

Persistent yet vulnerable: resurvey of an *Abies* ecotone reveals few differences but vulnerability to climate change

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Abstract. Climate change is shifting forest tree species distributions across elevational and latitudinal gradients, and these changes are often pronounced at ecotones where species meet their climatic bounds and are replaced by other species. Using an extensive ecotone composed of lower-montane white fir (*Abies concolor* var. *lowiana*) and upper-montane red fir (*Abies magnifica* var. *magnifica*) in the central Sierra Nevada range of California, USA, we (1) examined how the demographics of the ecotone have responded to recent climate using a field observational study and a historical dataset, (2) quantified climate drivers across species life stages using contemporary demographic data, and (3) tested the potential impacts of future climate on species-specific seedling survival and growth in a fully factorial growth chamber experiment that varied temperature, growing season length, and water availability. A re-examination of the ecotone midpoint after 35 yr suggested a reduction in *A. concolor* sapling and tree densities and a rise in *A. magnifica* proportional dominance between surveys. Seedling abundances across the ecotone indicated that *A. magnifica* tends to dominate the regeneration layer and currently forms an important component of the seedling community at elevations below those where *A. magnifica* saplings or trees begin to co-dominate stands. Observational and experimental assessments suggest that temperature and precipitation serve as important drivers, differentiating *A. concolor* vs. *A. magnifica* distributions, and are primary stressors at the seedling stage. Seedlings of both species were adversely affected by experimental climate treatments, although *A. concolor* exhibited greater survival and a more conservative growth strategy under extreme climatic stress than *A. magnifica*. Projections indicate that historical climate conditions will rise by an amount greater than the ecotone's current elevational extent by the end of the 21st century. Differential drivers of species abundances suggest that the projected climate will expand conditions that promote *A. concolor* abundance and impede *A. magnifica* abundance across the ecotone; however, disturbance activity and microclimatic conditions will also influence regeneration and overstory tree dynamics. Our study demonstrates the importance of quantifying species-specific responses to climate and indicates that widespread regeneration failure may be one possible consequence in which species exhibit strong sensitivity to projected climate conditions.

Key words: *Abies concolor*; *Abies magnifica*; climate change; climate envelope; climate tolerance; distribution shifts; ecotone; elevational gradient; growth chamber experiment; regeneration; Sierra Nevada; species demographics; species distribution.

INTRODUCTION

Species distribution shifts are an anticipated consequence of rapid, ongoing climate change (Thuiller 2004, Hamann and Wang 2006), and elevational and

latitudinal shifts in forest tree species have already been documented (Beckage et al. 2008, Lenoir et al. 2008). Historical shifts in species composition are likely to occur over longer time frames, from decades to millennia (Davis and Shaw 2001); however, the rate of anthropogenically driven climate change is projected to outpace both historical rates as well as the pace at which forest tree species will be able to migrate (Aitken et al. 2008, Lafontaine et al. 2018). Early signs of distribution

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shifts are expected to be most pronounced in forest ecotones, representing transition zones between ecological communities (McArthur and Sanderson 1999). Within montane forest ecotones, tree species are distributed across climatic gradients until they meet their climatic bounds and are replaced in dominance by another co-occurring tree species (Whittaker 1960). Climate change-induced distribution shifts of long-lived, sessile tree species will vary as a function of differential survival among species but can also differ across life stages within species. Identification of disparities among life stages (i.e., seedlings, saplings, and mature trees) through time can provide an early indication of species distributional shifts in co-occurring tree species, and forest ecotones provide an effective platform in which to evaluate the potential for climate-driven shifts in local species' distributions.

Distribution shifts across montane ecotones will occur as species track ecological niches under climate change (Aitken et al. 2008), and rapidly changing, interacting climate conditions will constrain niche suitability and breadth (Sexton et al. 2017). At a distribution's leading edge, the upward migration of favorable conditions—particularly warming temperatures and lengthening growing seasons—are expected to bolster the reproductive capacity of lower elevation and lower latitude species and permit species migration (e.g., migration of northern hardwoods into the boreal forest, Beckage et al. 2008). On the trailing edge, these same conditions will intensify climatic stressors and are likely to result in some combination of either canopy mortality or regeneration failure, leading to localized extirpation from a species' extant range (e.g., drought-induced contraction of *Pinus ponderosa* at its lowest elevational extent; Allen and Breshears 1998). A species' persistence potential will be determined by its ability to track its ecological niche under a rapidly changing climate. Upward or downward shifts may be possible under future temperature and precipitation regimes or through the emergence of microclimatic refugia (Millar et al. 2018, Stralberg et al. 2018, Millar 2019). The extent and speed at which distributional shifts occur across ecotones will depend on both the rate and degree of macro-climatic change, the abundance of favorable microclimatic niches suitable for continued species regeneration and survival, and the differential climate tolerances of co-occurring species.

Assessments of change within montane forest ecotones will be critical, given that higher elevations are warming faster than other regions, and evidence of climate-driven distribution shifts is mounting (Allen and Breshears 1998, Wason and Dovciak 2017). In the Sierra Nevada range of California, USA, where the climate has warmed by $\sim 1^{\circ}\text{C}$ over the 20th century (Safford et al. 2012), *Abies concolor* var. *lowiana* (Sierra Nevada white fir) and *Abies magnifica* var. *magnifica* (red fir) form an extensive, late-seral, elevationally stratified ecotone and

represent leading and trailing edge species across the ecotone, respectively. Prior research in the *A. concolor*-*A. magnifica* ecotone (Parker 1984, 1986, Barbour et al. 1990) has focused on identifying local drivers of each species' abundance and regeneration niche requirements. Both field observational (Parker 1984, 1986) and follow-up experimental studies (Barbour et al. 1990) found evidence to suggest that species' abundances are driven by microsite conditions within the ecotone and that *A. concolor*-*A. magnifica* germination and survival are linked to distinct regeneration strategies, in which *A. concolor* is favored in open/drier microhabitats while *A. magnifica* is favored in open/mesic and shaded/drier microhabitats. Additionally, regional examination of species' occurrences across the ecotone found that the duration of snow cover and snow water equivalent were dominant drivers of the upper elevation limit of *A. concolor* and the lower elevation limit of *A. magnifica* (Barbour et al. 1991). These historical studies highlighted the importance of microsite conditions on differential establishment within the ecotone but did not explicitly identify the climatic drivers of *A. concolor* and *A. magnifica* across life stages. Because climate is a fundamental determinant of species persistence, this information will be key in predicting the response of the ecotone to ongoing, rapid climate change.

To fill this knowledge gap, we revisited an *A. concolor*-*A. magnifica* ecotone in the central Sierra Nevada to investigate species-specific climatic drivers across life stages under both historical and projected future conditions and to assess the potential for distribution shifts in the ecotone under climate change. First, we established a field observational study to quantify abundances among species and across life stages. We then paired this contemporary assessment with Albert Parker's historical ecotone dataset (Parker 1984, 1986) to compare abundances among species and across life stages over a 35-yr period. Next, we quantified climate conditions driving variation among species and across life stages under in situ historical climate conditions and investigated seedling tolerances to future climate conditions using a fully factorial growth chamber experiment that manipulated temperature, growing season length, and water availability. Finally, we used these observational and experimental studies to evaluate current and future climatic sensitivity of the *A. concolor*-*A. magnifica* ecotone in California's Sierra Nevada range and to specifically investigate the following questions: (1) Are seedling and mature life stages coincident across the ecotone, as they were historically, or has demography shifted over the last 35 yr? (2) How do climatic drivers differ among species and across life stages under in situ historical and projected future climate conditions? (3) Given species climatic tolerances, what is the potential fate of these species across the ecotone under future climate scenarios?

STUDY AREA

The *A. concolor*-*A. magnifica* ecotone in the central Sierra Nevada range of California, USA separates the lower- and upper-montane vegetation zones (Parker 1984, Barbour et al. 1990). *Abies concolor* primarily grows in mixed-conifer stands from ~1,200 to 2,500 m in elevation and frequently co-occurs with *Calocedrus decurrens*, *Pinus lambertiana*, and *Pinus ponderosa* var. *ponderosa*. *Abies magnifica* forms pure stands from 1,600 to 2,700 m in elevation but can also co-occur with *Pinus contorta* var. *murrayana* and *Pinus monticola* (Bonner and Karrfalt 2008). Lower-montane *A. concolor* forests tend to occur on more productive sites with nutrient-rich soils and a shallow seasonal snowpack (Barbour et al. 1990, 1991), while upper-montane *A. magnifica* forests tend to occur on less productive sites with nutrient poor or disturbed soil and a deeper, seasonally persistent snowpack (Barbour et al. 1991). Historical fire return intervals averaged 16 yr in the lower montane and 40 yr in upper-montane forests (Van Wagtenonk et al. 2018).

We conducted our study in Yosemite National Park (hereafter Yosemite) and the Stanislaus National Forest (hereafter Stanislaus) in the central Sierra Nevada (Fig. 1). Both areas are characterized by warm, dry summers and cool, wet winters with the majority of precipitation falling as snow (Kittredge 1953). At the Yosemite Village weather station (2020 m elevation, Station ID: GHCND:USW00053150) that resides at the northern edge of Yosemite and southern edge of the Stanislaus study areas, 30-yr climate normals for the period 1981–2010 showed that mean annual temperature was 9.8°C, ranging from 2.3°C in December to 19.9°C in July (data available online: <https://www.ncdc.noaa.gov/>). Mean annual precipitation was 1,060 mm, with most falling precipitation in the winter season between November and March.

METHODS

Field study

1981 data.—Forest composition and structure were surveyed in 30 plots established in the Tioga Pass Road and Glacier Point areas of Yosemite (Parker 1986) between 1,960 and 2,330 m in elevation. Sample plots targeted stands that contained *A. concolor* and *A. magnifica* overstory trees in equal abundance (i.e., at the ecotone midpoint), and sampling consisted of 12 subplots nested within a 40 × 60 m plot grid. Trees (>10 cm diameter) were sampled for species and diameter at breast height (dbh; 1.37 m height) in 0.01-ha subplots (0.12-ha per plot). Saplings (>1.37 m height and <10 cm diameter) and established seedlings (<1.37 m height and >1-yr-old, younger seedlings have low rates of survival and cannot be reliably identified to species) were tallied by species in 0.005-ha (0.06 ha per plot) and 0.001-ha subplots (0.012 ha per plot), respectively. See Parker

(1984, 1986) for a full methodological description. For this comparative analysis, the total number of plots sampled in 1981 plots were subset to 12 (of 30) to best match the elevational range and aspect of plots sampled in 2016.

2016 data.—Forest composition and structure were surveyed in 60 plots distributed across the *A. concolor*-*A. magnifica* ecotone in Yosemite and the Stanislaus. Plots were divided among four regions—Tioga Pass Road and Glacier Point areas in Yosemite, and Crabtree and Herring Creek areas in the Stanislaus—and stratified across five ~150 m elevation bands between 1,675 and 2,425 m within each region (4 regions × 5 elevational bands × 3 plots = 60 total plots). For each elevation band and region, 10 candidate plot locations were randomly selected on north-facing aspects within ~750 m of a road or trail using a geographic information system (ESRI ArcGIS Desktop: Release 10.1, Redlands, California, USA). Plots were restricted to north-facing aspects to ensure that pre-identified plot locations had a high probability of being dominated by one or both fir species. Included in these were plot locations sampled by Parker (1984, 1986) in 1981 in Yosemite and relocated using detailed qualitative directions. Plot relocation was approximate, because historical plots were not monumented and geographic coordinates not collected in 1981. In the field, candidate plots were visited in sequence, and the first three plots within the *A. concolor* or *A. magnifica* forest type were selected for sampling. In rare instances on the Stanislaus, candidate plots were deemed unsuitable for sampling due to localized evidence of past tree harvest. Plots with evidence of tree harvest were not sampled because such disturbance history was not representative of conditions found in the broader plot network, and we did not possess historical records nor the means to accurately back calculate pre-treatment forest structure.

All trees and saplings were surveyed within a circular 0.1-ha fixed area plot, and species, live or dead status, and dbh were recorded. Established seedlings were assigned height classes (i.e., <0.25, 0.26–0.50, 0.51–1.00, and 1.00–1.37 m) and tallied by species in a 0.01-ha⁻¹ fixed area plot. Circular fixed area plots are standard forestry practice and were chosen for the 2016 sampling campaign to balance accuracy in capturing forest structure attributes and efficiency in plot layout necessary for visiting many plots within an extensive network. Overall, plot areas were similar among 1981 and 2016 sampling campaigns, and seedling, sapling, and tree size classes were held constant among sampling campaigns. To estimate seedling age cohorts, we destructively sampled basal stem segments from two to ten seedlings per species per plot depending on seedling availability on the Stanislaus (197 *A. concolor* and 191 *A. magnifica* seedlings across 30 plots). Destructive sampling was not permitted in Yosemite. Samples were returned to the laboratory and processed to determine age using

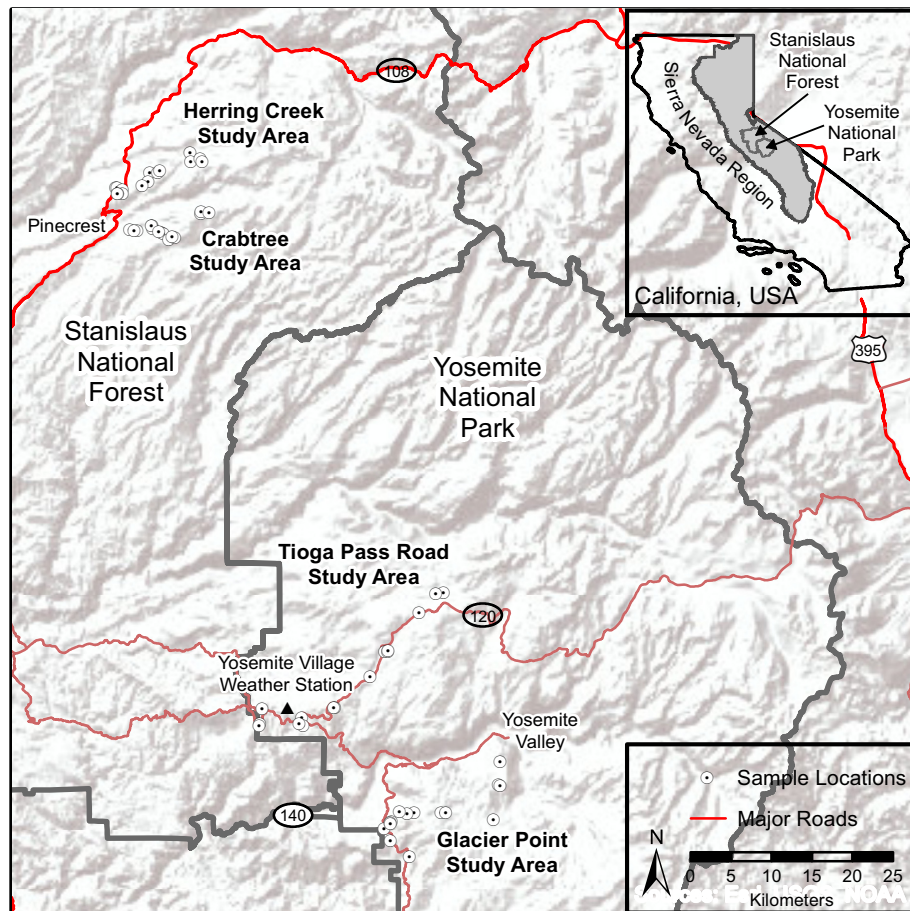


FIG. 1. Map of sampling locations in Yosemite National Park and the Stanislaus National Forest, Sierra Nevada Range, California, USA.

standard dendrochronology techniques (Stokes and Smiley 1996) and MeasureJ2X software (VoorTech Consulting ProjectJ2X: Version 5.0x, Holderness, NH, USA).

Data Processing.—Absolute (stems ha^{-1}) density and an *Abies* relative density index (i.e., proportional abundance of *A. concolor* and *A. magnifica* excluding non-*Abies* species) were computed for seedling, sapling, and tree life stages for each year. Regeneration was further evaluated by computing the proportion of seedlings to total *Abies* individuals in all life stages. Plots were treated as independent sample units.

Historical and projected climate data were extracted based on 2016 plot locations as scale-free point estimates generated using ClimateWNA v6.00 software (Wang et al. 2012, 2016). Mean annual climate normals were extracted for the 30-yr period preceding each sampling campaign (i.e., 1951–1980 and 1981–2010), and climate variability was computed as coefficient of variation using annual estimates of climate variables for the 1981–2010 climate period. Projected data represent future climate for periods 2040–2069 and 2070–2099 under the IPCC Fifth Report Representative Concentration Pathway (RCP) 8.5 (IPCC 2014) and were generated using an

ensemble of 15 global climate models from the Coupled Model Inter-Comparison Project 5. Climate variables included: mean annual temperature ($^{\circ}\text{C}$), mean annual precipitation (mm), mean annual radiation ($\text{MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), mean May to September precipitation (mm), precipitation as snow (mm), climatic moisture deficit (mm), annual temperature difference between the warmest and coldest months ($^{\circ}\text{C}$), and frost-free period (days).

Growth chamber experiment

Experimental Setup.—We conducted a three-way factorial experiment to investigate the effects of current and projected future temperature, soil drying, and growing season length conditions on *A. concolor* and *A. magnifica* seedling growth and survival ($n = 27$ treatment combinations). Each treatment was replicated with 14 seedlings per species. Locally collected seeds were obtained from the USDA Forest Service Placerville Nursery (seed zone 531, 1,980 m elevation) and stratified in cold, moist conditions for 30 d (Bonner and Karfalt 2008). Seeds were planted in soil collected at the

Crabtree sampling location and germinated under ambient temperature ($\sim 21^{\circ}\text{C}/10^{\circ}\text{C}$, day-time and night-time temperatures) and non-limiting moisture conditions for 60 d.

After establishment, seedlings were transferred to one of three growth chambers (Conviron CMP3000 and CMP4030, Winnipeg, Manitoba, Canada) programmed to represent mean summer temperature in the present (2001–2010), projected mid-21st century (2040–2069), and projected late-21st century (2070–2099) periods based on predictions made by the Canadian Centre for Climate Modelling and Analysis (CanESM2; Flato et al. 2000) under the RCP 8.5 emissions forcing scenario. Day-time temperatures were set at 24.0°C , 27.5°C , and 29.4°C , and night-time temperatures were set at 9.9°C , 11.6°C , and 14.6°C for present, mid-21st century, and late-21st century climate scenarios, respectively. Drying treatments emulated progressive soil drying by providing 2 mL of water at 7, 10, or 14 d intervals, such as might occur with decreasing snowpack and increasing evapotranspiration associated with climate change (Flint et al. 2008). Growing season length was manipulated by limiting the experiment length to 143, 154, and 189 d in accordance with predicted growing season lengths in the present, mid-21st century, and late-21st century time periods, respectively. The photoperiod of each chamber was set at 15 h, light intensity was set at $45\ \mu\text{mol}$ daily and $0\ \mu\text{mol}$ nightly, and pots were grouped by drying and growing season treatments within trays and randomized weekly to avoid any influence of position. At the end of each growing season treatment, seedlings were removed from chambers, and seedling status (live/dead) was recorded. Pots were dried under ambient conditions. Once dry, seedlings were extracted and weighed for root and shoot biomass.

Statistical analysis

Changes in the composition of seedling, sapling, and tree life stages between the 1981 and 2016 surveys was assessed by comparing estimates of density and the proportion of each species seedlings to total *Abies* individuals in all life stages. Due to some uncertainty in determining the location of Parker's 1981 plots, we restricted the 2016 and 1981 datasets to the Yosemite region and progressively constrained site characteristics to best match in aspect (290° to 70°) and elevation (2,000–2,235 m). Twelve plots from each sampling campaign were identified as sufficiently similar to support comparative analysis. Differences in absolute density between sample years and species were assessed using analysis of variance (ANOVA) and multiple pair-wise comparisons (Tukey's HSD, $\alpha = 0.05$). Binomial logistic regression weighted with total *Abies* individuals per life stage (Venables and Ripley 2002) was used to estimate proportional *Abies*-only relative abundance and standard errors. Differences between species and year were evaluated using

multiple pair-wise comparisons (Tukey HSD, $\alpha = 0.05$). Model assumptions were checked using standard diagnostic plots and outliers were identified for removal using Cook distances.

Patterns in *A. concolor* and *A. magnifica* absolute and relative abundance were evaluated across the ecotone in 2016 by producing summary statistics for each species life stage (mean ± 1 standard error, $n = 60$). Differences between species were assessed using ANOVA for absolute density and binomial regression for proportion variables, and multiple pair-wise differences were evaluated using Tukey HSD ($\alpha = 0.05$). The occurrence of species life stages were evaluated by computing the number of plots with seedling, sapling, and mature tree life stages present. Mortality was estimated for sapling and tree life stages by estimating the percentage of dead individuals by species (mean ± 1 standard error, $n = 60$).

To investigate climate drivers among species and across life stages under past climate conditions in situ, we fitted multivariate regression models predicting absolute and *Abies* relative density index for each species life stage using historical 30-yr climate normals and climate variability variables (Appendix S1: Table S1; 1981–2010) as candidate variables in model selection. Models were fitted by exhaustive model selection to minimize AIC/BIC (Burnham and Anderson 1998) using the 2016 data ($n = 60$). Absolute density was transformed to the $\log_{10}$ scale and predicted using linear regression models. *Abies* relative density index was predicted using binomial logistic regression models weighted with total *Abies* individuals per life stage. Model assumptions were confirmed using standard diagnostic plots, outliers were identified for removal using Cook's distances, and the absence of multicollinearity was confirmed by computing variance inflation factors.

Projected climate at the lower and upper elevational bounds of the ecotone was predicted using a two-step process. First, *Abies* relative density index-elevation binomial logistic regression models (see above) were fitted for each life stage, and inverse regression was used to identify elevations corresponding to the lower and upper ecotone bounds. The lower ecotone boundary was defined as the elevation that corresponded to 90% *A. concolor* relative abundance and 10% *A. magnifica* relative abundance, whereas the upper ecotone boundary was defined as the elevation that corresponded to 10% *A. concolor* relative abundance and 90% *A. magnifica* relative abundance. Model results for *A. concolor* and *A. magnifica* were inverse one another because relative abundances were computed using the *Abies*-only relative density index. Second, climate-elevation linear models were fitted for each climate variable by period (i.e., 1951–1980, 1981–2010, 2040–2069, and 2070–2099), and inverse regression was used to predict historical and projected climate at the elevations corresponding with the above-defined lower and upper ecotone boundaries. Note that the purpose of the climate-elevation models was only to produce climate estimates at the elevational

bounds of the ecotone and not to test a priori relationships between climate variables and elevation. Model assumptions were evaluated using standard diagnostic plots and outliers were identified for removal using Cook distances. Standard errors of inverse model predictions were computed using the delta method (Oehlert 1992, Jackson 2011).

Species-specific seedling tolerances to future climate conditions were further investigated in the growth chamber experiment. Binomial logistic regression was used to evaluate treatment effects (i.e., temperature, moisture, growing days) on seedling mortality (0, 1) and ANOVA was used to evaluate treatment effects on total biomass (g), aboveground biomass (g), belowground biomass (g), and root : shoot biomass ratio. The experimental design was balanced for seedling mortality, but disproportionate seedling death in some treatment groups resulted in an unbalanced design for biomass and root : shoot ratio response variables. The interacting effects of species and treatment were evaluated in two-way analyses to investigate performance differences between species, and multiple pair-wise comparisons were used to assess differences (Tukey HSD, $\alpha = 0.05$). Model assumptions were evaluated using standard diagnostic plots and outliers were identified for removal using Cook distances.

All data processing and statistics were conducted using R software programs (R Core Team 2019), including the *bestglm* (McLeod et al. 2020), *leaps* (Lumley and Miller 2017), *msm* (Jackson 2011), and *multcomp* (Hothorn et al. 2008) packages.

RESULTS

Ecotone composition

On north-facing aspects at the ecotone midpoint, our comparison of the 1981 and 2016 datasets found fewer *A. concolor* saplings and trees in 2016 than in 1981, but

no change in *A. magnifica* sapling or tree densities between years (Table 1). Seedling density did not differ between years in either species. In 1981, shared dominance between *A. concolor* and *A. magnifica* was indicated by statistically similar relative abundances and similar proportions of each species seedlings to total *Abies* individuals. In 2016, *A. magnifica* was found to be dominant in relative abundance and the proportion of *A. magnifica* seedlings to total *Abies* individuals was greater than the proportion of *A. concolor* seedlings to total *Abies* individuals.

Across the broader plot network established in 2016, *A. concolor* seedlings occurred in 65%, saplings occurred in 63%, and trees occurred in 80% of plots, with all life stages co-occurring in 55% of plots. *Abies magnifica* seedlings occurred in 65%, saplings occurred in 62%, and trees occurred in 68% of plots, with all life stages co-occurring in 58% of plots. Seedling, sapling, and tree absolute abundances did not differ between *A. magnifica* and *A. concolor*, due to high variation in plot estimates across the ecotone. *Abies magnifica* was greater in relative abundance in sapling and seedling, but not tree life stages (Appendix S1: Table S2). *Abies concolor* seedlings averaged 19.7 ± 14.9 (± 1 standard deviation) years old, and *A. magnifica* seedlings averaged 27.2 ± 19.8 (± 1 standard deviation) years old (Appendix S1: Table S3). These ages justified the use of 30-yr climate data in predicting seedling stage abundances. Sapling mortality averaged $5.5\% \pm 3.0\%$ for *A. concolor* and $2.4\% \pm 0.8\%$ for *A. magnifica*, while tree mortality averaged $9.4\% \pm 2.4\%$ for *A. concolor* and $7.4\% \pm 1.5\%$ for *A. magnifica*. Non-*Abies* species were a minor component (<25% of individuals) of stand densities across the ecotone.

Binomial regression models predicting each species relative density index with elevation (R^2 from 0.66 to 0.85; Fig. 2; Appendix S1: Table S4) exhibited inverse relationships across the ecotone, with *A. concolor*

TABLE 1. A comparison of *Abies* species absolute density and relative density index within each life stage, and the proportion of each *Abies* species seedlings to total *Abies* individuals (all life stages) from surveys in 1981 and 2016 across the ecotone’s midpoint in Yosemite National Park.

	1981†		2016†	
	<i>Abies concolor</i> ‡	<i>Abies magnifica</i> ‡	<i>Abies concolor</i> ‡	<i>Abies magnifica</i> ‡
Absolute density (ha ⁻¹)				
Seedlings	875 ± 248 ^a	1,590 ± 308 ^a	3,417 ± 1,573 ^a	6,417 ± 2,728 ^a
Saplings	171 ± 48 ^a	212 ± 57 ^a	58 ± 26 ^b	464 ± 154 ^a
Trees	168 ± 22 ^a	176 ± 25 ^a	88 ± 36 ^b	198 ± 49 ^a
<i>Abies</i> relative density index (proportion)				
Seedlings	0.35 ± 0.12 ^{ab}	0.65 ± 0.12 ^{ab}	0.35 ± 0.06 ^a	0.65 ± 0.06 ^b
Saplings	0.45 ± 0.11 ^{ab}	0.55 ± 0.11 ^{bc}	0.11 ± 0.15 ^a	0.89 ± 0.15 ^c
Trees	0.49 ± 0.08 ^{ab}	0.51 ± 0.08 ^{ab}	0.31 ± 0.10 ^a	0.69 ± 0.10 ^b
Proportion of seedlings out of all life stages				
Seedling : All individuals	0.27 ± 0.11 ^a	0.50 ± 0.10 ^{ab}	0.32 ± 0.06 ^a	0.60 ± 0.06 ^b

Note: Estimates include means ± 1 standard error and letters denote pair-wise statistical differences in each row ($\alpha = 0.05$).
†Elevation range (m) for 1981 is (2,042, 2,225) and for 2016 is (2,014, 2,231).
‡Sample size (n) = 12.

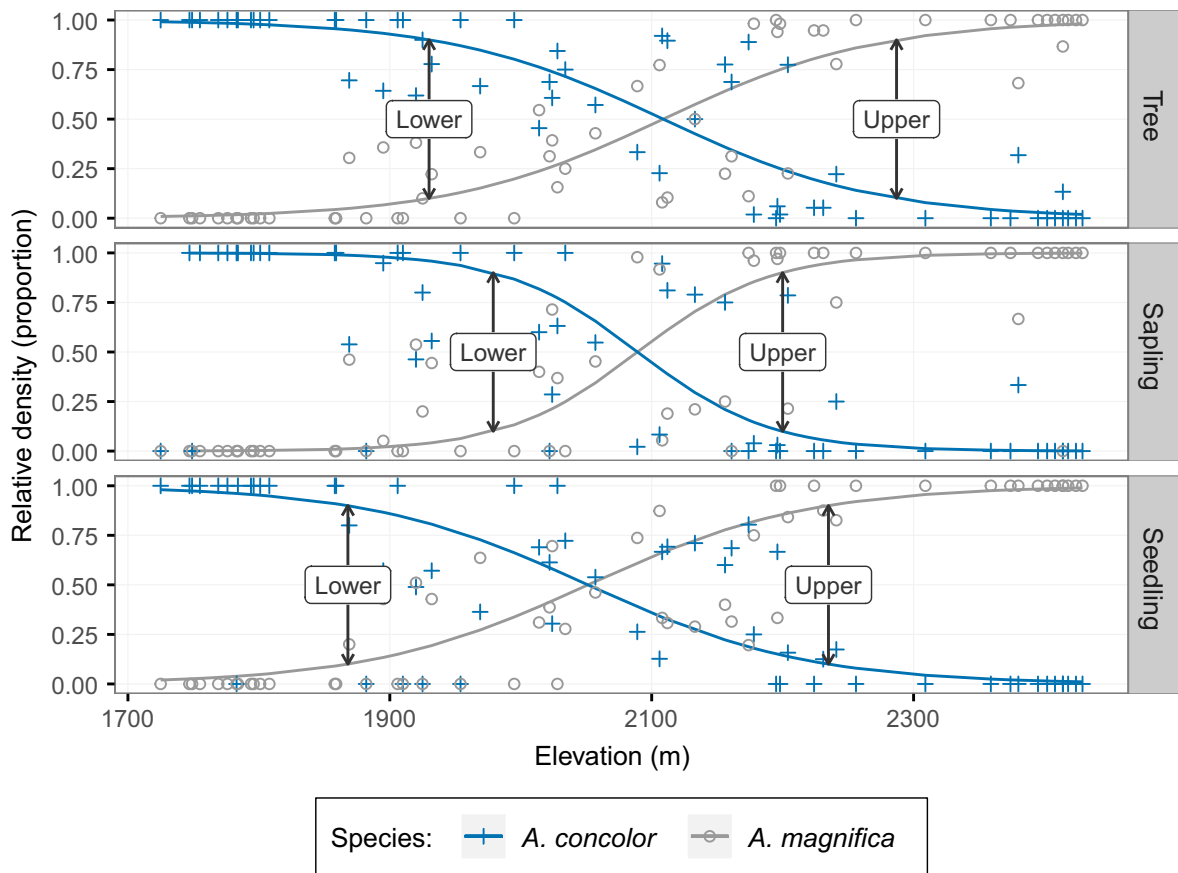


FIG. 2. Binomial logistic regression models predicting *Abies concolor* (pluses) and *Abies magnifica* (circles) relative density index with elevation show the transition in species composition across the ecotone in 2016. The elevational extent of the ecotone is indicated between lower and upper ecotone boundaries for each life stage. The lower ecotone boundary (Lower) is the elevation that corresponds with 90% *A. concolor*/10% *A. magnifica* relative abundance and the upper ecotone boundary (Upper) is the elevation that corresponds to 10% *A. concolor*/90% *A. magnifica* relative abundance. See Appendix S1: Table S4 for elevation model results and Appendix S1: Table S5 for estimates of the ecotone's elevation limits.

varying negatively and *A. magnifica* varying positively with elevation across all life stages on north-facing aspects. We found that the elevation limits and ranges comprising the *A. concolor* and *A. magnifica* ecotone (i.e., sites with shared species dominance between 10% and 90% *Abies* relative density index) differed depending on life stage (Appendix S1: Table S5). The elevational extent of the ecotone formed by seedlings extended into lower elevations than other life stages and encompassed a wider elevation range than other life stages from $1,868 \pm 23$ to $2,235 \pm 18$ m elevation with a midpoint of $2,051 \pm 13$ m. *Abies magnifica* seedling abundance in the lower portion of the ecotone was predominantly composed of seedlings in the smallest height class (<0.25 m height; Appendix S1: Fig. S1). Saplings spanned a narrower ecotone, occupying a mid-elevational position from $1,979 \pm 33$ to $2,200 \pm 22$ m elevation with a midpoint of $2,089 \pm 17$ m. Trees formed an ecotone at slightly higher elevations from $1,930 \pm 32$ to $2,287 \pm 31$ m with a midpoint $2,109 \pm$

16 m elevation. Based on these predictions, the elevational boundaries of the ecotone appeared to extend below, but not much above, the elevation range sampled in 1981 (Parker 1984, 1986).

Climate controls on ecotone species abundances

Differences in relative success between species and among life stages across the ecotone suggested distinct tolerances to past climate conditions. Mean 30-yr climate normals were the best predictors of *A. concolor* and *A. magnifica* densities. Climate variability predictors performed poorly in model selection and were, therefore, not included in final models. *Abies concolor* sapling and tree absolute density was negatively associated with mean annual radiation and precipitation as snow (Table 2; $R^2 = 0.69$ for saplings and 0.70 mature trees), while *A. concolor* seedlings were negatively associated with mean annual precipitation and mean annual radiation and positively associated with the frost-free period

TABLE 2. Linear regression model results predicting absolute density of *Abies concolor* and *Abies magnifica* life stages in 2016 using historical climate variables.

	Coefficient	SE	<i>t</i>	<i>P</i>	<i>r</i> ²
Tree: <i>Abies concolor</i>					
Intercept	8.563	1.862	4.599	<0.001	0.704
Mean annual radiation (MJ·m ⁻² ·d ⁻¹)	-0.309	0.101	-3.066	0.003	
Precipitation as snow (mm)	-0.008	0.001	-10.726	<0.001	
Tree: <i>Abies magnifica</i>					
Intercept	13.666	1.163	11.753	<0.001	0.773
Mean annual temperature (°C)	-1.134	0.087	-13.021	<0.001	
Mean May to September precipitation (mm)	-0.033	0.005	-6.172	<0.001	
Sapling: <i>Abies concolor</i>					
Intercept	12.5	2.079	6.013	<0.001	0.685
Mean annual radiation (MJ·m ⁻² ·d ⁻¹)	-0.543	0.113	-4.825	<0.001	
Precipitation as snow (mm)	-0.007	0.001	-8.494	<0.001	
Sapling: <i>Abies magnifica</i>					
Intercept	7.032	3.669	1.916	0.061	0.654
Mean annual temperature (°C)	-1.000	0.129	-7.755	<0.001	
Mean annual radiation (MJ·m ⁻² ·d ⁻¹)	0.297	0.140	2.117	0.039	
Mean May to September precipitation (mm)	-0.033	0.008	-4.136	<0.001	
Seedling: <i>Abies concolor</i>					
Intercept	13.595	3.844	3.537	0.001	0.639
Mean annual precipitation (mm)	-0.007	0.003	-2.501	0.016	
Frost-free period (days)	0.034	0.011	3.09	0.003	
Mean annual radiation (MJ·m ⁻² ·d ⁻¹)	-0.443	0.198	-2.232	0.03	
Seedling: <i>Abies magnifica</i>					
Intercept	17.384	2.022	8.598	<0.001	0.611
Mean annual temperature (°C)	-1.354	0.153	-8.844	<0.001	
Mean May to September precipitation (mm)	-0.045	0.009	-4.802	<0.001	

Note: Density is log₁₀ transformed.

($R^2 = 0.64$ for seedlings). Absolute densities in *A. magnifica* were negatively associated with mean annual temperature and mean May to September precipitation ($R^2 = 0.61$ for seedlings and 0.77 for mature trees), and sapling density was additionally positively associated with mean annual radiation ($R^2 = 0.65$ for saplings). *Abies concolor* and *A. magnifica* relative densities exhibited inverse relationships and life-stage predictor variables were similar to those in absolute density models (Appendix S1: Table S6).

Climate exposure at lower and upper ecotone bounds

Estimates of the breadth and range of climate conditions associated with the ecotone differed depending on which life stage was used to define the ecotone. When defined by seedlings, the ecotone was shifted toward warmer, drier sites at lower elevations compared with when defined by sapling or tree life stages. The breadth of climate conditions between the ecotone's lower and upper limits was similar for seedlings and trees but narrower for saplings (Appendix S1: Table S7). At the seedling ecotone boundaries, historical climate conditions from the 1981–2010 time period ranged from 7.2°C to 9.5°C in mean annual temperature, 113 to 147 d frost-

free period, 1,084 to 1,204 mm in mean annual precipitation, 502 to 571 mm in climatic moisture deficit, and 85 to 259 mm in precipitation as snow. At the sapling ecotone bounds, climate conditions ranged from 7.4°C to 8.8°C in mean annual temperature, 116 to 137 d frost-free period, 1,120 to 1,192 mm in mean annual precipitation, 508 to 550 mm in climatic moisture deficit, and 138 to 242 mm in precipitation as snow. Finally, at the tree ecotone boundaries, climate conditions ranged from 6.9°C to 9.1°C in mean annual temperature, 108 to 142 d frost-free period, 1,105 to 1,220 mm in mean annual precipitation, 492 to 559 mm in climatic moisture deficit, and 115 to 284 mm in precipitation as snow. Mean annual temperature, frost-free period, and climatic moisture deficit varied negatively with elevation, while mean annual precipitation and precipitation as snow varied positively with elevation (Fig. 3; Appendix S1: Table S8). Mean annual temperature, frost-free period, mean annual precipitation, and climatic moisture deficit intercepts shifted upward and precipitation as snow shifted downward in projected future climate periods. Regression model slopes remained parallel across climate periods. Mean annual temperature difference, mean annual radiation, and May to September precipitation exhibited significant associations with

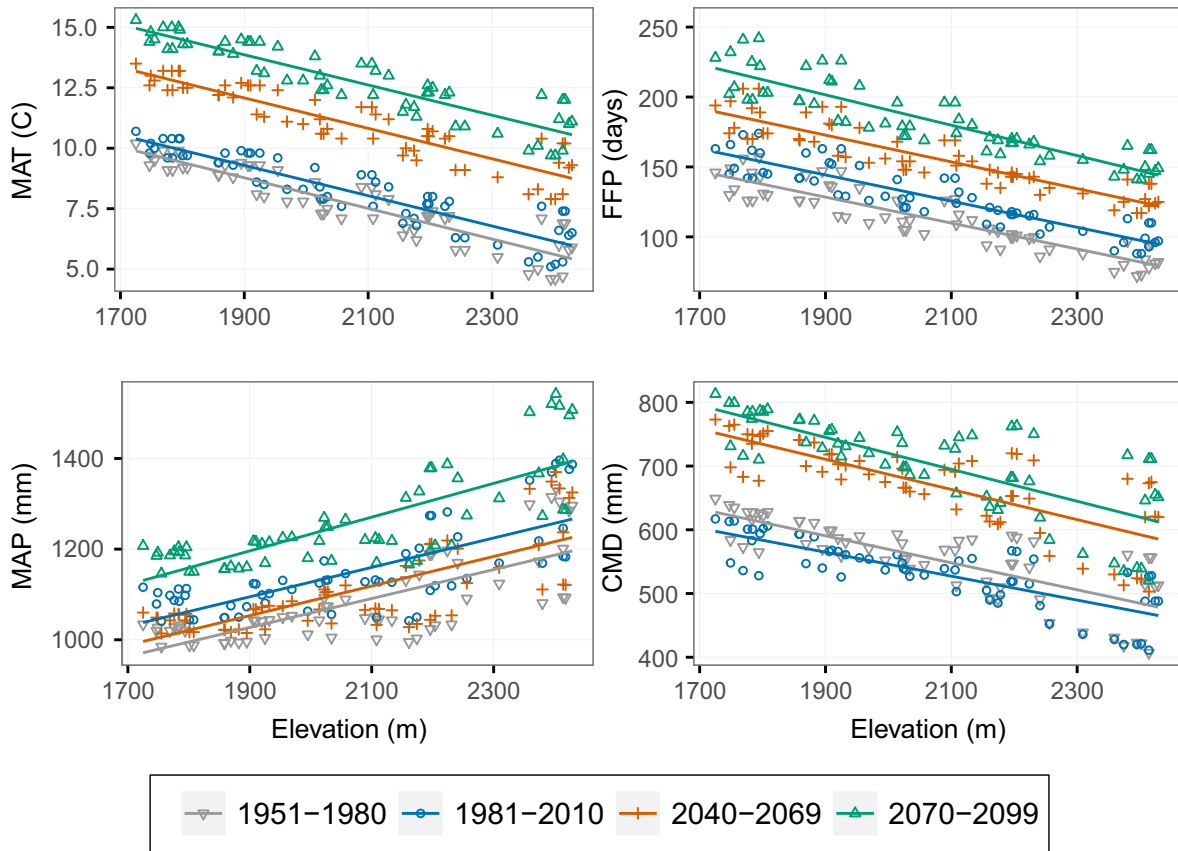


FIG. 3. Linear regression models predicting mean annual temperature (MAT, °C), frost-free period (FFP, days), mean annual precipitation (MAP, mm), and climatic moisture deficit (CMD, mm) with elevation by climate period. Climate periods 1951–1980 (inverted triangles) and 1981–2010 (circles) represent historical conditions, whereas periods 2040–2069 (pluses) and 2070–2099 (triangles) represent projected future conditions assuming relative concentration pathway (RCP) 8.5 emissions scenarios.

elevation, but correlation coefficients were below 0.2, so models were not used to predict climate conditions at ecotone bounds (Appendix S1: Table S8).

Between the 1951–1980 and 1981–2010 periods, climatic moisture deficit decreased across the ecotone due to concomitant increases in temperature ($\Delta 0.5^{\circ}\text{C}$) and precipitation ($\Delta 70\text{ mm}$; Appendix S1: Table S7). The frost-free period increased by 16 d across the ecotone and precipitation as snow decreased by 20–40 mm between time periods depending on elevational position. Climate conditions are expected to become more severe between the 1981–2010 and 2070–2099 time periods. Across the ecotone, climatic moisture deficit is expected to rise by 32% as a result of disproportionate changes in temperature ($+4.6^{\circ}\text{C}$) over precipitation ($+120\text{ mm}$). The frost-free period is anticipated to rise by 50+ days and precipitation as snow is projected to decline by 76% by the late-21st century. Notably, by the mid-21st century, mean annual temperature, frost-free period, climatic moisture deficit, and precipitation as snow at the upper elevation limit will meet or exceed conditions observed during the 1981–2010 period at the lower elevation limit.

Seedling performance in growth chambers

In the growth chamber experiment, both species experienced heightened mortality under greater temperature and moisture limitation (Fig. 4). *Abies magnifica* mortality also rose with the number of growing days. Under the projected late-21st century temperature treatment, mortality was complete for both species with more than two-thirds dying prior to the present (2000–2010) growing season length. *Abies concolor* seedlings performed better with lower overall seedling mortality ($57\% \pm 3\%$) than *A. magnifica* ($69\% \pm 3\%$) under all treatments (P -value < 0.001 ; Fig. 4).

In the seedlings that survived the treatments, *A. magnifica* allocated more shoot and root biomass than *A. concolor* across all climate treatments (P -value < 0.001 ; Table 3); however, differences in biomass declined under higher temperature and moisture limitation treatments (Fig. 4). Root : shoot ratio did not differ between species. Projected mid-21st century temperature had no effect on *A. concolor* aboveground biomass and a negative effects on *A. magnifica* aboveground biomass. Both species exhibited lower

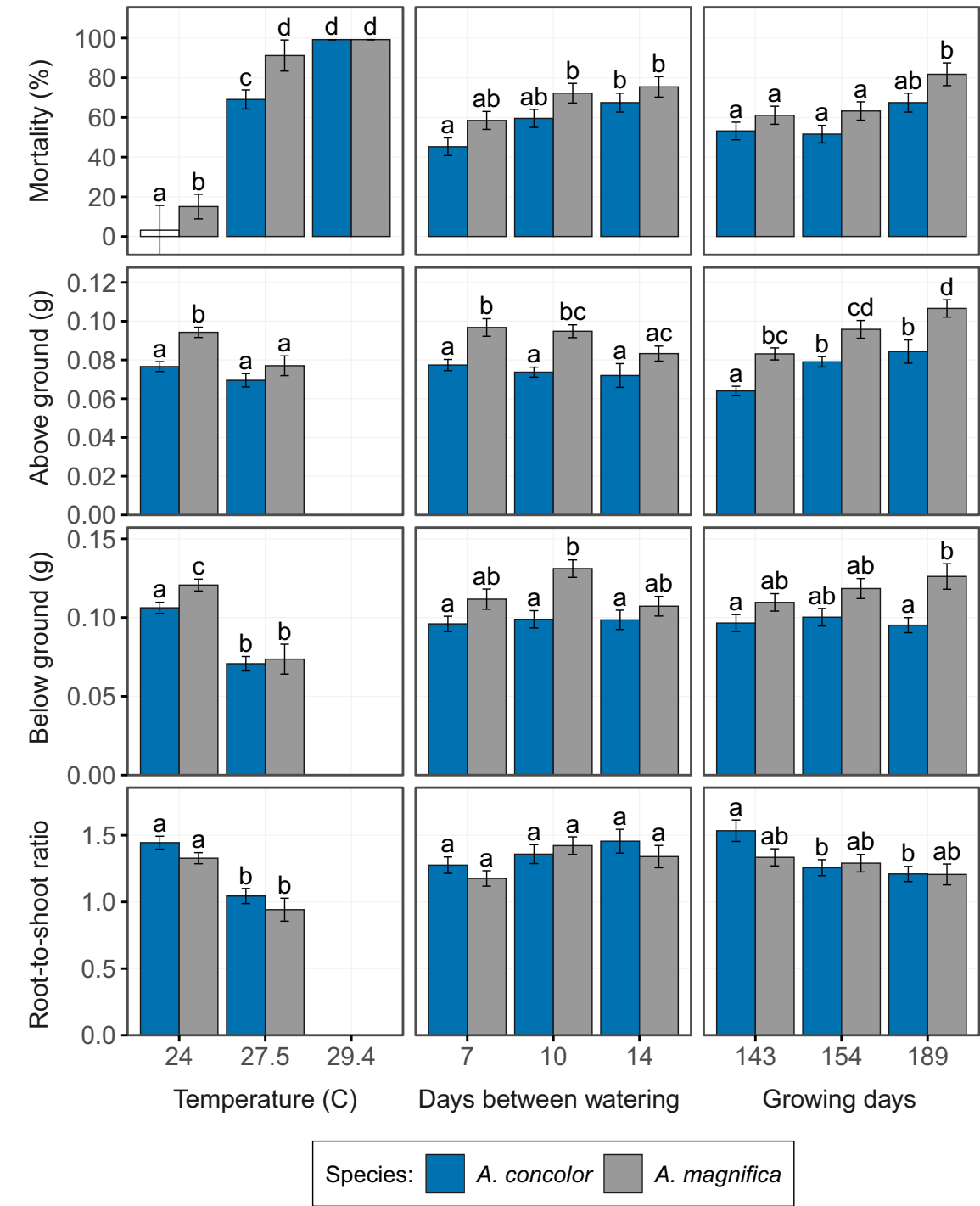


FIG. 4. *Abies concolor* and *Abies magnifica* seedling mortality (%), aboveground biomass (g), belowground biomass (g), and root : shoot ratio vs. temperature, moisture, and growing day treatments in the growth chamber experiment. Statistics include group means ± 1 standard error and letters denote pair-wise statistical differences in each panel ($\alpha = 0.05$).

belowground biomass, total biomass (not shown), and root : shoot ratio in the mid-21st century temperature treatment. The effect of projected growing season length differed by species. *Abies magnifica* aboveground and belowground biomass experienced positive effects, resulting in no change in root : shoot ratio. *Abies concolor* experienced converse relationships with growing season length having a positive effect on aboveground

TABLE 3. ANOVA results indicating growth chamber treatment effects on *Abies concolor* and *Abies magnifica* seedling total biomass (g), aboveground biomass (g), belowground biomass (g), and root : shoot ratio.

	Temperature	Moisture	Growing days
<i>Abies concolor</i>			
Total biomass (g)	20.38 (0.05)***	1.87 (0.01) ^{ns}	2.66 (0.01)*
Aboveground biomass (g)	2.23 (<0.01) ^{ns}	1.50 (<0.01) ^{ns}	8.09 (0.01)***
Belowground biomass (g)	32.29 (0.04)***	1.65 (<0.01) ^{ns}	3.01 (0.01)*
Root : shoot ratio	21.71 (4.72)***	0.07 (0.03) ^{ns}	12.31 (5.36)***
<i>Abies magnifica</i>			
Total biomass (g)	25.30 (0.06)***	8.30 (0.04)***	2.96 (0.014)*
Aboveground biomass (g)	7.84 (<0.01)**	6.693 (<0.01)**	6.17 (0.01)**
Belowground biomass (g)	21.24 (0.03)***	3.789 (0.01)*	0.29 (<0.01) ^{ns}
Root : shoot ratio	8.86 (1.40)**	2.85 (0.90)*	1.38 (0.43) ^{ns}

Note: Statistics include *F*-statistic (sum of squares) and significance level (*ns*, not significant, **P* < 0.10, ***P* < 0.05, ****P* < 0.01, ****P* < 0.001).

biomass but no effect on belowground biomass, resulting in a decline in root : shoot ratio. Moisture limitation had no effect on *A. concolor* aboveground biomass or belowground biomass. In *A. magnifica*, moisture limitation had a negative effect on aboveground biomass and a positive effect on belowground biomass in the intermediate drying treatment. Moisture limitation did not elicit an effect on root : shoot ratio in either species.

DISCUSSION

Under rapidly changing climate conditions, montane forest tree species may be at risk of local extirpation due to shifts in species dominance at ecotones as local conditions change and species are forced to migrate to track niche requirements (Millar et al. 2007, Aitken et al. 2008). A re-examination of the *A. concolor* – *A. magnifica* ecotone after 35 yr indicated a reduction in *A. concolor* sapling and tree abundance and a rise in *A. magnifica* relative abundance in all life stages between surveys. Across the entire ecotone, *A. magnifica* tended to dominate the seedling layer, but regeneration did not appear constrained in either species. The lower formation of the seedling ecotone (Fig. 2) indicated that *A. magnifica* seedlings are currently present in greater relative proportions at lower elevations than *A. magnifica* saplings or trees. Minor shifts in species composition is perhaps not surprising, as tree abundances can be dynamic, climate did not change dramatically between the 1951–1980 and 1981–2010 periods (relative to projected changes), and extensive high-severity disturbance events were absent prior to sampling.

Our findings from paired observational and experimental studies suggested that temperature and precipitation influence *A. concolor* and *A. magnifica* distributions across the ecotone and are primary stressors at the seedling stage. Future climate conditions are anticipated to change dramatically, as historical temperature and moisture regimes are projected to climb in elevation by an amount greater than the ecotone's current elevational extent by the mid- to late-21st century.

Moreover, findings from our growth chamber experiment suggested that proportional dominance in *A. magnifica* seedlings observed in the field is likely to be ephemeral, as *A. magnifica* seedlings exhibited substantial vulnerability to future climate conditions. Seedlings of both species performed adversely under projected temperature, moisture limitation, and growth season length treatments, suggesting the potential for widespread regeneration failure, although *A. concolor* exhibited greater survival and a more conservative growth strategy than *A. magnifica* (Fig. 4). Warming temperatures, longer growing seasons, and greater climatic moisture deficits are likely to exacerbate species-specific sensitivities in the regeneration phase and may result in compositional changes across the landscape.

Ecotone composition

Variation in the elevational distribution of life stages across the ecotone shows that *A. magnifica* seedlings currently form an important component of the regeneration community at elevations below those where *A. magnifica* saplings or trees begin to co-dominate communities. In contrast, *A. concolor* seedlings did not extend as high in elevation as *A. concolor* trees. Heightened *A. magnifica* seedling abundance was largely associated with seedlings in the smallest size class (<0.25 m height) and is suggestive of higher germination success and greater seedling survival (Parker 1986, Barbour et al. 1990), or could simply be due to greater seed production. Yearly seed production cycles are not always congruent between the two species (Gordon 1970); *Abies magnifica* produces seed, on average, every 2-3 years, while *A. concolor* production ranges from 3 to 9 years (Bonner and Karrfalt 2008). Such a regeneration response might also be expected if overstory mortality, as indicated by reductions in *A. concolor* saplings and trees at the ecotone midpoint between 1981 and 2016 (Table 1), extended into lower elevations and *A. magnifica* was able to establish in forest gaps and small openings where it could be a strong competitor (Parker 1986,

Barbour et al. 1990). In comparison with other studies investigating *Abies* spp. in the Sierra Nevada, *A. magnifica* tree abundances were equal to (Barbour et al. 2002) or less than (Meyer et al. 2019, Meyer and North 2019) those found in pure stands at similar or higher elevations, respectively, and *A. concolor* abundances were slightly less than those found in pure stands at similar elevations (Barbour et al. 2002) and in mixed-conifer stands at lower elevations (Knapp et al. 2021). Differences in abundance between 1981 and 2016 were notable, but need to be interpreted conservatively due a relatively small sample size, changes in sampling protocols, and the lack of certainty in the relocation of 1981 plots in 2016. Uncertainties aside, we can be confident that both species continued to reproduce prolifically and that abundance of each species aligned with historical patterns (Parker 1984, 1986, Barbour et al. 1990, 2002).

Looking forward, major shifts in the ecotone's composition may be spurred by amplifying disturbance regimes. Recent warming and drying trends have catalyzed disturbance processes that can alter species composition through directional changes in environmental conditions, favoring one competing species over another and/or abruptly altering successional trajectories through wind, fire, insect outbreak, or severe drought disturbance (Smith et al. 2009). Species dominance shifts are commonly observed in stands after drought-mediated, bark beetle attack, depending on outbreak severity and the prevalence of advanced regeneration (Diskin et al. 2011, Renwick et al. 2016, Young et al. 2020). Compositional shifts are also well documented after wildland fire as a function of fire severity (Crotteau et al. 2013), species adaptations (Lavoie and Sirois 1998, McKenzie and Tinker 2012), and distance to seed source (Shive et al. 2018). In Sierra Nevada *Abies* spp. communities, *Scolytus* bark beetle outbreaks, *Armillaria* root disease, and wildfire have, for a long time, shaped forest structure and community dynamics, and a rise in fine-scale disturbance activity across the ecotone might favor *A. magnifica* reproduction over *A. concolor* due to its better performance in canopy gaps (Parker 1986, Barbour et al. 1990).

Widespread disturbance-related mortality was not evident across our network of plots. Branch flagging was noted during our survey in 2016 and severe *A. concolor* mortality due to bark beetles has subsequently been documented at lower elevations on the nearby Stanislaus-Tuolumne Experimental Forest (Knapp et al. 2021) and elsewhere (Fettig et al. 2019, Restaino et al. 2019). Shifts in species abundance due to the 2012–2016 drought, if any, may not have been fully captured with the 2016 data, because a considerable portion of the fir mortality occurred between 2016 and 2018 (Knapp et al. 2021). *Abies magnifica* forest health-related crown loss has also recently been observed on moisture-limited sites along its lower elevational extent in Yosemite National Park (Meyer et al. 2019). Furthermore, this forest type is

increasingly experiencing high-severity fire, a poignant issue highlighted by the recent 2020 fire season that eclipsed prior seasons in extent and burned significant portions of the western Sierra Nevada forests (<https://www.fire.ca.gov/incidents/2020/>). While historical disturbance regimes may have promoted regeneration processes in these forests through gap and patch formation, extensive severe disturbance, as has occurred recently across California's forests, alters stand environmental conditions and risks widespread loss of advanced regeneration and seed bearing trees necessary to sustain contemporary forest species distributions in many areas.

Climate controls on ecotone species abundances and seedling performance

Individualistic species tolerances to climate and climate-influenced disturbances are a primary control of species abundances and distributional zonation, defining general habitat requirements and shaping forest composition and stand dynamics (Boucher-Lalonde et al. 2012, Copenhagen-Parry and Bell 2018). Inverse patterns of declining *A. concolor* and rising *A. magnifica* abundances with increasing elevation highlight the opposing climate drivers controlling individual species success (Table 2; Appendix S1: Table S4) and support observed segregation across elevational and climatic gradients (Parker 1984, Barbour et al. 1991). *Abies concolor* abundance within the ecotone appears to be driven by intolerance of cooler temperatures, short growing season lengths, and solar heating, while *A. magnifica* abundance appears to be driven by intolerance of warm temperatures, long growing seasons, and loss of the winter snowpack. Our growth chamber experiment reinforced the importance of seedling-stage climate drivers observed in the field observational study, with *A. magnifica* seedlings displaying greater overall mortality across temperature and drought treatments than *A. concolor*. Identifying species-specific climatic drivers and tolerances, as we have done here, will be instrumental in determining future patterns of tree species recruitment and persistence under ongoing, rapid climate change.

Demographics across the ecotone remain vulnerable to future changes in climate, which are anticipated to be far more severe than conditions observed during and prior to our sampling period (Fig. 3; Appendix S1: Table S7), and plant traits favoring greater heat and drought tolerance, especially in early life stages, are likely to have a distinct advantage under projected climate regimes (Mueller et al. 2005, Allen et al. 2010). In our climate change manipulation experiment, *A. concolor* exhibited higher survival and slower growth than *A. magnifica* in the face of projected greater temperature, moisture limitation, and growing season length, but these factors had adverse effects on seedlings in both species. While growth chamber experiments inherently lack the range of variation found in the natural environment and cannot fully replicate the numerous interacting

factors impacting species in early life stages, they can be used to effectively test hypothesized relationships in the drivers of seedling performance. Consistency between field observational and growth chamber results suggested that *A. concolor* and *A. magnifica* seedling success within the ecotone is likely to be vulnerable to increasingly severe climate conditions over the next century.

Our results corroborated past studies that concluded that climate is a strong driver of the establishment and persistence of *A. concolor* and *A. magnifica* (Oosting and Billings 1943, Parker 1984, 1986, Barbour et al. 1990, 1991) and that even minor increases in temperature can have a significant effect on both species' zonation (Barbour et al. 1991). Climatic sensitivity varies among species and will influence tipping points that drive overstory mortality and seedling recruitment for each species. Differential drivers of species' success suggest that projected warmer temperatures, longer growing seasons, and greater climatic moisture deficits may expand conditions that promote *A. concolor* abundance and impede *A. magnifica* abundance across the ecotone; however, *A. magnifica* continues to regenerate successfully across the lower and upper extents of the ecotone as of 2016.

Implications of climate change

Climate change is altering the boundary conditions that drive species demographics and disturbance regimes, two fundamental ecological processes that regulate species composition and distribution across contemporary ecosystems. Consistent with other studies examining future climate in the Sierra Nevada range (Mote et al. 2005, Cayan et al. 2008, Safford et al. 2012, Walton et al. 2016), climate projections used in this study indicate substantial future increases in temperatures and climatic moisture deficit. Across the *A. concolor* – *A. magnifica* ecotone, temperatures are projected to rise by 4.5°C, moisture deficits by 32%, and the frost-free period by 50+ days over historical conditions by the end of the 21st century (Appendix S1: Table S7; Wang et al. 2012, 2016). The precipitation phase will favor rain over snow as the warm season lengthens and winter temperatures rise, and soil water recharge will decline due to greater evaporation and runoff (Flint et al. 2008), limiting persistent soil moisture throughout the growing season (Bales et al. 2011). Soil moisture limitation, a critical bottleneck for seed germination and seedling establishment (Gray et al. 2005), will stress mature trees as well as limit new recruitment and establishment (Clark et al. 2016) and has the potential to drive extirpation of species from their historical distributions.

Climate change-induced effects on disturbance activity will be a compounding driver of forest composition change, as shifts in climate are anticipated to amplify fire and bark beetle activity in montane and subalpine forests, affecting *A. concolor* and *A. magnifica* (Meyer and

North 2019). Montane forest densification due to fire suppression has predisposed forests to greater disturbance risk and severity through the build-up of fuels and increased competition for limited resources (Young et al. 2017, Restaino et al. 2019). In two recent studies investigating the effects of drought on Sierra Nevada forests, interacting factors tied to climate, forest densification, and bark beetle activity have led to widespread severe mortality in conifers including *A. concolor* in the montane vegetation zone (Young et al. 2020, Knapp et al. 2021). Departures from historical fire frequencies are less pronounced in the *A. magnifica* zone and, while upper elevation *A. magnifica* forest composition and structure still reside within their natural range of variation, canopy decline and tree mortality are expected to increase with rising fire and beetle activity under future climates (Meyer et al. 2019, Meyer and North 2019). Local shifts in forest trajectories are expected to be catalyzed by disturbance (Smith et al. 2009). Evidence suggests that trailing edge species contractions may be more prevalent than leading edge range expansions (Zhu et al. 2012, Renwick et al. 2016), as mortality in extant species can occur abruptly due to disturbance processes, whereas migration typically requires longer time horizons (Renwick and Rocca 2015).

Under projected 21st century climate conditions, differing characteristics among leading and trailing edge species and communities may shape the future success across the ecotone we studied. For example, warming climate may exert less stress on leading edge metapopulations such as *A. concolor*, because gene flow will predominantly occur from populations pre-adapted to warm environments (Davis and Shaw 2001, Aitken et al. 2008). Additionally, trailing edge species such as *A. magnifica* adapted to short growing seasons may not take advantage of longer ones due to self-reinforcing phenological cues that drive seasonal growth onset and cessation (Davis and Shaw 2001, Aitken et al. 2008). Species that are less tolerant to drought and climate-related stress are likely to be less competitive than those with a broader tolerance envelope (Jump and Penuelas 2005, Valladares et al. 2014, Dobrowski et al. 2015). Patterns of disturbance risk linked to productivity gradients may also influence species success under future climates. Higher productivity sites at lower elevations have experienced greater forest densification from historical fire suppression, resulting in heightened risk of severe burning due to greater loading and continuity of fuels and heightened potential for bark beetle infestation due to greater drought stress associated with high tree densities. Because trees have a long lifespan, landscape-level shifts may be slow in the absence of widespread disturbance, especially if mature individuals are not abruptly culled and continue to produce seed. In this study, rising *A. magnifica* dominance in the middle of the ecotone and estimates of the ecotone's elevational extent based on life stage suggest that fluctuations in the ecotone may be responding to shifts in site conditions driven by

climate variation or disturbance effects. Close alignment between climate conditions and *A. concolor* and *A. magnifica* abundance and seedling performance suggest that projected heat and drought associated with climate change are likely to disrupt demographic rates across the ecotone and may lead to a shift in either or both species' distribution.

CONCLUSIONS

Ongoing climate change risks widespread disruption of processes that drive forest community composition and structure, and early signs of distribution shifts resulting from changes in regeneration and survival are expected in ecotones where species meet the boundaries of their climatic tolerances. A re-examination of the ecotone after 35 yr suggested a reduction in *A. concolor* sapling and tree densities and a rise in *A. magnifica* dominance across life stages. Seedling abundance across the ecotone indicated that *A. magnifica* currently forms an important component of the regeneration community at elevations below those where *A. magnifica* saplings or trees begin to co-dominate stands. In contrast, *A. concolor* seedlings did not reach the upper elevation limit where *A. concolor* trees cease to co-dominate stands. Predictive relationships between *A. concolor* and *A. magnifica* life stages and climate variables suggested that both species exhibited strong sensitivity to, and are potentially vulnerable to, projected warming and drought conditions. In fact, recent drought-driven mortality in our study region have likely shifted *A. concolor* and *A. magnifica* life-stage abundances since our investigation in 2016. Given that an upward shift in climate greater than the ecotone's current elevation extent is expected by the end of the 21st century, ecotone composition may be susceptible to widespread changes through mature tree mortality and regeneration failure despite the relative stability of the ecotone during the 1981–2016 sampling period. Our results demonstrated the importance of quantifying individual species' tolerances to climate and suggest that survival under changing climate conditions will be determined by responses to temperature, longer growing seasons, and drought. Furthermore, our comparison of current conditions with a historical dataset have provided insight into forest regeneration and composition dynamics to climate change up to the present, which is critical for predicting tree species responses to future climate scenarios.

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SUPPORTING INFORMATION

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Data (Nelson et al. 2021) are available from the US Forest Service Research Data Archive: <https://doi.org/10.2737/RDS-2021-0057>.