There was no effect of treeline position (lower, middle, upper) on any of the four size class proportions (MANOVA: N=28, F=0.33, p=0.94). As elevation increased, the proportion of small BC trees also increased (N=28, R^2=0.42, p<0.01; Figure 2 black line). Elevation had no effect on the proportion of medium BC (N=28, R^2=0.01, p=0.56). The proportion of both large BC trees (N=28, R^2=0.34, p<0.01; Figure 2 dashed line) and dead trees (N=28, R^2=0.28, p<0.01; Figure 3) decreased as elevation increased.

3.2 Bristlecone Neighbor Abundance

There were significant effects of some abiotic factors on proportion of small BC neighbors of the focal large BC trees (N=60, R^2_{Full Model}=0.19, p_{Full Model}=0.02). Specifically, elevation was positively correlated with the proportion of small BCs and distance from lower treeline was negatively correlated with proportion of small BCs (P=0.01, P=0.02, respectively; Figure 4). There was no effect of slope and aspect on proportion of small BC (P=0.10 and P=0.56, respectively).

There was no effect of elevation on BC DBH (N=69, R^2=0.02, p=0.21). However, there was a negative correlation between DBH and the total number of small and medium neighbors (small neighbors: N=69, R^2=0.10, p<0.01, Figure 5; medium neighbors: N=69, R^2=0.09, p=0.01), though these were weak relationships. There was no effect of DBH on large neighbors (N=69, R^2<0.01, p=0.74).
Figure 4. Correlation of proportion small BC with elevation and distance from lower treeline (m). Small BC neighbors represents trees under 3 m in height within 7 m radius of the focal BC tree. Total BC neighbors represents all sizes of trees within 7 m radius of the focal BC tree. As elevation increased, the proportion of small BC neighbors over total neighbors increased; however, it decreased as the distance from the lower treeline increased (N=60).

Figure 5. Correlation of diameter at breast height (m) on BC neighbor abundance. Y-axis represents trees within 7 m radius of the focal BC tree categorized by size classes. Light gray line and points represent abundance of small BC neighbors, dark gray line and points represent abundance of medium BC neighbors, and black dashed line and points represent abundance of large BC neighbors. As diameter at breast height of the focal BC increased, the abundance of BC neighbors varied among size; small and medium BC neighbors weakly decreased, and BC DBH had no effect on large BC neighbors.

DISCUSSION

Within each study site, there was no variation of size class among lower, middle, and upper positions on each mountain slope. However, we did find a large-scale pattern over a broader elevation gradient. In support of our hypothesis, at higher elevations, small trees made up a larger portion of the BC grove. This pattern may indicate increased recruitment at higher elevations, possibly due to warming temperatures. Additionally, we found that large trees make up a greater proportion of groves at lower elevation, which may indicate that past climatic conditions were more hospitable to recruitment at lower elevations than they are now. Medium trees were consistent throughout the elevational range, for they may represent a period of a non-climatic shift. As hypothesized, there was a greater abundance of dead BC compared to living at lower elevations, which supports the idea of a shifting treeline. Overall, these patterns suggest that recruitment rate is greater at higher elevations while mortality is greater at low. However, it is important to note that our inability to differentiate between dead *P. flexilis* and dead BC may have potentially caused an overestimation of dead trees recorded, since more *P. flexilis* are present at lower elevations (Hutchins and Lanner 1982).

The effects of elevation and distance from lower treeline showed contrasting trends on the abundance of small neighboring BC (Figure 6). The finding that small BC
abundance increased with elevation corresponds with our findings from the recruitment portion of our study, and demonstrates a macro-environmental shift in recruitment towards higher elevations. However, within a grove, small tree abundance increased towards the lower treeline, indicating recruitment may be more successful at the bottom of slopes. Although the weak correlation of this trend suggests that other environmental factors may be at play, gravity may be a dominant factor in recruitment at the lower treeline as it may cause pine cones and seeds to tumble downslope. Therefore, although on a local scale, position within a grove has a weak effect on forest structure, we did find an overarching pattern of increasing recruitment at higher elevations.

As climatic conditions become less harsh at the lower elevation limit of BC, other plant species that were previously unable to live in the harsh high-elevation conditions may be able to advance into those areas (Schlenz 2008). This may increase interspecific competition for resources, which may in turn increase BC mortality at their lower elevation limit and cause their range to shift. At higher elevations, where conditions are much harsher, BC will be more likely to persist, since other flora are less tolerant of these extreme conditions (Bliss 1962).

Although DBH of the large focal tree had no effect on the abundance of neighboring large trees, it was negatively correlated with medium and small neighbor trees. This pattern may suggest that intraspecific competition hinders recruitment. Since elevation had no effect on DBH, the possibility that elevation is driving this pattern is slim. This suggests that established large trees may limit the ability of small and medium trees to grow due to shade intolerance and limited resources (Schlenz 2008).

As the climate warms, not only will BC likely face a higher amount of inter- and intraspecific competition, they will also face an increased risk of infection by pathogens and viruses that would normally not survive in colder conditions. Catenazzi’s study on the fungal pathogen Batrachochytrium dendrobatidis found that amphibian species in the higher elevations of the Anduran mountain range that were previously untouched by B. dendrobatidis were becoming infected due to warming temperatures, which allowed the pathogen to more easily survive (2010). One similar parasite that might affect the future health of BC is the bark beetle, Dendroctonus ponderosae. Rising temperatures have been correlated with the outburst of bark beetle populations moving higher in latitude and elevation (Williams and Liebold 2002, Jonsson et al. 2009). If bark beetles continue migrating upwards, it is possible that they will infect more BC.

Species that inhabit BC forests may be affected by the upward shift in recruitment. A study by Rehm and Feeley found that cloud forests in the tropics are unable to shift to higher elevations fast enough to accommodate the changing climatic ranges of the species within them, stranding them in inhospitable environments (2015). This presents the possibility that species who rely on BC groves may face the same fate if the rate of temperature continues its gradual increase and BC are not able to expand their range fast enough (Scott et al. 2010). Our findings show that BC recruitment is increasing at higher
elevations; however, the rate of treeline encroachment was undetermined. Future studies could assess long-term treeline shift and the effects this may have on other species that inhabit this ecosystem. Furthermore, assessment of health along their elevational range may provide insight on the longevity of BC amidst anthropogenic climate change.

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REFERENCES


