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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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16

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19

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22

Abstract:

In response to climate warming, subalpine treelines are expected to move up in elevation since they 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 likely colonize newly available habitat first, potentially dominating 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 sub-alpine 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 many 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. Though limber pine is typically not dominant, and 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

45species differences in dispersal and establishment may result in future communities with very

46different specific composition.

47

48**Introduction:**

49   In response to climatic warming, species are generally expected to expand their ranges to

50higher latitudes and elevations and contract at lower latitude and elevational range margins

51(Parmesan & Yohe, 2003; Hayhoe *et al.*, 2004; Loarie *et al.*, 2008). The upslope leading range

52edge is at treeline in sub-alpine forests, an ecotone considered a sensitive biological indicator of

53climatic warming due to the strong, world-wide association between growing season temperature

54and treeline (Körner, 1998, 2012; Holtmeier, 2003; Körner & Paulsen, 2004; Millar *et al.*, 2004).

55Future treeline is generally expected to shift higher in elevation by as much as 700m by the year

562100 (Moen *et al.*, 2004; Kullman & Öberg, 2009). Despite these predictions, there is substantial

57variability in the speed of treeline response to warming in mountains around the world

58(Camarero *et al.*, 2017). This variation may be due to many factors, such as varying

59geomorphology, past human disturbance, lags in population dynamics, dispersal limitation, and

60biological interactions (competition, herbivory) (Grace *et al.*, 2002; Holtmeier, 2003; Harsch *et*

61*al.*, 2009; Speed *et al.*, 2010; Holtmeier & Broll, 2017). Variability in treeline advance hints that

62in addition to warming temperature, there are other factors influencing treeline advance, most of

63which remain unexplored.

64   Biotic interactions, such as competition, facilitation, and/or priority effects, are likely to

65have particularly strong effects on how range shifts occur (Baumeister & Callaway, 2006; Aitken

66*et al.*, 2008; Maestre *et al.*, 2009; Ettinger *et al.*, 2011; Kroiss & HilleRisLambers, 2014). In sub-

67alpine forests immediately below treeline, competitors from further downslope could displace

68 sub-alpine species through direct competition or through indirect mechanisms such as increased

69 exposure to disease or changing disturbance regimes associated with downslope species

70 (Flannigan *et al.*, 2000; Tomback & Resler, 2007). Alternatively, in harsh conditions like those

71 found in sub-alpine forests, species can have a "nurse effect," facilitating the establishment of

72 other species by positively modifying the microclimate through greater water retention, wind

73 blocking, creation of shade, or other ameliorating effects (Malanson *et al.*, 2007; Maestre *et al.*,

74 2009; Pyatt *et al.*, 2016). Interspecific differences in dispersal ability and establishment success

75 are likely to play major roles in how newly available habitat is colonized with priority effects

76 possibly trumping other responses to climate change. Species distribution models can predict the

77 future climate envelopes of species, but often ignore how other limitations affect species range

78 shifts under climatic warming. For example, in trees establishing outside of current forest range

79 limits, the lack of soil development or protection from harsh weather or ineffective dispersal may

80 preclude successful establishment.

81   Climate envelope models are often based on matching adult presence with climatic

82 conditions. Young individuals, however, not only encounter different micro-climates but often

83 have different climatic tolerances than do adults (Jackson *et al.*, 2009; Warren & Bradford, 2011;

84 Bell *et al.*, 2014; Kueppers *et al.*, 2016; Máliš *et al.*, 2016). Juvenile trees frequently occupy a

85 narrower range of climatic conditions, especially in water-limited areas (Zhu *et al.*, 2012;

86 Monahan *et al.*, 2013; Dobrowski *et al.*, 2015; Moyes *et al.*, 2015). Given this narrower filter for

87 juvenile survival, changes in recruitment are likely a major component of species range shifts

88 (Walck *et al.*, 2011). When propagules are plentiful, dispersal and range shift can happen rapidly,

89 but within slow-growing or slow-dispersing species, lags in range shifts can be decades to

90 centuries (Kroiss & HilleRisLambers, 2014). The narrow range of conditions suitable for

91establishment in sub-alpine trees and unforeseen biotic interactions complicate our ability to

92project how species' ranges will respond to increasing temperatures (Millar *et al.*, 2004, 2015;

93Körner, 2012; Conlisk *et al.*, 2017).

94   Treeline trees have shown recent dramatic stem growth increases in the mountains of the

95western US Great Basin, suggesting that temperature increases have recently improved growing

96conditions at the trees' upper elevation limit (Salzer *et al.*, 2009). The Great Basin is a region of

97low elevation basins and high elevation ranges, on which sparse montane forests occur at upper

98elevations. While the ranges of the Great Basin are generally arid, there is a substantial southwest

99to northeast gradient in the amount (low to high) and timing (Mediterranean to monsoonal) of

100precipitation with large daily and seasonal temperature ranges throughout the region. Above-

101treeline recruitment has increased in the western Great Basin, with evidence for increases in

102recruitment pulses in the last 130 years (Millar *et al.*, 2015). Great Basin sub-alpine forests are

103largely made up of Great Basin bristlecone pine (*Pinus longaeva* DK Bailey) and limber pine

104(*Pinus flexilis* James) with stands of Engelmann spruce (*Picea engelmannii* Parry) and quaking

105aspen (*Populus tremuloides* Michaux) on wetter slopes in the eastern Great Basin, and whitebark

106pine (*Pinus albicaulis* Engel) a treeline species in parts of the northern and eastern Great Basin.

107Great Basin bristlecone pine is notable for individual longevity with known trees over 5000 years

108old making them the oldest living nonclonal organisms on earth (Schulman, 1954).

109   Tree species with higher densities at treeline have range margins that better track

110warming temperatures in establishing above treeline (Kroiss & HilleRisLambers, 2014). Where

111bristlecone pine is present, it typically dominates at treeline with limber pine mixed in at lower

112elevations (Millar *et al.*, 2015). While there is overlap in the elevational ranges of the two

113species, there are range differences at both upper and lower elevations. At the upper extreme,

114bristlecone pine is found at higher elevations (3535m) than limber pine (3505m) in Nevada

115(Charlet, 1996). That seemingly slight difference reflects limber pine's much lower treeline

116density relative to bristlecone pine, and its absence from many treeline sites. The elevation

117difference is especially acute on dolomitic soil where the upper limit of limber pine (3030m) is

118considerably lower than that of bristlecone pine (3485m) (Wright & Mooney, 1965). For the

119lower range margin, limber pine is found considerably lower (1830m) than bristlecone pine

120(2060m) in Nevada (Charlet, 1996).

121   Recent establishment of young trees above the historical treeline in the western Great

122Basin has been observed, but much of that upslope establishment was typically downslope

123limber pine "leap-frogging" over bristlecone pine (Millar *et al.*, 2015). Shade-intolerant

124bristlecone pine encounters minimal competition from other tree species due to the harsh abiotic

125conditions of its habitat. There is minimal impact from pathogens in these forests and the

126sparseness of the vegetation limits the occurrence of fire (North *et al.*, 2009; Van de Water &

127Safford, 2011). The recent appearance of regeneration at and above treeline is evidence that

128climatic conditions have changed sufficiently at treeline in the last 50 years to allow for

129establishment. Given the observed treeline advance in the Great Basin, the few species involved,

130and limited human disturbance, Great Basin treelines provide a rare opportunity to examine the

131climate change-induced dynamics surrounding a discrete range margin.

132   It remains to be seen whether bristlecone pine will be able to track warming climate to

133higher elevations. Upper treeline is often a product of inhospitable upslope geomorphology

134limiting the ability of species to advance upslope under favorable climatic conditions (Grace *et*

135*al.*, 2002; Ernst *et al.*, 2003; Butler *et al.*, 2007). Even allowing for upslope migration, the rate of

136changing temperatures may be fast enough that species with long regeneration times like

137bristlecone pine are unable to migrate fast enough to avoid local extirpation (Neilson *et al.,* 2005;

138Van de Ven *et al.,* 2007; Aitken *et al.,* 2008; Loarie *et al.,* 2009). Minimum temperatures in the

139western Great Basin have increased an average of 1°C between 1910-2013 (Millar *et al.,* 2015),

140and regional temperatures are expected to rise an additional 2 - 4 °C by the late 21st century

141(Scalzitti *et al.,* 2016). Aside from the rate of climate warming, bristlecone pine may also be

142exposed to greater interspecific competition from other tree species, especially the better-

143dispersing limber pine, which could establish rapidly in newly available habitat at and above the

144current treeline.

145   We know little about the regeneration dynamics of sub-alpine trees and even less about

146these dynamics in dry forests like those found in the Great Basin (Barber, 2013; Conlisk *et al.,*

1472017). Part of this ignorance stems from the fact that in the last 500 years, treeline regeneration

148in the Great Basin appears to have been limited to the last 50 years. Surveys in the California

149White Mountains in the 1950s showed an absence of young trees indicating that adult treeline

150trees established in a period of more favorable, likely warmer, climatic conditions (Billings &

151Thompson, 1957). The lack of relict wood from smaller trees, which tends to persist on the

152surface for 100s to 1000s of years, suggests that there had been little regeneration at treeline for

153at least hundreds of years. While juvenile trees may have established at or above treeline in the

154past and then died before reaching maturity, once bristlecone pine and limber pine have survived

155to an age of 3-4 years, these small trees have extremely low mortality (Elliott, 2012; Barber,

1562013; Conlisk *et al.,* 2017). Most juvenile trees old enough to be observed in field surveys are

157very likely to persist into adulthood.

158   This study examines the species dynamics surrounding treeline in the Great Basin by

159specifically examining the following questions: 1) What are the major abiotic predictors of

160treeline advance, 2) What are the predictors of below-treeline adult basal area and above-treeline

161establishing juveniles and how consistent are the environmental associations of adult trees and

162juveniles of each species, and 3) How does the species composition of mature forest compare

163with the species composition of establishing juveniles below and above treeline? This research

164will examine whether differences exist between two key subalpine tree species in the US Great

165Basin and whether those differences have long-term consequences for the persistence of Great

166Basin bristlecone pine under rapidly warming treeline climate conditions.

167

168**Materials and Methods:**

169*Study Area:* The Great Basin of the interior United States West is defined by having internal

170drainage, Basin and Range geomorphology, and/or by its floristic composition. It extends from

171the crest of the Sierra Nevada in California in the west to the Uinta Mountains of Utah in the

172east, and with the Columbia River and Colorado River watershed divides forming the north and

173south boundaries, respectively (Figure 1). In the southern and central Great Basin, treeline is

174largely made up of Great Basin bristlecone pine (abbreviated PILO) and limber pine (PIFL). In

175the northern Great Basin, whitebark pine is the dominant treeline species. Occasional treeline

176stands of Englemann spruce (PIEN) and quaking aspen are also found throughout the Great

177Basin, especially in the cooler or wetter parts of the region.

178
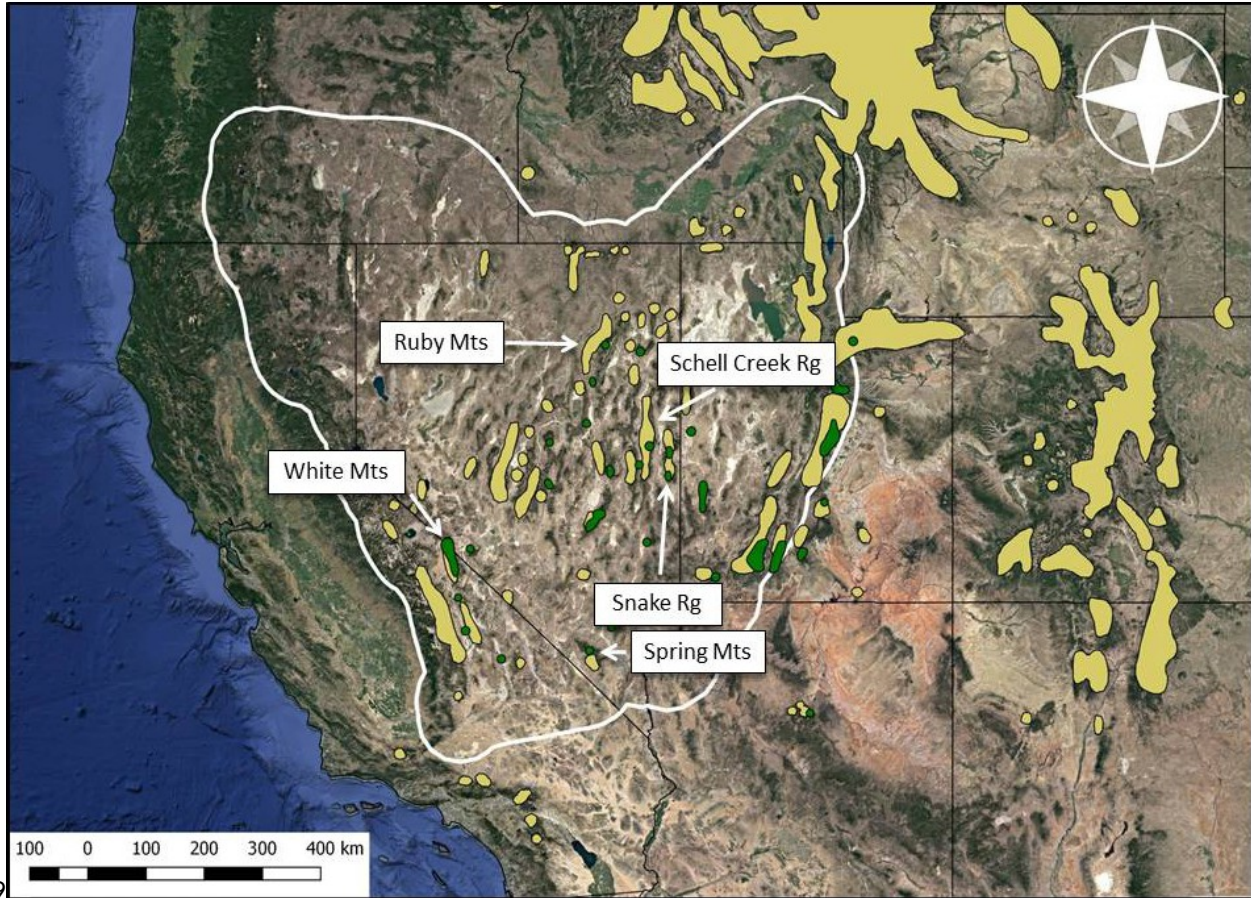
180**Figure 1:** The Great Basin, outlined in white, is centered on the state of Nevada which has most of the

181highest ranges in the bioregion. Sampling occurred in the mountain ranges labeled. Limber pine (yellow)

182and Great Basin bristlecone pine (green) range maps show their ranges in the Great Basin. This is the

183entire extent of the Great Basin bristlecone pine's range. Limber pine's range extends to the north into

184Canada. Species distribution vectors were downloaded from the USGS vegetation-climate modeling

185study (https://esp.cr.usgs.gov/data/little/). The background satellite image is a Google Earth image

186(www.earth.google.com) accessed via QGIS.

187

188

189   Soil type plays a large role in Great Basin tree species distributions. Bristlecone pine is

190mostly restricted to high-elevation carbonate (calcareous) soils, especially dolomite in the White

191Mountains (Schulman, 1954; Wright & Mooney, 1965), and limestone pockets throughout the

192Great Basin. On these soils, it is the dominant tree species with limber pine being rare or absent.

193Other major soil types include quartzite, a metamorphic sandstone, on which a mix of tree

194species generally coexist or different species can be locally dominant, and granite on which

195limber pine typically dominates and bristlecone pine is rare.

196   We sampled treeline in Great Basin mountain ranges in 2015 and 2016 that were of

197sufficient elevation to contain climatic treeline and supported both limber and bristlecone pine.

198Climatic treeline, as we use it, is treeline that is a function of temperature constraints as opposed

199to treeline determined by geology, disturbance, or other non-climatic effect (Körner, 2012). Since

200there is no reliable field method for distinguishing limber pine and whitebark pine juveniles

201(Hendrick, WH & Lotan, JE, 1971), we avoided sampling where those two species co-exist,

202eliminating an area in the northern Ruby Mountains from our study. These criteria allowed for

203sampling in the Snake Range, Schell Creek Range, southern Ruby Mountains, and Spring

204Mountains in Nevada and the White Mountains in California (Figure 1). Within each range, we

205sampled individual mountains or ridges that contained climatic treeline on all aspects that

206allowed safe access and where treeline appeared to result solely as a climatic effect, excluding

207avalanche chutes, cliffs, unstable scree, and recent landslides (Körner, 2007). This allowed for

208sampling on 13 distinct mountains or ridges in the five mountain ranges.

209

210***Plot placement and measurements:*** At each location, we identified treeline as the line

211connecting the uppermost forest patches of at least three trees growing to at least 3 m in height.

212This line is a generally recognized construct representing the upper margin of the treeline

213ecotone and is not associated with a particular elevation contour (Supplementary Figure 1)

214(Körner & Paulsen, 2004; Körner, 2007). We placed plots at the furthest distance upslope of

215treeline where juvenile tree densities were sufficient (i.e., clumps of three or more individuals)

216that upon reaching maturity the clump will represent future treeline. Plots were placed on all

217slopes and aspects that contained climatic treeline and met our criteria. We placed sequential

218plots measuring 30 m x 10 m (300 m^2) to form a modified 10 m wide belt transect upslope from

219and parallel to current treeline. Each 30 m length plot was placed parallel to and upslope from

220treeline but could be located up or down slope relative to the previous plot to follow the

221maximum elevation of juvenile tree clumps. Since we sought to maximize the number plots per

222peak or ridge aspect, the number of plots per peak or ridge aspect varied from 5-24. In each plot,

223we tallied all conifer individuals, identified individual trees to species, and aged them by

224nondestructively counting above-ground terminal bud scars, which is well-correlated with ring

225counts (Parent *et al.*, 2000; Millar *et al.*, 2004, 2015). These ages were binned into age classes to

226account for errors in whorl aging. We considered all trees < 100 years old to be a juvenile tree,

227although trees 50 – 100 years in age were very rare. With few exceptions, all trees encountered

228were either <50 years or were at least hundreds of years old. We excluded trees <5 years old to

229limit the effect of very young trees dying before reaching maturity (Barber, 2013). From each

230juvenile tree, vertical distance to current treeline was measured using a Laser Technology

231TruePulse 200 laser rangefinder. To avoid pseudoreplication, individual distances to treeline were

232averaged to give a plot-level distance to treeline. The elevation, slope, aspect, dominant soil type,

233and horizontal and vertical slope shape were recorded at the midpoint (15 m) of each plot.

234   To examine the surface characteristics in each plot, we took a point sample at 0.5 m

235intervals along a 30 m transect (N=60) recording substrate conditions that a seed would

236encounter if it landed or was buried there. At each point we recorded whether the point landed on

237soil subdivided into size class (0=bare soil, 1=gravel, 2=large rock or 3=bedrock), litter, downed

238wood, or vegetation identified to species. To evaluate abundance of adult trees as a

239representation of relative seed sources, we used basal area as a proxy for relative abundance. We

240estimated basal area of cone-producing adults for each tree species using a basal area prism

241(BAF=1M) at the two end points of the transect line which were averaged to give plot-level basal

242area for each species. We compared the demographics of upslope establishment with current sub-

243alpine adult demographics by pairing the above-treeline plots with plots selected in the closed

244forest below treeline in which the same plot-level and demographic data were collected. Since

245there were very few juvenile trees in the closed canopy, closed-forest plots were selected

246haphazardly where the aspect and relative position on the landscape matched its above-treeline

247pair.

248

249***Plot-level DEM predictors****:* For other potential model predictors of treeline advance, we used a

25030 m Digital Elevation Model (DEM) in QGIS (QGIS Development Team, 2016) to extract plot-

251level metrics. The DEM was used to calculate monthly total solar radiation (Wh/(m^{2}d)) and solar

252insolation time (h) for each plot using the QGIS GRASS plugin (GRASS Development Team,

2532016). For each month, we used the 15th as the target day to serve as an "average" day. We

254included an annual and a growing season (June-September) parameter for both solar radiation

255and insolation time. A DEM was also used to extract plot-level values of topographic water

256accumulation by using the Watershed (topographic convergence index) feature in ArcGIS

257(*ArcGIS Desktop*, 2016). Due to inconsistencies in field elevation measurements using a hand-

258held GPS, we used the DEM values for plot elevation.

259   These predictors (Table 1) were chosen because we believed that they were most likely to

260 affect successful establishment of young trees and therefore treeline advance. While the potential

261 predictors is a long list, we know that successful establishment of young trees, especially trees

262 establishing in the harsh conditions at treeline, is a result of many factors, both abiotic and biotic

263 (Kueppers *et al.,* 2016; Conlisk *et al.,* 2017).

264

265 **Table 1:** Potential predictors tested for treeline advance (distance from the above-treeline plot to

266 treeline), adult basal area, and juvenile density. *Basal areas were excluded from the treeline

267 advance models since there is essentially no adult basal area above treeline.

268

| **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*
> Limber pine (PIFL) basal area*
> Englemann spruce (PIEN) basal area*

269

270 ***Data Analysis*:** This design gave us a large number of plots and juvenile trees within plots, which

271 would likely result in a common problem with large sample sizes in which almost all predictors

272 are found to be "significant" (i.e. likely to have nonzero effect), but most with a very small effect

273 size and effects often correlated with each other (MacElreath, 2016). This presents a problem

274 with using standard statistical regression in that the resulting models are likely overfitted. In

275 addition, the large number of potential predictors make analysis with standard regression or

276 linear mixed effects models problematic. To avoid these problems of parameter selection, we

277 used the elastic net regularized regression method that combines the Least Absolute Shrinkage

278 and Selection Operator (LASSO) and ridge regression (Tikhonov regularization) to produce

279 regularized models that include only strong predictors, while shrinking weak predictor variables

280 toward zero (Guisan & Zimmermann, 2000; Friedman *et al.*, 2010). elastic net models have been

281 successfully used in a variety of ecological studies when dealing with a large number of potential

282 predictors, especially when those predictors have low predictive power (Prospere *et al.*, 2014;

283 Holdo & Nippert, 2015; Lemoine *et al.*, 2016). It is a feature of elastic net regularization that

284 choosing a model via shrinking coefficients towards zero will result in a model with most

285 coefficients very near zero. Because of this shrinkage, proximity to zero does not mean that a

286 predictor is unimportant—any predictor with a non-zero coefficient can be seen as important, in

287 that its inclusion in the model improves out-of-sample prediction of the response variable (Zou &

288Hastie, 2005). Specifically, we fit generalized linear models using penalized maximum

289likelihood (Glmnet) for the response variables of treeline advance (distance from the above-

290treeline plot to treeline), specific adult tree basal area, specific upslope juvenile density, the ratio

291of adult limber pine to bristlecone pine basal area, and the ratio of limber pine to bristlecone pine

292juvenile density. Models of the ratio of limber pine to bristlecone pine (PIFL:PILO) adult basal

293area and juvenile density were used to examine how the two species respond to climatic

294predictors in relation to each other. While elastic net models do not currently allow for using

295mixed effects, when we ran standard regression models, including spatial random effects did not

296improve the models. To fit these models, we used the R package glmnet (Friedman *et al.*, 2016),

297using the elastic net penalty and selecting values for the regularization parameter (λ) that

298minimize the mean cross-validation error over 100 runs of cv.glmnet.

299   For all models, coefficient values were plotted by nonzero (model-included) parameters

300using the library ggplot2 (Wickham, 2009) to show their relative effects on the response variable.

301Error bars were generated by nonparametric bootstrapping, using 1000 iterations. From the

302resulting regression parameters, we constructed 95% confidence intervals by taking the 2.5 and

30397.5 percentiles of the bootstrap estimates. These confidence intervals are provided only to show

304a visual estimate of parameter variability. They are not to be viewed as having statistical

305"significance." Parameters that are not shrunk to zero via elastic net by definition improve the

306model and so are included (Friedman *et al.*, 2010; Goeman *et al.*, 2016).

307

308**Results:**

309*Treeline Advance:* We surveyed 173 pairs of above and below treeline plots for a total of 346

310plots. Using the presence of at least three established juvenile trees within the plot as a measure

311of treeline advance, median vertical advance across all Great Basin sites including both species

312was 11.9 m (mean = 19.1 m) upslope with a maximum of 153 m (Figure 2). The majority of plots

313(62%) showed a potential treeline advance of between 5-25 m upslope. Given our measured

314slopes of 9 – 78%, this amounts to a ground distance of 8 – 279 m over which seeds dispersed.
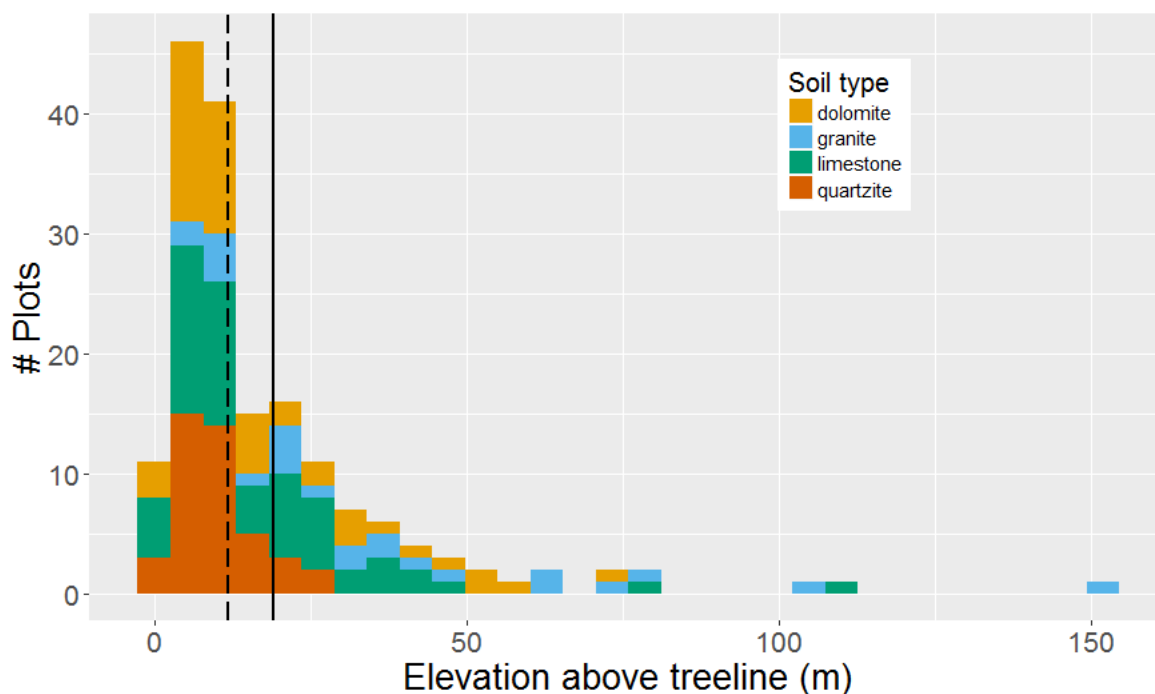

315

316**Figure 2:** The number of plots sampled by soil substrate and their vertical elevation above

317current treeline representing potential treeline advance. Median (11.9 m) and mean (19.1 m)

318elevations above treeline are shown with the dashed and solid lines, respectively.

319

320

321Soil was a factor in predicting potential advance with granitic soil showing larger advances of

32222.0 m compared with 9.6 m on carbonate dolomitic soil (Figures 2 and 3). Treeline advance was

323slightly, but insignificantly, higher (10.7 m) on carbonate limestone soil. Latitude, east aspect,

324and north aspect were the most negatively associated predictors implying that potential treeline

325advance is higher on south and west aspects and in mountain ranges further south. Quartzite soil

326is negatively associated with treeline advance relative to dolomitic soil (Figure 3), but still

327showed a median treeline advance equal to that of dolomite at 9.6 m. There was an effect of

328mountain range with treeline advance being higher in the Snake Range and the Schell Creek

329Range, but treeline was found to be advancing in all mountain ranges.
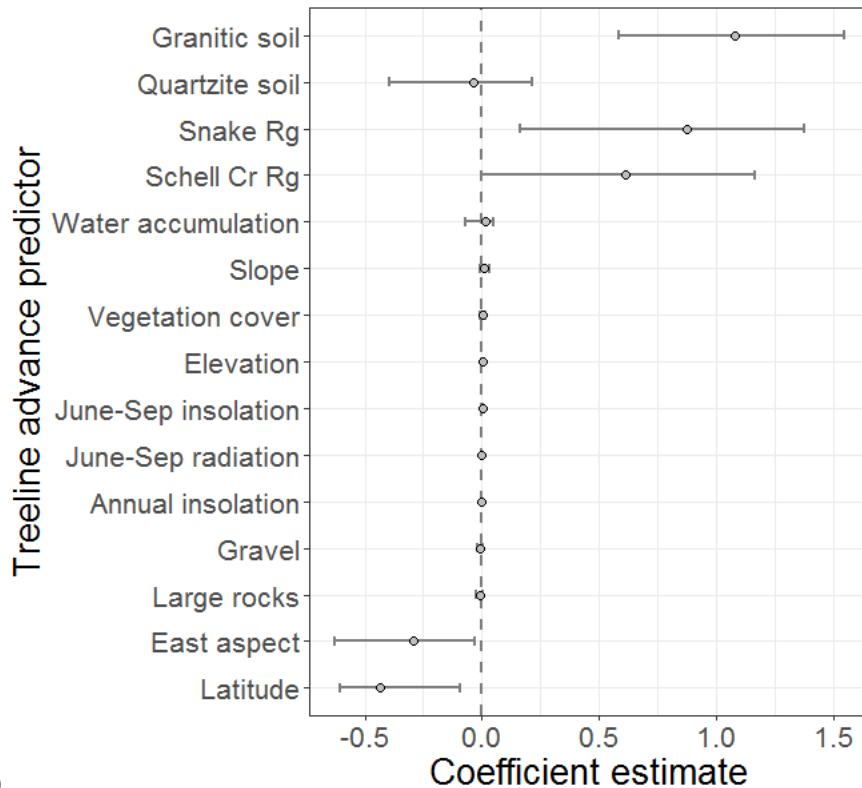
330

331Figure 3: Treeline advance predictors

332Rank of coefficients that predict treeline advance and the estimate of each coefficient relative to

333dolomite soils (which by default is assigned a coefficient of 0 to which the other soil types are

334compared). All points are non-zero coefficients chosen by glmnet using the elastic net penalty.

335Confidence intervals (95%) are included only as a visual estimate of parameter variability and

336*are not* meant to indicate the statistical significance of a parameter. Glmnet includes all

337parameters that improve a model and so are included in the model if they have a non-zero value.

338

339

340**_Life stage predictors_:** Models indicate that both bristlecone pine (Figure 4a) and limber pine

341(Figure 5a) adult basal area is largely explained by soil type. Since dolomite is set as the

342intercept by elastic net regularization, and since limestone has a similar effect as dolomite, they

343do not show up with a coefficient on the figures below. In the case of bristlecone pine, granite

344and quartzite soil both have a large negative effect relative to dolomite which would also make

345the inverse true: dolomite soils have a large positive effect relative to granite and quartzite.

346Mountain range also strongly predicted bristlecone pine adult basal area, having a strong positive

347association with the Spring Mountains and a negative association with the Snake Range. Adult

348bristlecone pine basal area was positively associated with cooler north-facing and east-facing

349slopes and negatively associated with latitude. As expected, adult limber pine basal area is

350positively associated with granitic and quartzite soils, thus indicating niche differentiation from

351bristlecone pine, which is positively associated with calcareous soils. Limber pine adult basal

352area was only moderately associated with mountain range but had a strong positive association

353with latitude indicating higher basal areas in the northern part of the study area. It also had a

354negative association with east aspect indicating higher treeline advance on warmer west-facing

355slopes. Both species had a number of other small, but non-zero, associations with basal area

356(Figures 4a and b).
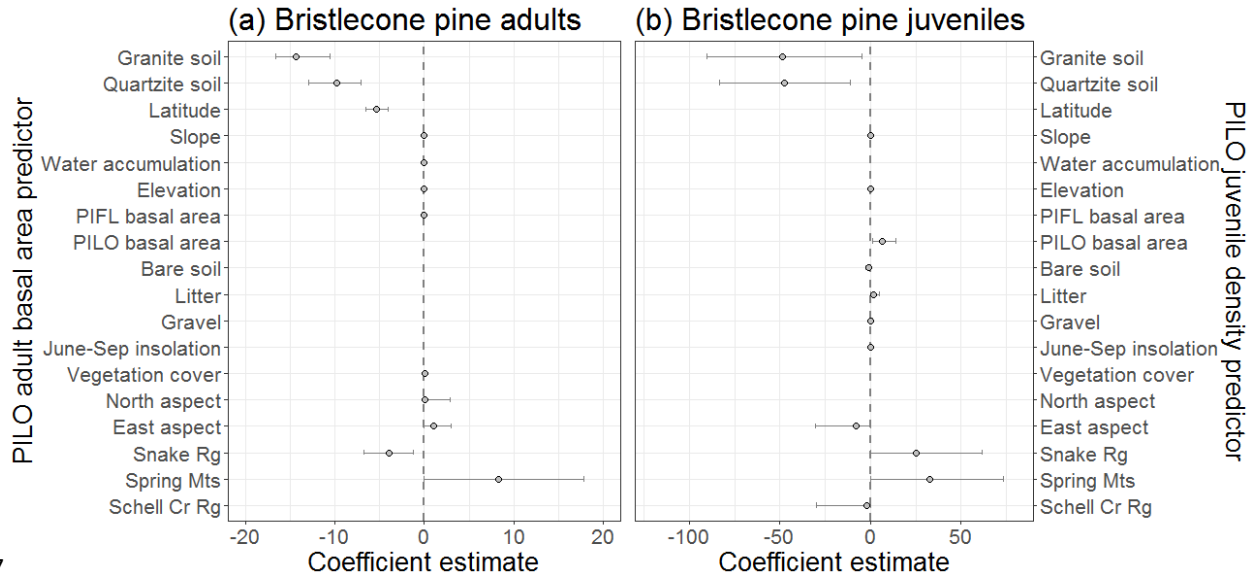
Figure 4: Bristlecone pine predictors

Slope coefficients for predictors of (a) adult bristlecone pine basal area below treeline and (b) established bristlecone pine juveniles above treeline. All points are non-zero 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 non-zero value.

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

374(positive for adults, negative for juveniles) indicating that while adults and juveniles share some

375predictors, they do not share all of them and for at least some predictors, respond oppositely.

376Models of limber pine above-treeline juvenile density included very few predictors, and shared

377only one of those predictors with the model for limber pine adults (Figure 5). Further, the only

378shared coefficient, quartzite soil, has an opposite sign for adults and juveniles. Most strikingly,

379while adult limber pine density was strongly associated with granitic soils, above-treeline

380juvenile density had no association with granitic soil. Limber pine juveniles responded to far

381fewer and different parameters than limber pine adults suggesting that limber pine juveniles have

382different and broader tolerances than adults.
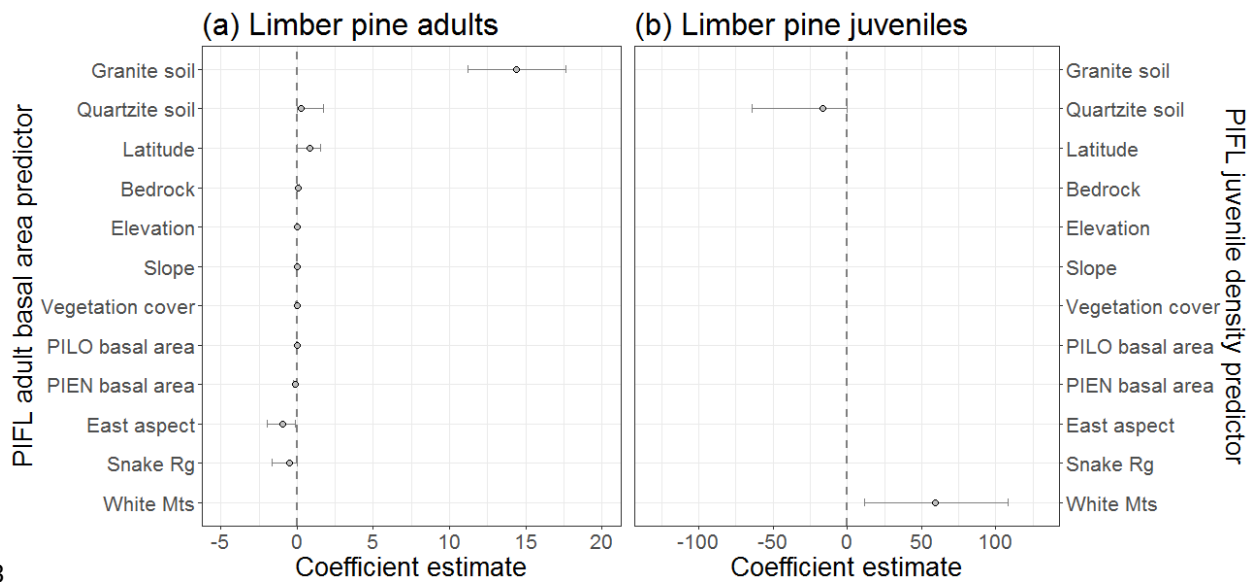
383
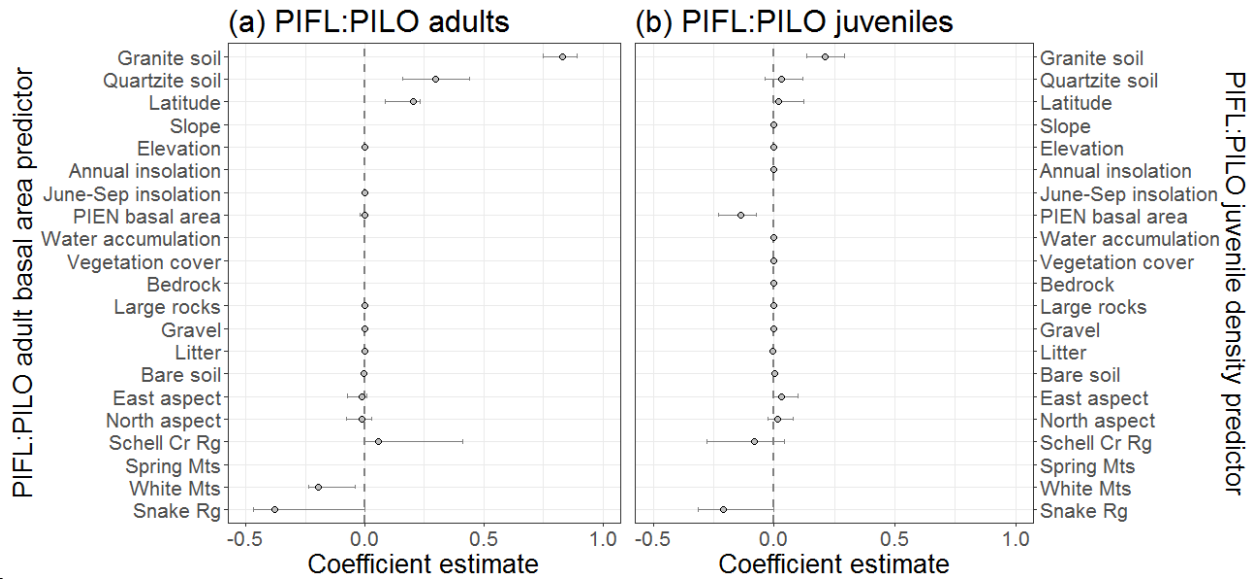384**Figure 5: Limber pine predictors**

385Slope coefficients for predictors of (a) adult limber pine basal area below treeline and (b)

386established limber pine juveniles above treeline. All points are non-zero coefficients chosen by

387glmnet using the lasso penalty. Predictors without a point were not found to improve the model

388and so, while not included, are shown here for comparison purposes. Confidence intervals (95%)

389are included only as a visual estimate of parameter variability and *are not* meant to indicate the

390statistical significance of a parameter. Glmnet includes all parameters that improve a model and

391so are included in the model if they have a non-zero value.

392

393   A positive coefficient for the ratio of limber pine to bristlecone pine adult basal area

394adults or juvenile density (PIFL:PILO) indicates a predictor that favors limber pine over

395bristlecone pine. For adult basal area there is a strong positive effect of granite soil on

396PIFL:PILO as expected (Figure 6a). There is also a strong positive association between latitude

397and adult basal area indicating a gradient of more bristlecone pine further south and more limber

398pine further north as well as positive and negative effects of individual mountain ranges. For

399juvenile density, models identify the same positive association of PIFL:PILO with granitic soil,

400due mostly to juvenile bristlecone pine's near absence on granite (Figure 6). While there are

401some shared predictors for adult and juvenile PIFL:PILO, many are unique and some of the

402predictors with smaller coefficients, such as those for north and east aspects, switch from

403negative (adults) to positive (juveniles) associations. A switch like this would indicate that for

404example on east aspects, adult bristlecone pines have a higher basal area than adult limber pine,

405but that for juveniles, bristlecone pines have a lower density than limber pines.

406   There is also a relationship between PIFL:PILO and substrate size. In adults, PIFL:PILO

407is positively associated with large rocks and gravel and negatively associated with bare soil and

408litter. In juveniles, PIFL:PILO is positively associated with bare ground, large rocks and bedrock

409while being negatively associated with gravel and litter. This would indicate that there is more

410limber pine relative to bristlecone pine on substrates composed of larger rock sizes.
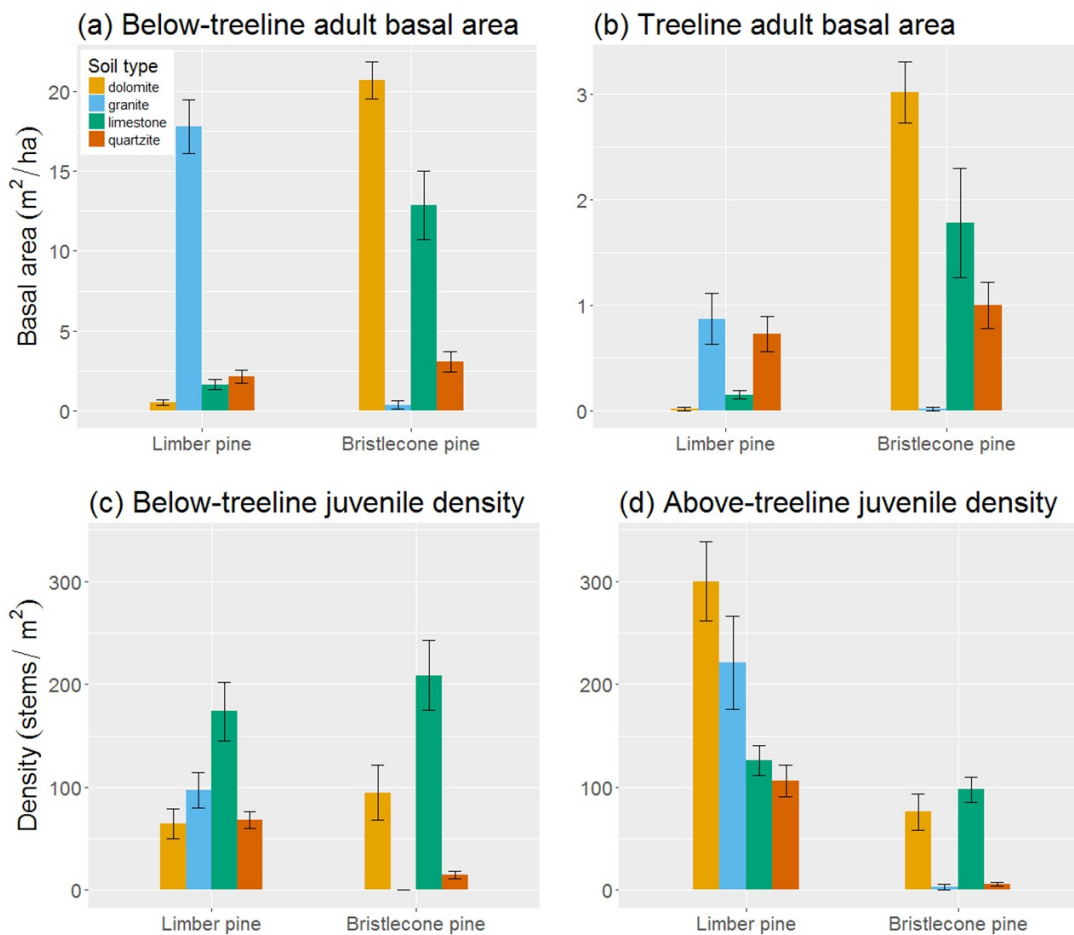
Figure 6: Limber pine : bristlecone pine predictors

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 non-zero 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 non-zero value.

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

428differences (Figure 7b). First, basal areas were lower at treeline as the trees become less dense at

429the edge of their tolerable range. Second, with the exception of granitic soils, limber pine basal

430area was considerably lower at treeline than that of bristlecone pine. This finding is consistent

431with general forest composition patterns in the Great Basin: when bristlecone pine is present in a

432stand, it is generally the dominant tree species at treeline, with some notable exceptions,

433especially on granitic soil.

434
435
436**Figure 7:** Comparisons of adult basal areas for limber pine and bristlecone pine in (a) the mid-

437stand below treeline forest and (b) at treeline and juvenile density (c) below treeline and (d)

438above treeline. Below-treeline and treeline basal areas are shown on different scales to allow

439visualization of the soil preference relationship. All error bars are 1 SE of the mean.

440

441

442   Below-treeline juvenile density of both species followed a similar pattern to adult basal

443area (Figure 7a,c). Bristlecone pine adults dominated on calcareous dolomite and limestone but

444had low basal area on granite. Below-treeline juvenile bristlecone pine had the same relationship

445with higher juvenile density on limestone and dolomite soils than limber pine. Where adult

446limber pine dominates on granite, the juvenile density is also high, unlike bristlecone pine

447juveniles which are almost entirely absent on granite (Figure 7c). However, limber pine juvenile

448density was higher generally on all soil types than the adult basal area relationship with soil type

449would imply. These relationships break down entirely above treeline where limber pine juveniles

450dominated on every soil type (Figure 7d). This is especially true on dolomite, a soil that is core

451bristlecone pine habitat, and on which very few adult limber pines were found (Figure 7b,d).

452Above-treeline bristlecone pine juvenile densities maintained the expected soil relationships

453based on adult basal area and soil type, but on every soil type, bristlecone pine juvenile density

454was considerably lower than limber pine juvenile density above treeline.

455

456**Discussion:**

457   Results from this study suggest three key findings. The first is that treeline is advancing

458in Great Basin mountains where bristlecone pine and limber pine are present. So far, the juvenile

459establishment would predict a region-wide increase for both species with a vertical mean of 19.1

460m since approximately 1950 (Billings & Thompson, 1957). The major predictors for higher

461advancing establishment relative to treeline are forest stands on granitic and limestone soils on

462south and west aspects and in more easterly mountain ranges like the Snake Range. However, we

463found upslope establishment in all mountain ranges included in the study. The second finding is

464that while bristlecone pine adults and above-treeline juveniles share some environmental

465predictors for their abundances, limber pine adults and above-treeline juveniles do not. The third

466finding is that juvenile limber pine density dominates that of bristlecone pine above treeline,

467especially on soils like dolomite where adult bristlecone pine dominates in currently established

468stands below treeline. Limber pine appears to have "leap-frogged" over bristlecone pine to

469dominate the newly expanding treeline in forests of the Great Basin, as found in a study of

470smaller extent (Millar *et al.*, 2015).

471   While these findings point to interesting potential changes in tree species composition

472above treeline, some caution is required in interpreting these results. We designated treeline as a

473line based on generally accepted criteria, but treeline is more accurately an ecotone between the

474sub-alpine forest and the alpine zone. Since it is an area of transition, determining this line can

475seem subjective. For the sake of consistency and clarity, experts have accepted a definition of

476treeline as being the line connecting clumps of trees at least 3 m in height (Körner, 1998, 2012;

477Paulsen *et al.*, 2000). We have adhered to this definition in measuring treeline advance distances

478while understanding that this measurement includes a certain amount of variance. Also, this

479study uses juveniles to project what treeline is likely to look like in the future since the juveniles

480(<100 years old) used for this projection are all under 3 m in height and do not meet the accepted

481definition of a "tree." Our findings rest on the premise that most established juvenile trees will

482survive to 3 m height in order to constitute a higher treeline. There is strong evidence in favor of

483this assumption, as previous studies have found very high (up to 99%) survival of bristlecone

484pine and limber pine once they become established after the first five years (Elliott, 2012;

485Barber, 2013; Conlisk *et al.,* 2017). Since we excluded juveniles under 5 years of age, it is likely

486that the vast majority of the juveniles measured will survive to adulthood. A pulse stress event

487that produced differential mortality between the two species might mean that the juvenile

488demographics seen today will not match the adult demographics of the future treeline.

489

490*Treeline advance*:

491   Studies predicting or showing treeline advance are common in the literature (Lescop-

492Sinclair & Payette, 1995; Grace *et al.*, 2002; Lloyd & Fastie, 2003; Truong *et al.*, 2007;

493MacDonald *et al.*, 2008; Elliott, 2011), as are studies showing a lack of treeline advance

494(Camarero & Gutiérrez, 2004; Gehrig-Fasel *et al.*, 2007; Payette, 2007; Harsch *et al.*, 2009;

495Dolanc *et al.*, 2013). Where treeline advance was not found, other treeline responses to warming

496are often seen such as sub-alpine infilling of trees (Millar *et al.*, 2004; Dolanc *et al.*, 2013),

497vertical release from the krummholz growth form (Lescop-Sinclair & Payette, 1995; Millar *et al.*,

4982004; Cairns, 2005), and growth changes (Wilmking *et al.*, 2004; Salzer *et al.*, 2009). Studies

499quantifying treeline advance have shown variable results given the difficulty in determining

500exact elevations for historic and current treeline. An even bigger problem is teasing apart the

501effects of recent anthropogenic warming on treeline advance from other human disturbance

502effects such as logging or grazing (Gehrig-Fasel *et al.*, 2007; Harsch *et al.*, 2009).

503   Compared with other studies that have quantified treeline advance, our mean vertical

504treeline advance of 19 m is relatively small. In the European Alps, treeline was found to advance

505115 m since 1900 in response to a 1.7°C temperature increase (Leonelli *et al.*, 2011). Studies in

506the Ural Mountains have documented a 40-80 m treeline advance in response to increased winter

507temperatures (Kammer *et al.*, 2009; Hagedorn *et al.*, 2014). The Scandes Mountains have seen a

50870-90 m increase in treeline elevation (Kullman & Öberg, 2009). There may be several reasons

509for this disparity. For example, the 1.7°C increase in the Alps is almost double the temperature

510increase documented in the western Great Basin (Millar *et al.,* 2015). In the Scandes Mountains,

511it is unclear whether that treeline advance response is a function of recent temperature increases

512or recent land abandonment (Gehrig-Fasel *et al.,* 2007). A recent study in the western Great

513Basin documented pine regeneration as much as 225 m from forest boundaries, which would

514equate to vertical distance of 35 – 220 m when factored with our measured range of slopes

515(Millar *et al.,* 2015). However, this study included other forest boundaries in addition to treeline

516possibly skewing their results.

517   One possibility for our lower treeline advance relative to other ranges may be the extreme

518longevity of bristlecone pine and limber pine, with adult trees on the landscape establishing

519during a warmer climatic period, perhaps during the Medieval Warm Period (950-1250$_{CE}$) but at

520least before the first climatic minimum of the Little Ice Age (1650$_{CE}$). Given the documented 1°C

521Great Basin temperature increase in the last century, the dry adiabatic lapse rate would project a

522100m increase in treeline. Our mean of 19.1 m is considerably less than this predicted value

523which suggests one of two options: 1) there is still significant upslope area that is climatically

524available for regeneration pointing to at least decades long lags in climate change response

525(Kroiss & HilleRisLambers, 2014), or 2) the climatic zone where trees were able to regenerate in

526the most recent regeneration period, the 'regeneration line', was historically well below the adult

527treeline and, as temperatures have increased, has only recently moved upslope through adult

528treeline to its current above-treeline location. If the current regeneration line is at the upper

529extent of climatically available habitat, the adiabatic lapse rate would estimate the historical

530regeneration line at 100 m below our "new" treeline, or 80 m below current adult treeline. This

531theory fits well with observations of a lack of regeneration near treeline in the mid-1900s and a

532current lack of recent treeline relict wood on the landscape, which tends to persist for 100s-1000s

533of years (Billings & Thompson, 1957; Wright & Mooney, 1965; LaMarche Jr, 1973). Other

534climatically extreme systems have seen similar lags (Payette, 2007).

535   There are other confounding factors concerning recent warming-induced treeline

536advance. For example, while temperature ultimately limits tree distributions, establishment filters

537such as water availability are more proximate limiters to range shifts (Lloyd & Graumlich, 1997;

538Daniels & Veblen, 2004; Moyes *et al.*, 2015; Conlisk *et al.*, 2017). We found soil type to be a

539strong predictor of higher treeline advance, especially on granitic soil. While granite is a

540relatively drier soil owing to its low water-holding capacity (Wright & Mooney, 1965), it is the

541only soil type in the study area dominated by limber pine at treeline. Other notable predictors

542include a positive association of treeline advance with topographic water accumulation and a

543negative association with large rocks and gravel. These responses indicate that treeline advance

544is likely facilitated by better water-holding soils and areas that accumulate more water. The large

545negative effects of latitude and east aspect are interesting in that they appear to indicate that

546treeline advance is greater in southern ranges on west-facing slopes. Taken together, treeline

547advance was highest in warmer areas where limber pine is the dominant treeline tree.

548

549*Life stage predictors:*

550   Species distribution models using climate niche are very common, especially those which

551use models to project future species distributions under climate change (Hijmans & Graham,

5522006). However, species distribution models are often based on matching adult distributions to

553climatic conditions, while not taking into account biotic interactions, dispersal effects, and life

554stage differences in climatic tolerances (Pearson & Dawson, 2003; Guisan & Thuiller, 2005;

555Heikkinen *et al.*, 2006; Araújo & Luoto, 2007). Mechanistic models which use knowledge of a

556species' physiology, ecological roles, population trends, and/or life stage differences can perform

557better than climate envelope models that rely only on climatic parameters (Hijmans & Graham,

5582006; Kueppers *et al.*, 2016; Ralston *et al.*, 2017). By comparing predictors for adults and young

559trees, we can learn about environmental filters for multiple life stages that will influence range

560shifts.

561   For bristlecone pine, predictors are similar for adults and above-treeline established

562juveniles. Both are positively associated with the Spring Mountains, the most southerly range.

563They are both negatively associated with granite and quartzite soils. Granite is a very porous soil

564and has a poor water holding capacity. Quartzite is usually darkly colored and so is warmer than

565white dolomite or light grey limestone, both being carbonate soils (Wright & Mooney, 1965).

566This would have the effect of increasing drought stress, especially on juvenile trees. Soil particle

567size also appears to have an effect on bristlecone pine establishment (but not on adult basal area).

568We found a small negative effect of increased bare soil (<1 cm particle size) and a small positive

569effect of gravel (1-20 cm particle size). Bristlecone pine seeds are small and generally gravity-

570dispersed with the seeds landing on the soil surface. These seeds are almost entirely consumed

571by seed predators. Seeds not consumed but on the soil surface also fail to germinate, likely due to

572the lack of surface moisture (Barber, 2013). Soils with larger particle size, however, may allow

573some seeds to fall between the soil particles, providing both protection from predation and a

574better microclimate for germination. Sub-alpine trees are often found growing from under "nurse

575rocks" suggesting that seeds protected from predators and desiccation are more likely to

576establish.

577   Limber pine juveniles do not appear constrained by the same environmental factors

578affecting limber pine adults. While adults have relatively small responses to a number of

579predictors, they are largely predicted by granitic soil. Juveniles are not well predicted by soil

580type, and in fact though limber pine juveniles were prevalent in almost every plot, few

581environmental variables were associated with juvenile density. Even high adult limber pine basal

582area failed to predict juvenile density. Since we observed high overall limber pine regeneration

583(Figure 7), as have other studies in the Great Basin (Millar *et al.*, 2015), this finding strongly

584suggests that limber pine juveniles have relatively wide environmental tolerances. Therefore,

585while there are strong environmental or dispersal filters operating on bristlecone pine juveniles,

586above-treeline limber pine juveniles appear to have less constrictive filters.

587   The relative ratios between limber pine and bristlecone pine (PIFL:PILO) and substrate

588size suggests a relative preference for limber pine in areas with larger rocks and exposed

589bedrock. This appears to be the case for both adults and juveniles. The difference in the limber

590pine to bristlecone pine ratio points either to a relative difference in limber pine's ability to

591establish on larger substrate sizes or to a difference in its ability to disperse to microsites with

592preferred substrates. Either way, the ratio indicates an important role for 'nurse rocks' whereby

593larger rocks provide more mesic microsites than low-texture surfaces for establishing seedlings

594by moderating temperature, blocking wind, and/or maintaining soil moisture (Resler *et al.*, 2005;

595Pyatt *et al.*, 2016). Both species would likely benefit from establishing near nurse rocks, thus a

596higher relative abundance of limber pine in larger substrates suggests that limber pine is better

597able to disperse to these preferred nurse rock microsites. While there is much less topographic

598texture in the Great Basin relative to the Rocky Mountains where many abiotic facilitation

599studies have taken place, it would appear that this nurse effect is still an important driver of

600species distributions. Interestingly, with limber pine and bristlecone pine in the Great Basin,

601there is no evidence of biotic facilitation wherein an individual above-treeline tree creates a more

602mesic microsite under which a tree island can form, as seen in whitebark pine treelines (Resler *et*

603*al.,* 2014; Tomback *et al.,* 2014).

604

605

606*Adult basal area and upslope juvenile density:*

607   Above-treeline limber pine juveniles established in higher densities than bristlecone pine

608throughout the Great Basin, especially on dolomite, a soil type that is known to be strongly

609associated with bristlecone pine (Wright & Mooney, 1965; Charlet, 1996). The assumption has

610been that bristlecone pine is dominant on dolomite because other species do not tolerate the high-

611pH, high-magnesium, and low-phosphorus soil (Wright & Mooney, 1965; Butler *et al.,* 2007;

612Maher *et al.,* 2015). In these stands, adult cone-producing limber pines are rare. However, it is on

613these soil types that limber pine regeneration is highest (Figure 7d). One reason for high

614regeneration likely has to do with water limitation. While deep-soil water is typically not in short

615supply for adult trees in Great Basin treelines (Salzer *et al.,* 2009), studies examining tree

616recruitment at and above treeline show that water is often limiting at the surface where young

617trees access it (Moyes *et al.,* 2013; Kueppers *et al.,* 2016; Conlisk *et al.,* 2017). Relative to

618quartzite and granite, carbonate soils (like dolomite and limestone) are lighter in color which

619reduces the surface temperature, and thus evaporative demand, while also having a finer grain

620and better water-holding capacity (Wright & Mooney, 1965). It is likely the improved water

621retention in dolomite and limestone make it more tolerable to juvenile trees. And despite the low

622numbers of adult limber pine on dolomite and limestone (Figure 7a and b), these soil types

623appear to be an amenable substrate for juveniles.

624   This contrast of many juvenile limber pines but few adults on dolomite soils raises an

625obvious question: how are all of these limber pine seeds getting there? Small-seeded bristlecone

626pine seeds are primarily dispersed by wind with the majority of regeneration occurring near adult

627trees (Benkman, 1995; Coop & Schoettle, 2009, but see Lanner *et al.*, 1984). The vast majority

628of these seeds are consumed by rodent seed predators (Barber, 2013; Maher *et al.*, 2015). Limber

629pine seeds are large and nutritious and so are targeted by Clark's nutcracker (*Nucifraga*

630*columbiana*), a high-elevation corvid that tears apart limber pine cones, removes the seeds and

631then travels up to 22 km away to cache the seeds for future consumption (Vander Wall, 1988;

632Lanner, 1996; Tomback *et al.,* 2005; Siepielski & Benkman, 2008). Since seeds are buried at an

633optimal depth for germination, are hidden from other seed predators, and at least some of the

634cached seeds are not consumed, limber pine seeds are "planted" throughout the landscape. This

635is also likely to provide an advantage for seeds which area cached (limber pine) near nurse

636objects over wind-dispersed seeds (bristlecone pine) (Malanson *et al.*, 2007; Tomback & Resler,

6372007)

638   Even among those seeds that are not consumed, successful establishment is rare, often

639occurring in pulses coinciding with multiple years of higher summer and autumn precipitation

640and lower summer temperatures (Barber, 2013; Millar *et al.*, 2015). Since no colonization above

641treeline was apparent in the mid-20th century, it is likely that the climatic conditions have

642changed enough in the last 50 years for what was climatically inhospitable habitat at and above

643treeline to recently become a large area of suitable seedling habitat. Ongoing research is

644examining the local and broad-scale genetic population structure between the two species to

645assess how differences in dispersal strategies might be resulting in genetic differentiation among

646populations. If limber pine does have a dispersal advantage, it may be more able than bristlecone

647pine to take advantage of a rapidly warming climate.

648   There is an interesting paradox concerning the elevational and latitudinal distributions of

649adult limber and bristlecone pines. While in bristlecone pine's range it is found at higher

650elevations than limber pine (Charlet, 1996; Millar *et al.*, 2015), limber pine's range extends far to

651the north relative to bristlecone pine (Figure 1). If cold tolerance were the only driver for these

652distributions, we would expect bristlecone pine to be found both higher up and further north.

653There are a number of possible explanations for this, although most are outside the scope of this

654paper. While limber pine's range extends far to the north relative to bristlecone pine, it also

655extends relatively further to the south, hinting that limber pine generally has either more genetic

656variation or phenotypic plasticity allowing it to live in a greater diversity of climatic conditions.

657Limber pine is known to grow well across an unusually wide range of elevations and conditions

658and while the high gene flow of this bird-dispersed species results in little genetic differentiation

659among populations, phenotypic plasticity with regard to stomatal density across elevational

660gradients has been noted which may account for this greater distribution of limber pine

661(Schoettle & Rochelle, 2000). A final speculative reason for this difference in elevational and

662latitudinal ranges may be that while temperature certainly limits both species' ranges, water

663limitation is an especially acute limiting factor in the Great Basin relative to much of limber

664pine's range (Moyes *et al.*, 2013; Kueppers *et al.*, 2016). While our ongoing research will seek to

665examine the relative effects of water stress on limber and bristlecone pine, we currently lack an

666understanding of the relative importance of water limitation on these species at treeline.

667

668*Significance*:

669   This study highlights the importance of recognizing differences in life stage tolerances to

670climatic conditions. At treeline, adults are exposed to the extreme cold and wind of winter while

671juveniles are protected under insulating snow. During the summer, adult trees can tap readily

672available water deep in the soil that is unavailable to seedlings facing summer drought. Matching

673adults to climatic conditions, such as in a species distribution model, is likely to be insufficient to

674predict species distributions since filters may differ significantly among life stages. This study

675also highlights that there are interspecific differences in the relationship between adult and

676juvenile responses to climatic parameters. Here, bristlecone pine adults and juveniles share some

677predictors while limber pine adults and juveniles do not, even though climatic conditions that

678support increased limber pine growth in adults have been shown to be the same that support

679limber pine recruitment (Millar *et al.*, 2015).

680   Treeline is advancing throughout the Great Basin, primarily through downslope limber

681pine "leap-frogging" over treeline bristlecone pine. This is happening even on soils types like

682dolomite that have historically been dominated by bristlecone pine adults. These forests are low-

683density stands, likely due to water limitation, shade intolerance, and limited suitable

684establishment micro-sites. If a species is able to establish first, it might be able to pre-empt other

685tree species, at least in the short term, which in these forests can extend to thousands of years.

686Priority effects can only occur when the initial colonizer is able to exclude subsequent species

687from establishing. Whether this is occurring with limber and bristlecone pine remains to be seen,

688but in these harsh conditions where both light and water limitations are acute and establishment

689microsites are rare, initial establishment may cause a priority effect even in the event of low-

690density establishment. While sub-alpine trees have been documented expanding their range

691downslope in some unusual slope conditions such as downslope cold air pooling (Millar *et al.*,

6922015), on most slopes, treeline advance upslope is also possibly happening in conjunction with

693contraction at the lower range margins (Kueppers *et al.*, 2016). If bristlecone pine is contracting

694at its lower range margin and unable to advance upslope because it is blocked by limber pine,

695bristlecone pine would face overall range contraction and possibly local extirpations. With

696individual bristlecone pines being the oldest known non-clonal individuals on earth, a loss of

697some of these populations would be a loss of great cultural significance.

698

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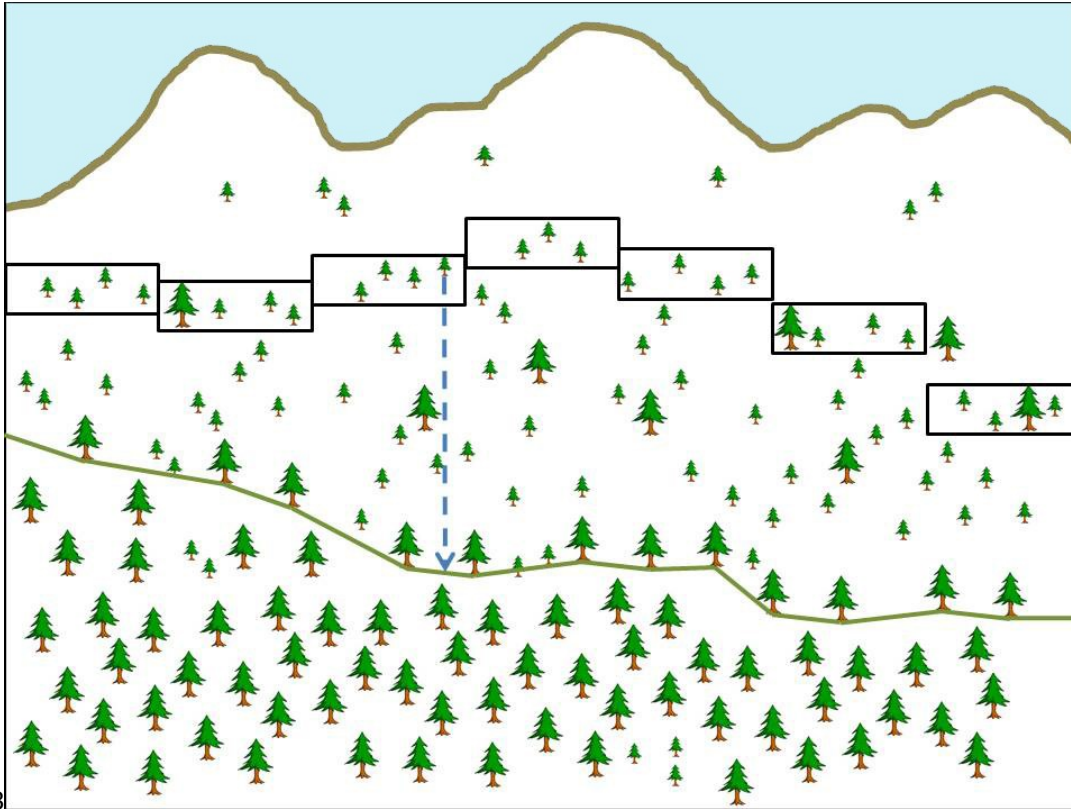
Supplement 1: Above-treeline Plot Placement

Plots were placed as a modified belt transect in which the plots (black rectangles) were

connected but allowed to move up and down in elevation each 30 m to meet our above-treeline

criteria. Vertical distance to treeline (blue dashed line) was measured from each tree in the plot

down the vertical fall-line to the line connecting the highest continuous adult trees (green line).