

THESIS

FOREST RANGE SHIFTS UNDER CLIMATE CHANGE: MICROENVIRONMENT
IMPACTS TO TREE RECRUITMENT AT A CLIMATIC ECOTONE

Submitted by

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ABSTRACT

FOREST RANGE SHIFTS UNDER CLIMATE CHANGE: MICROENVIRONMENT IMPACTS TO TREE RECRUITMENT AT A CLIMATIC ECOTONE

Warming across the western United States is projected to cause dramatic shifts in tree species recruitment, with the most pronounced changes in composition at range edges where species are at their thresholds of reproductive tolerance. Yet microenvironments experienced by juvenile trees can be decoupled from regional climate due to variations in canopy cover, microtopography, and organic matter. As a result, tree recruitment may be strongly controlled by microenvironments and not follow species range projections based on regional climate, even at ecotone boundaries in which species at their upper range distributions are predicted to increase in density. This is likely especially pronounced in undisturbed forests with dense canopy cover in which microclimate is more strongly de-coupled from regional climate. To address these hypotheses of tree recruitment at species range margins we conducted a field experiment and observational study at the upper montane – subalpine ecotone on the Colorado Front Range. We characterized site microenvironment and observed germination and survival of six common conifer species, Douglas-fir, ponderosa pine, lodgepole pine, subalpine fir, Engelmann spruce, and limber pine. To quantify water availability and wildlife limitations, we sowed seeds from five study species and applied treatments of simulated precipitation and wildlife exclusion. Strong recruitment limitations were observed for nearly all species in experimental and observational studies, with strong negative effects of low soil moisture and maximum temperature. Notably, only subalpine fir exhibited increased seedling dominance, likely due to

the limited light availability and cooler temperatures associated with shaded microenvironments. Recruitment success was unrelated to range position and do not match established migration predictions for these species. This research further illustrates the complexity of recruitment dynamics and the need to study regeneration at multiple scales.

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CHAPTER 1: MICROENVIRONMENT EFFECTS ON TREE SEEDLING RECRUITMENT AT A CLIMATIC ECOTONE

1.1 Introduction

The distribution and abundance of tree species in western forests of the United States are broadly defined by disturbance regimes and physiographic factors that influence water availability and temperature-related stress (Woodward and Williams 1987, Brown et al. 1996, Brown and Wu 2005, Soberón and Nakamura 2009, Davis et al. 2019a). Ongoing climate change in the western United States has geographically shifted portions of some tree species' niche space beyond their current distributions and is altering the recruitment dynamics of mixed-conifer forests, especially near climatic ecotones (Rehfeldt et al. 2006, Kelly and Goulden 2008, Ray et al. 2008, Wein et al. 2012, Gray and Hamann 2013). Recruitment dynamics will be a defining factor in how forest composition is altered by changing conditions, yet it is unclear how potentially novel climates will interact with local conditions to impact forests (Nedlo et al. 2009, Corlett and Westcott 2013, Kroiss and HilleRisLambers 2015).

The largest changes in tree species distributions in western North America are predicted to occur in the Rocky Mountains, where species already lag behind their optimal climate niche by as much as 60 m in elevation (Gray and Hamann 2013). Evidence of substantial range shifts is accumulating, with species failing to recover from large-scale environmental stressors such as drought (Bassman et al. 2003, Kelly and Goulden 2008, Chen et al. 2011). At the same time, these broad-scale shifts have highlighted the importance of microenvironment in buffering the effects of climate change on species composition and suggest that that species dynamics may become increasingly decoupled from regional shifts in climate (Jackson et al. 2009, Serra-Diaz et al. 2015, Davis et al. 2019b).

It is generally expected that, based on climate niche models, species will migrate upward in elevation and poleward in latitude, but it is predicted that migration will be limited and some species will experience range contractions overall (Chen et al. 2011, Zhu et al. 2012, Dobrowski et al. 2015). The speed with which climate is changing may exceed the ability of many species (e.g. K-selected species with long lags before juveniles reach reproductive maturity) to keep pace (Swetnam and Betancourt 2010, Fellows and Goulden 2012, Renwick and Rocca 2015). Likewise, experimental transplant and seed-sowing studies to stimulate the ability of tree species to migrate to higher elevations have provided mixed results (Moyes et al. 2015, Conlisk et al. 2017, Kueppers et al. 2017a). Many dominant species, such as Engelmann spruce (*Picea engelmannii*), are expected to lose more than two-thirds of suitable habitat by 2090 (Rehfeldt et al. 2006).

It is clear that microenvironment will play an increasingly important role in future climate scenarios, perhaps serving as the determining factor in the ability of tree species to both persist locally and to migrate to new areas (Von Arx et al. 2013, Serra-Diaz et al. 2015, McLaughlin et al. 2017). Climate-based models are an important tool, but they are unable to directly account for many of the key factors which determine seedling recruitment at smaller scales (Clark et al. 1998, 2016, Suggitt et al. 2011, Larson and Funk 2016). Microenvironment and understory conditions created by disturbance are especially influential determinants of tree recruitment and range shifts in the Rocky Mountains. Indeed, the effects of disturbance have been found to both facilitate rapid range expansions or restrict range shifts depending on the context (Kulakowski et al. 2013, Renwick et al. 2016). Successful regeneration depends on a series of favorable events; microenvironment effects such as understory vegetation and seedbed conditions necessary for one stage may prove constraining in different microenvironments or at

different life history stages (Callaway and Walker 1997, Clark et al. 2007, Kroiss and HilleRisLambers 2015).

Microenvironment conditions, primarily defined by microclimate, are essential in initiating seed germination and can strongly limit initial seedling establishment (Alexander and Noble 1971, Germino et al. 2002, Johnson et al. 2004, Maher et al. 2005). Requirements differ widely by species in the Rocky Mountains, with moisture retention properties of the microenvironment serving as the primary determinant of regeneration success, both for early survival and as a cue for germination (Alexander 1987, Brown and Wu 2005, Redmond and Barger 2013, Kroiss and HilleRisLambers 2015, Kueppers et al. 2017b, Andrus et al. 2018b). Precipitation patterns are only partially indicative of available moisture as microenvironment conditions (e.g. temperature, soil depth, canopy cover, slope, and seedbed) can greatly affect moisture retention (Maher and Germino 2006, Landhäusser et al. 2010, Kelsey et al. 2017). Additionally, certain forest floor covers, such as moss, can provide more consistent moisture, whereas others, such as leaf litter, have greater evaporative potential and can cause seedlings to be more prone to desiccation (Lamont et al. 1993, Wheeler 2009, Gray and Spies 2016).

Colorado Front Range forests are well-suited to study tree regeneration as the history and structure of these forests has been catalogued in depth (Daubenmire 1943, Alexander 1974, Peet 1981, Battaglia et al. 2018). Existing literature of Colorado upper montane and subalpine tree species suggest that new recruits experience limitations due to microenvironment conditions, primarily those related to microclimate, canopy openness, seedbed substrate, and surrounding understory vegetation (Table 1.1; Knapp and Smith 1982, Stohlgren and Bachand 1997, Buechling et al. 2017). Moisture is understood as a primary limitation to recruitment in western forests and snowpack is as an important source of long-lasting and slow releasing moisture in

subalpine forests (LaMalfa and Ryle 2008, Hu et al. 2010, Hill et al. 2019). Microenvironment has the potential to mitigate losses in soil moisture during periods of drought and consequently strongly influence tree recruitment dynamics, but has not yet been formally addressed within Colorado Front Range forests (LaMalfa and Ryle 2008, Kelsey et al. 2017, Andrus et al. 2018b).

We established a long-term study site at the upper montane-subalpine forest ecotone on the Colorado Front Range to investigate emerging range shifts and address knowledge gaps in microenvironment effects on tree regeneration in the southern Rocky Mountains (Figure 1.1). We investigated the range of available microenvironments in a closed canopy forest with co-occurring populations of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce and analyzed how these conditions served to influence seedling survival in the absence of disturbance. We hypothesized that (1) species at the upper end of their range would exhibit higher rates of survival overall, and (2) survival will be tied to the availability of suitable microenvironments, which will differ by species. Our results will help build understanding of site-scale limitations to southern Rocky Mountain tree species which are predicted to experience significant range shifts with climate change.

1.2 Methods

1.2.1 Study site

The study site is located in Boulder County in the Colorado Front Range north of Peaceful Valley at approximately 2700 m in elevation (Fig. 1.1). The site is in the mixed mesic forest type at the interface of upper montane and subalpine forest types per Peet (1981). Climate warming has been observed at this site over the last half-century with mean minimum

temperatures increasing especially rapidly, which likely favors species differently based on the range of their climatic tolerance and regenerative thresholds (Fig. 1.2). Mean annual precipitation is 618 mm, primarily in the form of snow with snowmelt occurring in May- June (PRISM Climate Group 2019). Mean growing season temperature ranges from a mean minimum of 5.2°C to a mean maximum of 19.4°C. During the study period (2017 and 2018), annual mean maximum and minimum temperatures were warmer than 70-year normals; notably, the warmest annual mean temperature in the last 70 years occurred in the second year of our study. The first year was wetter than typical (56 mm above 70-year normal growing season mean) while the second year experienced a significant drought during the growing season (total precipitation 91 mm below 70-year normal mean annual) (PRISM Climate Group 2019). Soils are derived primarily from Leighcan family till substratum with glacial till and alluvium parent material derived from igneous and metamorphic rock (NRCS 2019). When present, understory vegetation is dominated by ericaceous species. The site is free of recent major disturbance with no evidence of multi-tree blowdown, harvest, recent fire, or widespread insect outbreaks within the study site.

The study site was divided into three separate plots to obtain large enough numbers of all species. The site's slope and aspect are flat overall, but there are small-scale changes in elevation ($\pm$ 5-10 m) within each plot, which creates a rolling topography and significant variation in microtopography. Elevation across the entire site is fairly uniform and all plots are within 30 m in elevation of each other. The main plot (2.25 ha) is dominated foremost by lodgepole pine and then by subalpine fir, with sizeable patches of aspen and scattered individuals of all other study species. The north plot (0.15 ha) is slightly north-facing and near the cooling influence of a wet meadow and stream and is dominated by Engelmann spruce and subalpine fir. The south plot (0.80 ha) is positioned on a slightly more south-facing aspect and is primarily comprised of

lodgepole pine, ponderosa pine, and Douglas-fir. Limber pine is present throughout all plots, although it is never highly abundant, as is typical of this species in mixed stands (Table 1.2).

1.2.2 Field sampling

Study at the site began in 2016 with mapping, measuring, and tagging all live and dead adult stems ($\text{DBH} \geq 10 \text{ cm}$) within the study site. To capture potential regeneration of all of our study species, we established ninety-five 1 m^2 seedling quadrats using a stratified random design based on distance from a seed producing adult. Mature, seed-producing individuals of each study species were identified using the stem map and quadrats were placed at varying distances (1-10 m) and random cardinal directions from each of these seed trees. Within each 1 m^2 quadrat we quantified the abundance of germinants and established seedlings, germinant survival, and associated microenvironment characteristics over two growing seasons in 2017 and 2018. Survivorship and health status of new germinants was monitored throughout the growing season (June- September) in 2017 and 2018. Established seedlings (individuals with age > 1 year and height $< 1 \text{ m}$), within 1 m^2 quadrats were measured at the end of the growing season. Aspen was not included in the study as the majority of its reproduction occurs vegetatively and it was not possible to distinguish suckers from germinants without destructive sampling.

Quadrat microenvironment was characterized for seedbed cover, understory plant composition, canopy openness, and microclimate within all ninety-five 1 m^2 quadrats in the summers of 2017 and 2018. Seedbed cover was visually estimated to 1% class intervals of the percent cover in each quadrat of the following categories: bare mineral soil, exposed rock, leaf litter, moss, woody debris (with a diameter 5 mm or greater), fungi, lichen, scat, or other (shells, animal hair, etc.). Understory species were later lumped by growth form (graminoid, forb, shrub, and tree) for data analysis. Integrated, whole-growing season light levels were estimated for each

1 m² quadrat with a canopy photograph taken at 50 cm above the ground with a Nikon Coolpix camera fitted with a fish-eye hemispherical lens on a levelled and oriented tripod (Martin et al. 2010). A gap light index (GLI; the combined incident diffuse and direct beam radiation over a growing season expressed as a percent of full sun) was then computed for each photograph using Gap Light Analyzer (GLA ver. 2.0) software (Frazer et al. 1999). Microclimate was quantified by soil moisture, mean maximum temperature, and mean minimum temperature for the growing season. Soil moisture (volumetric water content, VWC) was measured with a Hydrosense II soil moisture probe via a mean of five spot measurements taken in each corner and the center of 1 m² quadrats following two major rainfall events in July and August 2018 (Hydrosense II, Campbell Scientific, Logan, Utah). Temperature data was collected independently from early June 2018 to October 1, 2018 in all ninety-five 1 m² quadrats using iButton ThermoChron sensors which recorded every two hours on the soil surface beneath the litter layer (Maxim Integrated, San Jose, California). Growing season temperatures were calculated as the mean of all daily minimum temperatures and the mean of all daily maximum temperatures from June 6, 2018 to October 8, 2018. Combined depth of litter and duff layers (litter depth) was assessed by averaging the depth of the center and each of the four corners of each quadrat from the litter or duff surface to mineral seedbed or bedrock.

1.2.3 Data and statistical analyses

1.2.3.1 Microenvironment characterization

We performed Spearman's rank correlation coefficient (r_s) analyses to characterize the relationships between six microenvironment variables (soil moisture, mean minimum temperature, mean maximum temperature, canopy openness, and litter depth) that we hypothesized are the most important to seedling establishment. Since we were seeking to identify

influential relationships among environmental factors, we only reported significant relationships, with $\alpha = 0.05$.

1.2.3.2 Seed germination and germinant survival

We tested if rates of germination and germinant survivorship were significantly different between species. Differences in seed germination totals between species were tested using a Kruskal-Wallis rank sum test. Kruskal-Wallis is a non-parametric alternative to ANOVA for data that is highly skewed, as is often the case with count data (Kruskal and Wallis 1952). Differences in germinant survivorship between species were tested with a generalized linear model (GLM) using a binomial distribution and a logit link function.

We also explored species-specific relationships between germinant survival rates in 2017 with microenvironment conditions using a mixed-effect generalized linear model with a binomial distribution and a logit link function. The model incorporated a random effect of quadrat to account for the fact that all microenvironment variables were collected at the quadrat scale. Analyses were performed separately for each species that had at least 24 individuals germinate in 2017 (subalpine fir, Engelmann spruce, and Douglas-fir); analysis could not be performed on lodgepole pine due to high mortality for that species (over 97%). Due to very low germination (sample size, $n=5$) and 100% mortality of germinants in the 2018 growing season, only 2017 survivorship was analyzed. A larger sample size for subalpine fir ($n= 427$ germinants across 68 quadrats) allowed for more complex models, which included additive predictors of mean maximum temperature, mean minimum temperature, soil moisture, canopy openness, litter depth, percent cover of litter, and percent cover of woody plant species. We also included up to two-way interactions of canopy openness $\times$ soil moisture, canopy openness $\times$ mean maximum temperature, canopy openness $\times$ mean minimum temperature, and soil moisture $\times$ mean

maximum temperature based on *a priori* ecological knowledge and our prior analysis of associations between canopy openness and microclimate variables at the study site. Models for Engelmann spruce and Douglas-fir only included additive predictors of soil moisture, canopy openness, and mean minimum temperature due to small sample sizes (24 Engelmann spruce germinants across 9 quadrats and 27 Douglas-fir germinants across 16 quadrats). Predictor variables were not highly correlated (Pearson's $r \leq 0.68$). We checked multicollinearity of the models using ordinary least-squares regression of the variance inflation factor. All predictor variables were < 3 in all models (Zuur et al. 2007). All possible models for each species were compared using all subsets selection to produce a final model that minimized the small-sample Akaike Information Criterion (AIC_C, Akaike 1973). All-mixed model GLMs were fit using the *glmer* function in the package *lme4* (Bates et al. 2015) and model selection was performed using the *dredge* function in the MuMIn package (Burnham and Anderson 2002).

1.2.3.3 Multivariate analysis

To characterize the relationships of microenvironment with where individual species established and where species survived versus germinated, we performed non-metric multidimensional scaling (NMDS). Multivariate analysis allowed us to visually compare microenvironment preferences simultaneously both by species and life history stage (seed germination versus germinant survival). NMDS calculates distance based on similarity and holds fewer assumptions than other ordination techniques, which is helpful when using ecological data (McCune and Grace 2002). Microenvironments favorable to seed germination may not be favorable to germinant survival and we were interested in observing how species moved through their microenvironment at different life history stages. Our first matrix was comprised of counts of germination and survival of subalpine fir, Engelmann spruce, Douglas-fir, and lodgepole pine in 2017. The second matrix was composed of 5 observed microenvironment factors: canopy

openness, soil moisture, litter depth, mean minimum temperature, and mean maximum temperature. We only included data from a subset of microenvironmental factors to ease interpretation based on significant relationships observed in GLM models. Microenvironment data was z-scaled due to account for differing units and species data was transformed by relativizing by species maximum to equalize common and uncommon species, which is a common approach in multivariate analysis to account for differing germination rates (McCune and Grace 2002). All statistical analyses were performed in R version 3.5.1 “Feather Spray” (R Core Team 2018).

1.3 Results

1.3.1 *Microenvironment characteristics*

We observed substantial range in microenvironment at the site scale; quadrat-level growing-season mean minimum temperature ranged from 5.8 to 11.1°C and mean maximum temperature ranged from 13.6 to 37.2°C. The variation in these observed seasonal soil surface temperatures was as wide as the entire range of site-level regional climate variability over the last half-century.

Microenvironment conditions were generally characterized by high litter cover, mid to low levels of light, and low soil moisture (Table 1.3). Understory light levels ranged from 8.2% to 48.4% of full sun, with overall lower light levels in the north plot than the main and south plots (south plot: 21.4%, main plot: 20.8%, north plot: 12.3%). We observed a strong positive relationship between canopy openness and mean maximum temperature ($r_s = 0.71$, $P < 0.0001$). Litter depth was negatively related to soil moisture ($r_s = -0.46$, $P < 0.0001$) and positively to mean minimum temperature ($r_s = 0.25$, $P = 0.02$; Fig. 1.3).

1.3.2 Germination, survival, and establishment

New germinants were observed for four of the six dominant conifer tree species at the study site. Despite the presence of reproductive-sized adults within 10 m of all quadrats, no germinants or established seedlings were observed for limber pine or ponderosa pine during the two seasons of data collection. Germination and germinant recruitment were dominated by subalpine fir: 69.4% of all germinants were subalpine fir and 82.2% of germinants that survived until the end of the growing season were subalpine fir. Furthermore, subalpine fir also dominated the seedling age class (age > 1 year and height < 1 m), with 88.7% of seedlings being subalpine fir (39,474 seedlings ha⁻¹) even in the portion of our study site with a greater abundance of ponderosa pine and Douglas-fir (Fig. 1.4, Fig. 1.5). ANOVA tests showed significant differences in germinant emergence ($P < 0.002$) and survival ($P < 0.0001$) among species. Douglas-fir (51.8%), Engelmann spruce (42.3%), and subalpine fir (32.6%) exhibited the highest survival rates of germinants, while lodgepole pine had low survivorship (3%). The majority of germination and subsequent germinant survival occurred in the 2017 growing season (615 germinants across all species); only five lodgepole pine germinants were observed in 2018 and none survived to the end of the growing season.

1.3.3 Microsite, germination, and germinant survival

Generalized linear models showed significant relationships between germinant survival and microenvironment for subalpine fir and Engelmann spruce (Table 1.4). Subalpine fir germinant survival was associated with lower mean growing season minimum temperature, lower mean growing season maximum temperature, higher soil moisture, and a more closed canopy (Table 1.4). Notably, there was an interaction of canopy openness and mean minimum temperature on subalpine fir survival (Fig. 1.6), such that subalpine fir survival was not

associated with mean maximum temperature in areas with greater canopy gaps (GLI = 16.1% and 25.2%), suggesting that there may be a threshold where increasing gap size causes maximum temperature to be a detriment to germinant survival. Survival of Engelmann spruce germinants was negatively associated with mean minimum temperature (Fig. 1.7). Douglas-fir germinant survival was not associated with any of the microenvironment variables examined.

Through NMDS analysis, we were visually able to explore and compare the microenvironments where seeds germinated compared to where they survived (Fig. 1.8). Subalpine fir seeds germinated and survived throughout the ordination space, while other species aligned themselves along particular environmental gradients. Both lodgepole pine and Engelmann spruce germinant survival were associated with areas with higher moisture and cooler mean minimum temperatures; however the sample size for lodgepole pine survival was very low ($n=3$) due to high mortality (97%). Douglas-fir germination and germinant survival was associated with darker microenvironments that had few canopy gaps and cooler mean maximum temperatures. Subalpine fir and lodgepole pine were present within a greater number of microenvironments, but they also had the two largest sample sizes. Of the microenvironment variables tested, only canopy openness ($P = 0.009$) was correlated with the species ordination.

1.4 Discussion

Current predictions of species ranges generally suggest preferential survival for drought adapted species, such as pines, and for populations at their upper range edges (Rehfeldt et al. 2006, Bell et al. 2014a). Surprisingly, we observed the strongest recruitment from subalpine fir, which has low drought tolerance, predicted to decline in abundance with warming, and at its lower range position at the study site. Comparisons of relative abundance of seedlings to adults

indicate a compositional shift from a mixed community to one heavily dominated by subalpine fir. While limited in scale, this study suggests that recent warming has not resulted in range contractions for subalpine fir in this undisturbed forest.

High abundance of subalpine fir at the tail end of its range suggest that the species is persisting at the site due to favorable microrefugia and that it may continue to be a dominant component of undisturbed mixed-conifer forests. Subalpine fir can tolerate a relatively wide range of environmental conditions (Niinemets and Valladares 2006, Serra-Diaz et al. 2015) and exhibits life history strategies that may provide added benefit in this type of undisturbed forest. The deeper roots of subalpine fir can reduce the risk of desiccation during seedling establishment by quickly penetrating through the dry litter layer (Knapp and Smith 1982), which is often deeper in an undisturbed forest and poses a heightened the risk of desiccation. Additionally, germinants of subalpine fir have been observed to emerge later than other species (Anderson and Winterton 1996), which reduces its susceptibility to early season drought events and is especially important in the southern Rocky Mountains where late season monsoonal rain is a primary source of growing season moisture.

While results from this study suggest a potential transition toward a subalpine fir dominated forest, previous research suggests that seedling recruitment of subalpine fir in spruce-fir stands is not necessarily indicative of future stand structure. Subalpine fir suffers high rates of loss from the canopy during subsequent life history stages, which more than off-sets its higher rates of seedling abundance (Veblen 1986, Andrus et al. 2018a). Anecdotal evidence from the north plot of the study site supports this hypothesis, as the vast majority (90.5%) of dead adult stems ($\text{DBH} \geq 10 \text{ cm}$) observed during stem mapping were subalpine fir and subalpine fir dominated early seedling recruitment (97.5% of all seedlings). While it is clear that subalpine fir

is able to compete and establish within a wide range of microenvironmental conditions, these findings may not fully suggest long-term forest structure due to the differing recruitment strategies of subalpine tree species (fecundity vs. persistence). Furthermore, these findings illustrate the complexity of recruitment dynamics and the need to assess multiple life history stages in accurately predicting future forest structure (Máliš et al. 2016, Andrus et al. 2018a).

Lack of disturbance may serve as a potential reason for lower levels of recruitment given disturbance adaptations for species such as lodgepole pine and ponderosa pine. Both species are fire-adapted and have specific site requirements of bare mineral soil seedbeds and open, heterogeneous canopy structures, which result from moderate to high frequency disturbance (Knapp and Seastedt 1986, Bonnet et al. 2005, Ziegler et al. 2017, Hansen et al. 2018). Altered disturbance regimes have been cited as a primary reason for low ponderosa pine recruitment in recent years and its projected distributional decline (Coops et al. 2005, Rehfeldt et al. 2006, Kemp et al. 2019). However, lack of disturbance and resulting movement along the successional pathway do not fully explain the shift to subalpine fir dominance. Both Engelmann spruce and Douglas-fir have similar life history strategies to subalpine fir yet are suffering low seedling recruitment. In particular, the low abundance of Douglas-fir is surprising considering its drought-tolerance, climatic distribution, and disturbance adaptations as predictive models favor Douglas-fir over ponderosa pine in warmer and drier climates (Coops et al. 2005). However, evidence of successful Douglas-fir recruitment on the Colorado Front Range has been mixed with some studies showing evidence of decline during the 20th century (Schoennagel et al. 2011) and others exhibiting continued recruitment (Battaglia et al. 2018).

While we made an effort toward a comprehensive study of microenvironment restrictions to germinant recruitment, we were not able to address all influential factors. Nearly all the

observed conifer species reproduce through episodic mastings events, which requires several consecutive years of favorable climate conditions for successful seed production, germination, and survival (Kelly and Sork 2002, Redmond et al. 2012, Buechling et al. 2016). Subalpine fir has one of the fastest and most frequent mastings cycles of these species, which would provide a greater number of regenerative opportunities (Franklin et al. 1974), whereas ponderosa pine, limber pine, Engelmann spruce, and Douglas-fir all have more infrequent mastings cycles, ranging from 2 to 7 years (Burns and Honkala 1990). Levels of frequency, synchrony, and volume of mastings have the potential to affect the amount of seed consumed versus dispersed by predators and competition among seedlings (Tomback et al. 2005, Vander Wall 2011).

While a range of microenvironment characteristics were observed at the study site, these conditions may not have actually encompassed the preferred conditions for all species. Light levels observed within quadrats were overall low and did not encompass the high light levels required by shade intolerant pine species (Niinemets and Valladares 2006). Levels of litter cover and depth were relatively high across the site, resulting in limited availability of bare mineral seedbeds, the preferred seedbed substrate of most species (Lamont et al. 1993, Feller 1998, Shepperd et al. 2006, Wolk and Rocca 2009). Herbivory may also play a role in accounting for some of our unexplained seedling mortality given that trampling by large ungulates, clipping of cotyledons by birds, and damage from insects have been observed to significantly affect regeneration of subalpine tree species in this region (Noble and Alexander 1977, Alexander 1987). Furthermore, seed consumption and caching by small mammals can affect spatial patterns of regeneration (Chambers and MacMahon 1994, Gómez-Aparicio 2008, Pansing et al. 2017).

Of microenvironment limitations measured, adequate soil moisture and mean maximum temperature emerge as driving factors to germinant survival. Positive correlations between soil

moisture and survival were observed for Engelmann spruce, subalpine fir, and lodgepole pine in statistical analysis. Despite being a drought-tolerant species, lodgepole pine still requires a minimum amount of soil moisture to successfully regenerate on the Colorado Front Range, as evidenced in recent studies at Niwot Research Station (Petrie et al. 2016, Conlisk et al. 2018, Lazarus et al. 2018). The small seed size of lodgepole pine (207,000 seeds kg^{-1}) compared to other drought-tolerant pines, such as ponderosa pine (26,500 seeds kg^{-1}) and limber pine (10,800 seeds kg^{-1}), may provide fewer stored nutrients for first-year tree seedlings, thus causing germinants to be more prone to desiccation (Schopmeyer 1974, Noble and Alexander 1977, Burns and Honkala 1990, Lazarus et al. 2018, Hill et al. 2019). Engelmann spruce seedlings are known to be strongly tied to cooler and wetter sites (Alexander and Noble 1971, Coates et al. 1991), displaying fatal heat girdling when prolonged surface temperatures exceeded 45°C (Alexander 1987). Temperatures experienced by germinants exceeded this threshold in 18.9% of quadrats and Engelmann spruce seedlings were not observed in any of these quadrats despite being within the dispersal radius of a seed producing adult (McCaughey et al. 1985). Douglas-fir seedling failures may also be tied to temperature limitations, as models for the cooler end of the species range suggest a surprisingly low mean summer temperature threshold of 17°C resulting in lower seedling densities; in our study over two-thirds of all plots exceeded this temperature threshold (Kemp et al. 2019).

Our results fail to support our hypothesis of directional range shifts and conversely suggest that species responses are unique and uncorrelated with other species at similar range positions (Carroll et al. 2017, Urza and Sibold 2017). Species responses are independent and affected by fine-scale microenvironment factors rather than overall site climate as microrefugia can moderate the stress of large-scale changes in climate (Serra-Diaz et al. 2015, Kelsey et al.

2017) and seed availability and disturbance can play an important role in determining seedling recruitment (Eriksson and Erlhén 1992, Clark et al. 2007, Landhäusser et al. 2010). Our findings showed similar trends to those suggested in Rehfeldt et al. (2006) for ponderosa pine, but Douglas-fir illustrated a contradictory trajectory and decline of Engelmann spruce was substantially milder. As such, this study provides greater support for the use of bioclimate models in conjunction with field observations to assess the ability of species to migrate (Coop et al. 2010, Clark et al. 2016).

Few studies have used field data to discuss potential range shifts for species at the upper montane – subalpine ecotone in the southern Rocky Mountains. We provide evidence that the future of Colorado forests is complicated, with trajectories defined by a web of site-specific factors that are difficult to predict across an entire ecotone. Subalpine fir's dominance of early recruitment suggests that it may begin to dominate in this forest in absence of stand replacing disturbance. While we did not observe evidence of upslope migration of the species at our site, we did observe important characterizations of microenvironment in relation to early seedling survival. The significant relationships observed between overstory canopy, soil surface temperatures, and germinant survival confirms the ability of microrefugia to buffer the larger-scale impacts of altered climate.

1.5 Tables

Table 1.1. Life history strategies of common montane and subalpine tree species in Colorado. Shade and drought tolerance levels were acquired from Niinemets and Valladares (2006) and range from 0 (no tolerance) to 5 (maximum tolerance) (Burns and Honkala 1990, Carey 1992, Anderson and Winterton 1996, LePage et al. 2000, Niinemets and Valladares 2006, Hill et al. 2019).

	Subalpine fir	Engelmann spruce	Lodgepole pine	Aspen	Douglas-fir	Limber pine	Ponderosa pine
Drought tolerance	2.02 ± 0.02	2.58 ± 0.30	4.21 ± 0.38	1.77 ± 0.23	2.62 ± 0.41	4.72 ± 0.22	4.32 ± 0.32
Shade tolerance	4.83 ± 0.15	4.53 ± 0.07	1.48	1.21 ± 0.18	2.78 ± 0.18	1.56 ± 0.15	1.64 ± 0.15
Seedbed preference	bare mineral soil, logs or other nurse objects that retain moisture	bare mineral soil, logs or other nurse objects that retain moisture	bare mineral or organic soil	bare mineral soil	bare mineral or organic soil	bare mineral soil	bare mineral soil
Disturbance adaptations	none	none	fire	fire; canopy or ground disturbance	none	none	fire
Range position at site	tailing	tailing	mid-range	mid-range	leading	mid-range	leading

Table 1.2. Basal area ($\text{m}^2 \text{ha}^{-1}$) and stems ha^{-1} for each species for each plot within the study site.

Species	Plot	Basal Area ($\text{m}^2 \text{ha}^{-1}$)	Stems ha^{-1}
Subalpine fir	Main Plot	7.63	248.89
Lodgepole pine	Main Plot	19.10	497.33
Engelmann spruce	Main Plot	0.32	6.22
Limber pine	Main Plot	1.49	45.33
Ponderosa pine	Main Plot	0.10	4.44
Aspen	Main Plot	3.69	238.22
Douglas-fir	Main Plot	0.58	11.56
Subalpine fir	North Plot	22.44	1028.53
Lodgepole pine	North Plot	5.07	116.57
Engelmann spruce	North Plot	21.87	486.84
Limber pine	North Plot	0.35	20.57
Ponderosa pine	North Plot	0	0
Aspen	North Plot	0.18	13.71
Douglas-fir	North Plot	0.32	13.71
Subalpine fir	South Plot	2.69	124.58
Lodgepole pine	South Plot	24.60	733.77
Engelmann spruce	South Plot	0.82	9.97
Limber pine	South Plot	1.01	41.11
Ponderosa pine	South Plot	4.56	59.80
Aspen	South Plot	0.97	49.83
Douglas-fir	South Plot	2.80	61.04

Table 1.3. Mean ($\pm$ standard error), minimum, and maximum values for microenvironment variables. Of microenvironment variables related to percent cover, only those with a mean percent cover of $\geq 5\%$ are included. Variables were assessed individually for quadrats where germinants of any species were observed in 2017 versus those where they were not observed.

	Quadrats with germinants (n=68)			Quadrats without germinants (n=27)		
	Mean ($\pm$ SE)	Minimum	Maximum	Mean ($\pm$ SE)	Minimum	Maximum
Litter cover (%)	82.3 (20.0)	8	99.5	80.2 (19.1)	28	98
Woody plant cover (%)	9.3 (15.3)	0	69.7	12.1 (19.7)	0	68.1
Available light (GLI)	17.4 (6.3)	8.2	43.7	26.5 (10.1)	10.3	48.4
Soil moisture (VWC)	6.5 (3.1)	0	14.4	7 (3.3)	0	13.8
Litter depth (cm)	4.7 (3.5)	1.2	20.6	3.2 (2.2)	0.9	10.3
Mean minimum temperature ($^{\circ}$ C)	8 (1.0)	6.2	11.1	8 (1.3)	5.8	10.5
Mean maximum temperature ($^{\circ}$ C)	19.8 (3.9)	13.6	29.6	23.9 (23.9)	15.7	37.2

Table 1.4. Generalized linear models of germinant survival on microenvironment characteristics by species.

Subalpine fir (<i>n</i>= 427 germinants, 68 quadrats; pseudo R^2= 0.19)				
	β log(odds)	SE	<i>z</i> value	<i>P</i> value
Intercept	-0.45	0.14	-3.34	< 0.001
Canopy openness	0.55	0.21	2.62	0.01
Soil moisture	0.46	0.11	4.10	< 0.001
Mean maximum temperature	-0.50	0.19	-2.64	0.01
Mean minimum temperature	-0.74	0.18	-4.15	< 0.001
Canopy openness $\times$ mean maximum temperature	-0.47	0.18	-2.68	0.01
Engelmann spruce (<i>n</i>= 24 germinants, 9 quadrats; pseudo R^2= 0.24)				
	β log(odds)	SE	<i>z</i> value	<i>P</i> value
Intercept	-1.10	0.94	-1.18	0.24
Mean minimum temperature	-2.96	1.94	-1.52	0.13
Douglas-fir (<i>n</i>= 27 germinants, 16 quadrats)				
	β log(odds)	SE	<i>z</i> value	<i>P</i> value
Intercept	0.07	0.39	0.19	0.85

1.6 Figures

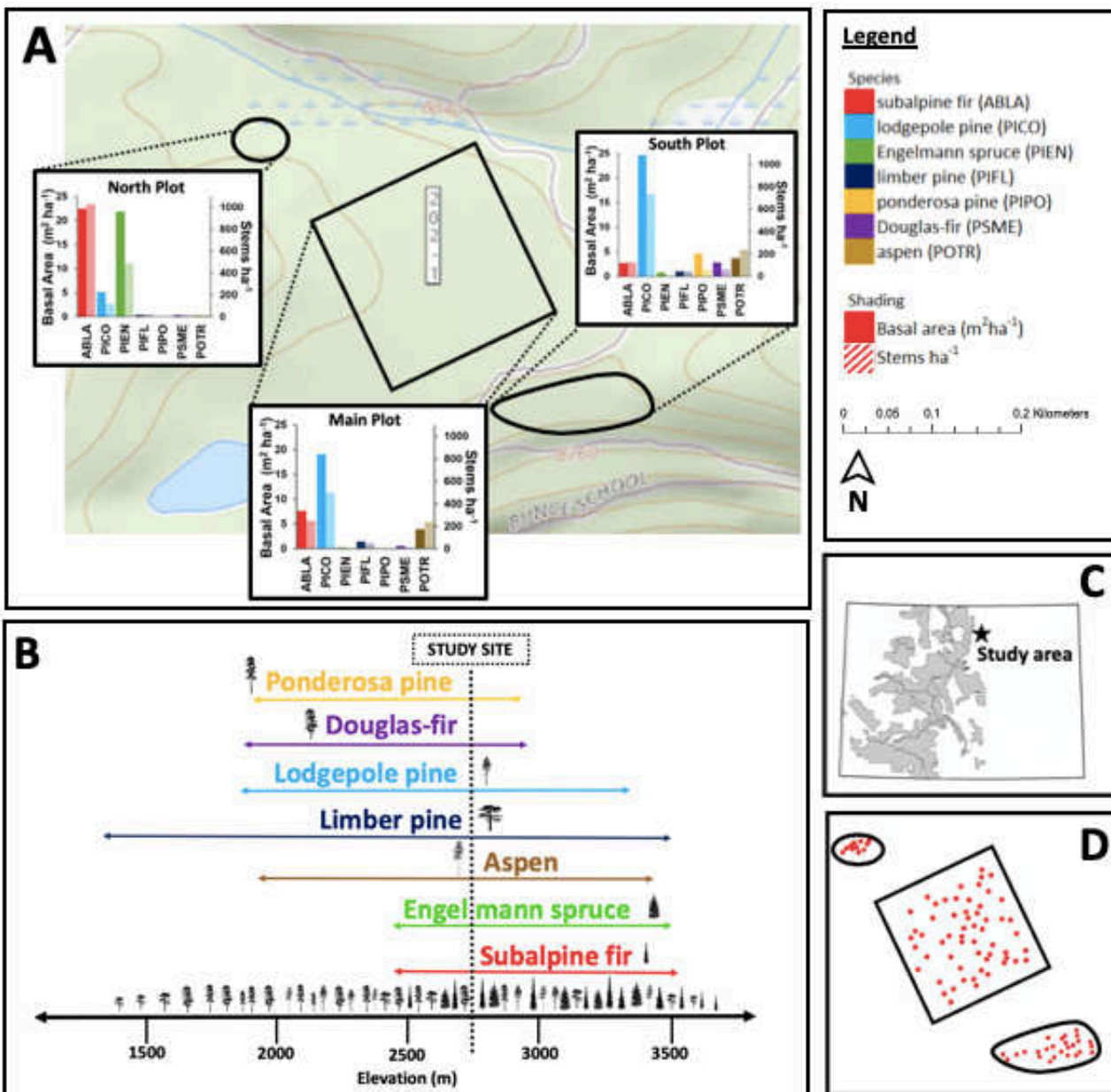


Figure 1.1. (A) Map of the study site with species composition of each study plot. Overall slope and aspect of the site is effectively neutral and differences within the site are defined by microtopography. Bars in histograms represent the basal area ($\text{m}^2 \text{ha}^{-1}$; solid bars) and density (stems ha^{-1} ; dashed bars) of each species within the three plots. Species at the study site are subalpine fir (ABLA), lodgepole pine (PICO), Engelmann spruce (PIEN), limber pine (PIFL), ponderosa pine (PIPO), aspen (POTR), and Douglas-fir (PSME). (B) Elevational distribution of study species in Colorado relative to location of the study site (dashed line). Information on species distributions is based on ranges reported by the Colorado State Forest Service. (C) Location of the study site within Colorado in the U.S. National Forest system. (D) Distribution of 1 m^2 quadrats within the three study plots.

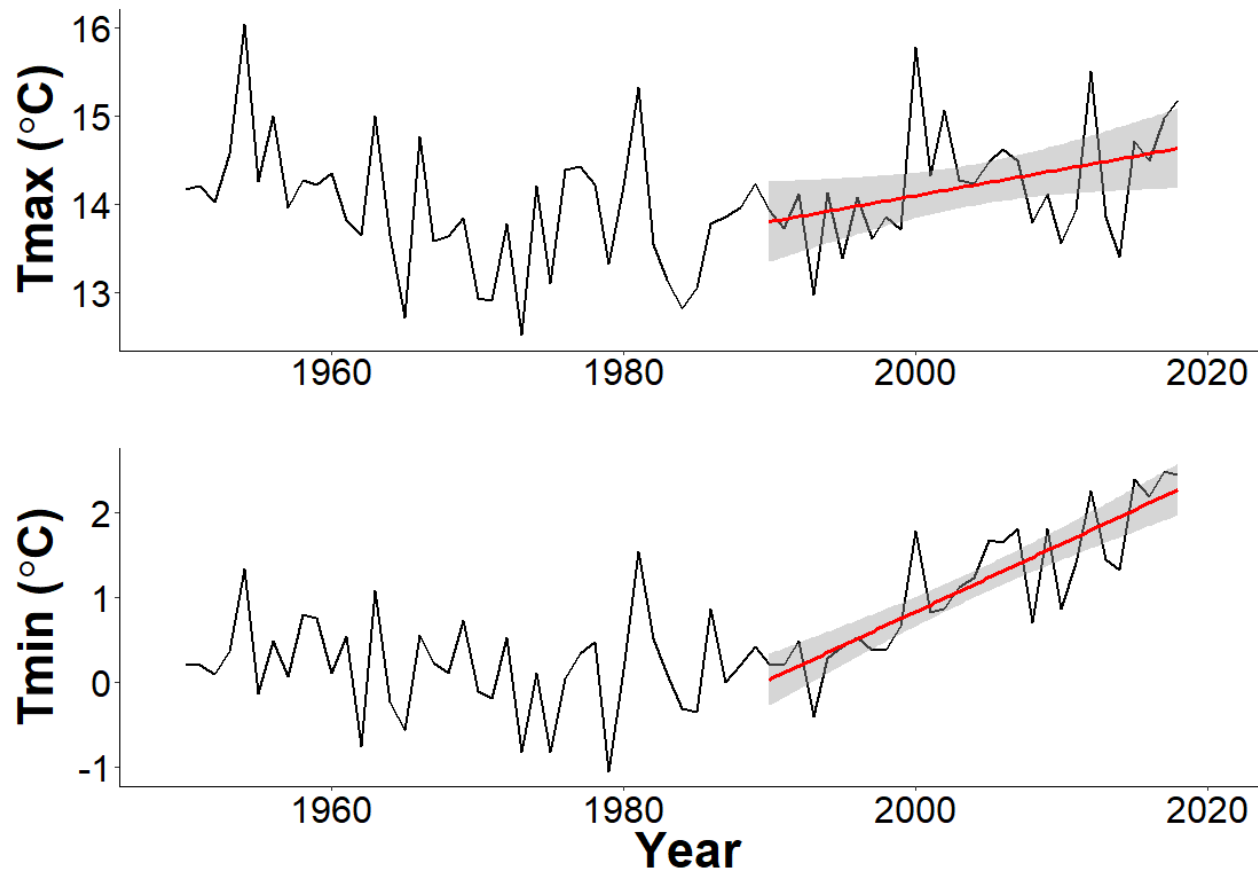


Fig. 1.2. Yearly mean minimum (Tmin) and maximum temperature (Tmax) for the study site. Red solid red lines represent trend lines and 95% confidence intervals for the last 28 years (1990-2018). Data from PRISM Climate group, Oregon State University.

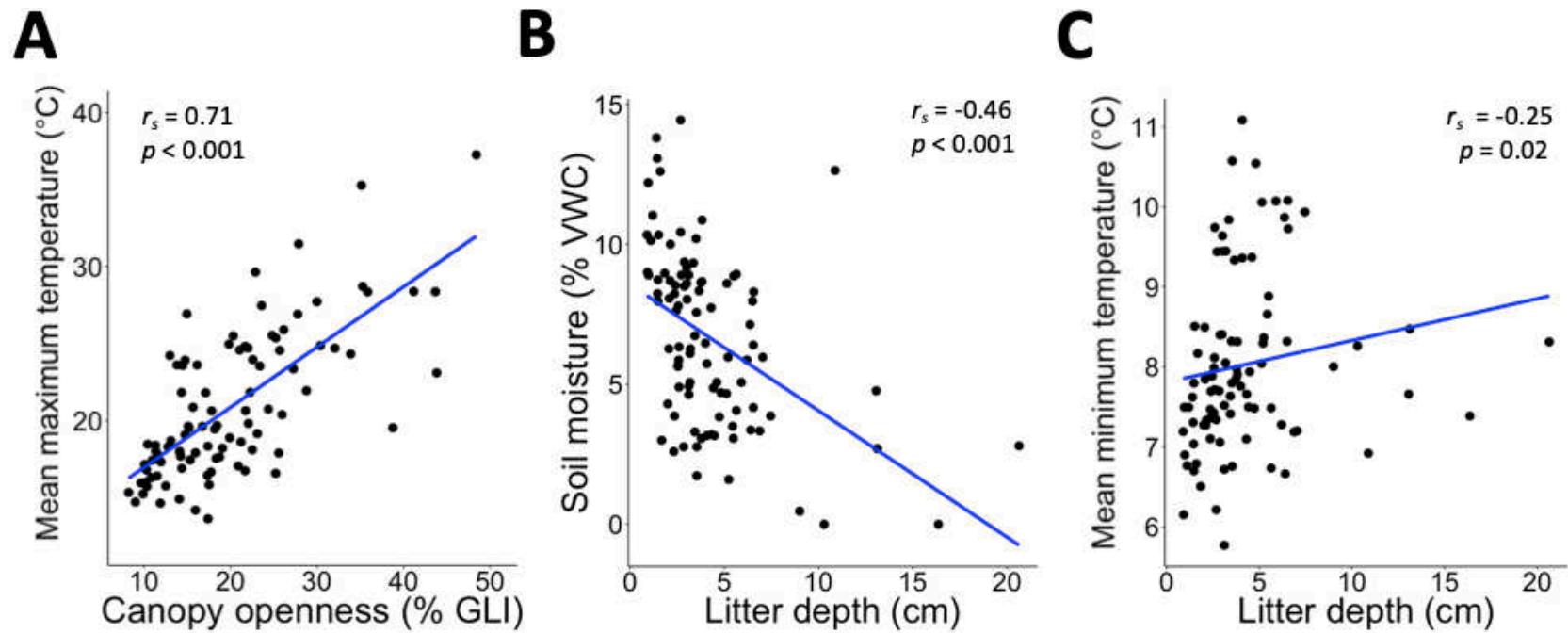


Fig. 1.3. Spearman rank correlation coefficients with fitted lines (blue) for: (A) canopy openness (GLI) and growing season mean maximum temperature (°C); (B) litter depth (cm) and soil moisture (VWC); and (C) litter depth and growing season mean minimum temperature.

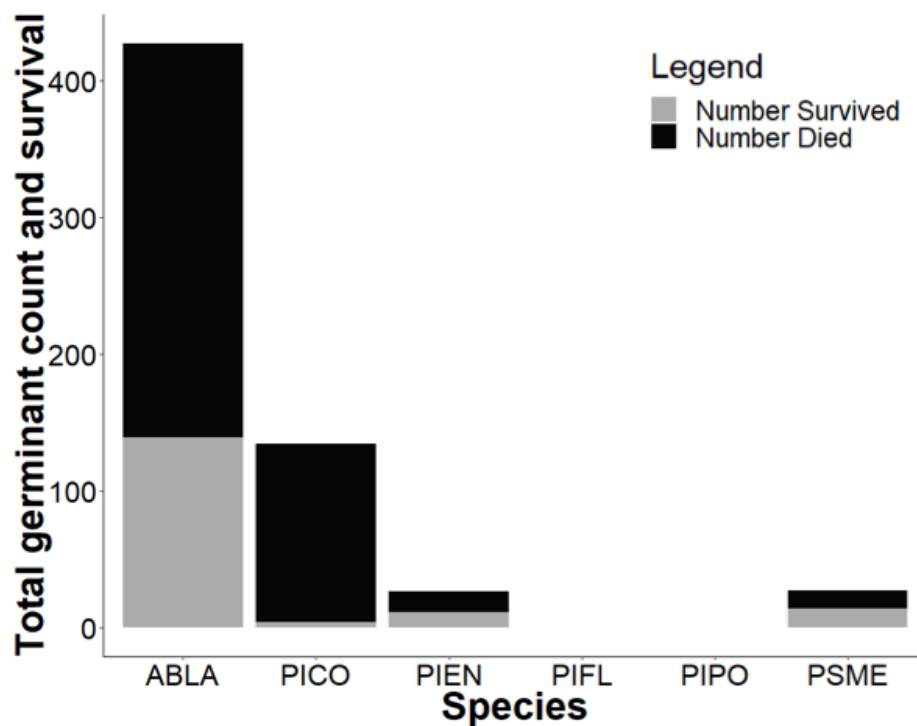


Fig. 1.4. Total germination and survival in 2017. Total height of each bar represents the total number of germinants that emerged in 2017 with the number of germinants surviving to the end of the growing season shown in light gray. In 2018, there were only 5 total germinants of all species combined; all were lodgepole pine and none survived the growing season. Species abbreviations are as follows: subalpine fir (ABLA), lodgepole pine (PICO), Engelmann spruce (PIEN), limber pine (PIFL), ponderosa pine (PIPO), and Douglas-fir (PSME).

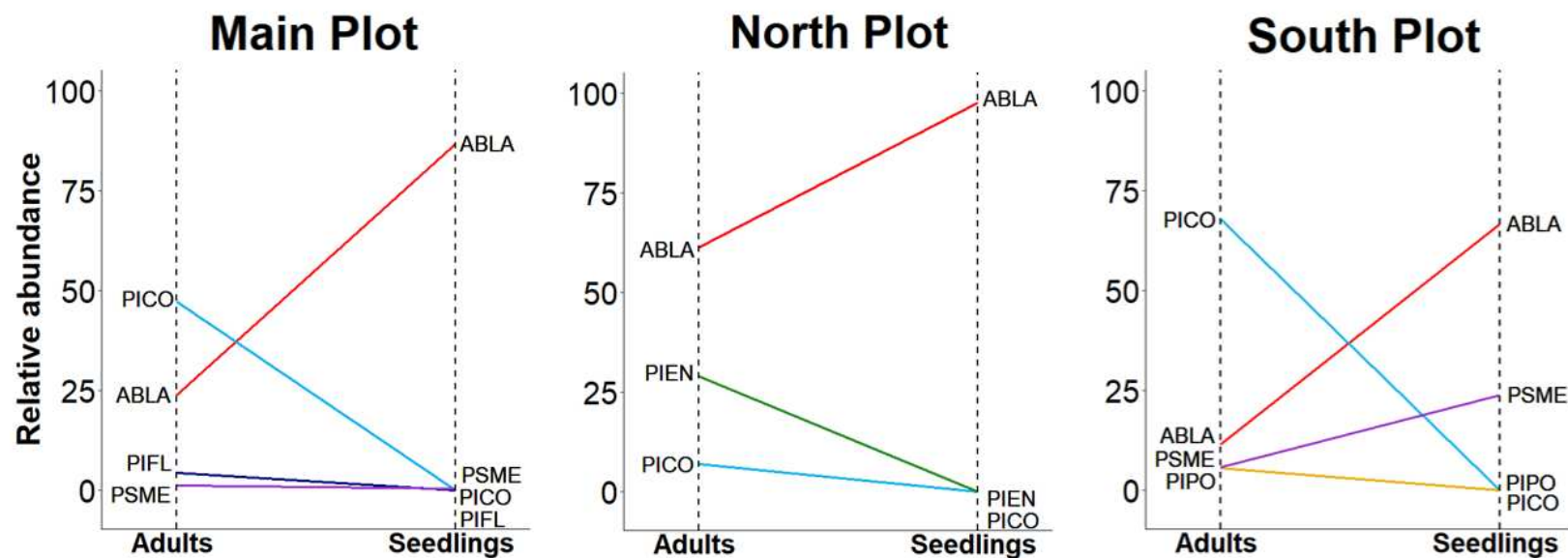


Fig. 1.5. Relative density of each species based on life history stage in: (A) main plot, (B) north plot, and (C) south plot. Only species that had a relative density of $\geq 1\%$ at either life history stage are plotted. Seedlings were defined as all individuals with age > 1 year and height < 1 m and adults were defined as individuals with DBH ≥ 10 cm. Species abbreviations: subalpine fir (ABLA; red), lodgepole pine (PICO; light blue), Engelmann spruce (PIEN; green), limber pine (PIFL; navy blue), ponderosa pine (PIPO; yellow), and Douglas-fir (PSME; purple).

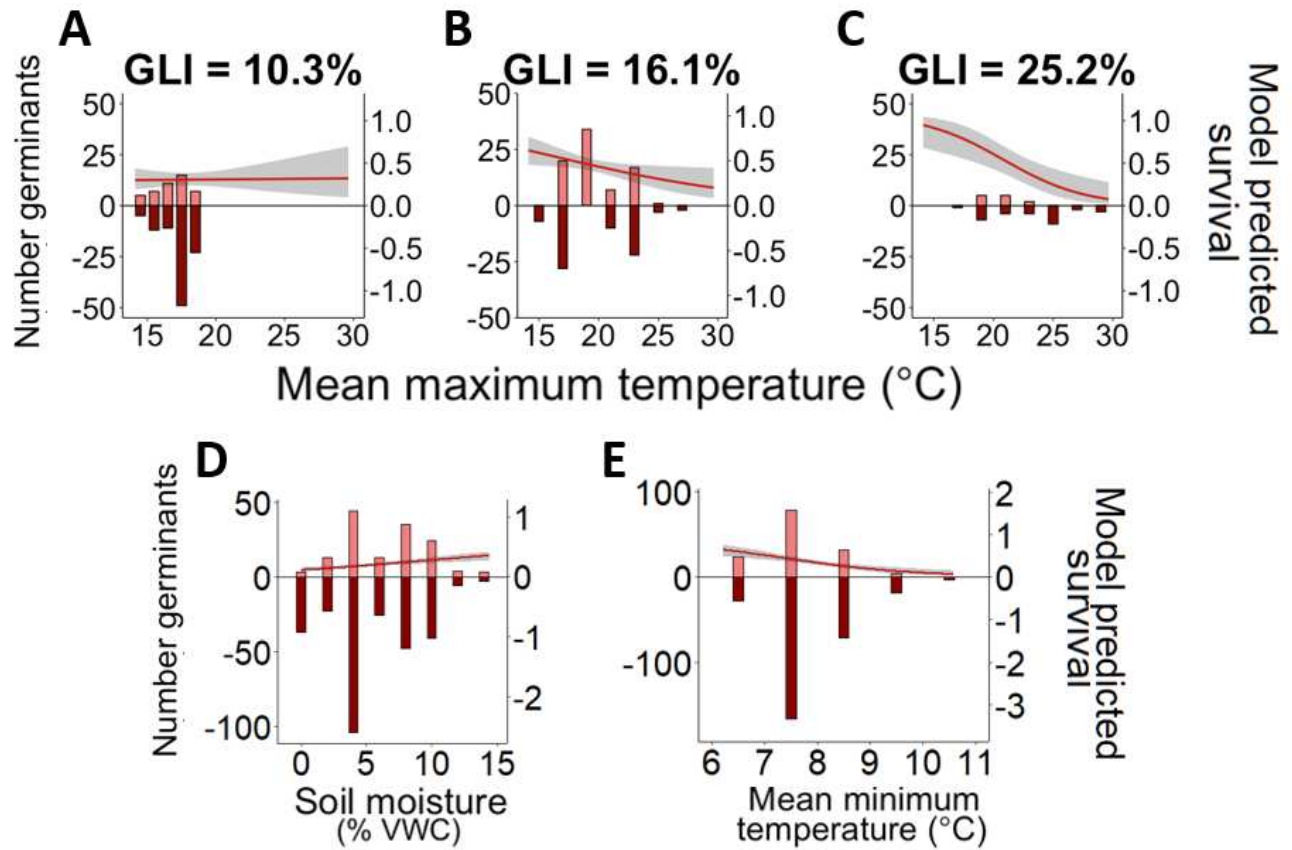


Fig. 1.6. Models of subalpine fir 2017 first year germinant survivorship as a function of: (A-C) mean maximum temperature (°C) at the range of canopy openings (GLI) observed: (A) lower quartile (GLI = 10.3%), (B) median (GLI = 16.1%), and (C) upper quartile (GLI = 25.2%); (D) soil moisture (VWC), and (E) mean minimum temperature (°C). Histograms display the observed number of seedlings that survived (pink bars) and observed number of seedlings that died (red bars). The modeled relationship (solid line, secondary y-axis) and 95% confidence interval (grey band) are overlaid. Pseudo R^2 values for all models are noted in Table 1.4.

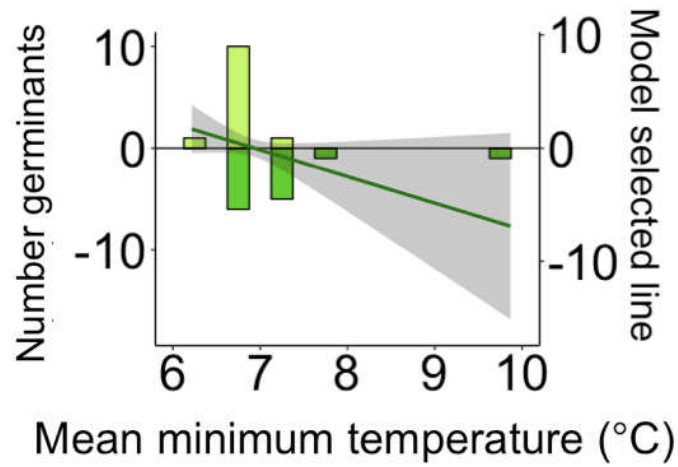


Fig. 1.7. Model of Engelmann spruce 2017 first year seedling survivorship as a function of growing season mean minimum temperature (°C). Histograms display the observed number of seedlings that survived (light green bars) and observed number of seedlings that died (dark green bars). The modeled relationship (solid line, secondary y-axis) and 95% confidence interval (grey band) are overlaid. Pseudo R^2 values for all models are noted in Table 1.4.

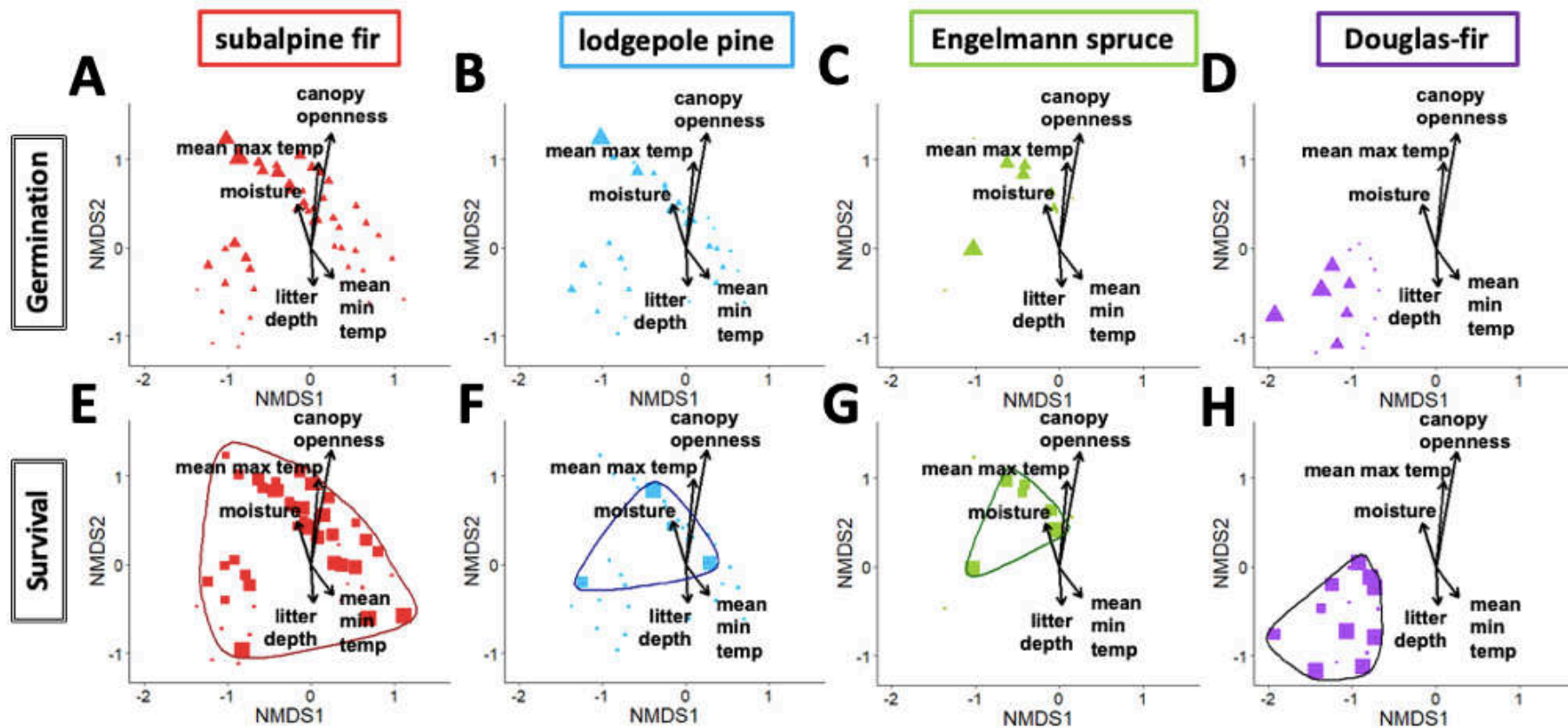


Fig. 1.8. Nonmetric multidimensional scaling (NMDS) ordination showing germination (top row) and survival (bottom row) with microenvironment factors (canopy openness, GLI; soil moisture, VWC; mean maximum temperature, °C; mean minimum temperature, °C; litter depth, cm) by species: (A and E) subalpine fir (red); (B and F) lodgepole pine (blue); (C and G) Engelmann spruce (green); and (D and H) Douglas-fir (purple). Symbol size is scaled by relative presence of germinants in each quadrat.

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CHAPTER 2: SOIL MOISTURE STRONGLY LIMITS DOUGLAS-FIR SEEDLING ESTABLISHMENT NEAR THE LEADING EDGE OF ITS DISTRIBUTION IN THE SOUTHERN ROCKY MOUNTAINS

2.1 Introduction

Changing climatic conditions in the western United States have begun to exceed thresholds for tree species regeneration across significant portions of their range, causing spatial shifts in regenerative niche (Kelly and Goulden 2008, Gray and Hamann 2013, Davis et al. 2019a). As climatically- suitable habitat shifts, species are generally predicted to migrate toward cooler and wetter edges of their range (Kelly and Goulden 2008, Bell et al. 2014b), while high rates of mortality from drought, insects, and disease raise questions of species persistence in the hotter and drier portions of their range. Together these processes make juvenile recruitment dynamics central to the persistence and migration of many species in the region (Breshears et al. 2005, Williams et al. 2013, Kueppers et al. 2017a).

There is growing evidence that climate change is affecting seed germination and seedling survival at multiple range positions (Liu and El-Kassaby 2015, Conlisk et al. 2017), highlighting the sensitivity of seedling establishment to even small changes in the environment. Soil moisture is especially important for seedling recruitment in dry forests of the western U.S. and is often the limiting factor in early regenerative stages (Moyes et al. 2015, Andrus et al. 2018b). Timing and regularity of precipitation is also important, with higher rates of germination and seedling survival occurring during periods of more consistent moisture (League and Veblen 2006, Kroiss and HilleRisLambers 2015). Yet precipitation in the western U.S. is predicted to shift toward less frequent and higher intensity events (IPCC 2018), suggesting that soil moisture may become

increasingly important for tree seedling establishment over the next century, even among species with drought adaptations (Kolb and Robberecht 1996, Hu et al. 2010).

While regional changes in climate are predicted to affect species persistence, populations may be able to regenerate during selectively favorable climatic periods or in certain microenvironments (Andrus et al. 2018b, Redmond et al. 2018). Indeed, climatic microrefugia, or areas on the landscape that support the persistence of populations within a regionally unsuitable climate, can allow for successful seedling establishment under increasingly arid conditions (Serra-Diaz et al. 2015, McLaughlin et al. 2017, Davis et al. 2019b). Fine-scale heterogeneity at the forest floor in light, moisture, and temperature create substantial variation in microenvironments and strongly impact tree recruitment (Moyes et al. 2015, McLaughlin et al. 2017). This variation in microenvironment can mitigate or even override the effect of warmer temperatures, thus altering the speed or extent of species range shifts (Munier et al. 2010, Serra-Diaz et al. 2015, McLaughlin et al. 2017).

Seed predation, germinant herbivory, and trampling are little-studied yet important limitations to conifer recruitment (Noble and Alexander 1977, Johnson and Fryer 1996, Shepperd et al. 2006). Seed predation can substantially reduce seed abundance (Johnson and Fryer 1996, Pesendorfer et al. 2016), clipping of germinant cotyledons by birds and small mammals can strongly reduce survival (Noble and Alexander 1977, Pesendorfer et al. 2016) and trampling is known to limit seedling recruitment due to the small size and vulnerability of seedlings (Noble and Alexander 1977, Bingham and Simard 2012).

This study examines how these local-scale factors as well as the timing and amount of precipitation influence tree seedling germination and survival of a widespread conifer. Douglas-fir (*Pseudotsuga menziesii*) is a drought-tolerant species of the montane zone of the Rocky

Mountains and has had varying recruitment success following recent disturbances (Restaino et al. 2016, Davis et al. 2019a, Hankin et al. 2019), with available moisture serving as the primary limitation to seedling regeneration (Rother et al. 2015). Bioclimate models predict that Douglas-fir will be favored in future climate scenarios, particularly at the montane – subalpine ecotone at its current upper range limit (Rehfeldt et al. 2006), yet to our knowledge no research has assessed Douglas-fir recruitment in this zone. We assessed the *in-situ* effects of augmented precipitation regimes, wildlife predation, and microclimate on germination and early seedling establishment of Douglas-fir at the montane-subalpine ecotone in the southern Rocky Mountains. We hypothesized: (1) Douglas-fir will have higher rates of germination and survival in watered treatments and in cooler and wetter microenvironments, and (2) wildlife will strongly limit seed germination and seedling survival.

2.2 Methods

The experiment was conducted at a permanent study site on the Colorado Front Range north of Peaceful Valley, Colorado, USA. The site is in a mixed mesic forest type at the interface of upper montane and subalpine forest types at 2700 meters in elevation. Mean annual precipitation is 618 mm, primarily in the form of snow with snowmelt occurring in May- June (PRISM Climate Group 2019). Mean growing season temperature ranges from a mean minimum of 5.2°C to a mean maximum of 19.4°C. Soils are derived primarily from Leighcan family till substratum with glacial till and alluvium parent material derived from igneous and metamorphic rock (NRCS 2019). The site is a closed canopy forest with low light levels and when present, understory vegetation is dominated by ericaceous species. It is free of recent disturbance with no evidence of major blowdown, fire, harvest, or widespread insect outbreaks. The slope is flat overall, but there are small-scale changes in elevation (± 10 m), which creating rolling

topography and significant variation in microtopography. All live and dead adult stems (DBH $\geq$ 10 cm) were measured and tagged in 2016 and 2017. The study area is dominated by lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*), with scattered clusters of aspen (*Populus tremuloides*), limber pine (*Pinus flexilis*), ponderosa pine (*Pinus ponderosa*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir.

Experimental treatments were installed throughout the study area using a blocked design with 24 replicates of 4 treatments stratified along a canopy gap gradient (Fig. 1). Block locations spanned the range of available light (% gap light index, GLI) observed in the study area and were chosen for low presence of competing plants and a sufficiently large area (4 m²) with the same seedbed, slope, and aspect throughout. Each replicate was composed of 4 treatments: control, uncaged (predator allowance), 25% water addition, and 50% water addition. The control served as a control for both predator allowance and water additions. All treatments with the exception of the uncaged treatment were covered with a square wire mesh cage with flange on all sides to prevent burrowing by small mammals. Two treatments included a moisture addition of 25% (2.2 L) or 50% (4.5 L) of mean weekly rainfall from mid-May to mid-September. Mean precipitation was calculated based on historical precipitation data from a SNOTEL station approximately 7 km southwest of the study site (NRCS SNOTEL Data Network 2019). Treatments were positioned within the site so that the watering treatments were always downslope of the other treatments to prevent water from flowing in.

The study period was much warmer and drier than 70-year normals; in 2018 we observed the warmest growing-season mean minimum and maximum temperatures of the past 70 years and only half of typical precipitation (PRISM Climate Group 2019). Ambient precipitation was so low that only the water addition treatments had typical growing season precipitation – 25%

water addition had a seasonal total of 19.5 cm (86% of mean); 50% water addition had 27.4 cm (121%) – while the control was in effect a drought treatment (51% of mean).

Ten seeds of Douglas-fir were sown into a randomly generated grid of cells in each treatment replicate, resulting in a total of 960 seeds sown or 240 seeds per treatment. All seeds were sown at least 8 cm apart to avoid competition between germinations. Seeds were obtained from the U.S. Forest Service Bessey Nursery from seeds collected within similar proximity (within 10 km) and elevation (2560 m) as the study site and stratified prior to sowing in the field following guidelines from the U.S. Forest Service Woody Seed Manual (Schopmeyer 1974). We also stratified and sowed seeds of ponderosa pine, lodgepole pine, subalpine fir, and Engelmann spruce, but these species did not germinate in sufficient numbers for study.

Microclimate was quantified with canopy openness (% gap light index, GLI) and soil surface temperatures (°C). Light levels were measured using digital hemispherical photos and computing GLI (the combined incident diffuse and direct beam radiation over a growing season expressed as a percent of full sun) using Gap Light Analyzer (GLA ver. 2.0) (Frazer et al. 1999, Martin and Canham 2010). Temperature data was collected independently from early June to October 1, 2018 in all 24 blocks using iButton Thermochron sensors which recorded every two hours on the soil surface beneath the litter layer (Maxim Integrated, San Jose, California). Growing season temperatures were calculated as the mean of all daily minimum temperatures and the mean of all daily maximum temperatures from June 6, 2018 to October 8, 2018.

2.2.1 Statistical analysis

We analyzed germination and survival rates of Douglas-fir. We used a repeated measures approach in a generalized linear mixed-effects model (GLMM) with a Poisson distribution to examine whether watering treatments and precipitation affected the timing of germination. The

model included fixed effects of total bi-weekly precipitation, watering treatment, observation date, random effect of treatment block, and a response variable of total bi-weekly germination. We included observation date as a second-order polynomial term to allow for the unimodal distribution of germination across time. Significant effects were tested in a type 3 ANOVA.

To model germination and survival rates, we used GLMMs with a binomial distribution and a logit link function. Each model included a random effect of block with fixed effects of treatment (control, 25% water, 50% water) and mean minimum and mean maximum growing-season soil surface temperature for each block. Germination and survival were run separately. Canopy openness and mean maximum soil surface temperature were highly correlated (Pearson's $r > 0.8$), and thus only mean maximum temperature was included in the model as we hypothesized that soil temperature was more important for early seedling establishment. Variance inflation factors for each predictor were all < 2 . Significant effects of treatment and differences between treatments were tested using a type 3 ANOVA and Dunnett-adjusted pairwise comparisons of means using the *emmeans* function (Lenth 2014).

The effect of wildlife exclusion was tested using a similar approach by fitting GLMMs and performing model selection for separate models of germination and survival. Both models had a fixed effect of treatment (caged or uncaged) and a random effect of block, with a binomial response of germination or survival. GLMMs were fit using the *glmer* function in the package *lme4* (Bates et al. 2015); analyses were done in R v. 3.5.1 “Feather Spray” (R Core Team 2018).

2.3 Results

GLI in the experiment ranged from 8.7% to 48.7% with a median of 17.4% (study site GLI ranged from 8.2% to 48.4% with a median of 17.7%). Growing season soil surface temperatures in study blocks ranged from a mean minimum of 6.1°C to a mean maximum of

39.9°C, which were warmer than PRISM 70-year mean growing-season minimum (5.2°C) and maximum (19.4°C) temperatures.

The germination rate across all treatments for Douglas-fir was 17.6% and survivorship was 82.8% with 140 surviving individuals. Repeated measures tests found watering treatments to be significantly correlated with the timing of germination ($P = 0.01$), such that non-watered treatments germinated later than those that received supplemental water (Fig. 2). However, the timing of precipitation was not associated with the timing of germination, although notably our statistical power is minimal with only one growing season of data.

Germination rates were nearly three times higher in the two watering treatments compared to the control (drought) treatment (Fig. 3A), whereas survival was similar across watering treatments (Fig. 3B). Soil surface mean maximum temperature was strongly negatively associated with Douglas-fir survival (Fig. 3C), whereas neither temperature variable was associated with germination (Table 2.1). There was no detectable effect of wildlife exclusion on germination or survival (Fig. 3A, 3B).

2.4 Discussion

This study provides evidence that Douglas-fir regeneration is limited by moisture and microclimate, even at the cooler and wetter edge of its range. Germination rates and timing were significantly increased with watering treatments during an unusually dry growing season. While warmer temperatures did not affect germination, survival was reduced by higher mean maximum temperatures, showing that hotter temperature can limit recruitment in absence of sufficient moisture and that the combined effects of drought and warmer temperatures are already affecting early recruitment. While heat and moisture limitations would be unsurprising in some portions of

its range, it is concerning that they caused recruitment failures at Douglas-fir's cooler and wetter range position given that it is predicted to fare better than many western species with climate change (Rehfeldt et al. 2006). Numerous studies have shown climate-related recruitment limitations to Douglas-fir at other areas within its range (Williams et al. 2013, Rother et al. 2015, Davis et al. 2019b, Hankin et al. 2019), but this study is the first documented field experiment of moisture and temperature limitations to Douglas-fir at its upper limit.

Many studies indicate that moisture stress is the defining determinant of Douglas-fir photosynthetic rates, root growth, germination rate, and nutrient uptake and allocation (Roberts et al. 2005, Rother et al. 2015). Germination rates and timing are significantly correlated with available moisture in numerous western species, including Douglas-fir (HilleRisLambers et al. 2013, Thomas and Wein 2017), and despite moderate drought-tolerance, vapor pressure deficit and water limitations on Douglas-fir recruitment have been observed throughout its range (Littell et al. 2008, Restaino et al. 2016, Davis et al. 2019a). Indeed, while Douglas-fir germinants have been shown to be more embolism resistant than other western species, this resistance is at the cost of hydraulic efficiency and may prove less advantageous in all circumstances except severe drought (Miller and Johnson 2017, Davis et al. 2019a). Ectomycorrhizal networks benefit Douglas-fir seedlings under drought conditions, but only when established prior to the onset of drought (Bingham and Simard 2012). Our results agree with these complexities surrounding moisture limitation as both severity and timing of moisture stress were significantly correlated with germination. The timing germination is a delicate balance; too soon and germinants risk early damage by late spring frost; too late and they are not sufficiently established to withstand summer drought (Petrie et al. 2017). In general, longer growing seasons resulting from climate change may increase overall growth and productivity (Carroll et al. 2017, Carroll et al. *in*

review), but they also lead to greater rates of transpiration, evaporation, and soil drying (Bassman et al. 2003).

Wildlife herbivory did not appear to affect germination or first year survival of Douglas-fir. However, germination rates in the uncaged and caged control treatments were low ($< 10\%$), likely due to limited water availability and we thus had limited power to detect differences. Further, seeds were sown in late spring rather than in the fall when Douglas-fir seeds naturally disperse and thus seed predation could only occur during a limited time period. Seed pilfering and germinant herbivory have been shown to affect rates and spatial patterns of seedling survival (Noble and Alexander 1977, Pesendorfer et al. 2016) and clipping of cotyledons has been cited as a main cause of early mortality in California populations of Douglas-fir (Maguire 1989). Germinants are a more attractive food source in the succulent stage, which is when they are also more vulnerable to desiccation. We hypothesize that water stress is the primary limitation on recruitment and that wildlife effects are only more pronounced during years of above average moisture.

A number of studies have set out to address questions of how climate warming and altered precipitation will affect recruitment of conifer species (Rother et al. 2015, Kueppers et al. 2017a), but few have investigated moisture limitations in a drought-tolerant species at its upper range edge. Models predict that Douglas-fir will gain habitat with warming (Rehfeldt et al. 2006), but do not account for the influences of climate-induced stress, wildlife, and microenvironment on early seedling establishment. We found that water availability was a fundamental limitation to germination and that germinant survival was limited to cooler microenvironments at our study area in the montane – subalpine ecotone of the southern Rocky Mountains. Douglas-fir populations near the leading edge of its range may thus experience

recruitment failure with increasing aridity despite drought adaptations and predictions of expansion. This field-based experiment illustrates the complexity in predicting species future ranges and the vulnerability of early seedling establishment to heat and water stress.

2.5 Tables

Table 2.1. Generalized linear mixed-effect models of Douglas-fir germination and survival on treatment and microenvironment.

Watering and precipitation on timing of germination		
	Chi square	<i>P</i> value
Intercept	48.23	< 0.001
Bout	50.85	< 0.001
Bout2	54.26	< 0.001
Watering treatment	10.53	0.01
Precipitation	0.31	0.58
Watering treatments		
<i>Germination model</i>		
	Chi square	<i>P</i> value
Intercept	0.61	0.43
Watering treatment	17.06	0.00
Mean maximum temperature	1.25	0.26
Mean minimum temperature	0.06	0.81
Dunnett- adjusted pairwise comparison of means	Odds ratio	<i>P</i> value
Control - 25% Water	0.39	0.01
Control - 50% Water	0.26	0.00
25% Water - 50% Water	0.67	0.24
<i>Survival model</i>		
	Chi square	<i>P</i> value
Intercept	3.37	0.07
Watering treatment	2.02	0.36
Mean maximum temperature	9.35	0.002
Mean minimum temperature	0.51	0.48
Dunnett- adjusted pairwise comparison of means	Odds ratio	<i>P</i> value
Control - 25% Water	0.37	0.41
Control - 50% Water	0.77	0.93
25% Water - 50% Water	2.09	0.48
Wildlife exclusion		
<i>Germination model</i>		
	Chi square	<i>P</i> value
Intercept	41.66	< 0.001
Wildlife exclusion treatment	0.64	0.42

<i>Survival model</i>	Chi square	<i>P</i> value
Intercept	6.10	0.01
Wildlife exclusion treatment	1.23	0.27

2.6 Figures

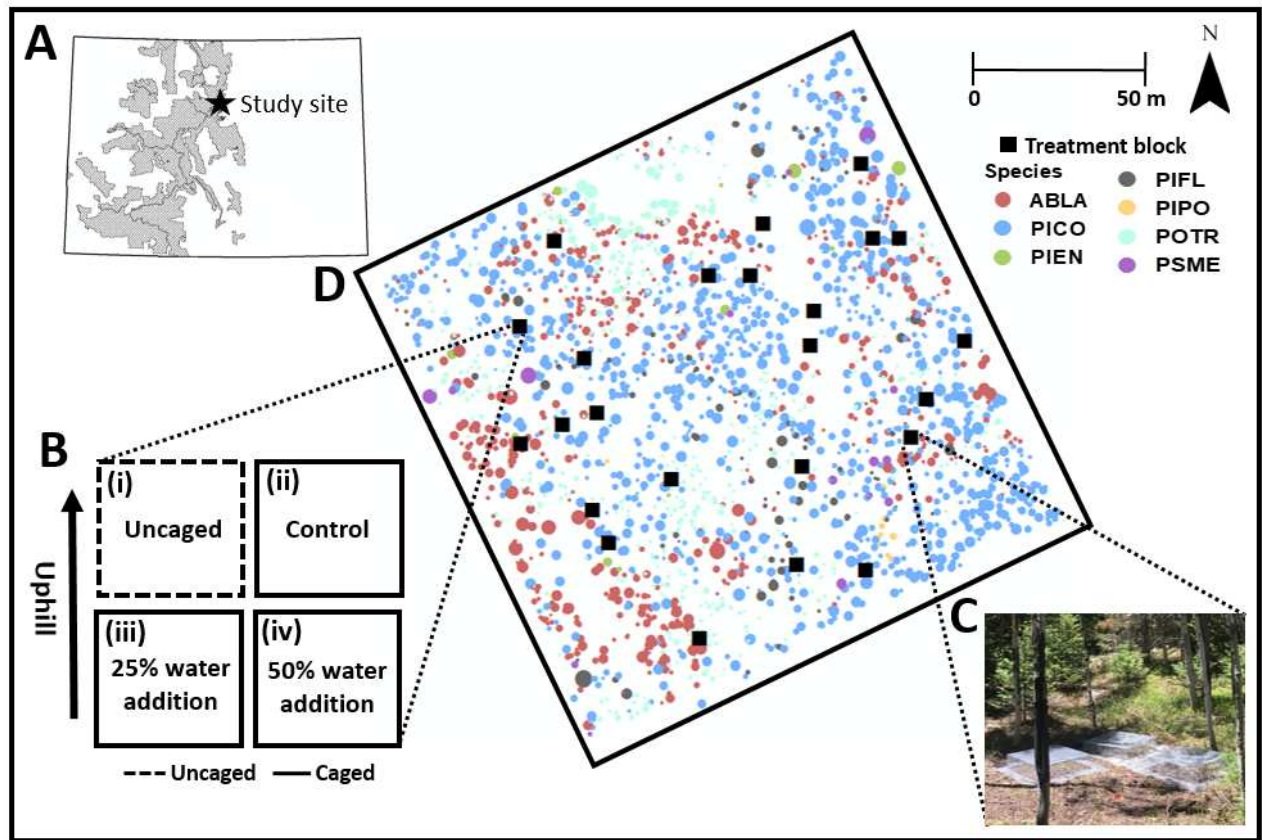


Fig. 2.1. Detail of study site and plot design including: (A) study site location within Colorado in relation to U.S. National Forest land; (B) four treatments: (i) wildlife allowance; uncaged, not watered; (ii) control (drought); caged, not watered; (iii) 25% water addition (typical moisture); caged; (iv) 50% water addition (excess moisture); caged; (C) photo of one treatment block; (D) stem map of site with treatment block locations (black squares). Species codes are as follows: ABLA, subalpine fir; PICO, lodgepole pine; PIEN, Engelmann spruce; PIFL, limber pine; PIPO, ponderosa pine; POTR, aspen; PSME, Douglas-fir.

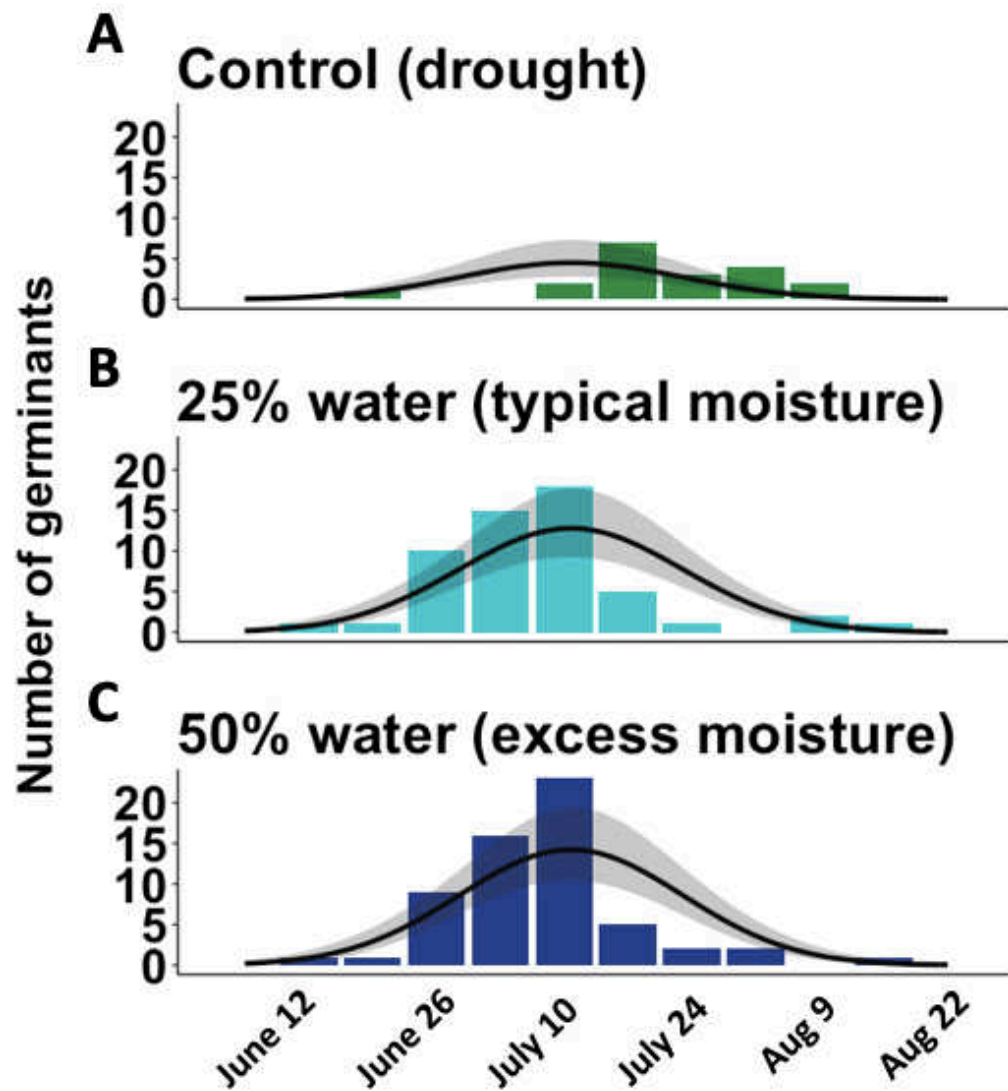


Fig. 2.2. Timing of Douglas-fir seed germination (number germinated seeds) by treatment: (A) control (drought); (B) 25% water (typical moisture); and (C) 50% water (excess moisture). Model predicted germination and 95% confidence intervals for each treatment is overlaid.

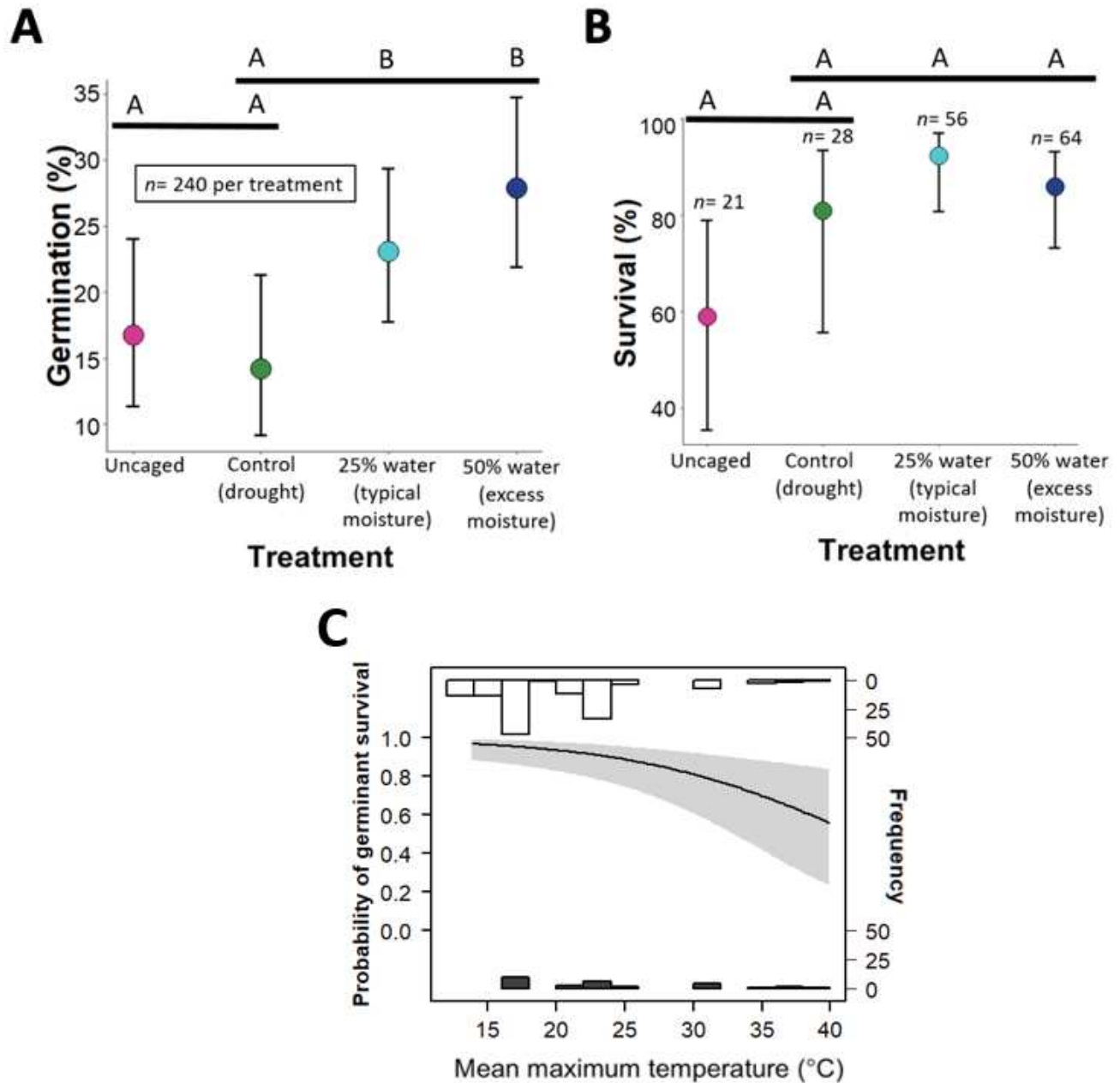


Fig. 2.3. Mean probabilities with upper and lower confidence intervals from mixed linear regression for: (A) germination and (B) survival of Douglas-fir by treatment. Sample sizes for germination (number seeds sown) and survival (number surviving germinants) are noted within boxes. Significantly different groups within each model by upper horizontal lines. Note different scales in the y-axis. (C) Predicted effect of mean maximum temperature (°C) on the probability of Douglas-fir germinant survival. Histograms (secondary y axis) show the observed frequency of juveniles that survived (white; top histograms) and died (gray; bottom histograms) across mean maximum temperature.

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