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Leap frog in slow motion: Divergent responses of tree species and life stages to climatic warming in Great Basin subalpine forests

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Abstract

In response to climate warming, subalpine treelines are expected to move up in elevation since treelines are generally controlled by growing season temperature. Where treeline is advancing, dispersal differences and early life stage environmental tolerances are likely to affect how species expand their ranges. Species with an establishment advantage will colonize newly available habitat first, potentially excluding species that have slower establishment rates. Using a network of plots across five mountain ranges, we described patterns of upslope elevational range shift for the two dominant Great Basin subalpine species, limber pine and Great Basin bristlecone pine. We found that the Great Basin treeline for these species is expanding upslope with a mean vertical elevation shift of 19.1 m since 1950, which is lower than what we might expect based on temperature increases alone. The largest advances were on limber pine-dominated granitic soils, on west aspects, and at lower latitudes. Bristlecone pine juveniles establishing above treeline share some environmental associations with bristlecone adults. Limber pine above-treeline juveniles, in contrast, are prevalent across environmental conditions and share few environmental associations with limber pine adults. Strikingly, limber pine is establishing above treeline throughout the region without regard to site characteristic such as soil type, slope, aspect, or soil texture. Although limber pine is often rare at treeline where it coexists with bristlecone pine, limber pine juveniles dominate above treeline even on calcareous soils that are core bristlecone pine habitat. Limber pine is successfully "leap-frogging" over bristlecone pine, probably because of its strong dispersal advantage and broader tolerances for establishment. This early-stage dominance indicates the potential for the species composition of treeline to change in response to climate change. More broadly, it shows how species differences in dispersal and establishment may result in future communities with very different specific composition.

KEYWORDS
climate envelope, elastic net regularization, Great Basin bristlecone pine, limber pine, *Pinus flexilis*, *Pinus longaeva*, range shift, regeneration, species distribution, treeline

1 | INTRODUCTION

In response to climatic warming, species are generally expected to expand their ranges to higher latitudes and elevations and contract at lower latitude and elevational range margins (Hayhoe et al., 2004; Loarie et al., 2008; Parmesan & Yohe, 2003). The upslope leading range edge is at treeline in subalpine forests, an ecotone considered a sensitive biological indicator of climatic warming due to the strong, world-wide association between growing season temperature and treeline (Holtmeier, 2003; Körner, 1998, 2012; Körner & Paulsen, 2004; Millar, Westfall, Delany, King, & Graumlich, 2004). Future treeline is generally expected to shift higher in elevation by as much as 700 m by the year 2100 (Kullman & Öberg, 2009; Moen, Aune, Edenius, & Angerbjörn, 2004). Despite these predictions, there is substantial variability in the speed of treeline response to warming in mountains around the world (Camarero et al., 2017). This variation may be due to many factors, such as varying geomorphology, past human disturbance, lags in population dynamics, dispersal limitation, and biological interactions (competition, herbivory; Grace, Berninger, & Nagy, 2002; Harsch, Hulme, McGlone, & Duncan, 2009; Holtmeier, 2003; Holtmeier & Broll, 2017; Speed, Austrheim, Hester, & Mysterud, 2010). Variability in treeline advance hints that in addition to warming temperature, there are other factors influencing treeline advance, most of which remain unexplored.

Biotic interactions, such as competition, facilitation, and/or priority effects, are likely to have particularly strong effects on how range shifts occur (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Baumeister & Callaway, 2006; Ettinger, Ford, & Hille Ris Lambers, 2011; Kroiss & HilleRisLambers, 2014; Maestre, Callaway, Valladares, & Lortie, 2009). In subalpine forests immediately below treeline, competitors from further downslope could displace subalpine species through direct competition or through indirect mechanisms such as increased exposure to disease or changing disturbance regimes associated with downslope species (Flannigan, Stocks, & Wotton, 2000; Tomback & Resler, 2007). Alternatively, in harsh conditions like those found in subalpine forests, species can have a "nurse effect," facilitating the establishment of other species by positively modifying the microclimate through greater water retention, wind blocking, creation of shade, or other ameliorating effects (Maestre et al., 2009; Malanson et al., 2007; Pyatt et al., 2016). Interspecific differences in dispersal ability and establishment success are likely to play major roles in how newly available habitat is colonized with priority effects possibly trumping other responses to climate change. Species distribution models can predict the future climate envelopes of species, but often ignore how other limitations affect species range shifts under climatic warming. For example, in trees establishing outside of current forest range limits, the lack of soil development or protection from harsh weather or ineffective dispersal may preclude successful establishment.

Climate envelope models are often based on matching adult presence with climatic conditions. Young individuals, however, not only encounter different microclimates but often have different climatic tolerances than do adults (Bell, Bradford, & Lauenroth, 2014; Jackson, Betancourt, Booth, & Gray, 2009; Kueppers et al., 2017; Máliš et al., 2016; Warren & Bradford, 2011). Juvenile trees frequently occupy a narrower range of climatic conditions, especially in water-limited areas (Dobrowski et al., 2015; Monahan, Cook, Melton, Connor, & Bobowski, 2013; Moyes, Germino, & Kueppers, 2015; Zhu, Woodall, & Clark, 2012). Given this narrower filter for juvenile survival, changes in recruitment are likely a major component of species range shifts (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). When propagules are plentiful, dispersal and range shift can happen rapidly, but within slow-growing or slow-dispersing species lags in range shifts can be decades to centuries (Kroiss & HilleRisLambers, 2014). The narrow range of conditions suitable for establishment in subalpine trees and unforeseen biotic interactions complicate our ability to project how species' ranges will respond to increasing temperatures (Conlisk et al., 2017; Körner, 2012; Millar, Westfall, Delany, Flint, & Flint, 2015; Millar et al., 2004).

Treeline trees have shown recent dramatic stem growth increases in the mountains of the western US Great Basin, suggesting that temperature increases have recently improved growing conditions at the trees' upper elevation limit (Salzer, Hughes, Bunn, & Kipfmueller, 2009). The Great Basin is a region of low-elevation basins and high-elevation ranges, on which sparse montane forests occur at upper elevations. While the ranges of the Great Basin are generally arid, there is a substantial southwest to northeast gradient in the amount (low to high) and timing (Mediterranean to monsoonal) of precipitation with large daily and seasonal temperature ranges throughout the region. Above-treeline recruitment has increased in the western Great Basin, with evidence for increases in recruitment pulses in the last 130 years (Millar et al., 2015). Great Basin subalpine forests are largely made up of Great Basin bristlecone pine (*Pinus longaeva* DK Bailey) and limber pine (*Pinus flexilis* James) with stands of Engelmann spruce (*Picea engelmannii* Parry) and quaking aspen (*Populus tremuloides* Michaux) on wetter slopes in the eastern Great Basin, and whitebark pine (*Pinus albicaulis* Engel), a treeline species in parts of the northern and eastern Great Basin. Great Basin bristlecone pine is notable for individual longevity with known trees over 5,000 years old making them the oldest living nonclonal organisms on earth (Schulman, 1954).

Tree species with higher densities at treeline have range margins that better track warming temperatures in establishing above treeline (Kroiss & HilleRisLambers, 2014). Where bristlecone pine is present, it typically dominates at treeline with limber pine mixed in at lower elevations (Millar et al., 2015). While there is overlap in the elevational ranges of the two species, there are range differences at both upper and lower elevations. At the upper extreme, bristlecone pine is found at higher elevations (3,535 m) than limber pine (3,505 m) in Nevada (Charlet, 1996). That seemingly slight difference reflects limber pine's much lower treeline density relative to bristlecone pine, and its absence from many treeline sites. The elevation difference is especially acute on dolomitic soil where the upper limit of limber pine (3,030 m) is considerably lower than that of bristlecone pine (3,485 m; Wright & Mooney, 1965). For the lower range margin,

limber pine is found considerably lower (1,830 m) than bristlecone pine (2,060 m) in Nevada (Charlet, 1996).

Recent establishment of young trees above the historical treeline in the western Great Basin has been observed, but much of that upslope establishment was typically downslope limber pine "leap-frogging" over bristlecone pine (Millar et al., 2015). Shade-intolerant bristlecone pine encounters minimal competition from other tree species due to the harsh abiotic conditions of its habitat. There is minimal impact from pathogens in these forests and the sparseness of the vegetation limits the occurrence of fire (North, Van de Water, Stephens, & Callins, 2009; Van de Water & Safford, 2011). The recent appearance of regeneration at and above treeline is evidence that climatic conditions have changed sufficiently at treeline in the last 50 years to allow for establishment. Given the observed treeline advance in the Great Basin, the few species involved, and limited human disturbance, Great Basin treelines provide a rare opportunity to examine the climate change-induced dynamics surrounding a discrete range margin.

It remains to be seen whether bristlecone pine will be able to track warming climate to higher elevations. Upper treeline is often a product of inhospitable upslope geomorphology limiting the ability of species to advance upslope under favorable climatic conditions (Butler, Malanson, Walsh, & Fagre, 2007; Ernst, Van de Ven, & Lyon, 2003; Grace et al., 2002). Even allowing for upslope migration, the rate of changing temperatures may be fast enough that species with long regeneration times like bristlecone pine are unable to migrate fast enough to avoid local extirpation (Aitken et al., 2008; Loarie et al., 2009; Neilson et al., 2005; Van de Ven, Weiss, & Ernst, 2007). Minimum temperatures in the western Great Basin have increased an average of 1°C between 1910 and 2013 (Millar et al., 2015), and regional temperatures are expected to rise an additional 2–4°C by the late 21st century (Scalzitti, Strong, & Kochanski, 2016). Aside from the rate of climate warming, bristlecone pine may also be exposed to greater interspecific competition from other tree species, especially the better-dispersing limber pine, which could establish rapidly in newly available habitat at and above the current treeline.

We know little about the regeneration dynamics of subalpine trees and even less about these dynamics in dry forests like those found in the Great Basin (Barber, 2013; Conlisk et al., 2017). Part of this ignorance stems from the fact that in the last 500 years, treeline regeneration in the Great Basin appears to have been limited to the last 50 years. Surveys in the California White Mountains in the 1950s showed an absence of young trees indicating that adult treeline trees established in a period of more favorable, likely warmer, climatic conditions (Billings & Thompson, 1957). The lack of relict wood from smaller trees, which tends to persist on the surface for 100s to 1,000s of years, suggests that there had been little regeneration at treeline for at least hundreds of years. While juvenile trees may have established at or above treeline in the past and then died before reaching maturity, once bristlecone pine and limber pine have survived to an age of 3–4 years, these small trees have extremely low mortality (Barber, 2013; Conlisk et al., 2017; Elliott, 2012). Most juvenile trees old enough to be observed in field surveys are very likely to persist into adulthood.

This study examines the species dynamics surrounding treeline in the Great Basin by specifically examining the following questions: (i) What are the major abiotic predictors of treeline advance? (ii) What are the predictors of below-treeline adult basal area and above-treeline establishing juveniles and how consistent are the environmental associations of adult trees and juveniles of each species? (iii) How does the species composition of mature forest compare with the species composition of establishing juveniles below and above treeline? This research will examine whether differences exist between two key subalpine tree species in the US Great Basin and whether those differences have long-term consequences for the persistence of Great Basin bristlecone pine under rapidly warming treeline climate conditions.

2 | MATERIALS AND METHODS

2.1 | Study area

The Great Basin of the interior United States West is defined by having internal drainage, Basin and Range geomorphology, and/or by its floristic composition. It extends from the crest of the Sierra Nevada in California in the west to the Uinta Mountains of Utah in the east, and with the Columbia River and Colorado River watershed divides forming the north and south boundaries, respectively (Figure 1). In the southern and central Great Basin, treeline is largely made up of Great Basin bristlecone pine (abbreviated PILO) and limber pine (PIFL). In the northern Great Basin, whitebark pine is the dominant treeline species. Occasional treeline stands of Engelmann spruce (PIEN) and quaking aspen are also found throughout the Great Basin, especially in the cooler or wetter parts of the region.

Soil type plays a large role in Great Basin tree species distributions. Bristlecone pine is mostly restricted to high-elevation carbonate (calcareous) soils, especially dolomite in the White Mountains (Schulman, 1954; Wright & Mooney, 1965), and limestone pockets throughout the Great Basin. On these soils, it is the dominant tree species with limber pine being rare or absent. Other major soil types include quartzite, a metamorphic sandstone, on which a mix of tree species generally coexist or different species can be locally dominant, and granite on which limber pine typically dominates and bristlecone pine is rare.

We sampled treeline in Great Basin mountain ranges in 2015 and 2016 that were of sufficient elevation to contain climatic treeline and supported both limber and bristlecone pine. Climatic treeline, as we use it, is treeline that is a function of temperature constraints as opposed to treeline determined by geology, disturbance, or other nonclimatic effect (Körner, 2012). Since there is no reliable field method for distinguishing limber pine and whitebark pine juveniles (Hendrick & Lotan, 1971), we avoided sampling where those two species coexist, eliminating an area in the northern Ruby Mountains from our study. These criteria allowed for sampling in the Snake Range, Schell Creek Range, southern Ruby Mountains, and

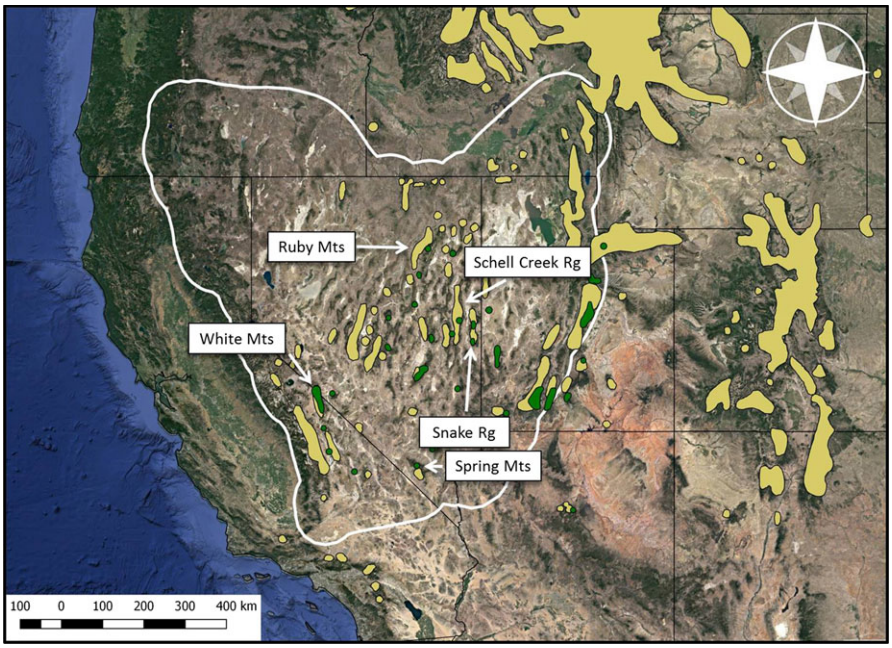

FIGURE 1 The Great Basin, outlined in white, is centered on the state of Nevada which has most of the highest ranges in the bioregion. Sampling occurred in the mountain ranges labeled. Limber pine (yellow) and Great Basin bristlecone pine (green) range maps show their ranges in the Great Basin. This is the entire extent of the Great Basin bristlecone pine's range. Limber pine's range extends to the north into Canada. Species distribution vectors were downloaded from the USGS vegetation-climate modeling study (https://esp.cr.usgs.gov/data/little/). The background satellite image is a Google Earth image (www.earth.google.com) accessed via QGIS [Colour figure can be viewed at wileyonlinelibrary.com]

Spring Mountains in Nevada and the White Mountains in California (Figure 1). Within each range, we sampled individual mountains or ridges that contained climatic treeline on all aspects that allowed safe access and where treeline appeared to result solely as a climatic effect, excluding avalanche chutes, cliffs, unstable scree, and recent landslides (Körner, 2007). This allowed for sampling on 13 distinct mountains or ridges in the five mountain ranges.

2.2 | Plot placement and measurements

At each location, we identified treeline as the line connecting the uppermost forest patches of at least three trees growing to at least 3 m in height. This line is a generally recognized construct representing the upper margin of the treeline ecotone and is not associated with a particular elevation contour (Fig. S1; Körner, 2007; Körner & Paulsen, 2004). We placed plots at the furthest distance upslope of treeline where juvenile tree densities were sufficient (i.e., clumps of three or more individuals) that upon reaching maturity the clump will represent future treeline. Plots were placed on all slopes and aspects that contained climatic treeline and met our criteria. We placed sequential plots measuring 30 m × 10 m (300 m^2) to form a modified 10 m wide belt transect upslope from and parallel to current treeline. Each 30 m length plot was placed parallel to and upslope from treeline but could be located up or down slope relative to the previous plot to follow the maximum elevation of juvenile tree clumps. Since we sought to maximize the number plots per peak or ridge aspect, the number of plots per peak or ridge aspect varied from 5 to 24. In each plot, we tallied all conifer individuals, identified individual trees to species, and aged trees less than 100 years by nondestructively counting above-ground terminal bud scars, which is well-correlated with ring counts (Millar et al., 2004, 2015; Parent, Morin, & Messier, 2000). These ages were binned into age classes to account for errors in whorl aging. We considered all trees <100 years old to be a juvenile tree, although trees 50–100 years in age were very rare. Since our ability to accurately age trees older than 100 with bud scars is limited, we binned all of these trees as adults. With few exceptions, all trees encountered were either <50 years or were at least hundreds of years old. We excluded trees <5 years old to limit the effect of very young trees dying before reaching maturity (Barber, 2013). From each juvenile tree, vertical distance to current treeline was measured using a Laser Technology TruPulse 200 laser rangefinder. To avoid pseudoreplication, individual distances to treeline were averaged to give a plot-level distance to treeline. The elevation, slope, aspect, dominant soil type, and horizontal and vertical slope shapes were recorded at the midpoint (15 m) of each plot.

To examine the surface characteristics in each plot, we took a point sample at 0.5 m intervals along a 30 m transect ($N = 60$) recording substrate conditions that a seed would encounter if it landed or was buried there. At each point we recorded whether the point landed on soil subdivided into size class (0 = bare soil, 1 = gravel, 2 = large rock, or 3 = bedrock), litter, downed wood, or vegetation identified to species. To evaluate abundance of adult trees as a representation of relative seed sources, we used basal

area as a proxy for relative abundance. We estimated basal area of cone-producing adults for each tree species using a basal area prism (BAF = 1M) at the two end points of the transect line which were averaged to give plot-level basal area for each species. We compared the demographics of upslope establishment with current subalpine adult demographics by pairing the above treeline plots with plots selected in the closed forest below treeline in which the same plot level and demographic data were collected. Since there were very few juvenile trees in the closed canopy, closed forest plots were selected haphazardly where the aspect and relative position on the landscape matched its above-treeline pair.

2.3 | Plot-level DEM predictors

For other potential model predictors of treeline advance, we used 30 m Digital Elevation Models (DEM) in QGIS (QGIS Development Team, 2016) to extract plot-level metrics. The DEM was used to calculate monthly total solar radiation (W hr/(m^2 day)) and solar insolation (hr) for each plot using QGIS GRASS (GRASS Development Team, 2016). For each month, we used the 15th as a monthly "average" day. We included annual and growing season (June–September) parameters for solar radiation and insolation time. A DEM was also used to extract values for elevation and topographic water accumulation by using the Watershed (topographic convergence index) feature in ArcGIS (*ArcGIS Desktop*, 2016).

These predictors (Table 1) were chosen because we believed that they were most likely to affect successful establishment of young trees and therefore treeline advance. The list of potential predictors is long since successful establishment of young trees in the harsh conditions at treeline is a result of many factors, both abiotic and biotic (Conlisk et al., 2017; Kueppers et al., 2017).

2.4 | Data analysis

This design resulted in a large number of plots and juvenile trees within plots, which resulted in a common problem with large sample sizes in which almost all predictors are found to be "significant" (i.e., likely to have nonzero effect), but most with a very small effect size and effects often correlated with each other (MacElreath, 2016). Models using standard statistical regression are likely overfitted. In addition, the large number of potential predictors makes analysis with standard regression or linear mixed effects models problematic. To avoid these problems of parameter selection, we used elastic net regularized regression that combines the least absolute shrinkage and selection operator (LASSO) and ridge regression (Tikhonov regularization). This produces regularized models that include only strong predictors, while shrinking weak predictor variables toward zero (Friedman, Hastie, & Tibshirani, 2010; Guisan & Zimmermann, 2000). Elastic net models have been successfully used in a variety of ecological studies when dealing with a large number of potential predictors, especially when those predictors have low predictive power (Holdo & Nippert, 2015; Lemoine et al., 2016; Prospere, McLaren, & Wilson, 2014). This regularization shrinks coefficients to 0 unless they substantially improve model fit and predictive performance in cross-validation. The elastic net model fitting procedure imposes regularization on the model parameters, strongly penalizing model complexity. It is a feature of elastic net regularization that choosing a model via shrinking coefficients toward zero will result in a model with most coefficients very near zero. Proximity to zero does not mean that a predictor is unimportant—any predictor with a nonzero coefficient is important in that its inclusion in the model improves out-of-sample prediction of the response variable (Zou & Hastie, 2005).

We fit generalized linear models using penalized maximum likelihood (Glmnet) for the response variables of treeline advance

TABLE 1 Potential predictors tested for treeline advance (distance from the above-treeline plot to treeline), adult basal area, and juvenile density

Potential model predictors
Mountain range
Ruby Mountains
Schell Creek Range
Snake Range
Spring Mountains
White Mountains
Soil type
Dolomite (calcareous)
Granite
Limestone (calcareous)
Quartzite
Elevation
Latitude
Longitude
Slope
Northness = cos(aspect)
Eastness = sin(aspect)
Topographic water accumulation
Annual insolation
Annual radiation
Growing season insolation
Growing season radiation
Percent bare soil
Percent gravel
Percent large rocks
Percent bedrock
Percent litter
Percent vegetation cover
Bristlecone pine (PILO) basal area[a]
Limber pine (PIFL) basal area[a]
Engelmann spruce (PIEN) basal area[a]

[a]Basal areas were excluded from the treeline advance models since there is essentially no adult basal area above treeline.

(distance from the above-treeline plot to treeline), specific adult tree basal area, specific upslope juvenile density, the ratio of adult limber pine to bristlecone pine basal area, and the ratio of limber pine to bristlecone pine juvenile density. Models of the ratio of limber pine to bristlecone pine (PIFL:PILO) adult basal area and juvenile density were used to examine how the two species respond to climatic predictors in relation to each other. While elastic net models do not currently allow for using mixed effects, when we ran standard regression models, including spatial random effects did not improve the models. To fit these models, we used the R package glmnet (Friedman, Hastie, Simon, & Tibshirani, 2016), using the elastic net penalty and selecting values for the regularization parameter (λ) that minimize the mean cross-validation error over 100 runs of cv.glmnet.

For all models, coefficient values were plotted by nonzero (model-included) parameters using the library ggplot2 (Wickham, 2009) to show their relative effects on the response variable. Error bars were generated by nonparametric bootstrapping, using 1,000 iterations. From the resulting regression parameters, we constructed 95% confidence intervals by taking the 2.5 and 97.5 percentiles of the bootstrap estimates. These confidence intervals are provided only to show a visual estimate of parameter variability. They are not to be viewed as having statistical "significance." Parameters that are not shrunk to zero via elastic net by definition improve the model and so are included (Friedman et al., 2010; Goeman, Meijer, & Chaturvedi, 2016).

3 | RESULTS

3.1 | Treeline advance

We surveyed 173 pairs of above and below treeline plots for a total of 346 plots. Using the presence of at least three established juvenile trees within the plot as a measure of treeline advance, median vertical advance across all Great Basin sites including both species was 11.9 m (mean = 19.1 m) upslope with a maximum of 153 m (Figure 2). The majority of plots (62%) showed a potential treeline advance of between 5 and 25 m upslope. Given our measured slopes of 9%–78%, this amounts to a ground distance of 8–279 m over which seeds dispersed.

Soil was a factor in predicting potential advance with granitic soil showing larger advances of 22.0 m compared with 9.6 m on carbonate dolomitic soil (Figures 2 and 3). Treeline advance was slightly, but insignificantly, higher (10.7 m) on carbonate limestone soil. Latitude, east aspect, and north aspect were the most negatively associated predictors implying that potential treeline advance is higher on south and west aspects and in mountain ranges further south. Quartzite soil is negatively associated with treeline advance relative to dolomitic soil (Figure 3), but still showed a median treeline advance equal to that of dolomite at 9.6 m. There was an effect of mountain range with treeline advance being higher in the Snake Range and the Schell Creek Range, but treeline was found to be advancing in all mountain ranges.

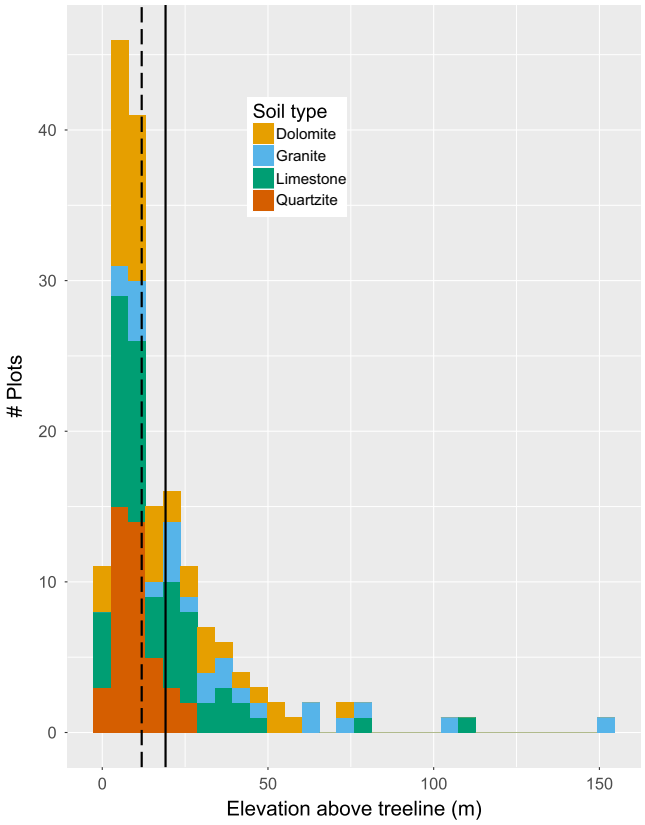

FIGURE 2 The number of plots sampled by soil substrate and their vertical elevation above current treeline representing potential treeline advance. Median (11.9 m) and mean (19.1 m) elevations above treeline are shown with the dashed and solid lines, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Life stage predictors

Models indicate that both bristlecone pine (Figure 4a) and limber pine (Figure 5a) adult basal area is largely explained by soil type. Since dolomite is set as the intercept by elastic net regularization, and since limestone has a similar effect as dolomite, they do not show up with a coefficient on the figures below. In the case of bristlecone pine, granite and quartzite soil both have a large negative effect relative to dolomite which would also make the inverse true: dolomite soils have a large positive effect relative to granite and quartzite. Mountain range also strongly predicted bristlecone pine adult basal area, having a strong positive association with the Spring Mountains and a negative association with the Snake Range. Adult bristlecone pine basal area was positively associated with cooler north-facing and east-facing slopes and negatively associated with latitude. As expected, adult limber pine basal area is positively associated with granitic and quartzite soils, thus indicating niche differentiation from bristlecone pine, which is positively associated with calcareous soils. Limber pine adult basal area was only moderately associated with mountain range but had a strong positive association with latitude indicating higher basal areas in the northern part of the study area. It also had a negative association with east aspect indicating higher

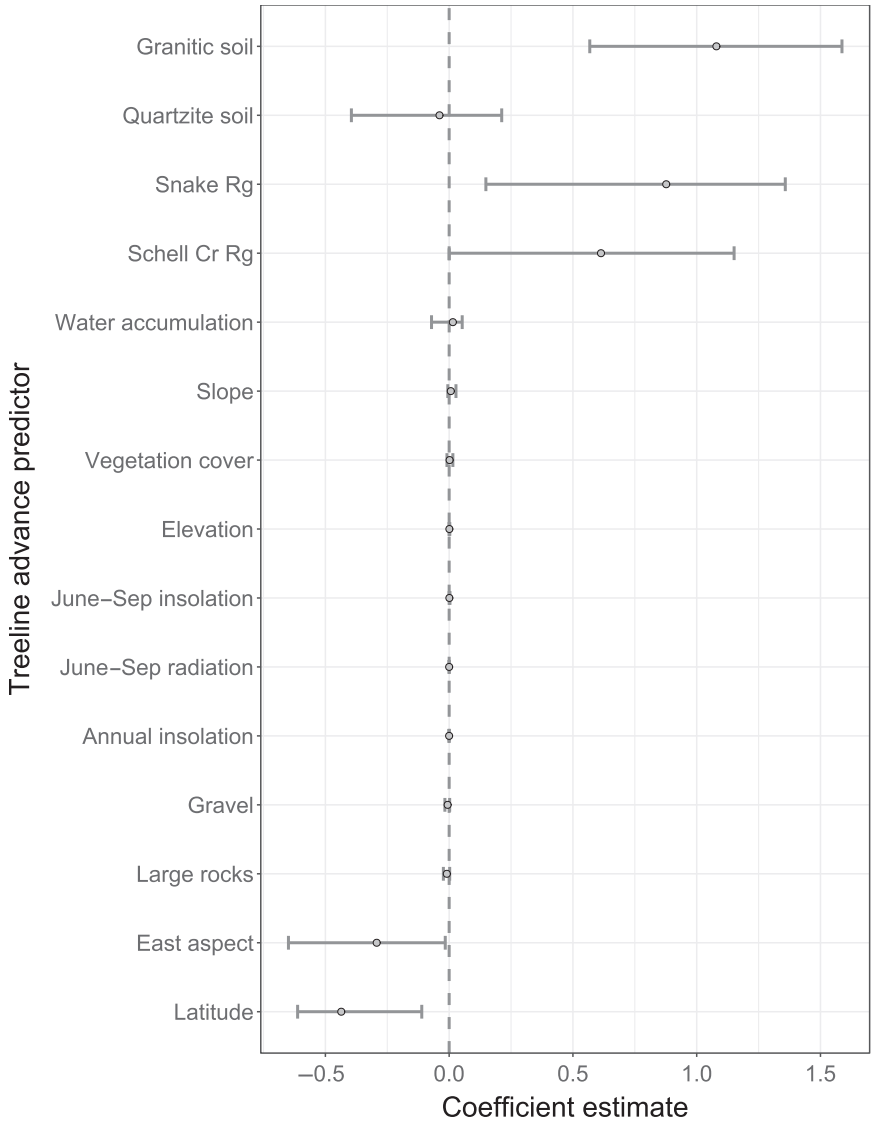

FIGURE 3 Treeline advance predictors. Rank of coefficients that predict treeline advance and the estimate of each coefficient relative to dolomite soils (which by default is assigned a coefficient of 0 to which the other soil types are compared). All points are nonzero coefficients chosen by glmnet using the elastic net penalty. Confidence intervals (95%) are included only as a visual estimate of parameter variability and *are not* meant to indicate the statistical significance of a parameter. Glmnet includes all parameters that improve a model and so are included in the model if they have a nonzero value

treeline advance on warmer west-facing slopes. Both species had a number of other small, but nonzero, associations with basal area (Figure 4a,b).

Models for above-treeline density of bristlecone pine juveniles had predictors that were similar to, but not the same as, those for adult basal areas (Figure 4b). Most of the corresponding regression coefficients have the same coefficient sign for both life stages, suggesting that bristlecone pine seedling environmental tolerances somewhat match those of adults. Exceptions include the Snake Range (negative association for adults, positive for juveniles) and east aspect (positive for adults, negative for juveniles) indicating that while adults and juveniles share some predictors, they do not share all of them and for at least some predictors, respond oppositely. Models of limber pine above-treeline juvenile density included very few predictors, and shared only one of those predictors with the model for limber pine adults (Figure 5). Furthermore, the only shared coefficient, quartzite soil, has an opposite sign for adults and juveniles. Most strikingly, while adult limber pine density was strongly associated with granitic soils, above-treeline juvenile density had no association with granitic soil. Limber pine juveniles responded to far fewer and different parameters than limber pine adults suggesting that limber pine juveniles have different and broader tolerances than adults.

A positive coefficient for the ratio of limber pine to bristlecone pine adult basal area adults or juvenile density (PIFL:PILO) indicates a predictor that favors limber pine over bristlecone pine. For adult basal area there is a strong positive effect of granite soil on PIFL:PILO as expected (Figure 6a). There is also a strong positive

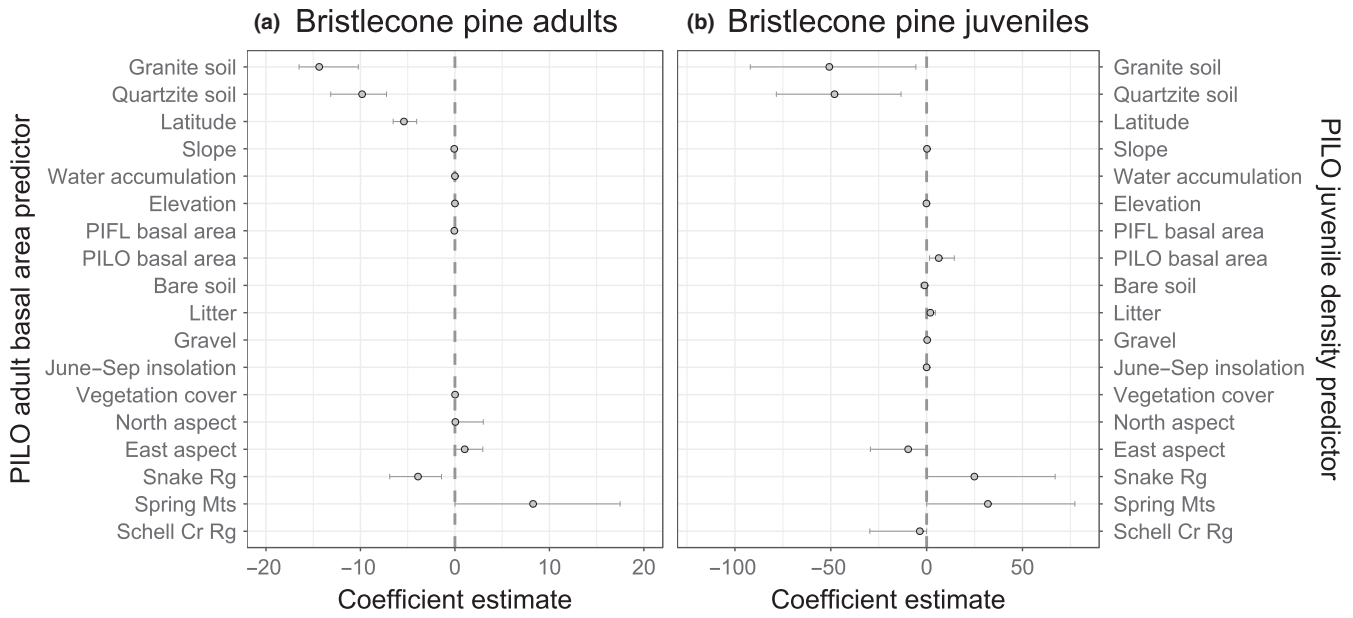

FIGURE 4 Bristlecone pine predictors. Slope coefficients for predictors of (a) adult bristlecone pine basal area below treeline and (b) established bristlecone pine juveniles above treeline. All points are nonzero coefficients chosen by glmnet using the elastic net penalty. Predictors without a point were not found to improve the model and so, while not included, are shown here for comparison purposes. Confidence intervals (95%) are included only as a visual estimate of parameter variability and *are not* meant to indicate the statistical significance of a parameter. Glmnet includes all parameters that improve a model and so are included in the model if they have a nonzero value

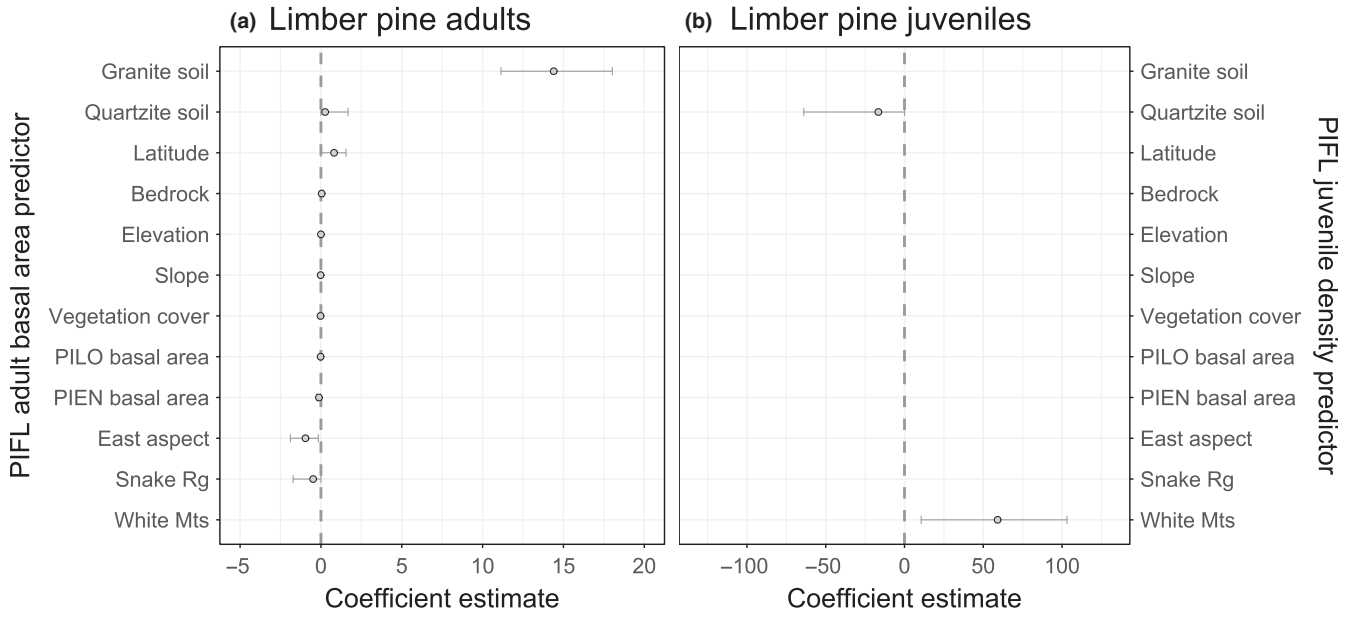

FIGURE 5 Limber pine predictors. Slope coefficients for predictors of (a) adult limber pine basal area below treeline and (b) established limber pine juveniles above treeline. All points are nonzero coefficients chosen by glmnet using the lasso penalty. Predictors without a point were not found to improve the model and so, while not included, are shown here for comparison purposes. Confidence intervals (95%) are included only as a visual estimate of parameter variability and *are not* meant to indicate the statistical significance of a parameter. Glmnet includes all parameters that improve a model and so are included in the model if they have a nonzero value

association between latitude and adult basal area indicating a gradient of more bristlecone pine further south and more limber pine further north as well as positive and negative effects of individual mountain ranges. For juvenile density, models identify the same positive association of PIFL:PILO with granitic soil, due mostly to juvenile bristlecone pine's near absence on granite (Figure 6). While there are some shared predictors for adult and juvenile PIFL:PILO, many are unique and some of the predictors with smaller

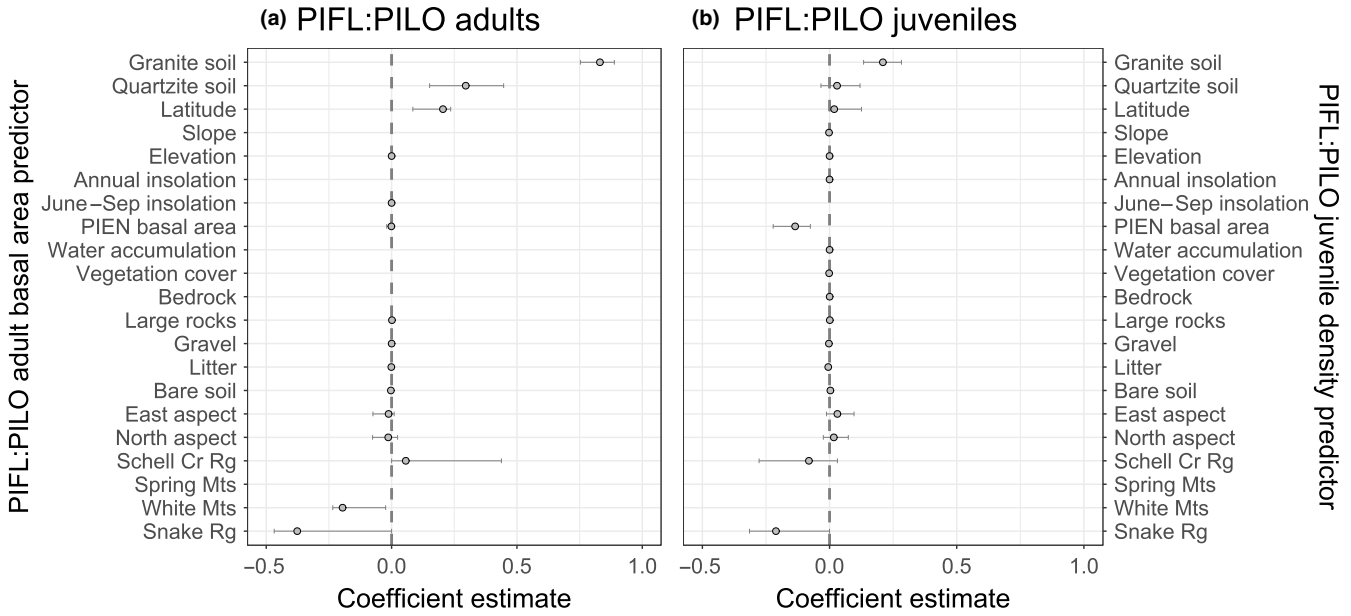

FIGURE 6 Limber pine: bristlecone pine predictors. Slope coefficients for predictors of the (a) relative limber pine to bristlecone pine adult basal area ratio and (b) relative limber pine to bristlecone pine juvenile density ratio above treeline. All points are nonzero coefficients chosen by glmnet using the lasso penalty. Predictors without a point were not found to improve the model and so, while not included, are shown here for comparison purposes. Confidence intervals (95%) are included only as a visual estimate of parameter variability and *are not* meant to indicate the statistical significance of a parameter. Glmnet includes all parameters that improve a model and so are included in the model if they have a nonzero value

coefficients, such as those for north and east aspects, switch from negative (adults) to positive (juveniles) associations. A switch like this would indicate that, for example, on east aspects, adult bristlecone pines have a higher basal area than adult limber pine, but that for juveniles, bristlecone pines have a lower density than limber pines.

There is also a relationship between PIFL:PILO and substrate size. In adults, PIFL:PILO is positively associated with large rocks and gravel and negatively associated with bare soil and litter. In juveniles, PIFL:PILO is positively associated with bare ground, large rocks, and bedrock, while being negatively associated with gravel and litter. This would indicate that there is more limber pine relative to bristlecone pine on substrates composed of larger rock sizes.

3.3 | Adult basal area and upslope juvenile density

Below-treeline adult basal area follows expected patterns with respect to soil type. Limber pine basal area was higher on granitic soil, while bristlecone pine basal area was higher on carbonate soils like limestone and dolomite (Figure 7a). Treeline adult basal area generally followed the same pattern, but there were two key differences (Figure 7b). First, basal areas were lower at treeline as the trees become less dense at the edge of their tolerable range. Second, with the exception of granitic soils, limber pine basal area was considerably lower at treeline than that of bristlecone pine. This finding is consistent with general forest composition patterns in the Great Basin: When bristlecone pine is present in a stand, it is generally the dominant tree species at treeline, with some notable exceptions, especially on granitic soil.

Below-treeline juvenile density of both species followed a similar pattern to adult basal area (Figure 7a,c). Bristlecone pine adults dominated on calcareous dolomite and limestone but had low basal area on granite. Below-treeline juvenile bristlecone pine had the same relationship with higher juvenile density on limestone and dolomite soils than limber pine. Where adult limber pine dominates on granite, the juvenile density is also high, unlike bristlecone pine juveniles which are almost entirely absent on granite (Figure 7c). However, limber pine juvenile density was higher generally on all soil types than the adult basal area relationship with soil type would imply. These relationships break down entirely above treeline where limber pine juveniles dominated on every soil type (Figure 7d). This is especially true on dolomite, a soil that is core bristlecone pine habitat, and on which very few adult limber pines were found (Figure 7b,d). Above-treeline bristlecone pine juvenile densities maintained the expected soil relationships based on adult basal area and soil type, but on every soil type, bristlecone pine juvenile density was considerably lower than limber pine juvenile density above treeline.

4 | DISCUSSION

Results from this study suggest three key findings. The first is that treeline is advancing in Great Basin mountains where bristlecone pine and limber pine are present. So far, the juvenile establishment would predict a region-wide increase for both species with a vertical

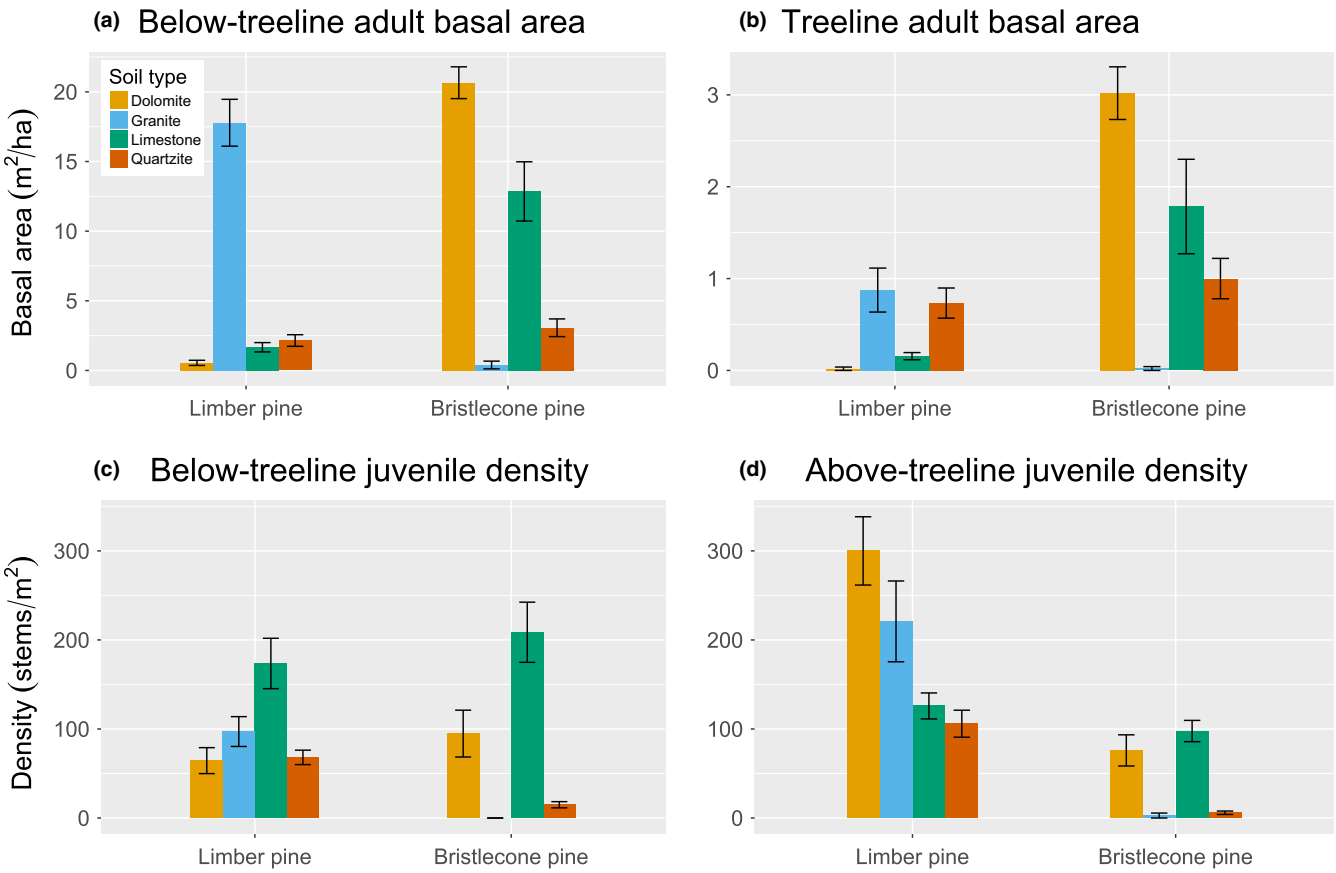

FIGURE 7 Comparisons of adult basal areas for limber pine and bristlecone pine in (a) the midstand below treeline forest and (b) at treeline and juvenile density (c) below treeline and (d) above treeline. Below-treeline and treeline basal areas are shown on different scales to allow visualization of the soil preference relationship. All error bars are 1 *SEM* [Colour figure can be viewed at wileyonlinelibrary.com]

mean of 19.1 m since approximately 1950 (Billings & Thompson, 1957). The major predictors for higher advancing establishment relative to treeline are forest stands on granitic and limestone soils on south and west aspects and in more easterly mountain ranges like the Snake Range. However, we found upslope establishment in all mountain ranges included in the study. The second finding is that while bristlecone pine adults and above-treeline juveniles share some environmental predictors for their abundances, limber pine adults and above-treeline juveniles do not. The third finding is that juvenile limber pine density dominates that of bristlecone pine above treeline, especially on soils like dolomite where adult bristlecone pine dominates in currently established stands below treeline. Limber pine appears to have "leap-frogged" over bristlecone pine to dominate the newly expanding treeline in forests of the Great Basin, as found in a study of smaller extent (Millar et al., 2015).

While these findings point to interesting potential changes in tree species composition above treeline, some caution is required in interpreting these results. We designated treeline as a line based on generally accepted criteria, but treeline is more accurately an ecotone between the subalpine forest and the alpine zone. Since it is an area of transition, determining this line can seem subjective. For the sake of consistency and clarity, experts have accepted a definition of treeline as being the line connecting clumps of trees at least 3 m in height (Körner, 1998, 2012; Paulsen, Weber, & Körner, 2000). We have adhered to this definition in measuring treeline advance distances while understanding that this measurement includes a certain amount of variance. Also, this study uses juveniles to project what treeline is likely to look like in the future since the juveniles (<100 years old) used for this projection are all under 3 m in height and do not meet the accepted definition of a "tree." Our findings rest on the premise that most established juvenile trees will survive to 3 m height to constitute a higher treeline. There is strong evidence in favor of this assumption, as previous studies have found very high (up to 99%) survival of bristlecone pine and limber pine once they become established after the first 5 years (Barber, 2013; Conlisk et al., 2017; Elliott, 2012). Since we excluded juveniles under 5 years of age, it is likely that the vast majority of the juveniles measured will survive to adulthood. A pulse stress event that produced differential mortality between the two species might mean that the juvenile demographics seen today will not match the adult demographics of the future treeline.

4.1 | Treeline advance

Studies predicting or showing treeline advance are common in the literature (Elliott, 2011; Grace et al., 2002; Lescop-Sinclair & Payette,

1995; Lloyd & Fastie, 2003; MacDonald, Kremenetski, & Beilman, 2008; Truong, Palmé, & Felber, 2007), as are studies showing a lack of treeline advance (Camarero & Gutiérrez, 2004; Dolanc, Thorne, & Safford, 2013; Gehrig-Fasel, Guisan, & Zimmermann, 2007; Harsch et al., 2009; Payette, 2007). Where treeline advance was not found, other treeline responses to warming are often seen such as subalpine infilling of trees (Dolanc et al., 2013; Millar et al., 2004), vertical release from the krummholz growth form (Cairns, 2005; Lescop-Sinclair & Payette, 1995; Millar et al., 2004), and growth changes (Salzer et al., 2009; Wilmking, Juday, Barber, & Zald, 2004). Studies quantifying treeline advance have shown variable results given the difficulty in determining exact elevations for historic and current treeline. An even bigger problem is teasing apart the effects of recent anthropogenic warming on treeline advance from other human disturbance effects such as logging or grazing (Gehrig-Fasel et al., 2007; Harsch et al., 2009).

Compared with other studies that have quantified treeline advance, our mean vertical treeline advance of 19 m is relatively small. In the European Alps, treeline was found to advance 115 m since 1900 in response to a 1.7°C temperature increase (Leonelli, Pelfini, Morra di Cella, & Garavaglia, 2011). Studies in the Ural Mountains have documented a 40–80 m treeline advance in response to increased winter temperatures (Hagedorn et al., 2014; Kammer et al., 2009). The Scandes Mountains have seen a 70–90 m increase in treeline elevation (Kullman & Öberg, 2009). There may be several reasons for this disparity. For example, the 1.7°C increase in the Alps is almost double the temperature increase documented in the western Great Basin (Millar et al., 2015). In the Scandes Mountains, it is unclear whether that treeline advance response is a function of recent temperature increases or recent land abandonment (Gehrig-Fasel et al., 2007). A recent study in the western Great Basin documented pine regeneration as much as 225 m from forest boundaries, which would equate to vertical distance of 35–220 m when factored with our measured range of slopes (Millar et al., 2015). However, this study included other forest boundaries in addition to treeline possibly skewing their results.

One possibility for our lower treeline advance relative to other ranges may be the extreme longevity of bristlecone pine and limber pine, with adult trees on the landscape establishing during a warmer climatic period, perhaps during the Medieval Warm Period (950–1250_{CE}) but at least before the first climatic minimum of the Little Ice Age (1650_{CE}). Given the documented 1°C Great Basin temperature increase in the last century, the dry adiabatic lapse rate would project a 100 m increase in treeline. Our mean of 19.1 m is considerably less than this predicted value which suggests one of two options: (i) there is still significant upslope area that is climatically available for regeneration pointing to at least decades long lags in climate change response (Kroiss & HilleRisLambers, 2014), or (ii) the climatic zone where trees were able to regenerate in the most recent regeneration period, the "regeneration line," was historically well below the adult treeline, and as temperatures have increased, has only recently moved upslope through adult treeline to its current above-treeline location. If the current regeneration line is at the upper extent of climatically available habitat, the adiabatic lapse rate would estimate the historical regeneration line at 100 m below our "new" treeline, or 80 m below current adult treeline. This theory fits well with observations of a lack of regeneration near treeline in the mid1900s and a current lack of recent treeline relict wood on the landscape, which tends to persist for 100s–1,000s of years (Billings & Thompson, 1957; LaMarche, 1973; Wright & Mooney, 1965). Other climatically extreme systems have seen similar lags (Payette, 2007).

There are other confounding factors concerning recent warming-induced treeline advance. For example, while temperature ultimately limits tree distributions, establishment filters such as water availability are more proximate limiters to range shifts (Conlisk et al., 2017; Daniels & Veblen, 2004; Lloyd & Graumlich, 1997; Moyes et al., 2015). We found soil type to be a strong predictor of higher treeline advance, especially on granitic soil. While granite is a relatively drier soil owing to its low water-holding capacity (Wright & Mooney, 1965), it is the only soil type in the study area dominated by limber pine at treeline. Other notable predictors include a positive association of treeline advance with topographic water accumulation and a negative association with large rocks and gravel. These responses indicate that treeline advance is likely facilitated by better water-holding soils and areas that accumulate more water. The large negative effects of latitude and east aspect are interesting in that they appear to indicate that treeline advance is greater in southern ranges on west-facing slopes. Taken together, treeline advance was highest in warmer areas where limber pine is the dominant treeline tree.

4.2 | Life stage predictors

Species distribution models using climate niche are very common, especially those which use models to project future species distributions under climate change (Hijmans & Graham, 2006). However, species distribution models are often based on matching adult distributions to climatic conditions, while not taking into account biotic interactions, dispersal effects, and life stage differences in climatic tolerances (Araújo & Luoto, 2007; Guisan & Thuiller, 2005; Heikkinen et al., 2006; Pearson & Dawson, 2003). Mechanistic models which use knowledge of a species' physiology, ecological roles, population trends, and/or life stage differences can perform better than climate envelope models that rely only on climatic parameters (Hijmans & Graham, 2006; Kueppers et al., 2017; Ralston, DeLuca, Feldman, & King, 2017). By comparing predictors for adults and young trees, we can learn about environmental filters for multiple life stages that will influence range shifts.

For bristlecone pine, predictors are similar for adults and above-treeline established juveniles. Both are positively associated with the Spring Mountains, the most southerly range. They are both negatively associated with granite and quartzite soils. Granite is a very porous soil and has a poor water-holding capacity. Quartzite is usually darkly colored and so is warmer than white dolomite or light gray limestone, both being carbonate soils (Wright & Mooney, 1965). This would have the effect of increasing drought stress,

especially on juvenile trees. Soil particle size also appears to have an effect on bristlecone pine establishment (but not on adult basal area). We found a small negative effect of increased bare soil (<1 cm particle size) and a small positive effect of gravel (1–20 cm particle size). Bristlecone pine seeds are small and generally gravity dispersed with the seeds landing on the soil surface. These seeds are almost entirely consumed by seed predators. Seeds not consumed but on the soil surface also fail to germinate, likely due to the lack of surface moisture (Barber, 2013). Soils with larger particle size, however, may allow some seeds to fall between the soil particles, providing both protection from predation and a better microclimate for germination. Subalpine trees are often found growing from under "nurse rocks" suggesting that seeds protected from predators and desiccation are more likely to establish.

Limber pine juveniles do not appear constrained by the same environmental factors affecting limber pine adults. While adults have relatively small responses to a number of predictors, they are largely predicted by granitic soil. Juveniles are not well predicted by soil type, and in fact though limber pine juveniles were prevalent in almost every plot, few environmental variables were associated with juvenile density. Even high adult limber pine basal area failed to predict juvenile density. Since we observed high overall limber pine regeneration (Figure 7), as have other studies in the Great Basin (Millar et al., 2015), this finding strongly suggests that limber pine juveniles have relatively wide environmental tolerances. Therefore, while there are strong environmental or dispersal filters operating on bristlecone pine juveniles, above-treeline limber pine juveniles appear to have less constrictive filters.

The relative ratios between limber pine and bristlecone pine (PIFL:PILO) and substrate size suggest a relative preference for limber pine in areas with larger rocks and exposed bedrock. This appears to be the case for both adults and juveniles. The difference in the limber pine to bristlecone pine ratio points either to a relative difference in limber pine's ability to establish on larger substrate sizes or to a difference in its ability to disperse to microsites with preferred substrates. Either way, the ratio indicates an important role for "nurse rocks" whereby larger rocks provide more mesic microsites than low-texture surfaces for establishing seedlings by moderating temperature, blocking wind, and/or maintaining soil moisture (Pyatt et al., 2016; Resler, Butler, & Malanson, 2005). Both species would likely benefit from establishing near nurse rocks, thus a higher relative abundance of limber pine in larger substrates suggests that limber pine is better able to disperse to these preferred nurse rock microsites. While there is much less topographic texture in the Great Basin relative to the Rocky Mountains where many abiotic facilitation studies have taken place, it would appear that this nurse effect is still an important driver of species distributions. Interestingly, with limber pine and bristlecone pine in the Great Basin, there is no evidence of biotic facilitation wherein an individual above-treeline tree creates a more mesic microsite under which a tree island can form, as seen in whitebark pine treelines (Resler, Shao, Tomback, & Malanson, 2014; Tomback, Chipman, Resler, Smith-McKenna, & Smith, 2014).

4.3 | Adult basal area and upslope juvenile density

Above-treeline limber pine juveniles established in higher densities than bristlecone pine throughout the Great Basin, especially on dolomite, a soil type that is known to be strongly associated with bristlecone pine (Charlet, 1996; Wright & Mooney, 1965). The assumption has been that bristlecone pine is dominant on dolomite because other species do not tolerate the high-pH, high-magnesium, and low-phosphorus soil (Butler et al., 2007; Maher, Barber, & Affleck, 2015; Wright & Mooney, 1965). In these stands, adult cone-producing limber pines are rare. However, it is on these soil types that limber pine regeneration is highest (Figure 7d). One reason for high regeneration likely has to do with water limitation. While deep soil water is typically not in short supply for adult trees in Great Basin treelines (Salzer et al., 2009), studies examining tree recruitment at and above treeline show that water is often limiting at the surface where young trees access it (Conlisk et al., 2017; Kueppers et al., 2017; Moyes, Castanha, Germino, & Kueppers, 2013). Relative to quartzite and granite, carbonate soils (like dolomite and limestone) are lighter in color which reduces the surface temperature, and thus evaporative demand, while also having a finer grain and better water-holding capacity (Wright & Mooney, 1965). It is likely the improved water retention in dolomite and limestone make it more tolerable to juvenile trees. And despite the low numbers of adult limber pine on dolomite and limestone (Figure 7a,b), these soil types appear to be an amenable substrate for juveniles.

This contrast of many juvenile limber pines but few adults on dolomite soils raises an obvious question: How are all of these limber pine seeds getting there? Small-seeded bristlecone pine seeds are primarily dispersed by wind with the majority of regeneration occurring near adult trees (Benkman, 1995; Coop & Schoettle, 2009; but see Lanner, Hutchins, & Lanner, 1984). The vast majority of these seeds are consumed by rodent seed predators (Barber, 2013; Maher et al., 2015). Limber pine seeds are large and nutritious and so are targeted by Clark's nutcracker (*Nucifraga columbiana*), a high-elevation corvid that tears apart limber pine cones, removes the seeds, and then travels up to 22 km away to cache the seeds for future consumption (Lanner, 1996; Siepielski & Benkman, 2008; Tomback, Schoettle, Chevalier, & Jones, 2005; Vander Wall, 1988). Since seeds are buried at an optimal depth for germination, are hidden from other seed predators, and at least some of the cached seeds are not consumed, limber pine seeds are "planted" throughout the landscape. This is also likely to provide an advantage for seeds which area cached (limber pine) near nurse objects over wind-dispersed seeds (bristlecone pine; Malanson et al., 2007; Tomback & Resler, 2007).

Even among those seeds that are not consumed, successful establishment is rare, often occurring in pulses coinciding with multiple years of higher summer and autumn precipitation and lower summer temperatures (Barber, 2013; Millar et al., 2015). Since no colonization above treeline was apparent in the mid-20th century, it is likely that the climatic conditions have changed enough in the last

50 years for what was climatically inhospitable habitat at and above treeline to recently become a large area of suitable seedling habitat. Ongoing research is examining the local and broad-scale genetic population structure between the two species to assess how differences in dispersal strategies might be resulting in genetic differentiation among populations. If limber pine does have a dispersal advantage, it may be more able than bristlecone pine to take advantage of a rapidly warming climate.

There is an interesting paradox concerning the elevational and latitudinal distributions of adult limber and bristlecone pines. While in bristlecone pine's range it is found at higher elevations than limber pine (Charlet, 1996; Millar et al., 2015), limber pine's range extends far to the north relative to bristlecone pine (Figure 1). If cold tolerance were the only driver for these distributions, we would expect bristlecone pine to be found both higher up and further north. There are a number of possible explanations for this, although most are outside the scope of this paper. While limber pine's range extends far to the north relative to bristlecone pine, it also extends relatively further to the south, hinting that limber pine generally has either more genetic variation or phenotypic plasticity allowing it to live in a greater diversity of climatic conditions. Limber pine is known to grow well across an unusually wide range of elevations and conditions and while the high gene flow of this bird-dispersed species results in little genetic differentiation among populations, phenotypic plasticity with regard to stomatal density across elevational gradients has been noted which may account for this greater distribution of limber pine (Schoettle & Rochelle, 2000). A final speculative reason for this difference in elevational and latitudinal ranges may be that while temperature certainly limits both species' ranges, water limitation is an especially acute limiting factor in the Great Basin relative to much of limber pine's range (Kueppers et al., 2017; Moyes et al., 2013). While our ongoing research will seek to examine the relative effects of water stress on limber and bristlecone pine, we currently lack an understanding of the relative importance of water limitation on these species at treeline.

4.4 | Significance

This study highlights the importance of recognizing differences in life stage tolerances to climatic conditions. At treeline, adults are exposed to the extreme cold and wind of winter, while juveniles are protected under insulating snow. During the summer, adult trees can tap readily available water deep in the soil that is unavailable to seedlings facing summer drought. Matching adults to climatic conditions, such as in a species distribution model, is likely to be insufficient to predict species distributions since filters may differ significantly among life stages. This study also highlights that there are interspecific differences in the relationship between adult and juvenile responses to climatic parameters. Here, bristlecone pine adults and juveniles share some predictors while limber pine adults and juveniles do not, even though climatic conditions that support increased limber pine growth in adults have been shown to be the same that support limber pine recruitment (Millar et al., 2015).

Treeline is advancing throughout the Great Basin, primarily through downslope limber pine "leap-frogging" over treeline bristlecone pine. This is happening even on soils types like dolomite that have historically been dominated by bristlecone pine adults. These forests are low-density stands, likely due to water limitation, shade intolerance, and limited suitable establishment microsites. If a species is able to establish first, it might be able to preempt other tree species, at least in the short term, which in these forests can extend to thousands of years. Priority effects can only occur when the initial colonizer is able to exclude subsequent species from establishing. Whether this is occurring with limber and bristlecone pine remains to be seen, but in these harsh conditions where both light and water limitations are acute and establishment microsites are rare, initial establishment may cause a priority effect even in the event of low-density establishment. While subalpine trees have been documented expanding their range downslope in some unusual slope conditions such as downslope cold air pooling (Millar et al., 2015), on most slopes, treeline advance upslope is also possibly happening in conjunction with contraction at the lower range margins (Kueppers et al., 2017). If bristlecone pine is contracting at its lower range margin and unable to advance upslope because it is blocked by limber pine, bristlecone pine would face overall range contraction and possibly local extirpations. With individual bristlecone pines being the oldest known nonclonal individuals on earth, a loss of some of these populations would be a loss of great cultural significance.

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