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A climate-driven tree line position model in the White Mountains of California over the past six millennia

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Abstract

Aim: Position of the alpine tree line ecotone around the globe corresponds to a growing season isotherm of approximately 6°C. Accordingly, tree lines are important indicators of Holocene global and regional environmental change. A central line of inquiry in tree line ecology is to better understand the mechanisms that dictate tree line position on the landscape, as well as the environmental conditions that cause upslope and downslope shifts in its position at centennial to millennial time-scales. Here, we present a climate-driven model to predict tree line position over the past 6,000 years.

Location: Sheep Mountain, located in the White Mountain Range of California, USA.

Time period: 4750 BCE to present.

Major taxa studied: Great Basin bristlecone pine (*Pinus longaeva* BK Bailey).

Methods: We use a climate-driven tree line position model that utilizes a topoclimate raster surface of growing season average temperature to predict the spatial position and area of the alpine tree line ecotone across the mountain range. We then produce a time series of tree line position predictions at 500-year intervals from 4750 BCE to present, and compare the predictions to the growth dates and spatial locations of 61 remnant bristlecone pine samples from above modern tree line.

Results: The model indicates that tree line position in the White Mountains, CA migrated downslope throughout the Holocene until approximately 750 CE, rebounded slightly upslope by 1250 CE, and has since likely remained stationary. Applying the model under present-day climatic conditions suggests the current tree line at Sheep Mountain may be out of climatic equilibrium by up to 250 vertical metres in some places.

Conclusion: The results support independent conclusions from global tree line analyses, underscore the temperature sensitivity of the tree line ecotone, and further develop our understanding of climate-driven tree line dynamics.

KEYWORDS
bristlecone pine, dendroclimatology, Great Basin, Holocene, palaeoclimate, topoclimate, tree rings

1 | INTRODUCTION

The alpine tree line ecotone is the transition between the highest elevations of closed subalpine forest and treeless alpine tundra, and is a valuable indicator of past and present global environmental change (Holtmeier & Broll, 2005; Kullman & Kjällgren, 2006). While the primary factors influencing the location of this boundary on the landscape vary with spatial scale, decades of research suggest global tree line position is controlled by temperature (Jobbagy & Jackson, 2000; Körner, 2012; Wardle, 1971). Three independent studies provide specific evidence that an average growing season temperature of approximately 6°C best explains the location of the alpine tree line ecotone, across latitudes, climate zones and species (Bruening, Tran, Bunn, Weiss, & Salzer, 2017; Körner & Paulsen, 2004; Paulsen & Körner, 2014).

The climate sensitivity of the alpine tree line ecotone makes it an important palaeoclimatic proxy (Holtmeier & Broll, 2005; Kupfer & Cairns, 1996). Downslope migration of multiple tree lines around the globe have been mapped throughout the Holocene, and have been shown to track centennial to millennial-scale changes in average global temperature (Carrara & McGeehin, 2015; Kullman & Kjällgren, 2006; Salzer, Bunn, Graham, & Hughes, 2013). At shorter time-scales, regional and site-specific tree line positions are influenced by other environmental factors including precipitation and growing season length, and topographic effects such as snowpack and wind mechanics (Holtmeier & Broll, 2005; Weiss, Malanson, & Walsh, 2015). Evidence of seedling establishment above tree line at various locations around the globe shows these communities may be responding to rising atmospheric temperatures (Batllori & Gutiérrez, 2008; MacDonald, Kremenetski, & Beilman, 2008; Millar, Westfall, Delany, Flint, & Flint, 2015). However, the mechanisms that influence tree line ecotone movement are not fully understood, nor consistent (Liang, Wang, Eckstein, & Luo, 2011), and more work is needed to understand climate-driven ecological change at the landscape scale.

Great Basin bristlecone pine (*Pinus longaeva*, DK Bailey) is a dominant tree line-forming species in the White Mountains of California (Figure 1a). At high elevations, the climate is characterized by extremes; hot, dry summers are followed by harsh and frigid winters, and most precipitation falls as snow. This species is extremely long lived, allowing for multimillennial ring-width chronologies. Due to the aridity (Sheep Mountain, CA receives approximately 520 mm of precipitation per year, PRISM 2004), ancient wood remnants can be found well above the modern tree line (Figure 1b–d). These can be precisely cross-dated, providing spatial and temporal information about tree line dynamics and palaeoclimate in the mid to late Holocene (LaMarche, 1973; Lloyd & Graumlich, 1997; Salzer et al., 2013; Scuderi, 1987). LaMarche (1973, 1974) developed the first timeline of tree line position movement in the White Mountains, CA and linked downslope migration of tree line position throughout the late Holocene to climate dynamics in the Great Basin. Salzer et al. (2013) reconstructed temperature and bristlecone pine tree line movement at Sheep Mountain, CA, and Mount Washington, NV, throughout the latter half of the Holocene. The authors built a ring-width chronology from exclusively "temperature-sensitive" trees, meaning a sample was added to the chronology only during the period it was at or near the tree line ecotone. This strategy improved the resultant temperature reconstruction by effectively isolating the temperature-limited growth signal.

Recently, we developed a regional climate-based tree line position model in the White Mountains of California (Bruening et al., 2017). Here, we (1) expand on our previous work by applying the tree line model from the mid-Holocene to present at 500-year intervals; (2) assess prediction accuracy over time by comparing predicted tree line positions to the locations and dates of 61 cross-dated remnant bristlecone pine samples collected above modern tree line at Sheep Mountain, CA; and (3) discuss how our results fit with other analyses of tree line dynamics throughout the Holocene.

2 | METHODS

2.1 | Seasonal mean temperature

At Sheep Mountain in the White Mountains, CA (37.52° N, 118.20° W), we built seasonal mean temperature (SMT) models from observed temperatures at the tree line ecotone (Bruening et al., 2017). We used 50 thermochron iButton sensors (Maxim Integrated, San Jose, CA, model DS1922L-F5) to record hourly temperatures (October 2014–September 2015) in living trees dispersed across a 1.5 km^2 area of complex alpine topography at tree line. We aggregated each sensor's hourly values into a set of monthly averages, yielding 50 unique time series.

The objective was to identify differences in climate signature due to topographic position within the network of sensors. Because these monthly data reflected the anomalously warm weather experienced at Sheep Mountain from October 2014 to September 2015, we corrected each of the 50 aggregated monthly time series to better reflect the site's average climate, while preserving the subtle differences among the 50 datasets. We derived monthly climate normals from 120 years of average temperature (1895–2015) obtained from PRISM (PRISM 2004), and calculated the ΔT between each month's climate normal and the site-average of the 50 time series from Sheep Mountain (the difference between circle and square points for each month in Figure 2). We applied the monthly ΔT corrections to each of the 50 time series, allowing us to adjust the entire data to be more reflective of the previous 120-year climate at Sheep Mountain, while preserving differences among the time series due to differences in complex topography among the sensor locations.

2.2 | Palaeoclimate

The oldest remnant bristlecone pine sample found at Sheep Mountain dates to 4408 BCE. Accordingly, we chose a date range to encompass the entire period from the earliest date of the oldest remnant sample, to the best estimate of when the tree line at Sheep

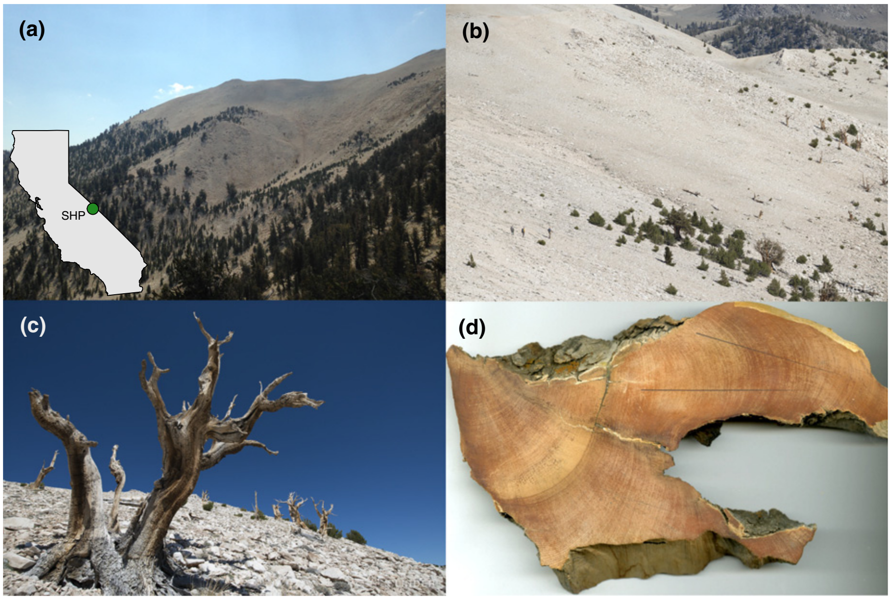

FIGURE 1 (a) The alpine tree line ecotone on Sheep Mountain (SHP), CA. (b) The ecotone is characterized by a dolomite substrate with sporadic, low-density bristlecone pine stands and abundant remnant wood above the highest elevations where trees are found. (c) Standing Great Basin bristlecone pine snags and subfossil remnant wood segments are common above the modern tree line. (d) Cross-section from a remnant found above tree line on Sheep Mountain (Figure 6, SHP025), dating from 2585 to 1597 BCE. The likelihood of significant weathering precludes identifying the absolute establishment and mortality dates from remnant samples. Photo credit for a, b, and c: Chris Linder

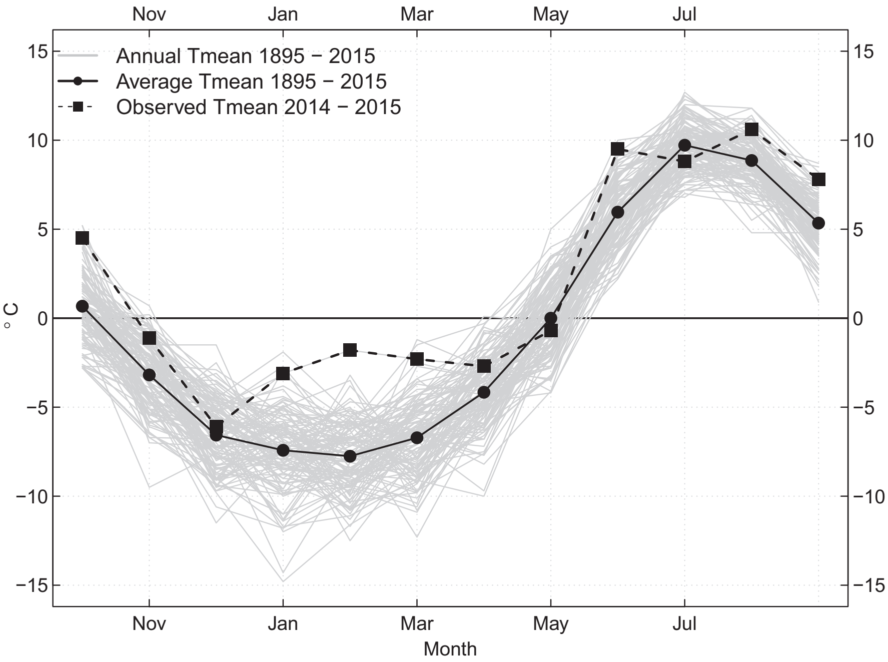

FIGURE 2 Site-average observed monthly mean temperatures from October 2014 to September 2015, calculated from the network of 50 sensors (square symbols), average climate normal (round symbols) and annual PRISM-modelled monthly mean temperatures 1895 to 2015 at Sheep Mountain, CA. The ΔT (°C) anomalies (difference between the site-average observed temperatures and 120 year average climate normal) were used to adjust the monthly observed temperatures from each sensor to better represent the average monthly temperature profile at this site

Mountain established its current position, in 1250 CE (see Salzer et al., 2013). We obtained monthly mean temperature anomalies from the CCSM3 TraCE palaeoclimatic simulations (see Liu et al., 2009; UCAR 2011; Figure 3) smoothed with a 500-year spline. We chose a 500-year interval between extraction dates spanning 4750 BCE to 1250 CE. Each set of anomalies was then applied to the observed, aggregated monthly values from Sheep Mountain (described in section Seasonal Mean Temperature), rendering datasets of the 50 monthly time series, representative of each 500-year time interval from 4750 BCE to 1250 CE.

We used lasso regressions with 10-fold cross-validation and 10 repeats per fold (Kuhn, 2008) to model monthly mean temperature across the White Mountains above 3,000 m for each time interval, using 10-m resolution topographic predictor variables of elevation, slope, aspect-derived eastness and southness indices, topographic convergence and position indices, and solar radiation values. From the modelled set of monthly temperature raster surfaces, we calculated SMT surfaces for each time interval, per methods developed by Bruening et al. (2017). The final output was a 10-m resolution raster surface of SMT for each time period.

2.3 | Tree line model and ecotone classification

We developed a three-ecotone model to predict tree line position from each modelled SMT raster surface. From a macro-perspective, tree line is described as a line boundary between areas

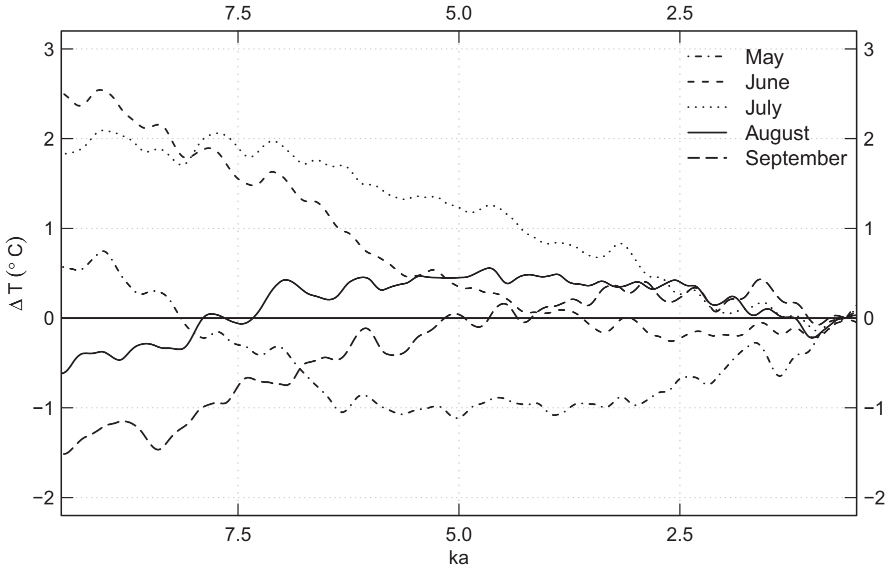

FIGURE 3 Modelled 2 metre air temperatures in the White Mountains, CA (UCAR 2011). Data are monthly temperatures from the growing season shown with a 500-year spline, relative to the formation of the modern tree line in approximately 1250 CE

where environmental conditions allow for woody biomass accumulation and areas where environmental conditions are too harsh. However, at a specific site, it is rarely such a distinct boundary. Rather, tree line is the ecotone between closed montane forest and alpine tundra, where environmental gradients subject to spatial and temporal variability result in a scattered and broken transition zone from montane forest to the treeless alpine (Figure 1a, b). Thus, we define tree line as an ecotonal zone instead of a line boundary.

Informed by conventions developed by Körner (2007, 2012), we used Google Earth to digitize a line through the middle of the present-day tree line ecotone at Sheep Mountain, and extracted values from our modelled, present-day SMT raster along the line. We calculated 25% and 75% probability estimates (6.10 and 6.38°C, respectively) from the resulting distribution of temperatures as upper- and lower-bound isotherms to the tree line ecotone, and used these isotherms to constrain the tree line ecotone at each time period. Areas on the landscape with SMT <6.10°C were classified as alpine, and areas with SMT >6.38°C were classified as subalpine, resulting in a three-ecotone model: alpine, tree line and subalpine (Figure 4).

2.4 | Remnant wood samples

We used 61 remnant wood and standing snag bristlecone pine samples collected from above modern tree line on or near Sheep Mountain to estimate the accuracy of the tree line position models (Figure 5). GPS coordinates were recorded (and later differentially corrected) to map the location of each sample. Samples were collected and prepared using standard methods in dendrochronology (Stokes & Smiley, 1968). Growth rings were annually cross-dated using COFECHA software and dplR (Bunn, 2008, 2010; Holmes, 1999) to establish absolute calendar dates for the inner- and outermost rings. Collectively, the remnants span 5,737 continuous calendar years, with the oldest sample spanning 4409–3958 BCE, and the youngest sample from 88 BCE to 1328 CE.

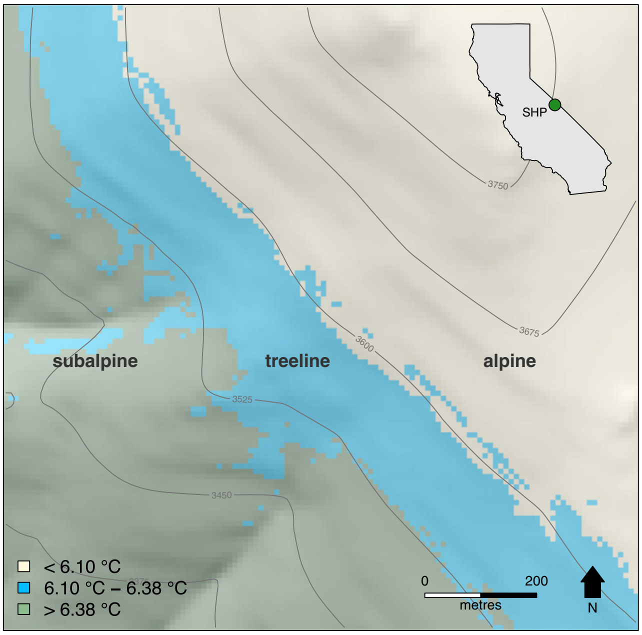

FIGURE 4 Sample tree line ecotone position model, from the southwest slope of Sheep Mountain, CA. Pixel width represents 10 horizontal metres and contour lines represent 75 vertical metres

3 | RESULTS

3.1 | Tree line position predictions

The model suggests continuous downslope tree line position movement from 4750 BCE until around 750 CE (a change of approximately 250 vertical metres in some places) followed by a slight rebound uphill between 750 and 1250 CE (Figure 5). Both modelled and observed tree line position at Sheep Mountain has remained relatively stable from 1250 CE until present day (Figure 5a; Salzer et al., 2013). We estimate the change in elevation of tree line ecotone

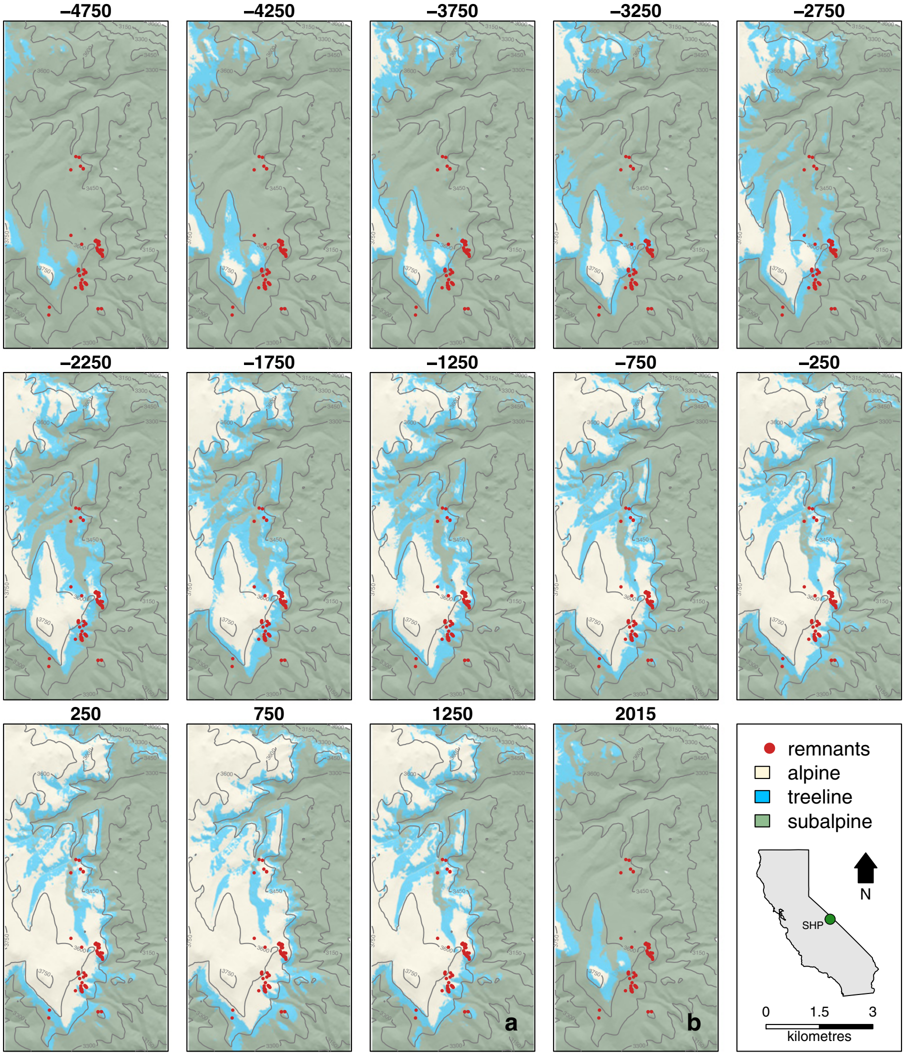

FIGURE 5 Great Basin bristlecone pine tree line position predictions over the past 6 millennia at Sheep Mountain, CA. Red points represent remnant locations. (a) Modelled position of the current tree line at Sheep Mountain, based on temperatures from 1250 CE, the period of modern-day tree line establishment in the Great Basin. (b) Forecast of tree line ecotone potential position, based on observed temperatures (October 2014–September 2015) at Sheep Mountain. Contour lines represent 150 vertical metres

over the past six millennia at Sheep Mountain to be up to 100 m more than reported by LaMarche (1973) and Salzer et al. (2013) at the same location.

Predicted tree line position based on the previous 120 years of climate (Figure 2) at Sheep Mountain reveals striking potential for future upslope migration of the tree line ecotone, and resulting expansion of the subalpine ecotone (Figure 5b). In this simulation, tree line position moves uphill anywhere from 150 to 250 vertical metres, translating to several horizontal kilometres in some areas. All projections in Figure 5 are driven exclusively from modelled and observed temperature data, and should be interpreted as theoretical potential positions based on climate, rather than known historical tree line positions.

3.2 | Remnant samples and model accuracy

The model correctly predicts tree line or subalpine conditions for 90% (55 of 61) of the subfossil remnant wood and standing snag samples during the earliest time interval each sample was alive (Figure 6). A remnant was only considered correctly classified if its earliest growth ring occurred during a period of tree line or subalpine ecotone as predicted by the model. Of the correctly classified samples, 25 were located in regions of subalpine classification and 29 were located in regions of tree line classification. Many of the remnants are spatially clustered, which somewhat reduces the weight of the 90% success rate; however, comparisons to all available remnants are the best means of assessing model accuracy.

4 | DISCUSSION

Our climate-driven approach sets this analysis of Holocene tree line position apart from others dependent on the locations of remnant wood; this study is unique in that it uses remnant samples to assess the accuracy of temperature-driven predictions of tree line position, with results similar to those obtained directly from the growth location of remnants. The success of remnant-dependent analyses depends upon the availability, amount of weathering and age of remnant samples across a wide elevational range. The results can be stepwise in nature, dependent on the age and location of samples

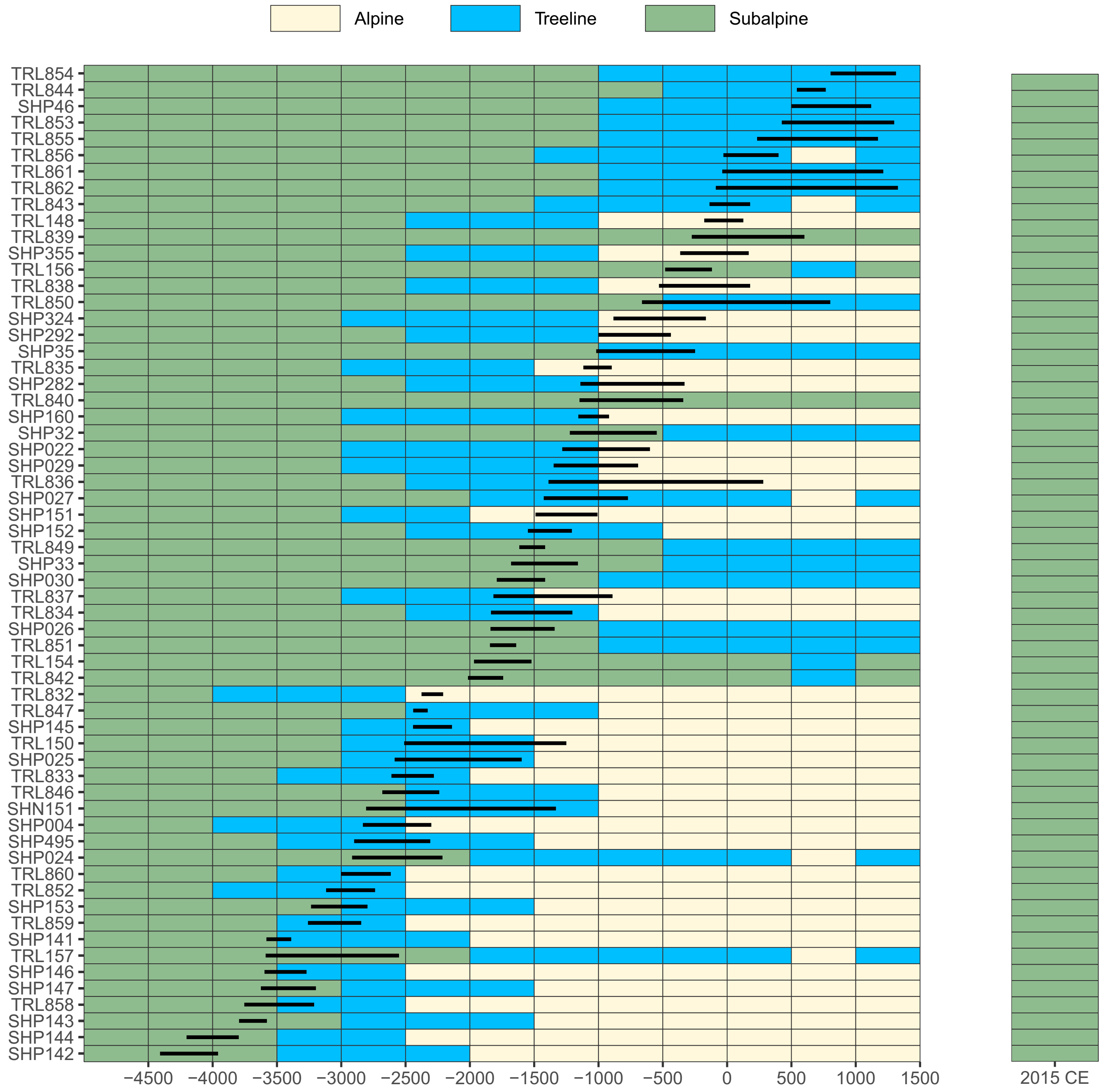

FIGURE 6 Ecotone predictions from Figure 5 at the spatial location of each dated remnant sample (rows) for each time interval (columns), with the remnant growth dates determined from annually resolved tree rings overlaid in black. Extreme weathering may have removed up to hundreds of rings from either side of the sample (pith-side or bark side), so we make no attempt to estimate the absolute establishment or mortality dates, and only show the years with ring-widths present. The right-most panel is the modern-day prediction, showing subalpine conditions at all remnant growth locations (Figure 5b). The *x*-axis values represent the threshold between two consecutive models. For example, the model centred on 4250 BCE is our best estimate of tree line position from 4500 to 4000 BCE

that are spatially and temporally discontinuous. Due to the vagaries of sampling and preservation, these analyses may fail to adequately reflect tree line dynamics during all periods. In contrast, our climate-driven results depict potential tree line position across the entire landscape, although validation is only possible at the locations where remnants are present for each time period.

4.1 | Model accuracy and remnant samples

Remnant wood above tree line has been subject to hundreds or thousands of years of weathering. In most cases, the entire trunk is not preserved. Samples are cross-sections or increment cores from the widest available part of the remnant. It is impossible to know exactly from what part of the tree the sample originated, and the inner and outermost dates may be hundreds of years from the establishment and mortality dates, due to weathering. Accordingly, we adopted a conservative method to compare the model's results at each remnant's location to the life span of each remnant (Figure 6). We used only the years during which we have annually resolved ring-widths, and did not attempt to estimate establishment or mortality dates. Rather, we characterize agreement between the tree line model and a remnant only if the earliest growth ring falls within a period of subalpine or tree line classification at the remnant's location. For example, the earliest growth ring from sample TRL832 is 2376 BCE, during which the model classifies its location as alpine environment. In this instance, there are only 124 years between the earliest dated ring and the last year of tree line classification at its location according to the model; however, there is not an objective way to estimate the number of years between the earliest dated ring and the sample's establishment date. This drawback necessitates a conservative characterization of disagreement between the life span of TRL832 and the ensemble predictions at its location.

Conversely, samples with growth rings that extend forward into a period of alpine prediction (samples SHP004, TRL837, TRL836) were not determined to be incongruous to the model, because downslope migration of tree line position is controlled by mortality (Lloyd & Graumlich, 1997). As growing conditions within the tree line ecotone become less favourable (due to a lower SMT or shorter growing season), individual trees start to die and establishment rates fall (Körner, 2012). A sustained imbalance between establishment and mortality rates will initiate a downslope shift in tree line position. While mature trees may persist on the landscape despite conditions being too harsh for seedling establishment, these individuals become increasingly rare and isolated above the ecotone as tree line position migrates downslope (Carrara & McGeehin, 2015).

Our predictions are site-specific approximations of the low-temperature controls on alpine tree line dynamics in the Great Basin over the past six millennia, and provide insight into how the tree line ecotone responds to millennial-scale climate change. An iterative process revealed a 500-year interval between predictions as a reasonable balance between the site's rate of atmospheric cooling and slow nature of tree line demography (Stephenson & Mantgem, 2005); shorter intervals yielded changes in tree line position that were difficult to detect or interpret, while longer intervals decreased prediction resolution and may have failed to reflect important perturbations in potential tree line position. The model's success rate suggests that temperature is the most consistent influence on tree line position in the White Mountains over long time periods. Our predictions are driven by temperature limitation only, and exclude any influence of non-temperature-related drivers. The following section addresses other relevant influences on tree line position.

4.2 | Mechanisms influencing tree line position

Tree line position is stable when rates of seedling establishment and adult mortality are in equilibrium within the ecotone. Bristlecone pine forests do not require much recruitment activity to sustain this equilibrium, as tree line mortality rates are low compared to montane forests (Lloyd & Graumlich, 1997; Stephenson & Mantgem, 2005). Research has shown that large quantities of seeds are consistently dispersed throughout the ecotone and above, and while many seedlings do not survive and mature to reach adulthood, enough persist to maintain tree line position (Barber, 2013; Körner, 2012; Kullman, 1993).

During periods of long-term temperature change, tree line position will shift up or downslope. Movement of the tree line ecotone also lags changes in climate with site and species-specific mechanisms likely (Bruening et al., 2017; Harsch, Hulme, McGlone, & Duncan, 2009; Körner, 2012; MacDonald et al., 2008; Millar et al., 2015). Attempts to quantify this lag have yielded varying results, perhaps in part due to differences in species, latitude, and site-specific topographic features (Dullinger, Dirnbo¨ ck, & Grabherr, 2004; Lloyd, Rupp, Fastie, & Starfield, 2002; Rupp, Chapin, & Starfield, 2001). Cooling climatic conditions decrease the likelihood a seedling reaches adulthood, slowing the rate of establishment and forcing an imbalance in the demographic equilibrium (Lloyd & Graumlich, 1997). The added stress of lower SMTs causes mature trees to be less resilient and more vulnerable to mortality (Körner, 2012). Over time, this imbalance may cause a decrease in tree line elevation (Körner, 1998; Paulsen & Körner, 2014). As the regional climate cooled throughout the Holocene (UCAR 2011; Figure 3), our model shows the seasonal mean isotherm at Sheep Mountain migrated downslope, and suggests tree line position followed (Figure 5).

An investigation of tree mortality across plots in the nearby Sierra Nevada discovered a substantial decrease in mortality rate with increasing elevation, and estimates of forest turnover at the upper tree line below one percent per year; however, determining causes of mortality for individual trees at tree line is fraught with difficulty (Stephenson & Mantgem, 2005). Over centuries, a cooling climate may act to increase stress on individuals at the highest elevations, while the direct causes of mortality may be more opportunistic and non-climate-related, and affect individuals that may otherwise survive without the added climatic stress (Das, Stephenson, & Davis, 2016).

Lloyd and Graumlich (1997) proposed that periods of intense drought acted to increase mortality of foxtail pine (*Pinus balfouriana* Grev. & Balf, a close relative of bristlecone pine) within the alpine tree line ecotone in the Sierra Nevada. In this scenario, warmer temperatures punctuated by several severe and prolonged multidecadal droughts during 1000–1400 CE caused an increase in mortality and subsequent downslope movement of tree line, due to decreased snowpack and subsequent increased winter desiccation in seedlings usually protected from the extreme cold and winter weathering. The authors propose a “gradient of vulnerability” within the tree line ecotone, induced by low temperatures during droughts, suggesting trees at the highest elevations are more susceptible to mortality due to increased stress; a theory directly supported by Das et al. (2016). While climatic cooling likely accounts for a baseline rate of mortality, the additional stress of prolonged, severe drought or biotic influence (such as bark beetles or defoliators) could act to further increase mortality within the tree line ecotone (Das et al., 2016; Lloyd & Graumlich, 1997). In contrast, preliminary evidence of increased bristlecone pine seedling recruitment during, and soon after, wet periods suggests an opposite effect. A large recruitment pulse observed in the White Mountains, CA from 1960 to 1987 CE coincided with above average precipitation. Barber (2013) used a mixed model, including 5-year averages of precipitation and minimum and maximum temperatures, to explain approximately half of the variance in recruitment rates during the past century. Together with our results, this evidence indicates temperature is the primary factor driving tree line ecotone position across millennia and acts gradually, whereas drought stress is likely important in driving more rapid and extreme changes in tree line position, with the potential for significant synergistic effects between temperature- and drought-related forcings.

Further, distinct stochastic events may have also influenced Holocene tree line position through rapid and intense, yet short-lived, atmospheric cooling. Aerosols from volcanic eruptions have initiated widespread and anomalously cool conditions in the past, forcing departures from the normal climate at the tree line ecotone (Mass & Portman, 1989; Sigl et al., 2015). Past eruptions have influenced the climate for several years, and may have acted to temporarily decrease the elevation of the tree line ecotone isotherm (approximately 6°C). Multiple closely spaced eruptions, as occurred in the mid 6th-century CE, could have had a stronger and lengthier atmospheric cooling effect (Sigl et al., 2015), inducing elevated mortality rates within the tree line ecotone in areas above the position of the volcanically forced 6+°C isotherm. Unfortunately, remnants found above tree line are not, by nature, intact samples. Weathering over millennia can erode hundreds of growth rings, so building an environmental record of short-lived tree line excursions from tree rings is challenging. Additionally, the CCSM3 TraCE palaeoclimatic simulations (UCAR 2011) used to obtain the Holocene temperature anomalies do not include volcanic aerosols, nor it reflect subgrid scale climatic phenomena such as persistent pressure systems or seasonal cloudiness in its simulations, so any influence from such is not reflected in our results.

We acknowledge possible amplifying effects between temperature and moisture availability at shorter temporal scales. However, we propose that both (1) the precipitation necessary for a recruitment pulse and (2) short-term droughts associated with widespread mortality at tree line could occur multiple times between any two predictions in Figure 5. Thus, in effect, the temperature requirement for tree line persistence becomes the most important variable across millennia, with the primary factor affecting tree line position dependent upon the temporal scale of interest. As far as we know, this intuitive finding is largely undiscussed, and points to the varied characteristics of palaeoclimatic evidence and complex nature of climatically induced ecological change, rather than a contradiction in evidence or mechanism. A future analysis of temporal variation within the remnants' climate-growth response may help clarify the interaction of climate drivers and the response of tree line across temporal scales.

4.3 | Significance and future response

Our model is in agreement with other tree line analyses in Western North America (Carrara & McGeehin, 2015; LaMarche, 1973; Pisaric, Holt, Szeicz, Karst, & Smol, 2003; Salzer et al., 2013; Scuderi, 1987). Our findings are also in good agreement with prior global-scale studies of tree line dynamics. The modelled topoclimate surface predicts a growing season isotherm of 6+°C at tree line, which is similar to independent analyses of modelled estimates and in situ observations of tree line temperatures globally. Körner and Paulsen (2004) estimate an average air temperature of 6–7°C at tree line from observed hourly temperatures over a 3-year period from 46 sites around the globe between 68° N and 42° S latitude. A decade later, this team modelled a tree line isotherm of 5+°C from 376 tree line positions around the globe (Paulsen & Körner, 2014). Our site-specific approach (along with Bruening et al., 2017) replicates these global findings using in situ observations, bolstering the conclusions of Paulsen and Körner (2014). Another global analysis (Harsch et al., 2009) of tree line advance across 166 sites concludes diffuse tree lines (like the tree line at Sheep Mountain) are more likely to advance upslope in response to increased SMT than abrupt or krummholz tree lines, a function of the direct link between diffuse tree line position and growing season temperatures that our model reproduces.

However, our prediction of potential tree line position based on recent observed temperatures (Figure 5b) conflicts with several studies regarding recent atmospheric warming may manifest changes in tree line position. Liang et al. (2011) documented an increase in stand density associated with warmer temperatures at a tree line site on the south-eastern Tibetan Plateau without evidence of a concurrent upslope movement in tree-line position. Further, Batllori, Camarero, Ninot, and Gutie′rrez (2009) demonstrate that seedling survival within the alpine ecotone may be controlled primarily by microsite conditions and available recruitment habitat, rather than the growing season temperature that sustains tree line ecotone position. The authors suggest these differences between limiting factors may alter the response of the tree line ecotone to a warming climate unpredictably. However, both these studies and our results are site-specific, and are not necessarily in contradiction to other given site- and species-specific effects, and the relatively long lag between warmer temperatures and upslope tree line movement we propose at this site. Our results are based on 120 years of empirical climate data, and corroborate two global tree line analyses. Assuming natural demographic processes will eventually move the tree line ecotone upslope to the position of the 6°C growing season isotherm, our estimate of potential maximum tree line ecotone position in the White Mountains of California predicts large future changes, both here and potentially in other alpine environments.

There is evidence of recent seedling establishment far above tree line in the Great Basin (Millar et al., 2015). In isolation, such observations are insufficient to demonstrate tree line advance. Körner (2007) warns explicitly against interpreting observations of seedling establishment above tree line as indicative of ecotone migration forced by a warming climate without long-term evidence. He argues that microsite conditions near the ground decouple from the free atmosphere, and are generally warmer and more favourable to early life stage processes. Only after seedlings reach a height of approximately three metres is there sufficient evidence to support an upslope migration of tree line position. This has not yet been observed above tree line in the Great Basin. Work by Barber (2013) in this mountain range demonstrates the average height of bristlecone pine seedlings 90–110 years old was 1.1 m with a standard deviation of 0.27 m. Assuming a linear growth rate, it could take hundreds of years for seedlings to mature enough to warrant a robust upslope migration of tree line position, and we speculate that a multicentury lag exists between sustained climate change and tree line position change at this site. Additionally, there is new evidence that Great Basin bristlecone pine demography may be slower to respond to recent warming that other species (*Pinus flexilis* James), further complicating predictions of post-industrial warming-induced tree line position change for this species (Smithers, North, Millar, & Latimer, 2017).

5 | CONCLUSIONS

Our results indicate that (1) average growing season temperature is an excellent first approximation of tree line position when topography is accounted for, and (2) from 4750 BCE to present, the modelled position of a 6+°C growing season topoclimate isotherm accurately predicts the movement of tree line position compared to 61 remnant samples from above tree line in the White Mountains, CA. The predictions are based on the low-temperature forcing of tree line position, independent from other possible effects. They should be interpreted as a spatiotemporal analysis of tree line dynamics and climate-limited potential tree line position, rather than precise and independent predictions.

These results are not contradictory to evidence from other studies of non-temperature-related factors driving tree line position at shorter time-scales (e.g. Lloyd & Graumlich, 1997), and further develop the known history of global Holocene tree lines and regional ecological change. Multiple factors continuously interact to affect the tree line ecotone. Future tree line dynamics studies could benefit from combining analyses of the demographic processes of recruitment, establishment and mortality, as all are affected by environmental conditions that fluctuate spatio-temporally. In the face of rapid and sustained climate change, a deeper understanding of how the unique and valuable tree line ecotone will respond is crucial, and necessitates future exploration of the climatic drivers of alpine tree line position.

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DATA ACCESSIBILITY

All topographic GIS layers in this analysis were generated using standard methods from a publicly available 10-metre resolution digital elevation model (DEM), obtained from the United States Geological Survey. The seasonal mean temperature (SMT) raster layers used in this analysis are available from Pangaea: https://doi.org/10.1594/PANGAEA.877972.

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BIOSKETCH

This author team is interested in the palaeoclimatic signal preserved in the tree rings of the ancient bristlecone pine. Some of our previous analyses have focused on the high-frequency temperature response observed in near-tree line bristlecone pine, and the topographic and topoclimatic influences on tree growth and tree line position.

Author contributions: A.G.B. and M.W.S developed the idea and methods; J.M.B., A.G.B. and M.W.S. collected the climate data; J.M.B. and A.G.B. analysed GIS and climate data; M.W.S. performed all dendrochronological data collection and analysis; and J.M.B. led the writing of the manuscript.

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