Plant Soil
https://doi.org/10.1007/s11104-020-04732-9

REGULAR ARTICLE

Mechanisms of species range shift: germination and early survival of Great Basin bristlecone pine and limber pine

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Received: 16 January 2020 / Accepted: 1 October 2020

Abstract

Aims To examine the potential mechanistic predictors of germination and first-year survival in two species of Great Basin sub-alpine trees along an elevation gradient on three soil types.

Methods Using a network of experimental gardens, we sowed limber pine and Great Basin bristlecone pine along elevational gradients at three sites on three different soil types. We collected germination and first-year survival data of each species while measuring temperature, soil water content, and other environmental variables to examine the potential predictors of first-year survival in these two species.

Results Thanks to consecutive anomalously wet and dry years, we found germination and first-year survival to be largely limited by soil type, soil water content, and precipitation timing. Limber pine germination and survival showed weak negative responses while bristlecone pine germination and survival showed stronger negative responses to temperature.

Conclusions Young trees are more sensitive to water limitation than to temperature and soil type has a strong moderating effect on water availability. Precipitation timing affected this availability with winter snowpack being less important in establishment than summer monsoonal rain. These results point to the importance of substrate and understanding limitations on all life stages when attempting to predict species range shifts.

Keywords *Pinus longaeva* · *Pinus flexilis* · Recruitment · Sub-alpine forest · Treeline · Great Basin

Abbreviations

GS	Growing season
GDD	Growing degree days
SWC	Soil water content
VWC	Volumetric water content
T_{max}	Daily maximum temperature
T_{min}	Daily minimum temperature

Introduction

In response to climatic warming, species are expected to expand their ranges to higher latitudes and elevations, and contract at lower latitude and elevational range margins (Parmesan and Yohe 2003; Lenoir et al. 2008; Pauli et al. 2012; Moritz and Agudo 2013). However,

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Responsible Editor: Rafael S. Oliveira.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11104-020-04732-9) contains supplementary material, which is available to authorized users.

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biotic interactions like competition, facilitation, and priority effects are likely to affect how range shifts occur (Baumeister and Callaway 2006; Kroiss and HilleRisLambers 2014). In sub-alpine forests, downslope competitors may displace sub-alpine species through direct competition or through indirect mechanisms such as increased exposure to disease or changing disturbance regimes associated with downslope species (Flannigan et al. 2000; Tomback and Resler 2007). In general, high-elevation plant communities may be especially sensitive to climate change since extreme abiotic conditions there generate narrow climatic niches (Harte and Shaw 1995; Debinski et al. 2000).

Climate envelope models often match mature tree presence with climatic conditions. However, young individuals encounter different micro-climates and often have narrower environmental tolerances than mature trees (Jackson et al. 2009; Zhu et al. 2012; Dobrowski et al. 2015; Máliš et al. 2016). Understanding the mechanisms of establishment is essential for projecting how tree species' ranges will respond to increasing temperatures (Millar et al. 2004; Conlisk et al. 2017a). The upslope leading range edge of sub-alpine forests (the treeline ecotone) is a sensitive biological indicator of climatic warming due to the strong association between growing-season temperature and treeline (Holtmeier 2003; Körner and Paulsen 2004). Future treeline is generally expected to shift higher in elevation by as much as 700 m by the year 2100 (Moen et al. 2004; Kullman and Öberg 2009). However, in many mountain areas throughout the world, treeline has not been observed to advance upslope (Harsch et al. 2009). In addition to temperature, other conditions such as water limitation, exposure, or snow pack may limit upslope establishment (Germino and Smith 1999; Frost and Epstein 2014; Rehm and Feeley 2015; Kueppers et al. 2016; Conlisk et al. 2017a; Brodersen et al. 2019).

In many sub-alpine systems, young trees germinate and survive above treeline while small enough to be coupled with warmer summer surface temperatures and insulated by snow from winter temperatures, wind abrasion, and desiccation, even if they could not survive there as adults more coupled with atmospheric conditions. Treeline seedlings passively warmed at night have increased seedling photosynthetic rates and seedlings in microsites protected from frost are more likely to survive (Germino and Smith 1999; Maher et al. 2005; Maher and Germino 2006). In addition to surface and air temperatures, seedlings are sensitive to soil moisture limitation (Moyes et al. 2013, 2015; Kueppers et al. 2016; Brodersen et al. 2019). Of particular interest are conditions in which the response to environmental change differs among co-occurring species and what that might mean for future treeline species composition in a warming and drying future. Site characteristics such as soil type and nurse features (rocks, shrubs, other trees, etc.) are also likely to have effects on the ability of trees to establish above current treeline with soil properties such as water holding capacity and albedo directly affecting soil water content and temperature.

In many sub-alpine systems, conifers have very high survival once established, and the earliest life stages are particularly important in predicting future forests (Paulsen et al. 2000; Leck et al. 2008; Barber 2013). The germination and seedling stages are especially sensitive to climate and these early life stages are likely important bottlenecks to treeline shifts (Germino and Smith 1999; Malanson et al. 2007; Conlisk et al. 2017b; Lazarus et al. 2018; Brodersen et al. 2019).

The Great Basin of the western US includes nearly 200 distinct mountain ranges, many of which have ridgelines extending above treeline. Daily 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 continue to rise an additional 2–4 °C by the late twenty-first century (Scalzitti et al. 2016). Great Basin treeline 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 northeastern Great Basin. For the two most common Great Basin subalpine conifers, Great Basin bristlecone pine, and limber pine, germination and first-year survival are likely the most significant bottlenecks to survival into maturity, but the relative importance of the factors that limit establishment, and how they differ between these co-occurring species, is largely unknown and likely dependent on other factors such as elevational position relative to treeline (Kueppers et al. 2016). Understanding the limitations on these earliest life stages is important in predicting future forest composition and how the subalpine forest extends its range upslope of treeline. This study examines the micro-site conditions that are associated with Great Basin treeline conifer germination and first-year survival. Using a network of experimental gardens, we examine the environmental conditions that are associated with germination and first-year survival of bristlecone pine and limber pine. Specifically, we ask: 1) what are the key factors that drive germination and survival for limber pine and bristlecone pine and 2) how are temperature and soil water content associated with elevation? We predict that high temperatures at the soil-atmosphere interface and low soil water content are the most limiting factors of germination and survival for limber pine and bristlecone pine. We also predict that soil temperature and water content will be negatively and positively associated with elevation, respectively, leading to higher germination and survival at higher elevations. We also predict that the differing physical properties of differing soil types will affect temperature and soil water, and hence affect germination and survival.

Materials and methods

Study area

The White Mountains are a 97 km-long mountain range in the western Great Basin (Fig. 1). Bristlecone pine is usually the dominant species at treeline, but typically downslope limber pine comprises the majority of treeline advance in these forests, with young trees "leap-frogging" over treeline bristlecone pine (Millar et al. 2015; Smithers et al. 2017). In the White Mountains, soil type has played an important role in tree species distributions. Bristlecone pine is mostly restricted to high-elevation carbonate soils, especially dolomite, where limber pine is usually rare (Schulman 1954; Wright and Mooney 1965). Dolomitic soils are weathered carbonaceous rock, medium- to fine-grained and light grey to white in color. On quartzite soils, which are weathered metamorphic sandstone rock and are relatively finely grained and dark grey in color, a mix of tree species generally coexists. On granitic soils, which are weathered from intrusive plutonic igneous bedrock, are light in color, and course-grained, limber pine is typically the dominant species. All three soil types weather to shallow, rocky, sandy loams with a high proportion of surface cover by coarse rock. However, these soil types have very strikingly different soil properties including large differences in pH, calcium, magnesium, and water holding capacity (Wright and Mooney 1965).

Data collection We installed transects of experimental plots in the White Mountains from lower to upper treeline at three sites: Bighorn Peak, Campito Mountain, and Trail Canyon (Table 1). We chose transect locations based on differing soil type and having an upper and lower treeline. In the White Mountains, Great Basin bristlecone/limber pine forests are largely relegated to northern aspects with the southern aspects too warm and dry to support forests. All transects were placed on a northwestern aspect as that was the only aspect on which we found suitable stands on all three soil types. Since we had one transect per soil type, the effects of soil type cannot be separated from those of site, but we expect that soil type contributes strongly to site effects. On each transect, plots were placed at 10 m (vertical) intervals, from 10 m below lower treeline to 20 m above upper treeline (Fig. 2). Plots were placed roughly along a direct upslope transect but were moved slightly off the fall line to avoid placing a plot directly under a tree's canopy or to place the plot closer to a tree or snag for instrumentation placement. Each plot was covered in an anchored exclosure cage of 0.6 cm mesh hardware to exclude seed predators. We excavated the soil to remove all vegetation and natural seeds and buried cages measuring 15 cm wide × 50 cm long × 15 cm high to 10 cm depth (Barber 2013; Maher et al. 2015). We collected seeds from 5 cones of 20 trees per species in each of the three study sites in the year before sowing. Seeds were tested for viability and stored at 4 °C, were mixed to randomize provenance, and then were sown. This same seed stock had a germination success rate of 86% under greenhouse conditions in standard potting soil (Smithers, unpublished data).

Seed cohorts were sown in October 2014, 2015, and 2016 in separate exclosures to allow for winter cold stratification and were monitored for the following growing season (2015, 2016, and 2017 growing seasons, respectively). We will refer to the cohort by the growing season year (for example, the 2015 cohort refers to the cohort sown in 2014 and monitored in the 2015 growing season). For the 2015 cohort, we sowed 30 viable seeds of bristlecone pine and of limber pine in each plot. Many seeds of both species, but especially bristlecone pine, fall to the soil surface when cones open. However, many older trees are found growing from under a rock or other facilitative structure. If seeds

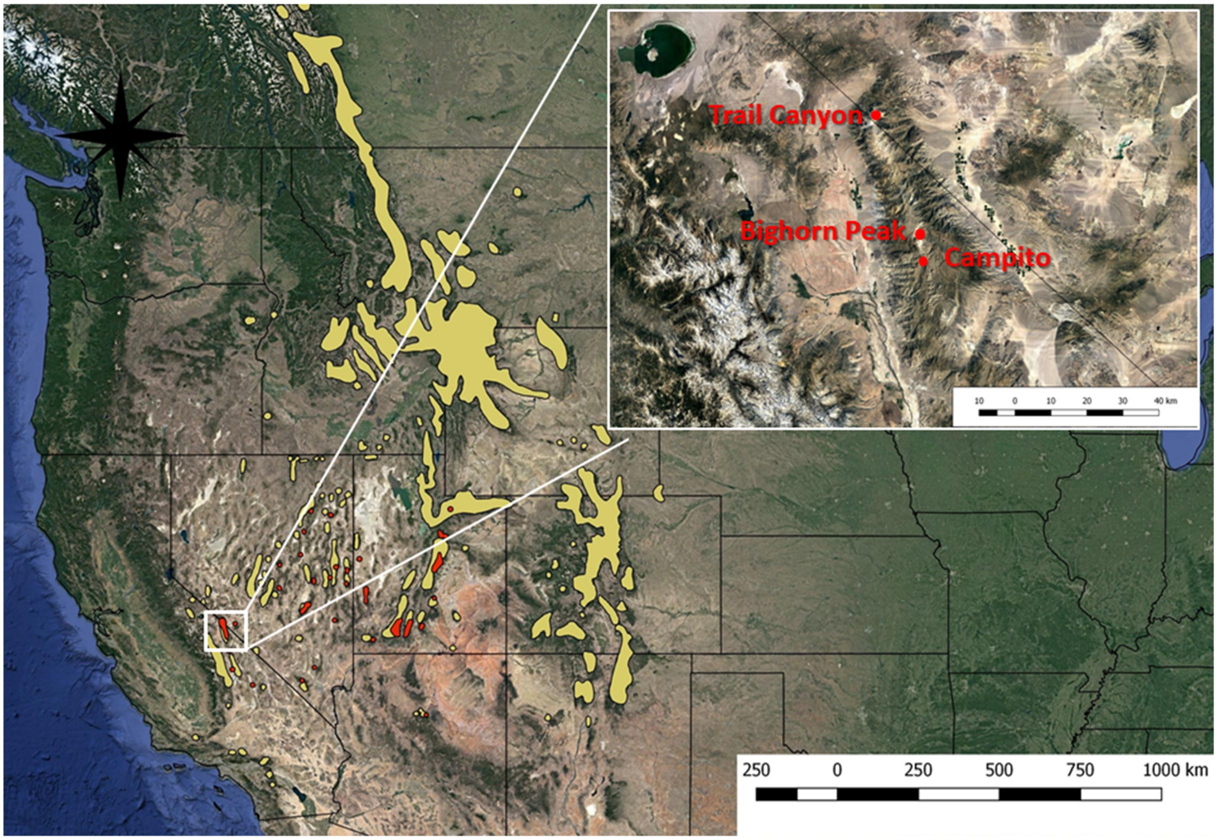

Fig. 1 Limber pine (yellow) and Great Basin bristlecone pine (red) range. The insert shows the White Mountains with each of the three transects. Species distribution polygons are from the USGS vegetation-climate modeling study (https://esp.cr.usgs.gov/data/little/)

are harvested from cones and cached by Clark's nutcrackers (*Nucifraga columbiana*), they are typically buried in caches about 5 cm below the soil surface. Therefore, we sowed ten seeds per species in each of three treatments: on the soil surface, under a fist-sized rock, and 5 cm below the soil surface ($n = 60$ seeds per plot for a total per site: Trail Canyon = 1080, Bighorn Peak = 780, and Campito = 720). Seeds of each species and treatment were sown in a line with at least 5 cm between each seed. Due to very low 2015 germination rates of surface and rock treatments, in 2016 and 2017 the surface and rock treatments were abandoned, and 10 seeds were buried per species ($n = 20$ per plot). These seeds were sown in consistent locations within the exclosure so that any emerging seedlings outside those areas could be removed and not counted in the event that they were natural germinants. However, due to very low natural germination rates, this never occurred. We monitored plots weekly in 2015, bi-weekly in 2016, and monthly in 2017, at which time emergent and live seedlings were counted. A seedling was considered to be alive (and therefore, to have survived to that date) if any of the cotyledon or true needles remained green. At the time of monitoring, we measured soil water content (FieldScout TDR 100, Spectrum Technologies, Inc.) with 12 cm probes. We averaged three readings per plot for soil water content (% soil water volume) taken immediately adjacent to the plot cage.

Precipitation records were aggregated from the White Mountains Research Center Barcroft weather station (WMRC 2017), located 3.6 km from Bighorn Peak, 9.3 km from Campito Mountain, and 31.6 km from Trail Canyon. In 2016, precipitation data was not available and so was interpolated using 4 km PRISM data (PRISM Climate Group 2004), corrected by the measured 2015 and 2017 weather data using a linear model. We collected plot-level air and soil surface temperatures using ibutton thermochrons (Maxim Integrated DS1921G-F5) which were equalized for any temperature sensing variation. At each plot, we placed

Table 1 Sites and site characteristics for the study

Site	No. plots	Elevation (m)	Soil Type	Dominant species
Bighorn Peak	13	3439–3563	Dolomite	Bristlecone pine
Campito Mountain	12	3319–3418	Quartzite	Bristlecone pine
Trail Canyon	18	3006–3217	Granite	Limber pine

thermochrons on the north side of the exclosure cage at soil level to directly measure the temperature at the soil-air interface as opposed to placing them underground, which is a more common practice as a proxy to approximate air temperature (Körner and Paulsen 2004). This placement allows for a more integrated measure of the total temperature experienced by a seedling. We also placed thermochrons under the north side canopy of the nearest tree (to effectively shade the thermochron) at roughly 2 m above ground level. Each thermochron was wrapped with screen mesh and placed inside a ¾" white PVC T-fitting to shield solar exposure (Ackerly et al., 2010). We set the thermochrons to record at 4-h intervals daily, replacing the loggers each October and June from 2014 to 2017. Missing data from loggers was interpolated using linear regression models ($R^2 > 0.9$ for all interpolations) from the nearest two loggers and corrected based on prior data with linear models.

Data aggregation From the raw temperature data, we derived potential predictors for germination and seedling survival including growing season, daily, and

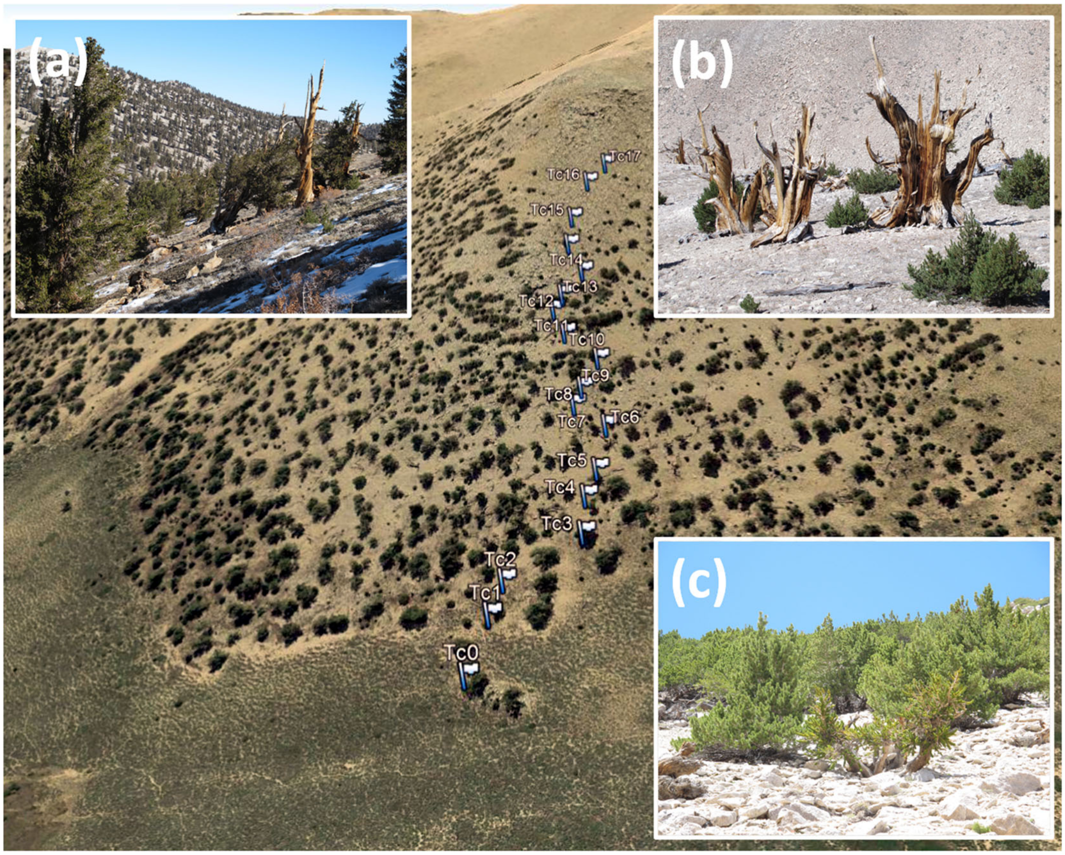

Fig. 2 The layout of the experimental garden transects from below lower (Tc0) to above upper (Tc17) treeline for the Trail Canyon site. Inset photos are of the three sites: Campito Mountain, quartzite soil (a), Bighorn Peak, dolomite soil (b), and Trail Canyon, granite soil (c). Background figure created in Google Earth

extreme maximum and minimum temperatures (Table 2). Extreme maximum and minimum temperatures are the highest and lowest temperatures, respectively, from each month. We defined the growing season conservatively as occurring from May through September. Since snow acts as insulation over the soil, it minimizes the variation between the daily maximum (T_{max}) and the daily minimum (T_{min}) soil surface temperatures. We calculated snow days as the sum of days with a $T_{max} – T_{min}$ of ≤1 °C from January – June (Total snow days) and for May only (May snow days). We calculated daily maximum, minimum, and overall growing degree days (GDD). We calculated GDD as the sum of days with a mean temperature above 5 °C (Moyes et al. 2013). Daily mean temperatures were determined by taking the mean of the daily T_{min} and T_{max}. At each plot we measured canopy cover over the plot with a spherical densiometer, slope, and aspect.

Data analysis We used binomial logistic generalized linear models with limber pine and bristlecone pine germination and survival as the response variable to a variety of measured and derived predictors. We used a Pearson correlation matrix to identify predictor variables that covaried and then used univariate binomial logistic models to “weed” out the predictor that explained less of the variation between the two covarying predictors. We then used the accepted predictors to construct multivariate models to predict our response variables: limber pine germination, limber pine survival, bristlecone pine germination, and bristlecone survival. We defined positive germination as the number of seedlings that had emerged since the beginning of the growing season. Since germination at the beginning of the growing season occurred in one pulse, we used the maximum number of seedlings per plot as the number of germinated seedlings. While a minor pulse of germination can occur in early fall, these were not included in our germination modeling since we were unable to separate fall germination from late-season mortality. We defined survival as the number of individual seedlings that survived until the last plot measurement before September 15th, which was chosen as the date before which fall germination was unlikely and after which mortality is minimal.

We modeled specific germination and survival with multiple centered and scaled predictors (Table 2). Since each site was located on a unique soil type, soil type is included as a site characteristic. We fit binomial models using all combinations of these predictors and their first-order interactions which we ranked using the Akaike Information Criterion (AIC). For predictor coefficient

Table 2 Potential predictors for seedling germination and survival of Great Basin bristlecone pine and limber pine. Abbreviations below are: meters above sea level (MASL), May – September growing season (GS), and volumetric water content (VWC). “Monthly” predictors are for June in germination models and for July in survival models

Potential GLM predictors
Year
Species
Elevation (MASL)
Soil type
Slope (%)
Canopy cover (%)
Total snow (# days under snow)
May snow (# days under snow)
GS mean daily max soil temp (°C)
GS mean daily max air temp (°C)
GS mean daily min soil temp (°C)
GS mean daily min air temp (°C)
Mean daily mean soil temp (°C)
Mean daily mean air temp (°C)
Extreme high soil temp (°C)
Extreme high air temp (°C)
Growing degree days soil (°C)
Growing degree days air (°C)
Mean soil water content (% VWC)
Extreme low soil water content (% VWC)
Total annual precipitation (mm)
Winter precipitation (mm)
GS precipitation (mm)
Month mean soil temp (°C)
Month mean air temp (°C)
Month mean max soil temp (°C)
Month mean max air temp (°C)
Month mean min soil temp (°C)
Month mean min air temp (°C)
Month extreme high soil temp (°C)
Month extreme high air temp (°C)
Month extreme low soil temp (°C)
Month extreme low air temp (°C)
Month soil water content (% VWC)
Month extreme low soil water content (%VWC)
Month growing degree days soil (°C)
Month growing degree days air (°C)

estimation, we calculated the mean of the predictor coefficients from all models that had a δAIC <4. When predictors were highly correlated ($r \geq 0.7$), we used only the predictor that had the lowest AIC value in a univariate model. If a predictor was not included in any model combination with a δAIC <4, it was excluded from the overall model. We determined importance values for each predictor by calculating the proportion of models with a δAIC <4 that included that predictor with a "Deviance explained" (DE) value as a pseudo-R^2 value showing how much better the model fits the data than the null (intercept only) model (McFadden and McFadden, 1974). We calculated DE as 1- (Residual deviance/Null deviance). All models were fitted as GLMs with a binomial distribution in the R Environment (R Core Team 2018). The MuMIn package was used for parameter estimations, model analysis, and importance value calculations (Barton 2018).

Results

Regional weather conditions for 2015–2017 showed considerable interannual variation in temperature and precipitation. The 2014–2015 winter was historically dry and warm, but a strong monsoonal pattern led to high 2015 summer precipitation and lower mid-summer temperatures. The 2015–2016 water year (Oct. 1 – Sept 30) had average temperature and precipitation but a moderately dry summer. The 2016–2017 water year was historically wet but included a historically very warm and dry summer (Table 3).

Temperature effects Growing season maximum air and soil surface temperatures increased rapidly from early May through June with the warmest temperatures in July (Fig. 3). In 2015, a July wet period resulted in mid-summer cooling. Despite differences in site elevation, temperatures were generally similar among the sites. Growing degree days (GDD), maximum temperatures, mean temperatures, and days under snow all showed non-linear and site-specific relationships with plot elevation (Online Resource 1, 2). Plots generally had more days under snow at mid-elevation relative to the highest elevations, likely due to low canopy closure allowing wind to blow snow from the highest elevations allowing increased surface insolation and subsequent snow melting.

Soil water content Overall, there was a significant correlation between soil water content and elevation across all sites with higher plots having higher growing season soil water content ($p < 0.001$, $R^2 = 0.5$). However, within each site, soil water content showed non-linear relationships with elevation (Online Resource 3). Lower and higher plots generally had higher soil water content, while there was considerable variation among sites. By late June, Bighorn Peak had higher overall water content than plots at either Campito or Trail Canyon, which had the lowest soil water content (Fig. 4a). This pattern held in the dry 2016 growing season and in the remarkably dry 2017 growing season (Fig. 4b). For the overall 2015–2017 period, Bighorn Peak had the highest water content (6.5 ± 0.3%), followed by Campito (6.1 ± 0.3%) and Trail Canyon (2.8 ± 0.1%).

Germination and survival In 2015, 35% of all seeds from all sowing treatments germinated and emerged. Of those seeds that germinated in 2015, 45% survived until September (Table 3). Bristlecone pine had higher germination (42%) than limber pine (28%) in 2015 while limber pine seedlings had higher survival (65% vs. 32%). In 2016 and 2017, limber pine had both higher germination and survival. In 2017, bristlecone pine had very low germination (0.5%) and none of those seedlings survived through August. Overall, high germination was followed by high seedling survival in 2015. In 2016, moderate germination preceded low seedling survival. In 2017, low germination preceded moderate seedling survival (Table 3).

Since there was relatively high seedling survival from the 2015 cohort, we continued to monitor those plots during the 2016 and 2017 seasons. From the seeds sown in 2014, both species had a pulse of germination in early July of 2015 followed by high mortality in July and August (Fig. 5). Bristlecone pine germination appeared to peak slightly earlier than for limber pine. In late September, there was another pulse of germination followed by mortality. Few seedlings died over the winters. In July of 2016 there was another pulse of germination from the original 2014 planting, followed by mortality and then another fall germination pulse. Although there was no detectable germination pulse in early summer 2017, a few seedlings emerged in the fall of 2017. At least some seeds were still germinating three years after sowing. Both bristlecone pine and limber pine had their highest proportion of living seedlings at Bighorn Peak (dolomite soil) and their lowest at

Table 3 Precipitation and air temperatures for the years 2015–2017 with bristlecone pine and limber pine germination and survival. Precipitation data are from the White Mountains Research Station Barcroft weather data. Winter (January – May) and growing season (June – September) temperatures are the mean daily maximum soil temperatures (± SE) of all plots across all elevations in the study. *2016 growing season precipitation records were unavailable and so were extracted from 4 km PRISM data, corrected by the measured 2015 and 2017 weather data using a linear model

	Winter		**Growing season**		**Bristlecone pine**		**Limber pine**		**Total**	
	Precip (mm)	Temp (°C)	Precip (mm)	Temp (°C)	Germ (%)	Survival (%)	Germ (%)	Survival (%)	Germ (%)	Survival (%)
2015	88	4.1 ± 0.1	113	22 ± 0.08	42	32	28	65	35	45
2016	121	2.6 ± 0.1	30*	24 ± 0.08	17	1	34	27	25	18
2017	312	1.1 ± 0.1	44	27 ± 0.09	0.5	0	25	38	3	35

Campito Mountain (quartzite soil). Due to very low first-year survival in the 2016 and 2017 cohorts, we did not monitor them beyond the first year.

Elevation among sites lacked linear relationships with germination and survival for both species within or among sites (2015: Figs. 6, 2016: Online Resource 4, 2017: Online Resource 5). Inter-annual differences in germination and survival were apparent with 2015 having relatively high germination and survival compared with 2017, which had low germination and very limited survival at only the highest elevations. Seedling germination and survival were most strongly predicted by soil type, soil water content, and soil surface temperature (Fig. 7). Higher soil water contents predicted higher germination and survival in both species (Online Resource 6), however bristlecone pine germination and survival were more strongly negatively correlated with low soil water content (Fig. 7). Granitic (Trail Canyon) and quartzite (Campito) soils had a negative effect on limber pine germination and survival and bristlecone pine survival, relative to dolomitic soil (Bighorn Peak). Bristlecone pine germination had a strongly positive response to granitic soil. At least some of the difference in germination and survival success among sites is likely a function of differences in soil water holding capacity. For both species, germination was much lower in response to extreme low soil water content in June while survival showed stronger positive responses to mean values of soil water content over the month of July.

Soil effects on germination and survival Lower soil surface temperatures were mostly positively associated with germination and survival for both species, with bristlecone pine having a stronger positive response. Mean June soil surface temperature was weakly

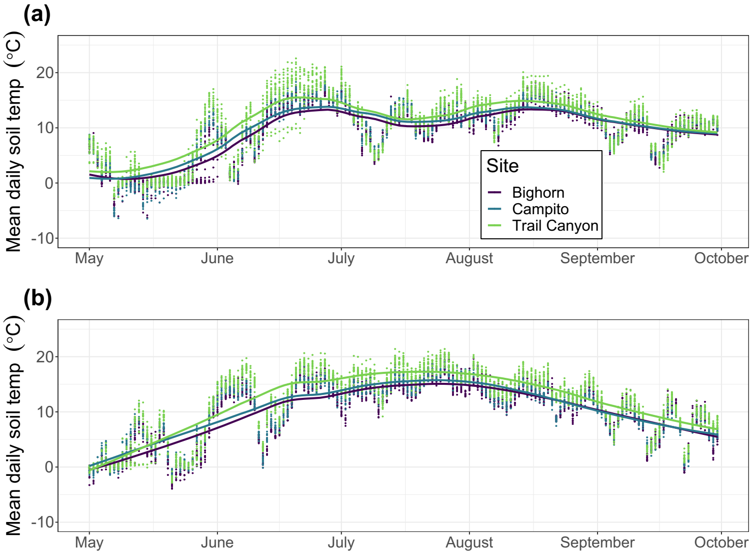

Fig. 3 Daily maximum soil surface temperatures for 2015 (a) and 2016 (b). Each point is one plot reading, color-coded by site. Lines are non-linear LOESS regression (span = 0.5) with standard error bars removed for clarity. Sites shown are Bighorn Peak (dolomite), Campito Mountain (quartzite) and Trail Canyon (granite)

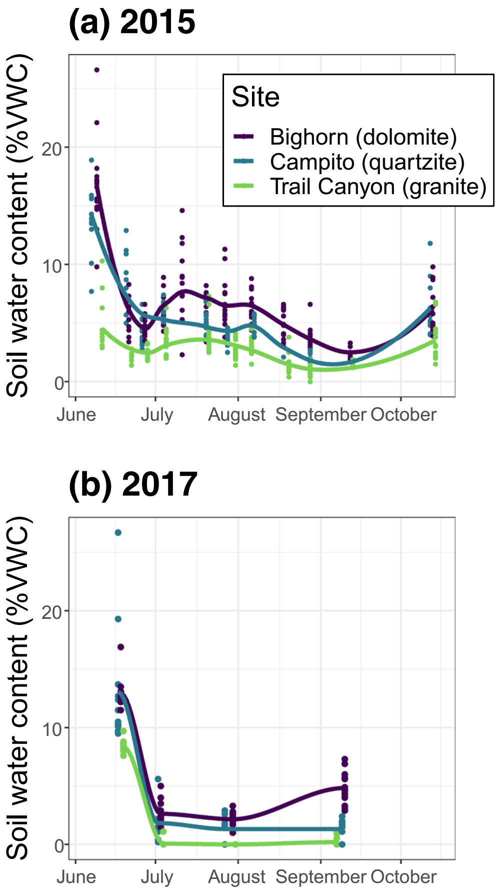

Fig. 4 Soil water content across the growing season in 2015 (a) and 2017 (b) for each site. Each point represents a plot and is color-coded by site: Bighorn Peak (dolomite), Campito Mountain (quartzite), and Trail Canyon (granite). (LOESS lines span = 0.5)

negatively associated with germination while July mean soil surface temperature was more strongly negatively associated with survival in both species (Fig. 6). GDD was not found to be an important predictor for germination but was an important predictor of bristlecone pine survival. Days under snow cover had positive effects on germination (May snow) and negative effects on survival (Total snow) in both species. Canopy cover (Fig. 7, Online Resource 7) had small positive effects on seedling germination but was slightly negatively associated with survival. The linear models were better at predicting bristlecone pine germination (DE = 0.44) and survival (DE = 0.69) than limber pine germination (DE = 0.40) and survival (DE = 0.30). We found no relationship between elevation and either germination or survival for either species and likewise no relationship between elevation and either temperature or soil water content. For germination and survival of both species, all models with first-order interactions were sufficiently penalized by AIC to exclude them from the final models and model-averaged coefficients and so were not included in the final analysis.

Discussion

Results from this study point to three key findings. First, successful recruitment of both species is strongly associated with soil water content and, to a lesser degree, soil surface temperature while neither variable was correlated with elevation as hypothesized. Bristlecone pine germination and establishment were more positively associated with soil water content compared with limber pine. Higher soil surface temperatures had negative effects on both germination and survival of both species. While bristlecone pine germination and survival showed a negative response to increased soil surface temperature, survival showed a strongly positive response to GDD, a metric strongly controlled by temperature. The second key finding is that there were strong effects of site on germination and survival related to differences in temperature and water holding capacity among the soil types. Both limber pine and bristlecone pine germination and limber pine survival were highest at the dolomite site (Bighorn Peak). Bristlecone pine survival showed a surprisingly positive response on granitic soil (Trail Canyon) despite there being very few adult bristlecone pines in this stand. The third key finding is that inter-annual soil surface temperature and precipitation variability had strong effects on germination and survival. The winter prior to the 2015 growing season was among the driest on record, yet 2015 had the highest rates of germination and survival. The winter prior to the 2017 growing season was among the wettest on record and had the lowest germination rates. Limber pine germination and survival were strongly predicted by growing season precipitation. Winter precipitation appears to play a limited role in growing season soil moisture and thus on recruitment in this system.

While these findings point to interesting predictors of seedling success, caution is required in interpreting the results. Although these experimental gardens were planted in situ, the conditions of the experiment were not totally natural. Each sample site was chosen based on elevation (every vertical 10 m) and placed where there was enough soil to anchor an exclosure cage.

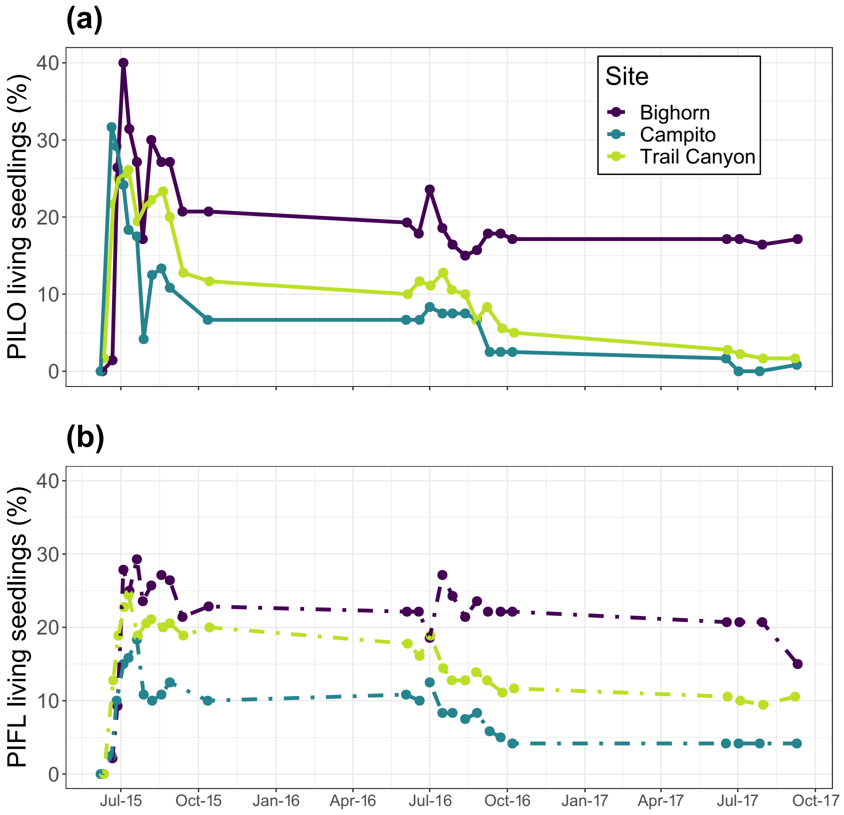

Fig. 5 Living seedlings from the 2015 cohort over the 2015–2017 period for bristlecone pine (a) and limber pine (b). Points are the percentage of living seedlings (# of alive seeds/#seeds planted *100) including all plots at each site

Micro-site characteristics are important to seedling establishment, especially in high elevation forests where seedling establishment is rare (Kroiss and HilleRisLambers 2014; Maher et al. 2015; Pansing et al. 2017; Davis and Gedalof 2018). While we took efforts to choose plot sites where there was open soil, there is likely to be variation in plot site quality that is not a function of the measured parameters. This is reflected in our values for deviance explained, indicating that there are parameters that affect germination and survival of these two species that we have not captured. Also, since each site is on a unique soil type and on non-overlapping elevation ranges, we are unable to examine the effects of soil type and elevation independently of site. However, these soil types have very different characteristics (Wright and Mooney 1965), so site differences are likely to be dominated by soil type. These factors likely help explain some of the unexplained variance.

Temperature effects One of our hypotheses was that germination and survival would be positively associated with temperature. Given the cool temperatures in these high-elevation forests, water is generally assumed to not be a limiting factor for adult trees (Holtmeier 2003; Salzer et al. 2009). At treeline, adult bristlecone pines are growing at unprecedented rates in response to recent warming and average precipitation, suggesting that adult trees were limited by temperature and not precipitation (Salzer et al. 2009). There is a well-accepted consensus that treeline, as determined based on adult presence, is controlled by cold air temperatures and that water availability plays a limited role (Körner and Paulsen 2004; Piper et al. 2006; Körner 2007, 2012; Rossi et al. 2008). However, this treeline framework relates to upright mature trees that are greater than 3 m in height, which are likely able to access water well below the soil surface, and where forests have a relatively closed canopy. Adult trees are coupled with air temperatures while young trees are coupled with temperatures near the soil surface. Seedlings at treeline are far more susceptible to a variety of stressors that can lead to mortality (Harsch and Bader 2011). For example, summer temperatures at the soil surface can be as much as 25 °C warmer than at the leaf-level of adult trees

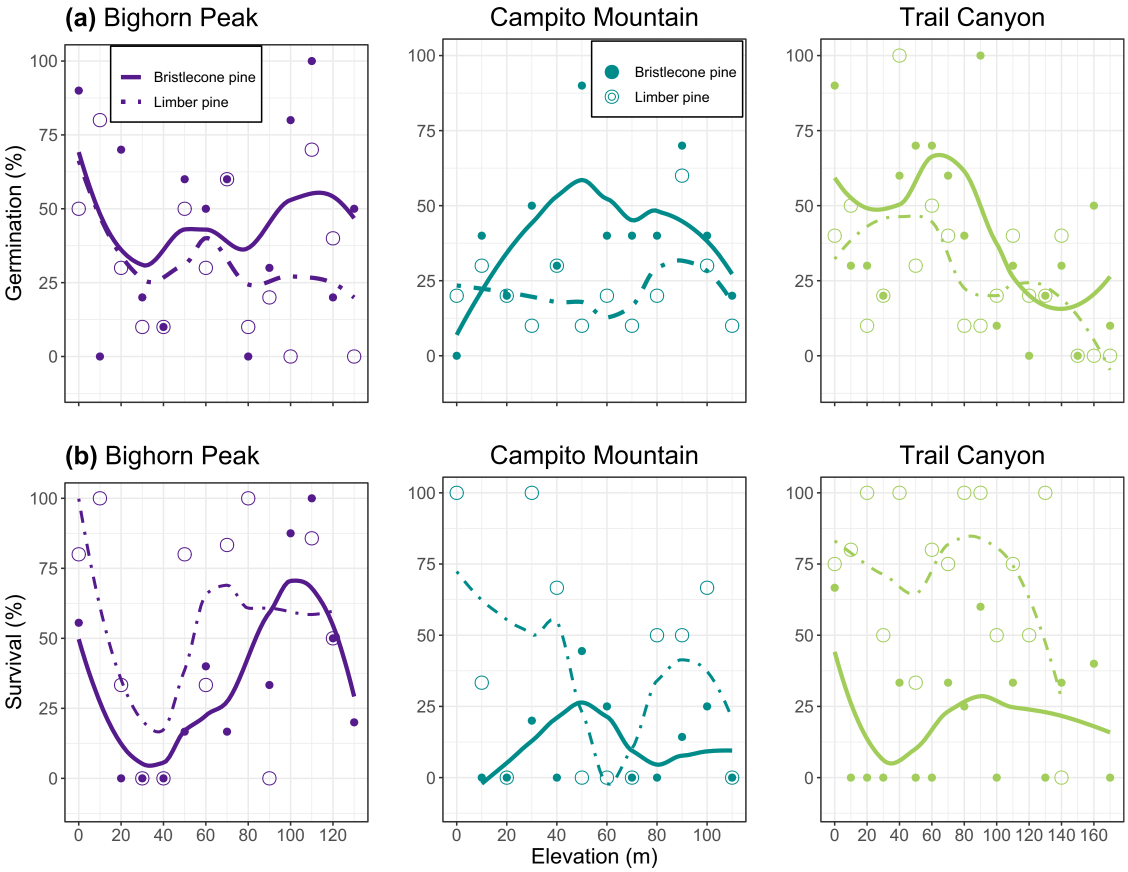

Fig. 6 Germination (a) and survival (b) of seedlings for the 2015 growing season by site and species

which can lead to opposite responses of adults and young trees to the same weather conditions (Smithers et al. 2017).

While we collected temperature data at soil level and in the atmosphere, soil-level temperatures were far more predictive than atmospheric temperatures. Whereas adult trees have shown higher growth with recent warming (Salzer et al. 2009), we found that higher temperatures were generally correlated with lower germination and survival success for young trees. One caveat to this is that in bristlecone pine young trees, higher GDD was associated with higher survival. This indicates that for bristlecone pine, an increase in the amount of time available for growth is correlated with higher survival, but only if soil surface temperatures are generally low and soil water moisture is high. While both species showed negative responses to higher soil surface temperatures, bristlecone pine showed a stronger response indicating that limber pine is more tolerant of higher soil surface temperatures.

Soil water content Our results suggest that water limitation is the primary driver of germination and first-year survival for these species at treeline, especially for bristlecone pine. Young trees are only able to access water in the top few centimeters of soil and so are more susceptible to water limitation. Recent studies in the Rocky Mountains have also found this to be the case (Moyes et al. 2013; Kueppers et al. 2016). Adult trees are known to have increased mortality in response to drought stress (van Mantgem et al. 2009; Allen et al. 2010; McDowell and Allen 2015; Young et al. 2017), but the effects of drought stress are even more acute in more sensitive, early life stages (Harsch and Bader 2011; Dobrowski et al. 2015). In the Great Basin, where establishment occurs infrequently, recruitment pulses are largely driven by precipitation, but with complicated multi-year effects (Millar et al. 2015). Treeline, as

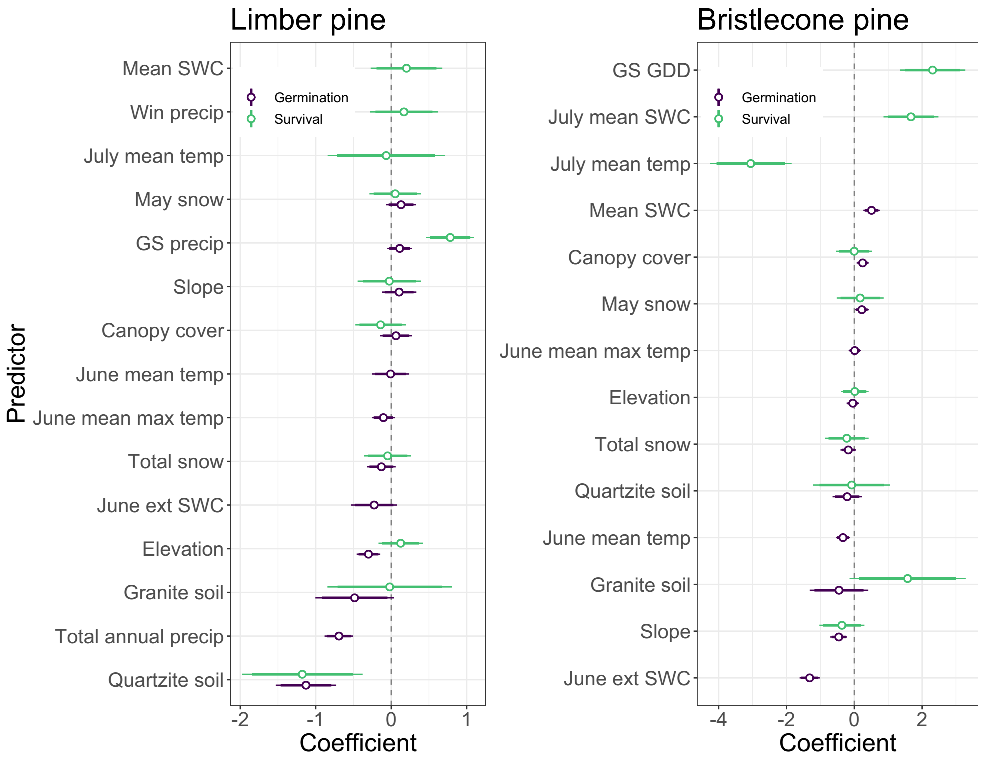

Fig. 7 Mean coefficient estimates from all binomial models with a δAIC <4 for limber pine and bristlecone pine germination (purple) and survival (green). Error bars are the 90% and 95% confidence intervals but are not meant to represent "significance." Parameter inclusion here by default makes them "significant" since they are included in the best model(s) as determined by AIC. The lack of a coefficient value for a predictor indicates exclusion of that parameter from the models. 2016 and 2017 years had strong negative coefficients for both species for germination and survival but are excluded here for scale. All temperatures seen here are soil temperatures. The following abbreviations are used: Win (winter), GS (growing season), soil water content (SWC), growing degree days (GDD), and extreme (ext)

defined by adult presence, may be determined by temperature. However, since adult trees are young trees first, and since young trees appear to be limited by water availability, treeline appears mechanistically controlled by water, at least in these dry systems.

At the largest scale across all sites, our results show that elevation is positively correlated with soil water content, but there is no correlation of elevation and soil water content within sites. At that smaller within-site scale, there is considerable variation among plots in soil water content owing to fine-scale topographic, canopy, and soil texture differences. Within site, soil water content was generally variable with a mid-elevation low where adult trees are more abundant. Given the increased canopy cover and longer snow retention (Online Resource 2) at mid-elevation, we might have expected increased soil water content at mid elevations in response to decreased insolation. Alternate hypotheses could include the increased water uptake by adult trees or decreased temperature-driven evaporation in the cooler temperatures of low-elevation (cold air pooling effects) and high-elevation (adiabatic cooling effects) plots.

Warming temperatures are widely expected to result in upslope migration of treeline, but we found that summer water availability is the primary constraint on seedling survival. With increased temperature comes increased effective soil drying due to increased vapor pressure deficit, even if the amount of precipitation stays constant. In most years, these forests have minimal regeneration and rely on sporadic pulse events with multiple favorable years (Millar et al. 2015). With increased effective soil drying, it is likely that what was a "favorable" weather year for regeneration may be less so and that the time in between regeneration pulses will increase. Depending on how quickly range contraction takes place at the lower range margins where mortality events have already been noted (Bentz 2019; Millar et al. 2019), these lags at the leading edge of range expansion could cause significant range reductions in the short-term. They could even cause local extirpations where the leading-edge establishment lag far exceeds the trailing edge extinction rate. For tree species with individuals that can live for thousands of years, it is also possible that these differences in regeneration pulse timing are of little consequence.

Site and soil effects Limber pine and bristlecone germination and establishment were both negatively associated with the quartzite soil site. Germination in both species was negatively associated with the granite soil site, but in both species, survival was less negatively associated with the site than was germination. Bristlecone pine survival was even positively associated with the granite soil site. Limber pine and bristlecone pine germination and establishment were both higher a the the dolomite soil site. This is unsurprising for bristlecone pine, which is strongly associated with calcareous soils, but mature limber pines are rare at treeline on dolomite soils (Wright and Mooney 1965). There are no mature limber pines at the Bighorn Peak site and yet this area is currently experiencing very high recruitment of limber pine juveniles (Millar et al. 2015; Smithers et al. 2017). Seeds are likely able to disperse into the area via Clark's nutcracker (*Nucifraga columbiana*) from the nearest seed source on the opposite slope (~0.5 km away), but the causes of their prior exclusion and only recent recruitment remain a mystery. Dolomite soil properties (high pH, high magnesium, and low phosphorus) exclude many plant species and it was assumed that since bristlecone pines are able to tolerate dolomite soil, it has a refuge from competition there (Billings and Thompson 1957; Wright and Mooney 1965). However, recent research suggests that limber pine is able to thrive on dolomite soil at the earliest life stages (Smithers 2017), somewhat older juvenile life stages (30–50 years old) (Millar et al. 2015; Smithers et al. 2017), and on a diversity of carbonate soils in mature age classes (Steele 1990; Charlet 2007).

While dolomite soils of Bighorn Peak have certain undesirable chemical properties, they have relatively desirable physical properties. Dolomite soils are light in color and reflect light, keeping soil surface temperatures cooler (Smithers 2017). Even at high elevations, soil surface temperatures can get very high. In this study, maximum July soil surface temperatures were regularly above 30 °C and occasionally exceeding 40 °C (Fig. 4). All other things being equal, dolomite soils are cooler than quartzite and granite (Smithers 2017). Dolomite soils are also finer in texture than quartzite or granite resulting in higher soil moisture (Wright and Mooney 1965). Quartzite has a finer texture than granite, but quartzite's darker color results in it getting relatively warmer (and thus drier) than dolomite, likely explaining the low germination and survival at Campito. Granite soil is both warm and has a coarser texture making it the soil with the least water holding capacity. These site-specific attributes may have led to interesting elevation differences among the sites. All three sites were located on the same aspect and contained an upper and lower climatic treeline. However, the three sites had different, non-overlapping, elevation ranges. Differences in site elevations of treeline are likely an effect of the physical properties of the soil (Table 1).

Inter-annual variation in germination and survival Winter precipitation may not be as important to germination and first-year survival as summer monsoonal precipitation. In 2014–2015, California had one of its driest and warmest winters ever recorded (NOAA National Centers for Environmental Information 2016). In the winter of 2016–2017, California had one of the wettest winters on record. Given our results that show soil water content to be a major driver of seed germination and seedling survival, we would have expected the 2015 growing season to be a poor season for seedling survival relative to 2017. Our results show the opposite response (Fig. 7 and Online Resource 4). The reasons for this likely have to do with precipitation timing and water phase (rain versus snow) trumping precipitation amount. Typically, monsoonal thunderstorms are most common in July and August, the warmest and most stressful months for a first-year seedling. While the winter prior to the 2015 growing season was very dry, a late spring storm ushered in a wet summer driven by monsoonal moisture from the south, resulting in spatially unpredictable but frequent afternoon thunderstorms and higher overall summer precipitation (Table 3). It is likely that this late spring storm was beneficial to seeds that emerged in late June when the soil surface temperatures were still relatively cool. In 2017, the growing season was preceded by abundant precipitation and deep snow, much of which did not melt off until July causing germination to be slightly delayed. By the time that germination was possible, soil surface temperatures were very warm with maximum soil surface temperatures between 30 and 40 °C for most plots. June–August 2017 soil surface temperatures in the region were the warmest ever recorded (Western Regional Climate Center 2017), so once the snow melted, soils dried quickly (Fig. 5b). This short period between soil surface temperatures under snow being too cold for seeds to germinate and soil surface temperature being very warm and dry likely led to germination not occurring or rapid mortality of those seeds which did germinate.

These two years with very different weather patterns provide insight into the interspecific differences we saw in germination and survival. Thanks to wetter conditions in 2015, bristlecone pine had relatively high germination and survival. In 2016 and 2017, bristlecone pine had much lower germination and survival than limber pine. From these results limber pine appears to have more steady germination and survival in a variety of climatic conditions. Bristlecone pine appears to have poor germination and survival unless there is anomalously high available water. In a future of warmer and dryer conditions, limber pine may be better able to germinate and survive the earliest life stages than bristlecone pine which relies on increasingly infrequent wet summer conditions unless climatic warming is also associated with an increase in summer monsoonal precipitation.

The results from these two very different years also lead to some inference about what drives recruitment patterns in these forests. For bristlecone pine and limber pine in the Great Basin, winter precipitation may have relatively little to do with successful establishment compared with the effects of growing season precipitation. Given the data observed in 2017, it is possible that abundant winter precipitation may even be a detriment to germination success since persistent snowpack can delay germination to later in the growing season when soil surface temperatures are too warm for the very vulnerable period immediately after emergence. The exceptionally dry 2014–2015 winter showed that winter precipitation, or the lack thereof, is much less important than the amount and timing of summer precipitation. Lags as long as six years in the relationship between various climate parameters and recruitment have been detected in these species, indicating that after this first-year bottleneck, predicting recruitment success gets even more complicated (Millar et al. 2015).

This study supports the growing body of research showing that when predicting species range shifts under climate change, we must consider the life stages that have the strongest bottlenecks rather than simply focusing on the presence or absence of adults. Climate change is affecting not just temperature but the timing and phase of precipitation, which has a strong effect on seedling recruitment. In water-limited systems of the western US, these changes in precipitation are likely to be the primary limitation to forests expanding their ranges.

Acknowledgments We thank Connie Millar and Adelia Barber for invaluable direction and input and research technicians Iris Allen, Jamey Wilcher, and Asa Holland. Thank you to the White Mountains Research Center for logistic support, and to the Andrew Latimer and Malcolm North Labs for reviewing and improving this manuscript. We thank three anonymous reviewers for their constructive comments to this manuscript.

Author's contributions BVS originally conceived of the idea. BVS and MPN conceived and designed the experiments. BVS performed the experiments. BVS and MPN analyzed the data. BVS and MPN wrote the manuscript.

Funding This project was generously supported by the USDA Forest Service, the White Mountain Research Center, California Native Plant Society, Davis Botanical Society, and UC Davis Jastro-Shields Graduate Research Scholarship.

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