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Drought to deluge: sensitivity to meteorological variation in trees of the eastern Sierra Nevada

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**DROUGHT TO DELUGE: SENSITIVITY TO METEOROLOGICAL
VARIATION IN CONIFERS OF THE EASTERN SIERRA NEVADA**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Katherine M. Ross

June 2020

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ABSTRACT

Drought to deluge: sensitivity to meteorological variation in trees of the eastern Sierra Nevada

Katherine Ross

Warming due to climate change will be felt throughout California. Increased climatic variability is also expected, and will impact physiological processes beyond what is predicted from changes in mean conditions. Knowledge of how these changes will affect dominant forest species in the Sierra Nevada is critical for anticipating secondary effects on water resources, wildlife, and other ecosystem services. In order to better understand the effect of weather variability on tree growth, I compared the sensitivity of four regionally dominant tree species to variable temperature and precipitation across a 500 m elevation gradient at annual and seasonal temporal scales.

My first chapter takes advantage of the end of a historic multi-year drought and included an unusually wet winter, to understand how very dry and very wet conditions constrain photosynthesis and growth. All species demonstrated phenotypic plasticity in response to temporal differences in precipitation on both inter-annual and seasonal timescales. Net photosynthesis in *Pinus contorta* decreased from an early season 2016 average of 12.4 to 6.89 μmol CO_2 m^{-2} s^{-1} later in the summer, but increased 14.1% between seasons in the wet year. By contrast, elevation had almost no effect on instantaneous photosynthetic gas exchange, CO_2 response curve

parameters, or stem water potential in any of the years for any of the species. My results show these species demonstrated considerable ability to tolerate and recover from an extreme drought event.

In my second chapter, I examined sensitivity of these species at longer time scales, by comparing tree age structure and variability in annual ring growth at these same elevations. I also assessed sensitivity of annual ring-width to variation in April 1 snow water content, a proxy for total water year precipitation over an 88-year period starting in 1929. I found higher snow water content had a positive effect on RWI at the lower elevations, but this effect was reversed at the highest site. Snow water content of the previous year was also important for some sites and species, supporting the idea that conditions over multiple years are involved in controlling growth. The age and size structure of *P. contorta* were not consistent with upslope migration, though a distributional shift for *Abies magnifica* is possible at the highest elevation.

In addition, I sought to understand community belief systems about climate change in the vicinity of two National Forests near my field sites. This aspect of my research may help forest managers frame management actions and policies to better communicate with these citizenries. My third chapter quantified the underlying belief systems and attitudes towards climate change expressed by local community members near the Inyo and Sierra National Forests. I used a combination of two previously developed survey instruments: 12 statements assessing a respondent's adherence to one of four dominant cultural types posited by Cultural Theory, and the

Global Warming's Six Americas survey developed by the Yale Program on Climate Change Communication. Despite the demographic similarities between the two National Forests, their populations differed in both their acceptance of and attitudes toward climate change and in their expressed agreement with the four cultural types.

My results provide reasons for optimism in the face of climate change in the eastern Sierra Nevada. With regard to the social context, even though acceptance of climate change was not universal, it was expressed by the majority of participants in both Forests. While significant ecological impacts are evident, tree at my sites demonstrated the capacity to respond plastically to dramatic meteorological variation in their photosynthetic rates, water status, and growth. One of the study species even appears to be responding distributionally. Increasing climate variability will likely subject these trees to new extreme events in the future, but thus far, they have shown an unexpected ability to tolerate and recover from extreme drought.

ACKNOWLEDGEMENTS

INTRODUCTION

Climate change is widely recognized as the major environmental challenge of our time. Rising atmospheric CO_2 concentration, driven by increasing anthropogenic greenhouse gas emissions are correlated with increases in mean surface air temperature (Hartmann et al. 2013, Myhre et al. 2013). Warming will continue over the coming century, with an increase in mean global surface temperature compared to the 1850-1900 baseline likely to exceed 2° C by 2100 (Collins et al. 2013). But it is not only mean conditions that are changing. Greater climatic variability, and a corresponding increase in the frequency of extreme temperature and precipitation events, may impact natural and human systems beyond what is predicted by changes in mean conditions (Cubasch et al. 2013). Plant physiological processes, especially water relations, appear to be more vulnerable to changing variability and extreme events than changes in mean conditions (Reyer et al. 2013). As large-scale reductions in emissions are unlikely in the near term, an understanding of the long-term ecosystem effects of rising CO_2 concentrations and associated climatic changes are an important goal for adaptation.

Understanding plant sensitivity to climatic changes is important for predicting future vegetation patterns to manage effectively for conservation, especially in forest ecosystems. Dominant tree species profoundly influence vegetation structure and have traditionally been used to identify vegetation communities in the Sierra Nevada (Storer and Usinger 1963). Evidence suggests that tree species are already responding

to climate change. Based on long-term snow depth manipulations, Loik et al. (2013) found reduced snow depth corresponded with reduced annual growth for *Pinus jeffreyi*, but not *P. contorta*, portending directional changes in species composition at certain elevations on the eastern side of the Sierra Nevada. Tree mortality in the Sierra Nevada is correlated with increases in climatic water deficit due to rising temperatures (van Mantgem and Stephenson 2007), while documentation of forest mortality associated with warming and drought in recent decades is at least consistent with idea that climate change is contributing factor on a global scale (Allen et al. 2010).

The relevance of the effects of climate change to forest management, through both impacts on ecosystem services and outcomes of management actions, are well documented. Widespread climate induced forest mortality, especially coupled with drought conditions, can increase fire risk and severity (Anderegg et al. 2013). Loss of forest cover also has numerous consequences for the hydrologic cycle, including changes in snow accumulation and melt patterns and increased evapotranspiration and surface runoff, which can affect water budgets and reduce water quality (Adams et al. 2012). At the same time, public attitudes in the U.S. towards the existence of climate change and the role of government in addressing it are strikingly divided along political and, to a lesser extent, geographic lines (Borick 2010). As a result, skepticism of climate science is common within communities most directly impacted by these changes, and can be a barrier to advancing management actions (Bierbaum et

al. 2013). Framing policies and actions in ways that are consistent with underlying belief systems and cultural values can reduce opposition (Kahan 2012), making an understanding of a community's beliefs about climate change important to successful public engagement (Maibach 2011).

My dissertation comprises three chapters. The first two examine the impact of conifer sensitivity to meteorological variability at four elevations in the eastern Sierra Nevada over two different timescales (Figure *i*-1). Both focus on the effects of very wet and very dry weather conditions. The first chapter focuses on short term impacts by investigating seasonal and inter-annual patterns in water status, photosynthesis, and needle growth. The second chapter investigates longer term impacts, looking at size and age structure across elevations, and comparing annual ring-growth to an 88-year record of April 1st snow water content, which approximates total water year precipitation. The final chapter investigates community belief systems about climate change near the Inyo and Sierra National Forests, the former of which include the field sites from the first two chapters.

a)
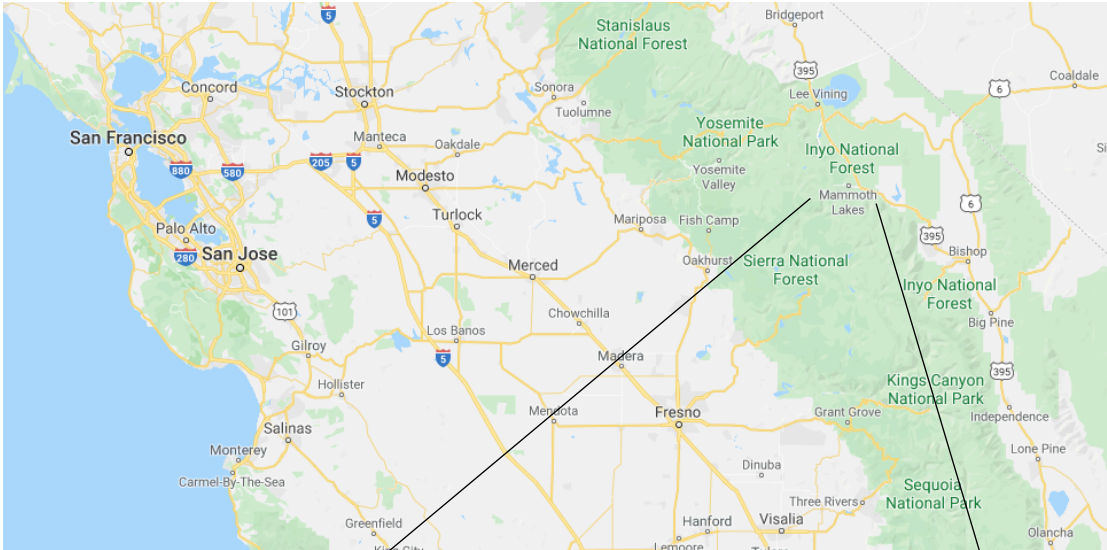
b)
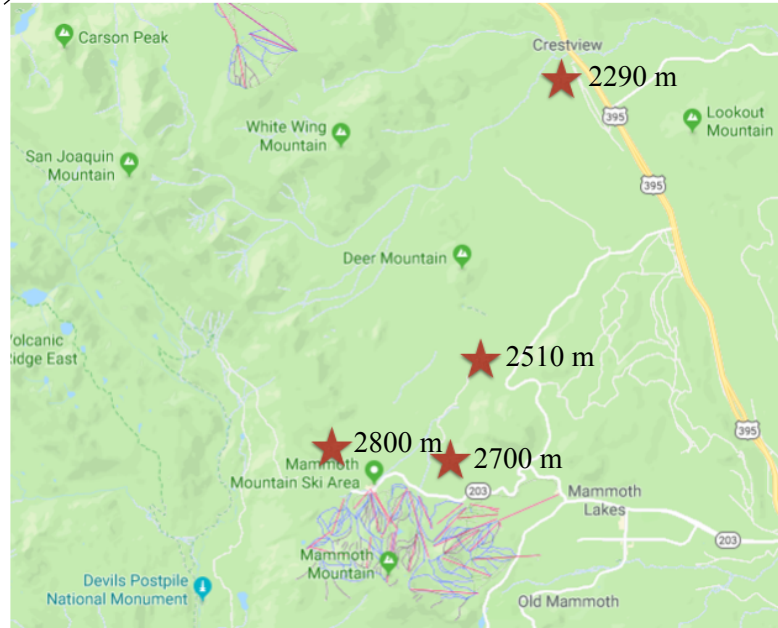
Figure *i*-1. a) Map including the Sierra and Inyo National Forests and Mammoth Lakes, CA. b) Map of Mammoth Lakes and the study sites.

CHAPTER 1:

Photosynthetic sensitivity to historic drought and deluge years for conifers in the eastern Sierra Nevada

Introduction

Warming under climate change will be felt throughout California, with greater increases in temperature expected in inland locations and during the summer months (Pierce et al. 2013), but more frequent occurrences of anomalously warm winter temperatures also likely (Swain et al. 2016). Projections of future precipitation trends in California suggest greater inter-annual variability and that the incidence of extreme years will likely increase by the end of the century (Berg and Hall 2015, Swain et al. 2018). At the same time, higher temperatures make extremely warm and dry conditions more likely to co-occur, increasing risk of drought (Diffenbaugh et al. 2015). Both rising temperatures and reduced precipitation enhance climatic water deficit (CWD), or the extent to which evaporative demand exceeds available soil moisture (Stephenson and Das 2011). Moreover, warming reduces winter snowpack, exacerbating the effect of low precipitation on the state's water resources for both human and natural systems (Berg and Hall 2017).

Phenotypic plasticity across both time and space can increase plant fitness and provide a mechanism through which species can respond to climate change. Especially for long-lived species, the ability of individuals to adjust physiological processes in response to environmental conditions over time may be sufficient to

allow populations to persist even under rapid, human-induced environmental changes (Chevin et al. 2013). Fotelli et al. (2019) found Aleppo pine exhibited considerable plasticity in needle water potential, net photosynthesis, and stable carbon isotope ratio (a measure of Water Use Efficiency) in response to both seasonal and inter-annual variation in temperature and precipitation, as well as clear recovery from drought effects as soil water availability increased. Inter-annual variation in the timing of leaf unfolding, flowering, and fruit maturation increased modeled fitness across the ranges of three European tree species, primarily by improving fitness in the margins of the niche (Duputié et al. 2015). However, effects were not consistent across species; phenological plasticity improved fitness in the warmer areas of their distributions for two species, but negatively affected the fitness of the third, which the authors attributed to unmet chilling requirements for breaking bud dormancy under warmer conditions (Duputié et al. 2015). These results indicate that plasticity is not uniformly adaptive for all species when it comes to coping with the impacts of climate change.

Physiological processes can vary considerably along environmental gradients within a species' range, which may provide insight into the effects of climatic changes on ecophysiological patterns and processes. Reed and Loik (2016) found that stem water potential and photosynthesis increased with elevation for sagebrush (*Artemisia tridentata*) in the eastern Sierra Nevada during the extreme drought year of 2014, consistent with increased precipitation and soil moisture at higher elevation sites. Experimental watering significantly increased photosynthetic rates and stomatal

conductance, but only at the lowest, driest site (Reed and Loik 2016). Zhang and

Cregg (2005) found that the morphological and physiological traits of Ponderosa

pines grown in a common garden experiment changed significantly along a mesic-to-

xeric gradient of three sites. Height, DBH, and needle length, which were greater at

more mesic sites, also showed significant differentiation based on source population.

In contrast, water potential and carbon isotope discrimination differed between sites,

but did not vary among populations, suggesting physiological plasticity is important

in allowing these trees to grow in differing environments (Zhange and Cregg 2005).

Likewise, Wertin et al. (2012) observed that loblolly pine seedlings grown at two

locations near the warm and cool extremes of the species current range had similar

responses to experimentally elevated water stress, temperature, and CO_2

concentration.

     Spatial and temporal physiological plasticity can interact to influence tree

sensitivity to future climate warming. In a common garden experiment in the

Colorado Rockies across three sites spanning a range of ~6° C, Carroll et al. (2017)

found both Lodgepole and Ponderosa pine showed considerable phenological

plasticity. Growing season length, as determined by the onset of bud break, increased

by an average of 40.5 days between the coldest and the middle sites, but only ~5 days

between the middle and warmest site (Carroll et al. 2017). Potts et al. (2017) found

strong seasonal responses in photosynthetic traits, but these responses were not

uniform across their three study species in southern Arizona; compared to Douglas fir

and southwestern white pine, Ponderosa pine had higher rates of photosynthesis during the cooler seasons. Changes in relative stomatal limitation for the three species followed similar patterns over time, but differed between species consistent with the study site's position within their respective elevational distributions. Ponderosa pine, which was near its upper range limit, experienced lower relative stomatal limitation than Douglas fir, which was near the lower edge of its elevational range (Potts et al. 2017). Together these results suggest greater physiological sensitivity in Douglas fir at this site, with potential consequences for community composition under future warming (Potts et al. 2017).

While predictions of future precipitation in the Sierra Nevada suggest considerable spatial and temporal variability, rising temperatures will increase CWD throughout the region (Rapacciuolo et al. 2014). This may lead to increased drought stress, especially for conifer species that are water limited at their lower elevation margins (Das et al. 2013). In California, there have recently been years of precipitation exceeding one standard deviation of the long-term mean, including 2011 and 2017, that have "bookended" the historic drought of 2012-2016. The degree to which the water relations, photosynthesis and growth of conifer saplings are sensitive such meteorological variability is not clear. Notably, the historic drought, followed by the exceptionally wet winter of 2016-2017, provides an opportunity to capture historically minimal and maximal water relations, photosynthesis, and growth of trees. In order to better understand historic variation in the physiology of young trees

in response to spatial and temporal changes in precipitation, we compared the physiological sensitivity of four conifer species over three years and at four different elevations, spanning the lower distributional edge of conifers at the Sierra Nevada – Great Basin Desert ecotone in eastern California. We hypothesized that

(1) Photosynthesis, stomatal conductance, and stem water potential would differ between species, but would (a) generally increase with elevation and (b) decrease over the course of the growing season, corresponding to trends in precipitation and soil moisture. This prediction assumes that temperatures are lower and soil moisture is greater at high compared to lower elevations, and that sapling physiology tracks the seasonal pulse of snow derived soil water.

(2) Photosynthesis, stem water potential, and growth would reflect the tremendous inter-annual variation in precipitation between the last year of the drought in 2016 and summer following the very snowy winter of 2017, but that trees at lower elevations, which are more likely to be water limited, would be more sensitive to this variation.

(3) Stomatal, as compared to biochemical, limitations on photosynthesis would be lower at higher elevations and in wetter years, reflecting patterns of precipitation and soil water availability.

Materials and Methods

Study Site and Species

This study was conducted along an elevation gradient that extends across approximately 500 m of the lower portion of a desert-to-forest ecotone, from the Great Basin Desert sagebrush steppe to the subalpine forest of eastern California, USA. We selected four study sites in the area around Mammoth Lakes, CA based on their elevation and accessibility. These sites are at approximately 2290 m, 2510 m, 2700 m, and 2800 m; the linear distance between the farthest two sites is approximately 12 km. The soils at all four sites are derived from geologically recent volcanic deposits, primarily well-drained rhyolitic pumice (Rinehart and Ross 1964, Huber and Rinehart 1965). The lowest site represents the lower distributional edge of conifers in this area, while the highest site is below the tree line. Four conifer species from the family Pinaceae, *Abies magnifica* A. Murray*, Pinus contorta* subsp. *murrayana* (Balsf.) Critchf.*, P. jeffreyi* Balf.*,* and *P. albicaulis* Engelm. occur at these sites. *P. contorta* is present at all four sites, *P. jeffreyi* at the lowest two, *A. magnifica* at the highest three, while *P. albicaulis* occurs at the highest site only. Six individuals of each species were haphazardly selected at their respective sites in June of 2016. At the 2510 m site, only four individuals of *P. jeffreyi* could be located that were small enough to access needle-bearing branches. For this species and site, measurements were made only on these four individuals. Physiological measurements were conducted for the next three summers. Individuals were < 5 m in height to ensure accessibility of needle-bearing branches. All individuals received direct sunlight

during the morning, ensuring that photosynthetic measurements were conducted on fully induced needles.

Meteorology

The eastern Sierra Nevada receives the majority of its precipitation over the winter between the months of October and March and much of it falls as snow. The growing season begins when the snow has melted, usually in March to May, though this occurs later at higher elevations and the timing varies considerably between years. Climate and meteorological information for Mammoth Pass, near the highest site, was obtained from the California Data Exchange Center of the California Department of Water Resources (cdec.water.ca.gov). Data for Crestview CA, near the lowest site, were obtained from the Western Regional Climate Center (wrcc.dri.edu). Data included daily and/or monthly minimum, maximum, and average air temperature, and incremental and accumulated precipitation. Daily temperature and precipitation were also compiled for the growing seasons of 2016, 2017, and 2018 for both stations. Records from Crestview started in November 1993. At Mammoth Pass starting dates differed, but all variables were recorded after 2005, and snow water content was available staring in 1929.

Photosynthesis and Water Potential

Instantaneous gas exchange measurements and stem water potential were measured twice for each individual tree during the 2016, 2017, and 2018 growing seasons in June (hereafter referred to as 'early summer') and again in late August or

early September ('late summer'). Due to the heavy snow pack in 2017, June measurements were not possible at the highest site, where trees were still covered with snow on June 25.

Stem water potential was measured for branches taken from heights of 0.5-1.25 m above the ground between 07:30 and 09:30 h local time. Water potential was measured on distal branch samples averaging 12 cm long using a Scholander-type pressure chamber.

Net photosynthetic rates and stomatal conductance were measured using an open-mode portable photosynthesis system (Model LI-6400; LI-COR) with a 6400-02 LED source. Five to six fascicles, for *P. contorta,* and one to two fascicles, *P. jeffreyi* and *P. albicaulis,* were arranged in a single layer inside the chamber. Fascicle length and width were measured for determination of leaf area. For *A. magnifica*, a terminal node was placed inside the chamber in their natural orientation. Leaf area was visually estimated relative to the two by three cm area of the chamber. Conditions inside the leaf cuvette included a light saturating PAR of 1500 μmol photons m^{-2} s^{-1}, a CO_2 concentration of 400 μmol mol^{-1}, and a flow rate of 500 μmol s^{-1}. Measurements were recorded when all three stability criteria were met, usually requiring three to four minutes, and occurred between approximately 09:00 and 10:30 h. In addition, CO_2 response curves (Farquhar et al. 1980) were conducted for each individual once per year, in June of 2016 and 2018 and in August of 2017. Response curves were also taken in June 2017 for the lowest site only. For CO_2 response curves, net

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photosynthesis was measured at 14-16 CO_2 concentrations ranging from 150-1800 μmol mol^{-1}. Photosynthesis (A_{net}, g_s, and C_i) and microclimatic conditions (T^{air}, T^{leaf}, and VPD^L) were recorded at reference CO_2 concentrations of 400, 300, 200, 100, 50, 400, 400, 500, 600, 700, 800, 900, 1000, 1200, 1500, and 1800 μmol mol^{-1}. Needles from the most recent mature flush were used for all gas exchange measurements. Needles were exposed to chamber conditions for approximately 4 minutes and until all three stability variables indicated the measurements were stable. Response curves were conducted between approximately 07:00 and 14:00 h.

In August 2018, one branch was removed from each individual tree to determine needle and node length for the 2014-2018 cohorts. For the pine species, the longest needles in five fascicles from each cohort were measured from each branch, starting with the most proximal part of the branch, and moving distally along a randomly selected side. Their average was used as estimate of needle length for that individual and year. For *A. magnifica*, which has much greater variation in needle length within cohorts, the node length for each year was measured along the central part of the branch. The width in the widest part of each node was also measured. Needles were dried at 65˚C for 48 hours and weighed to determine needle biomass.

Analysis

For each individual, instantaneous, needle-level net photosynthesis (A) and stomatal conductance (g_s) were calculated as the mean of three successive subsamples over 30 seconds. Intrinsic water use efficiency (*i*WUE) was calculated as the ratio of

A to g_s. The CO_2 response curve parameters maximum carboxylation efficiency

(V_{cmax}) and maximum rate of electron transport (J_{max}) were estimated using the 'fitaci'

function in R's plantecophys package, which fits the Farquhar-Berry-von Caemmerer

model (Duursma 2015). Stomatal limitation was estimated visually, following

methods in Long and Bernacchi (2003).

     Water potential, stomatal conductance, net photosynthesis, V_{cmax}, J_{max}, and

needle growth were determined for six individuals of each species at each site,

totaling 24 individuals of *Pinus contorta*, 10 individuals of *P. jeffreyi,* six individuals

of *P. albicaulis,* and 18 individuals of *A. magnifica.* Linear mixed effects models,

with individual tree as a random effect, and elevation, year, and/or season as fixed

effects were made for each species using the 'nlme' package in R (Pinheiro et al.

2018). Differences between elevations, years, and seasons for the response variables

were tested with an ANOVA of each model. All analyses were done in R version

3.5.1 (R core Team 2018). All figures were made using 'base' R (R core Team 2018)

or 'ggplot2' (Wickham 2016).

Results

Meteorology

     From 2006 to 2018, average summer air temperature (between June-

September) was 14.9˚C (±2.28) at 2315 m and 11.9˚C (±2.29) at 2835 m, a decrease

consistent with the adiabatic lapse rate (Figure 1-1a). By contrast, average winter air

temperatures (December-February) were -2.54˚C (±1.94) and -2.60˚C (±1.99) for the

lower and higher stations, respectively. A simple linear regression showed no trend in average summer temperatures, but a small and significant ($p < 0.05$) positive trend in average winter temperatures at both stations over the entire 14-year period. Based on a Welch two sample t-test, average temperature in the study years did not differ from the previous decade at either station.

As expected, precipitation was greater at the higher elevation. Mean total annual precipitation (by water year 1 October - 30 September) was 521 mm at the lower site and 1293 mm at the higher site. Both sites experienced considerable between-year variation (Figure 1-1b), but total annual precipitation varied more at the lower site, which had a coefficient of variation of 82.9% compared to 33.8% at the higher site. The second year of data collection (2017) corresponded with an unusually wet winter, with April 1st snow water content at Mammoth Pass greater than two standard deviations above the mean snow water content since 1929 (SM Figure 1-1). Summer rainstorms also contributed precipitation, although this was a relatively small fraction of the annual total. June-September precipitation was about 3.3% of total precipitation in water year 2016 and just over 2% in water year 2017.

Water Potential

The effects of year, season, and their interaction on stem water potential (Ψ) were significant for all four species (Table 1-1). In the wetter year of 2017, Ψ was higher (less negative) overall and increased later in the season. By contrast, it tended to decrease later in the season in the drier years, though for some species and years it

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did not change at all (Figure 1-2). Contrary to the first hypothesis, elevation had no effect on Ψ for any of the species.

Needle Photosynthesis

Almost all photosynthetic gas exchange parameters were significantly affected by year, season, and their interaction for all four species (Table 1-2). Like stem water potential, stomatal conductance decreased for all species over the season during the drier years but increased during the wet year of 2017, and was higher in the wet year overall (Figure 1-3a and 1-3b). The effect of elevation was not significant for *P. contorta* or *A. magnifica*, but stomatal conductance was slightly greater at the lower site for *P. jeffreyi* (Figure 1-3e).

Net photosynthesis was strongly related to stomatal conductance across all species, years, and elevations. For the three pine species, it followed the same general pattern as stomatal conductance, dropping later in the season in the drier years, but not in 2017 (Figure 1-3c and 1-3d). Net photosynthesis for *A. magnifica* was lower in 2017 and 2018 than in 2016 and decreased later in the season all three years, though the within season difference was greatest in 2016. Net photosynthesis for *A. magnifica* was also significantly higher at the highest site (Figure 1-3f), the only significant effect of elevation observed in this response variable.

For all four species, year and season had a significant effect on iWUE (Table 1-2), which tended to be highest in the late season of drier years (Figure 1-4). Elevation was also significant for *P. contorta* and *P. jeffreyi* though this was likely

driven by unusually low iWUE measured at the lowest site in the late season of 2018

(Figure 1-4a and 1-4b). A post hoc test examining pairwise comparisons (Tukey

Contrasts) showed no significant difference for iWUE between any two elevations.

Farquhar- von Caemmerer Photosynthetic Model

Compared to stem water potential, net photosynthesis, and stomatal

conductance, the patterns of the A-C_i response curve parameters were less consistent

across species. For *P. contorta*, both maximum carboxylation efficiency (V_{cmax}) and

maximum rate of electron transport (J_{max}) differed significantly between years, but

neither elevation nor year × elevation were significant (Table 1-4). V_{cmax} was higher in

2016 compared to other two years, while J_{max} was slightly, but significantly, lower in

2018 (Figure 1-5a). Both variables differed significantly between years for *A.*

magnifica, and the year and elevation interaction was significant. Similar to *P.*

contorta, V_{cmax} was higher in 2016, while J_{max} was similar across elevations in 2016,

and increased over the three years but only at the highest site (Figure 1-5b). For *P.*

jeffreyi, J_{max} differed significantly between years, but was highest in 2016 and lowest

in 2018. Year, elevation, and their interaction all had a significant effect on $V_{cmax,}$

which was higher at 2510 m (the higher elevation) in 2016 and 2017, but not in 2018.

It also decreased from 2016 to 2017 at both sites. For *P. albicaulis*, there were no

differences between years for either parameter (Table 1-4).

Stomatal limitation of photosynthesis was strongly associated with air

temperature for the three pine species, but not for *A. magnifica* (Table 1-4). For *P.*

contorta, elevation and year, but not their interaction were significant. Post hoc pairwise comparisons showed that stomatal limitation was greater in 2017 than in 2016, but found no significant differences between any two elevations, though it was greatest at the highest elevation (Figure 1-6a). Stomatal limitation in *P. jeffreyi* and *P. albicaulis* differed significantly between years. It decreased over the three years in *P. albicaulis* (Figure 1-6c), while for *P. jeffreyi*, it was highest in 2017 (Figure 1-6b). Both year and the interaction of year and elevation had a significant effect on stomatal limitation in *A. magnifica* (Table 1-4). At the lower two elevations, it increased across all three years, while at the highest elevation, it was highest in 2017, the wetter year (Figure 1-6d).

Needle Length and Biomass

For *P. contorta,* needle length was shorter at the lowest two sites in 2014 and 2015, during the height of the drought. Similarly, *P. jeffreyi*, which occurs only at the lowest two sites, also had significantly shorter needle length in 2014 and 2015. In contrast, *P. albicaulis*, which occurs only at the highest site, had significantly shorter needle length in 2017, the wettest year (Figure 1-7). Node length and width for *A. magnifica* followed a similar pattern, with significant effects of elevation, year, and their interactions (Table 1-5). At the lowest site, nodes were shorter in 2014 and 2015, the driest years, while at the highest site they were shorter in 2016 and 2017. Needle biomass generally followed the same pattern as needle length for all four species, with biomass increasing in the wetter years at the lower elevations, but decreasing at

the highest ones (Table 1-5). Needle length and biomass were largely uncorrelated with rates of net photosynthesis (SM Figure 1-2).

Discussion

Total annual precipitation in the study region, as measured by April 1st snow water content, has had considerable inter-annual variability over the past century. The recent 2012-2014 drought represents an extreme event in its combination of high temperatures and low precipitation (Griffin and Anchukaitis 2014). The winter of 2015 was particularly notable for its low snow levels—there was essentially no snow at the highest site on April 1st—a consequence of an unusually warm winter and a rex block high pressure system over Pacific Ocean (Williams et al. 2015). Though the wet 2017 water year was not unprecedented in terms of total precipitation, it does represent a dramatic increase in comparison to the prior drought years, and it markedly delayed the melt date and the onset of the growing season, especially at the higher elevations. Contrasting the two high and low elevations produced the expected patterns of lower temperatures—at least during the growing season—and increased precipitation at the higher elevation, but also less inter-annual variability. Trees at higher elevations not only received more moisture, it was more reliable between years than at lower elevations.

All four conifer species demonstrated phenotypic plasticity in response to temporal differences in precipitation on both seasonal and inter-annual timescales. Late season gas exchange and water potential were most sensitive to differences in

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water year, and the seasonal effects in the wetter year (2017) were reversed from the other two years for stomatal conductance, net photosynthesis, and water potential. Grulke (2010) found seasonal differences in iWUE of both white fir and Jeffrey pine, with greater efficiency later in the summer when conditions were drier, suggesting these species can adjust growth rates under both high and low water availability. In the present study, iWUE was similarly higher later in the season in 2016 and 2018, but not in the wetter year of 2017. On the whole, inter-annual differences in these physiological traits manifested primarily in late summer measurements, suggesting favorable early season conditions across all three years. Contrary to the hypotheses and despite observed elevational differences in temperature, precipitation, and soil moisture (SM Figure 1-3), elevation had almost no effect on instantaneous photosynthetic gas exchange, CO_2 response curve parameters, or water potential in any of the years for any of the species. The species were relatively insensitive to spatial variation in the physical environment at the scale captured by this elevation gradient. Therefore, we conclude that conifer sapling physiology in this area is sensitive to variability in inter-annual precipitation, but not to elevation.

Needle growth did show elevational differences for *P. contorta* and *A. magnifica*, suggesting the integrated measure was more reflective of differences in water availability than instantaneous photosynthetic gas exchange or water potential. Similarly, Carroll et al. (2017) found needle size was significantly greater at their warmest site for Ponderosa, though not for Lodgepole pine, while net photosynthesis

did not vary for either species. However, in the present study it was the interaction of year and elevation that was consistently significant for needle growth, with the effect of the heavy snow year contrasting at the low and high elevations. At the lowest two elevations, growth increased in the wettest year (2017), probably as a consequence of greater soil moisture in spring and summer. Meanwhile at the highest elevation, growth was depressed, probably because the deep, long-lasting snowpack delayed the emergence of the needles. Indeed, for some individuals in both pine species the delay was so severe that the needles never emerged, and the 2017 needle cohort was completely missing the following summer. Duputié et al. (2015) found phenological plasticity decreased fitness in the cold margins of the range for all three of their European study species, while in the warmer areas it improved fitness for two of the species, as warmer temperatures increased growth rates. For *P. contorta* in this study, needle growth did not differ across all elevations in 2016 at the end of the drought, but was much greater at the lowest elevation in higher water years (Figure 1-6). This suggests at lower elevations, warmer air temperatures and an earlier melt date meant the pines could take advantage of the wetter year. At the highest elevation, likely due to snowpack persistence and the shortened growing season, individuals could not exploit the increase in available water. In contrast to the pines, within-year differences in node width between elevations for *A. magnifica* were more evident in the drier years (especially 2015) but converged in wet years, suggesting the growth of *A. magnifica* was more sensitive to drought conditions than the pine species. This

species was also primarily able to take advantage of the increase in available water in 2017 at the lower elevations.

Ψ had been recorded in 2014 and 2015 for individuals of both *P. contorta* and *P. jeffreyi* at the lowest elevation. Over this five-year period, stem water potential increased with total annual precipitation up to approximately 500-550 mm (as in 2018), but was not significantly higher in 2017, despite total precipitation being nearly three times as much (Figure 1-8). This suggests there may be a threshold above which increased precipitation exceeds the water needs of these species, though observations over a greater number of years would be necessary to be certain. Interestingly, total annual precipitation at the highest elevation did not drop below 500 mm even at the height of the drought (Figure 1-1b), supporting the supposition that sufficient water was available to the trees at this site.

Maximum carboxylation efficiency (V_{cmax}) was significantly higher in 2016 compared to the subsequent two years for three of the four species. It was also higher in this year for *P. albicaulis*, though this difference was not significant, likely in part because of the small sample size. This suggests the amount of active ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) decreased during and after the wet winter across all species and elevations, perhaps as a result of reduced nitrogen availability if the high-water year flushed nitrogen from the system or made it otherwise unavailable. No patterns emerged across species or sites in linear electron transport (J_{max}), which tracked changes in V_{cmax} for *P. jeffreyi*, but not for *P. contorta*

or *A. magnifica*. Unlike Potts et al. (2017), we found patterns in species' relative

stomatal limitation differed over time in ways not that were not predictable from their

elevational distributions. For *P. albicaulis*, occurring only at the highest site, relative

stomatal limitation was greatest in 2016, and decreased the next two years. For *P.*

contorta, *A. magnifica,* and *P. jeffreyi,* it was significantly greater in the wet year for

2017 across sites (Figure 1-6), in contrast to hypothesis three. This was somewhat

surprising because stomatal opening should not be limited by soil water availability in

wet years. Elevation was significant only for *P. contorta,* and for this species it was

greater at the highest site, contradicting our expectations. It was strongly tied to air

temperature for all three pine species and marginally for *A. magnifica,* with higher air

temperature associated with greater stomatal limitation. It is possible that our

measurements of stomatal limitation were too greatly influenced by short term

(hourly or shorter) conditions to reflect responses to yearly or elevational differences

in water availability.

Over the three years of the study, total precipitation had coefficients of

variation of 76.0% and 38.5% at the lowest and highest elevation respectively, while

mean net photosynthesis ranged from 6.89 to 16.0 μmol CO_2 m^{-2} s^{-1} (Table 1-3). In

general, the biological variation over time was dampened compared to the physical

variation between years, suggesting these trees can effectively withstand temporal

changes in climatic factors. Moreover, across all species and years (2016-2018), the

lowest recorded stem water potential was a relatively wet -1.85 MPa. However, in

2014 and 2015, Ψ was -2.35 MPa for *P. jeffreyi* at the lowest site. Thus, we conclude

that both species were already rehydrating in 2016, when April 1st snow water content

was 96.0% of the long-term average. Even at the lowest elevation, the trees in this

study were doing well after experiencing an historic drought. This recent California

drought represents the most severe event over the past 1200 years, driven by

unusually low, though not unprecedented, amounts of precipitation combined with

temperatures that reached record highs (Griffin and Anchukaitis 2014). It is likely that

in the 18,000 years since the last glacial maximum in California, these species have

experienced multiple drought events that challenged their survival and productivity in

similar ways. Thus far, they have shown the ability to readily tolerate and recover

from such dramatic meteorological variation.

Table 1-1. Differences in elevation, year, and season for mid-morning stem water potential of the four study species. Table shows F and p-values from an ANOVA of a linear mixed effects model for each species, with individual tree as a random factor. Significant effects ($p < 0.05$) are in bold.

Species	Source of Variation	df	F	p-value
Pinus contorta	Elevation	3	1.2195	0.3273
	Year	2	**14.1346**	**<0.0001**
	Season	1	**11.2945**	**0.0011**
	Year*Season	2	**27.3967**	**<0.0001**
Pinus jeffreyi	Elevation	1	0.7754	0.4042
	Year	2	**9.7573**	**0.0003**
	Season	1	**10.2073**	**0.0026**
	Year*Season	2	**4.5190**	**0.0163**
Pinus albicaulis	Year and Season	4	**20.1702**	**<0.0001**
Abis magnifica	Elevation	2	0.0850	0.9189
	Year	2	**14.7706**	**<0.0001**
	Season	1	**12.1320**	**0.0008**
	Year*Season	2	**25.0932**	**<0.0001**

Table 1-2. Differences in elevation, year, and season for stomatal conductance (g_s), photosynthesis (A), and intrinsic Water Use Efficiency ($iWUE$) of the four study species. Table shows F and p-values from an ANOVA of a linear mixed effects model for each response variable and species, with individual tree as a random factor. Significant effects ($p < 0.05$) are in bold.

Species	Dependent Variable	Source of Variation	df	F	p-value
Pinus contorta	Stomatal Conductance	Elevation	3	2.439	0.0914
		Year	2	**46.545**	**<0.0001**
		Season	1	**62.090**	**<0.0001**
		Year*Season	2	**19.475**	**<0.0001**
	Net Photosynthesis	Conductance	1	**1140.352**	**<0.0001**
		Elevation	3	1.355	0.2826
		Year	2	1.624	0.2009
		Season	1	1.492	0.2241
		Year*Season	2	**12.448**	**<0.0001**
	Intrinsic Water Use Efficiency	Elevation	3	**3.4166**	**0.0352**
		Year	2	**38.27**	**<0.0001**
		Season	1	**46.1141**	**<0.0001**
		Year*Season	2	**6.1626**	**0.0028**
Pinus jeffreyi	Stomatal Conductance	Elevation	1	**8.8446**	**0.0156**
		Year	2	**10.8836**	**0.0001**
		Season	1	**16.2456**	**0.0002**
		Year*Season	2	**31.8599**	**<0.0001**
	Net Photosynthesis	Conductance	1	**414.047**	**<0.0001**
		Elevation	1	2.430	0.1535

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		Year	2	**7.214**	**0.0017**
		Season	1	2.929	0.0928
		Year*Season	2	2.953	0.0606
	Intrinsic Water Use Efficiency	Elevation	1	**13.34**	**0.0053**
		Year	2	**20.94**	**<0.0001**
		Season	1	**9.91**	**0.0027**
		Year*Season	2	**12.74**	**<0.0001**
Pinus albicaulis	Stomatal Conductance	Year and Season	4	**8.00275**	**0.0002**
	Net Photosynthesis	Conductance	1	**194.7266**	**<0.0001**
		Year and Season	4	**8.4470**	**0.0002**
	*Intrinsic Water Use Efficiency	Year and Season	4	**18.328**	**<0.0001**
Abies magnifica	Stomatal Conductance	Elevation	2	0.2293	0.7975
		Year	2	**28.6508**	**<0.0001**
		Season	1	**50.6795**	**<0.0001**
		Year*Season	2	**11.0989**	**<0.0001**
	Net Photosynthesis	Conductance	1	**486.341**	**<0.0001**
		Elevation	2	**4.880**	**0.0211**
		Year	2	**4.163**	**0.0185**
		Season	1	**14.919**	**0.0002**
		Year*Season	2	**26.698**	**<0.0001**
	Intrinsic Water Use Efficiency	Elevation	2	1.184	0.3300
		Year	2	**27.278**	**<0.0001**
		Season	1	**12.225**	**0.0007**
		Year*Season	2	**12.568**	**<0.0001**

Year*Elevation	4	1.009	0.4075
Season*Elevation	2	**4.316**	**0.0163**

Table 1-3. Mean net photosynthesis (±standard deviation) for each species by year and season. All values are in µmol CO_2 m^{-2} s^{-1}.

Species	Year	Season	A_{net}
Pinus contorta	2016	early	12.4 (±3.11)
		late	6.89 (±2.10)
	2017	early	11.6 (±2.54)
		late	13.2 (±2.60)
	2018	early	11.6 (±2.25)
		late	9.12 (±3.18)
Pinus jeffreyi	2016	early	16.0 (±1.72)
		late	8.09 (±3.07)
	2017	early	10.0 (±3.02)
		late	13.7 (±1.58)
	2018	early	13.4 (±1.67)
		late	10.9 (±1.90)
Pinus albicaulis	2016	early	10.6 (±2.34)
		late	7.42 (±2.92)
	2017	early	NA
		late	10.1 (±1.80)
	2018	early	9.46 (±3.29)
		late	7.54 (±3.13)
Abis magnifica	2016	early	13.1 (±2.55)
		late	6.8 (±2.35)
	2017	early	11.5 (±2.19)
		late	10.5 (±2.32)
	2018	early	9.78 (±2.07)
		late	9.05 (±2.59)

Table 1-4. Differences in elevation and year for CO_2 response curve parameters of the four study species. Table shows F and p-values from an ANOVA of a linear mixed effects model for each parameter and species, with individual tree as a random factor. Significant effects ($p < 0.05$) are in bold.

Species	Response Variable	Source of Variation	df	F	p-value
Pinus contorta	CO_2 - Vcmax	Elevation	3	2.935	0.0583
		Year	2	**9.311**	**0.0004**
		Year*Elevation	6	0.962	0.4616
	CO_2 - Jmax	Elevation	3	0.0933	0.9629
		Year	2	**7.3374**	**0.0017**
		Year*Elevation	6	1.8927	0.1024
	CO_2 - stomatal limitation	Air Temperature	1	**46.6838**	**<0.0001**
		Elevation	3	**4.0500**	**0.0211**
		Year	2	**8.0007**	**0.0011**
		Year*Elevation	6	0.9804	0.4496
Pinus jeffreyi	CO_2 - Vcmax	Elevation	1	**8.593**	**0.0190**
		Year	2	**15.044**	**0.0001**
		Year*Elevation	2	**3.801**	**0.0399**
	CO_2 - Jmax	Elevation	1	0.0640	0.8066
		Year	2	**8.6284**	**0.0020**
		Year*Elevation	2	2.1252	0.1456
	CO_2 - stomatal limitation	Air Temperature	1	**63.8582**	**<0.0001**
		Elevation	1	0.2285	0.6454
		Year	2	**19.1079**	**<0.0001**
		Year*Elevation	2	2.7102	0.0922

Pinus albicaulis	CO_2 - Vcmax	Year	2	2.6625	0.1235
	CO_2 - Jmax	Year	2	2.2320	0.1632
	CO_2 - stomatal limitation	Air Temperature	1	**9.2984**	**0.0138**
		Year	2	**4.6438**	**0.0412**
Abies magnifica	CO_2 - Vcmax	Elevation	2	1.541	0.2461
		Year	2	**23.369**	**<0.0001**
		Year*Elevation	4	**2.919**	**0.0376**
	CO_2 - Jmax	Elevation	2	2.461	0.1191
		Year	2	**5.377**	**0.0101**
		Year*Elevation	4	**3.788**	**0.0131**
	CO_2 - stomatal limitation	Air Temperature	1	3.7323	0.0632
		Elevation	2	2.3250	0.1320
		Year	2	**26.6030**	**<0.0001**
		Year*Elevation	4	**3.5700**	**0.0174**

Table 1-5. Differences in needle length and biomass by elevation and year for the four study species. Table shows *F* and *p*-values from an ANOVA of a linear mixed effects model for each response variable and species, with individual tree as a random factor. Significant effects ($p < 0.05$) are in bold.

Species	Response Variable	Source of Variation	df	F	*p*-value
Pinus contorta	Needle Length	Elevation	3	**22.4669**	**<0.0001**
		Year	4	**16.1952**	**<0.0001**
		Year*Elevation	12	**10.8107**	**<0.0001**
	Needle Biomass	Elevation	3	**8.0212**	**0.0011**
		Year	4	2.3009	0.0663
		Year*Elevation	12	**10.8252**	**<0.0001**
Pinus jeffreyi	Needle Length	Elevation	1	0.0621	0.8096
		Year	4	**27.5735**	**<0.0001**
		Year*Elevation	4	**7.0490**	**0.0004**
	Needle Biomass	Elevation	1	0.01606	0.9023
		Year	4	**12.96265**	**<0.0001**
		Year*Elevation	4	**5.96657**	**0.0012**
Pinus albicaulis	Needle Length	Year	4	**15.4519**	**<0.0001**
	Needle Biomass	Year	4	**12.78932**	**<0.0001**
Abies magnifica	Node Width	Elevation	2	**7.4383**	**0.0057**
		Year	4	**8.3184**	**<0.0001**
		Year*Elevation	8	**7.5872**	**<0.0001**
	Needle Biomass	Elevation	2	**4.4635**	**0.0301**
		Year	4	**7.2764**	**0.0001**
		Year*Elevation	8	**7.2134**	**<0.0001**
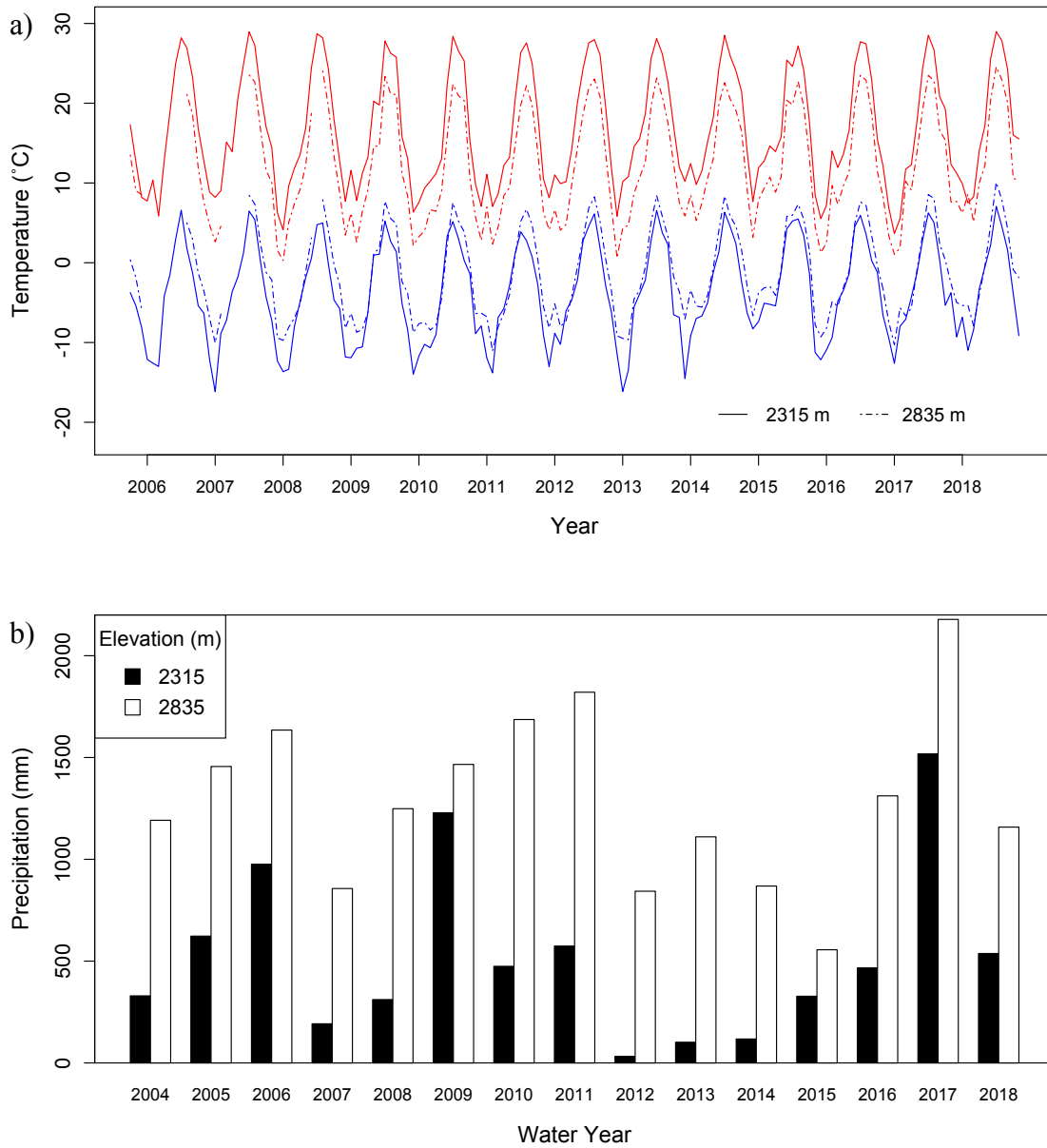
Figure 1-1. (a) Monthly maximum (red), and minimum (blue) air temperature at 2315 m (solid lines) and 2835 m (dashed lines) from October 2005 through November 2018. Broken lines indicate missing data. (b) Total annual precipitation (by water year, October 1 to September 30) at 2315 m (black) and 2835 m (white).
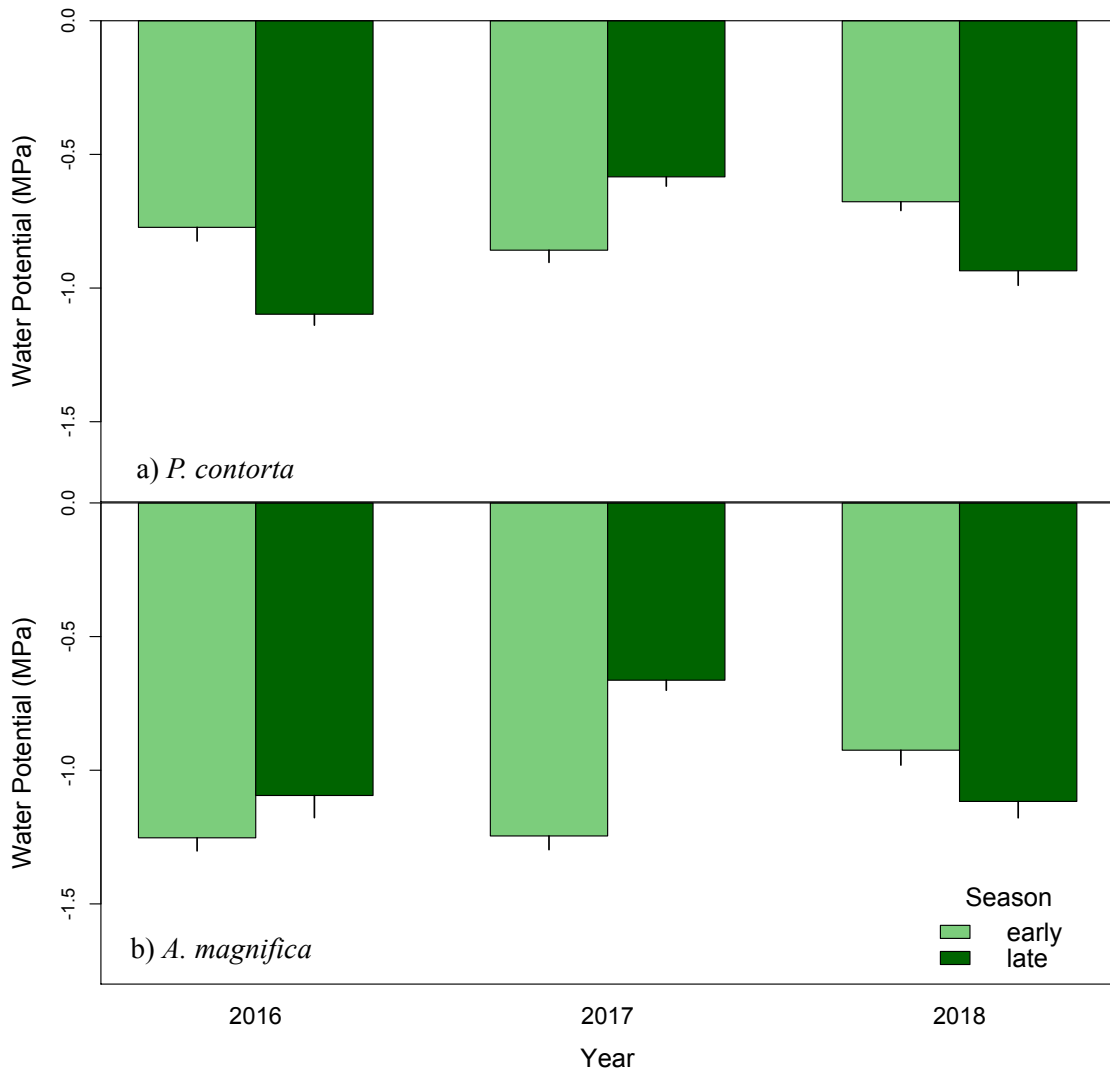
Figure 1-2. Stem water potential for *P. contorta* (a) and *A. magnifica* (b) in early and late summer 2016-2018. Data are means aggregated across four sites (*n* = 24) and three sites (*n* = 18) for *P. contorta* and *A. magnifica*, respectively. Error bars are one standard error.
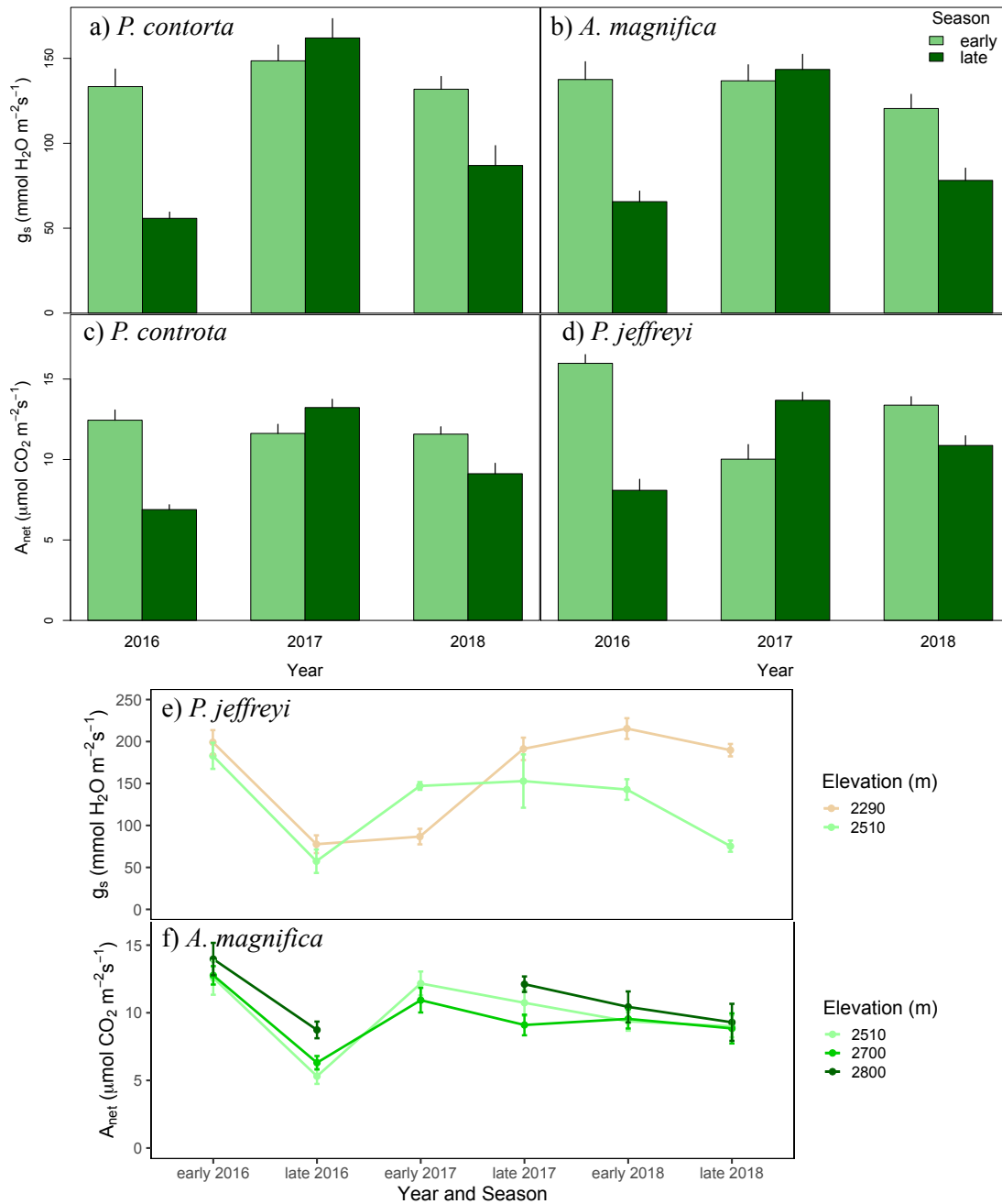
Figure 1-3. Early and late summer season stomatal conductance for (a) *P. contorta* and (b) *A. magnifica,* net photosynthesis of (c) *P. contorta* and (d) *P. jeffreyi* from 2016-2018. Data are means aggregated across four sites ($n = 24$), three sites ($n = 18$), and two sites ($n = 10$) for *P. contorta, A. magnifica*, and *P. jeffreyi*, respectively. Effect of year, season, and elevation of (e) stomatal conductance of *P. jeffreyi* and (f) net photosynthesis of *A. magnifica.* Data are means from each measuring time and site ($n = 6$). Error bars are one standard error.
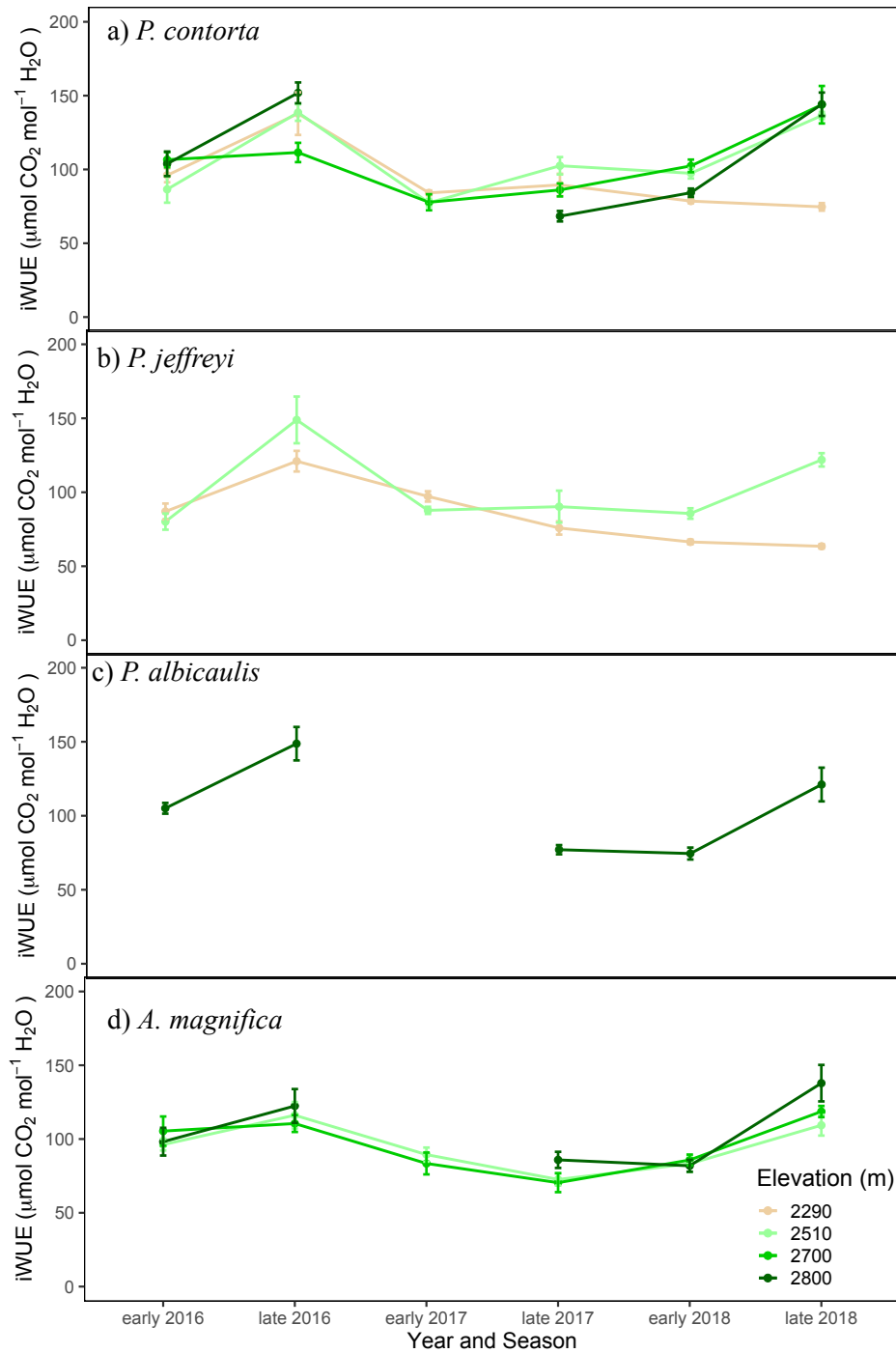
Figure 1-4. Intrinsic water use efficiency (iWUE) for (a) *P. contorta*, (b) *P. jeffreyi*, and (c) *P. albicaulis*, and (d) *A. magnifica*. Data are means from each measuring time and site (*n* = 6). Error bars are one standard error.
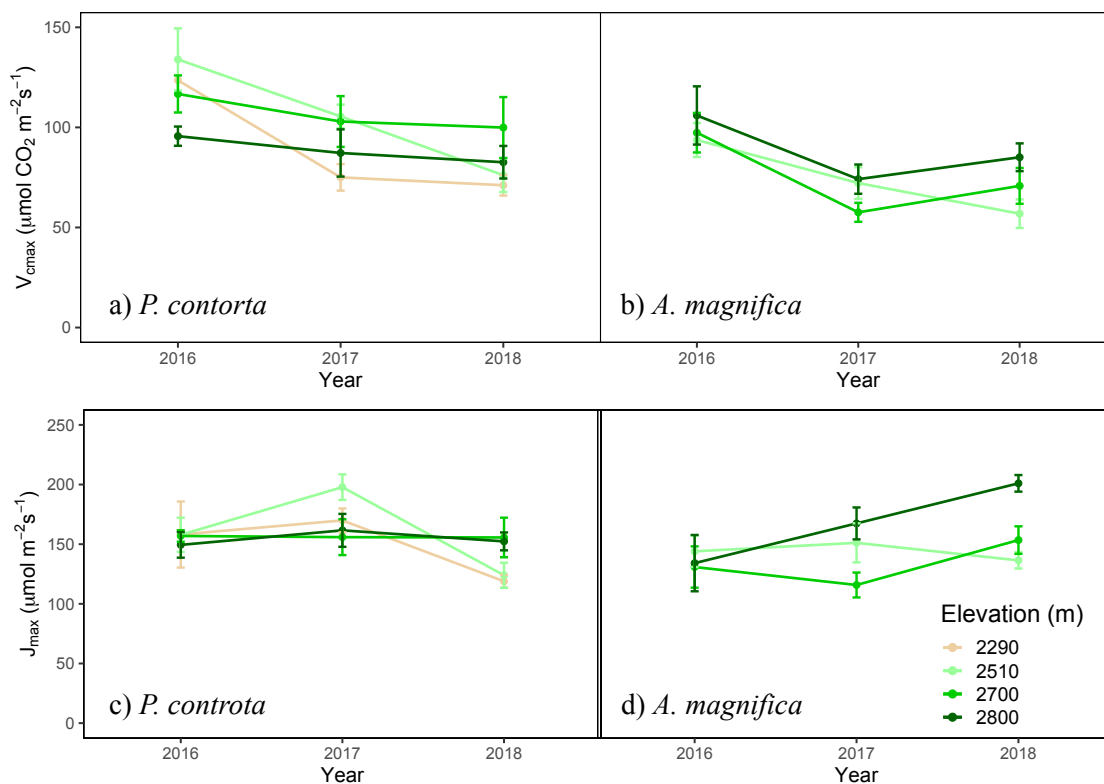
Figure 1-5. Maximum carboxylation efficiency for (a) *P. contorta* and (b) *A. magnifica* and maximum electron transport rate for (c) *P. contorta* and (d) *A. magnifica* by year and elevation. Data are means from each measuring time and site ($n = 6$). Error bars are one standard error.
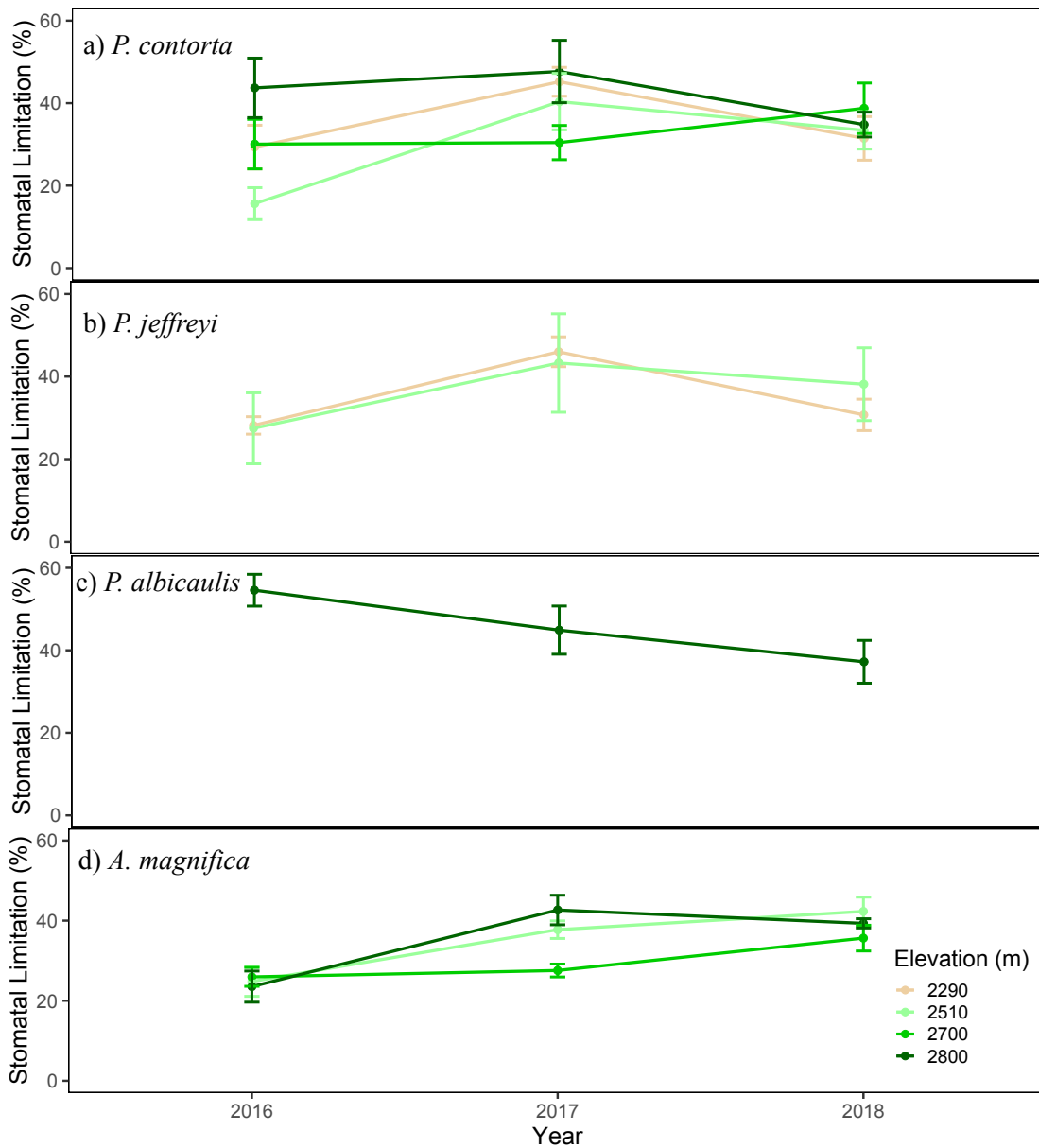
Figure 1-6. Stomatal limitation by year and elevation for (a) *P. contorta*, (b) *P. jeffreyi*, (c) *P. albicaulis*, and (d) *A. magnifica*. Data are means from each measuring time and site (*n* = 6). Error bars are one standard error.
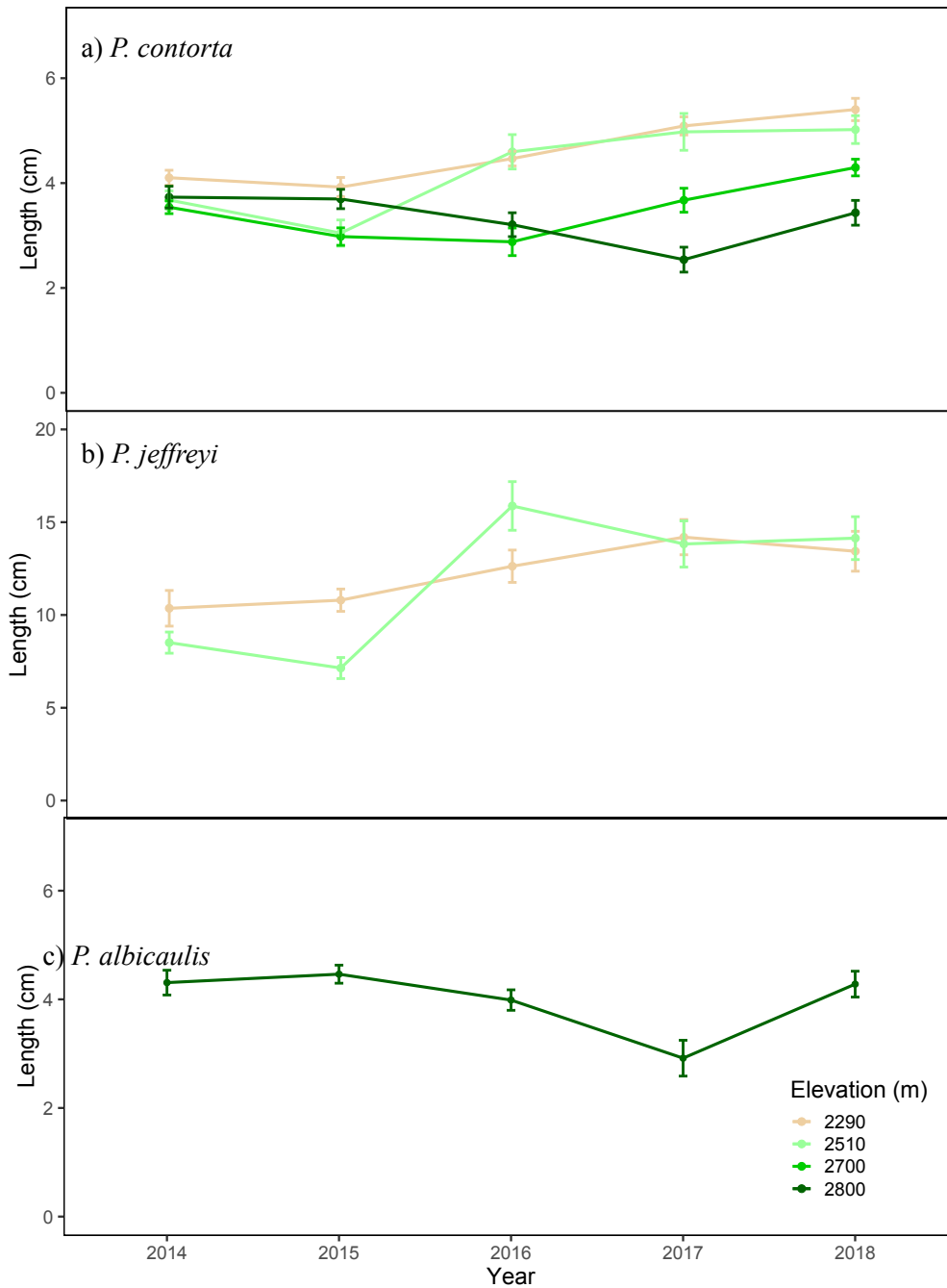
Figure 1-7. Needle length for (a) *P. contorta*, (b) *P. jeffreyi,* and (c) *P. albicaulis* by cohort year and elevation. Data are means from each cohort year and site (*n* = 6). Error bars are one standard error.

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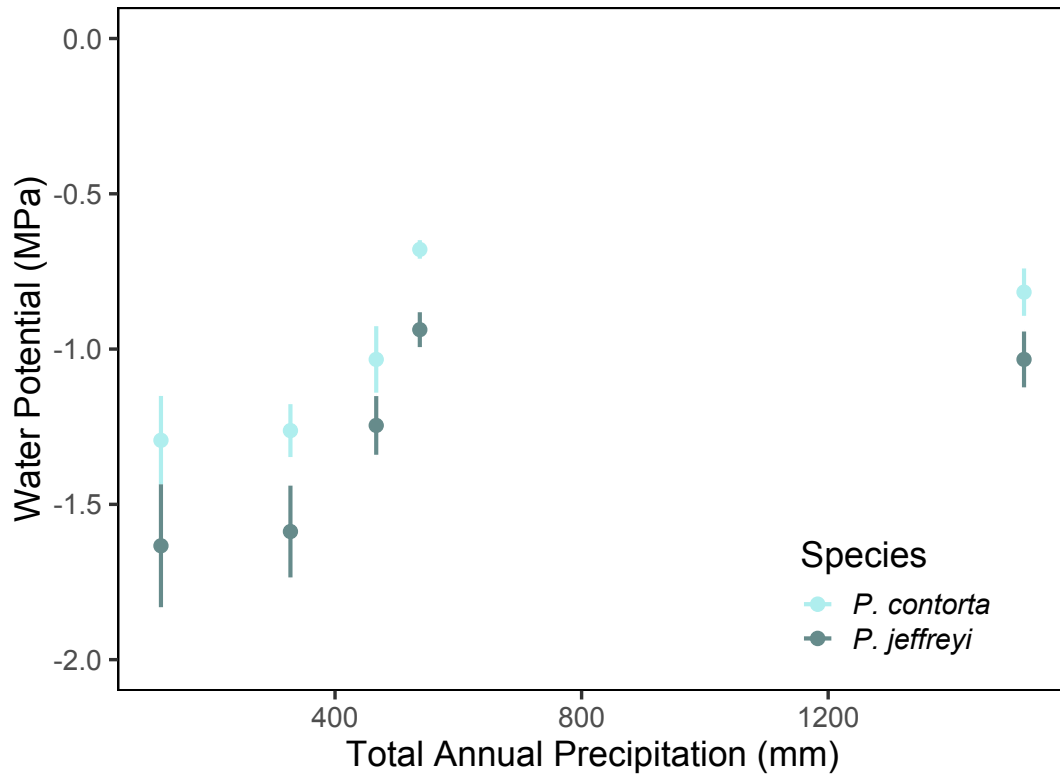
Figure 1-8. Stem water potential for *P. contorta* and *P. jeffreyi* at the lowest site (2290 m) as a function of total water year precipitation from 2014-2018. Data are means from each year and species (*n* = 6). Error bars are one standard error.

Supplementary Material Figure 1-1. April 1st snow water content from Mammoth Pass from 1929-2018. Black and grey dotted lines are one and two standard deviations, respectively, above and below the mean.
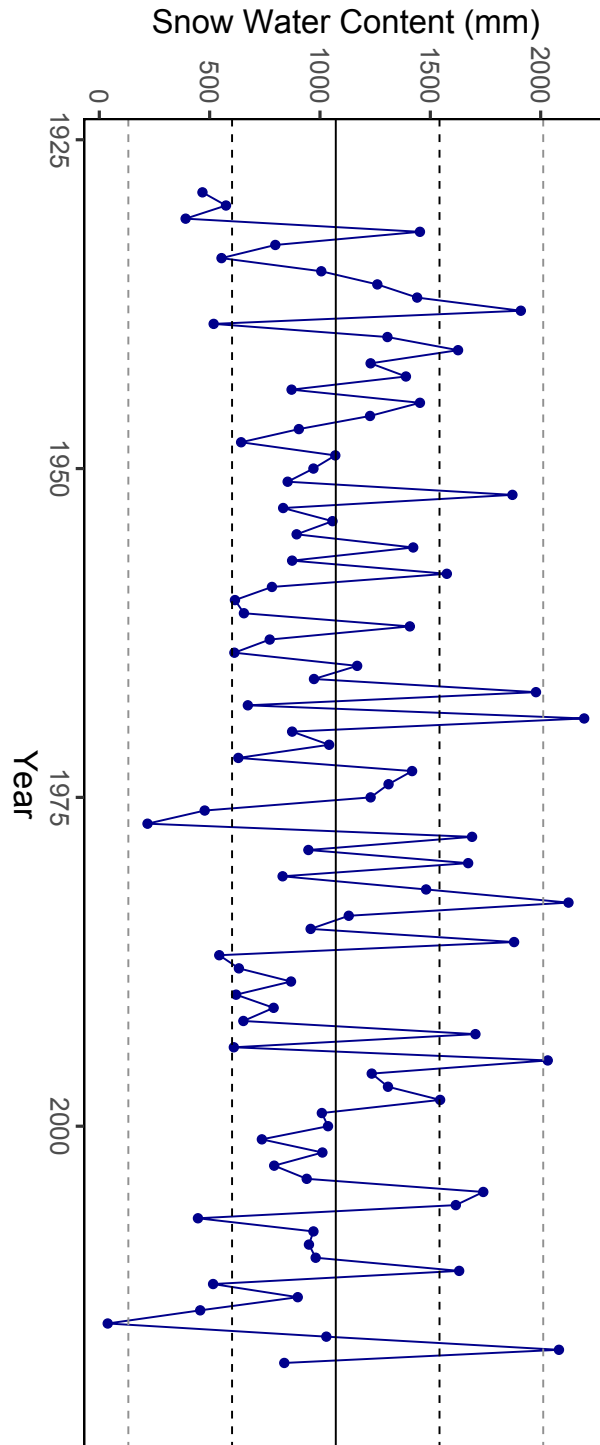
Supplementary Material Figure 1-2. Fascicle biomass compared to net photosynthesis of *P. contorta* by cohort year and elevation. Data are measurements from each individual.
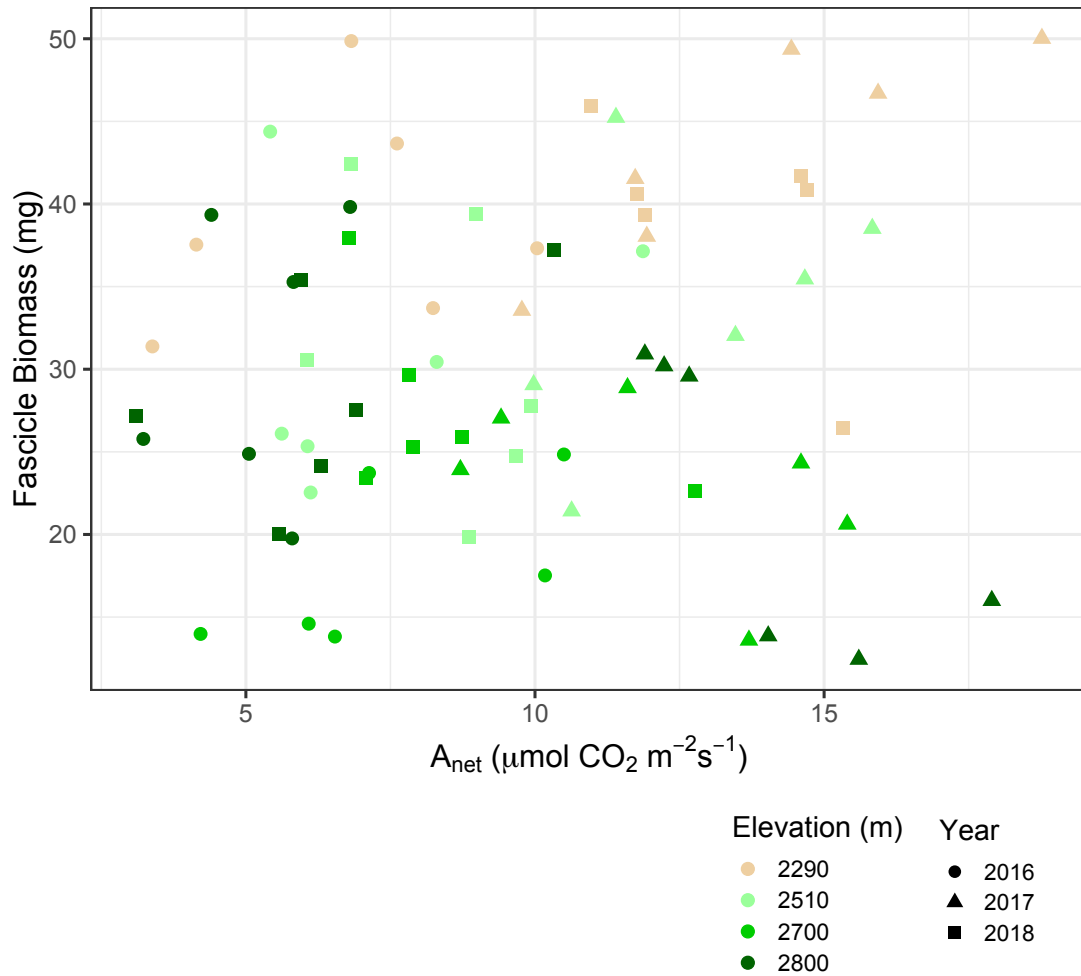
Supplementary Material Figure 1-3. June gravimetric soil water content integrated over the top 20 cm. Data are means (*n* = 10) from each elevation and time. Error bars are one standard error.
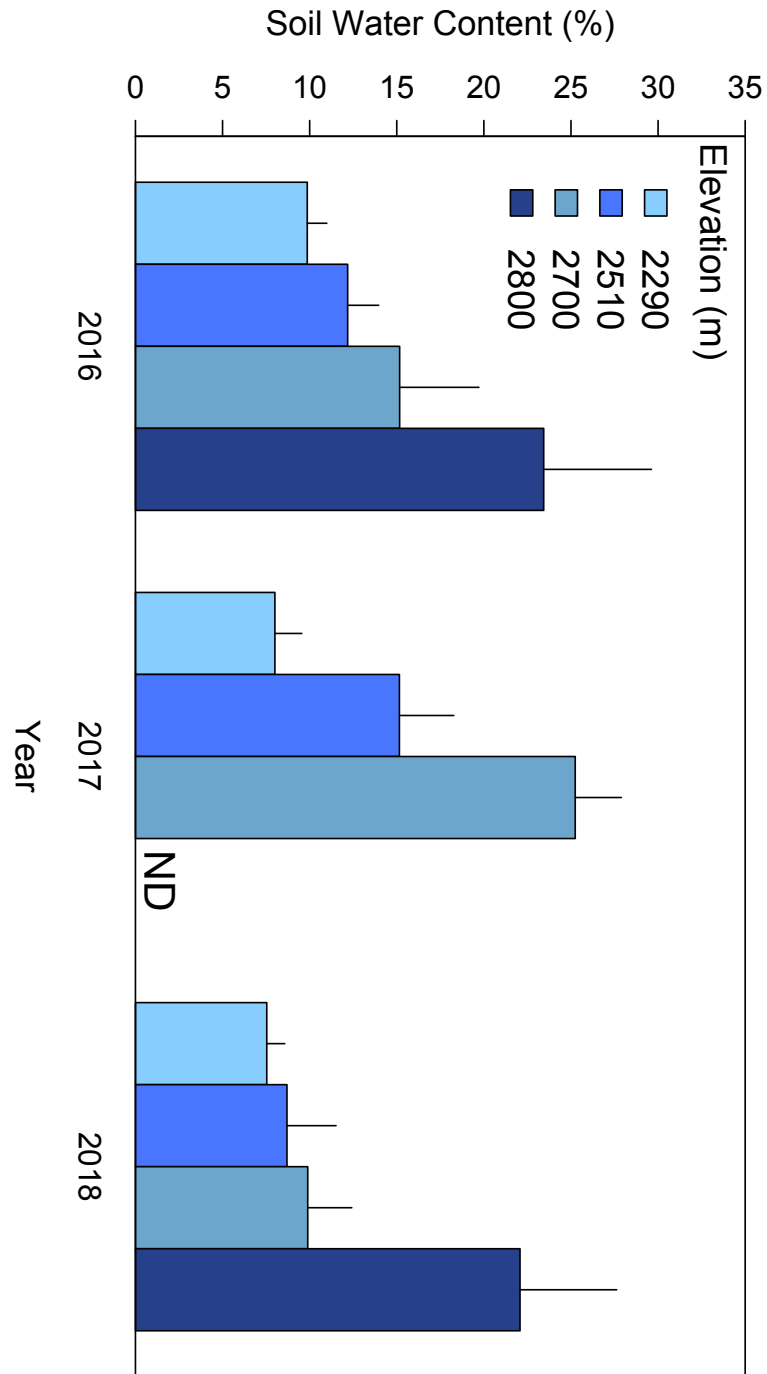
CHAPTER 2:

Sensitivity in ring-growth varies by elevation in eastern Sierra Nevada conifers

Introduction

Population level shifts in species' spatial distribution in response to changing climatic conditions are well documented (Parmesan 2006). However, the ways in which species' physiological sensitivities and population dynamics will influence range limits are not well understood (Sexton et al. 2009). Warming under climate change is generally expected to result in poleward and upslope distributional shifts, which may be characterized by expansion of the upper range margin, but may also include contraction of the lower range margin, increases in mean elevation, "leaning" distributions, and range-wide changes in abundance (Breshears 2008). Changing climatic variability, especially increased occurrence of extreme events, is also expected to influence the effects of environmental change, especially physiological responses (Reyer et al. 2013).

Forests throughout California have experienced changes in structure and composition over the past two centuries including an increase in forest density (particularly for small trees), reduced basal area, and an increased dominance of oaks relative to pines (McIntyre et al. 2015). In the Sierra Nevada, the density of large diameter trees has decreased over the past 80 years, largely due to increased mortality, while the density of small trees has significantly increased over the same time period (Lutz et al. 2009, Dolanc et al. 2014). Guarín and Taylor (2005) attributed the greater

abundance of intermediate and small trees to fire suppression policies, noting that high establishment rates coincided with fire cessation and that these size classes were dominated by less fire tolerant species. Dolanc et al.'s (2014) comparison of burned and unburned plots implicated fire suppression in forest density increases in mid-elevation forests, but small tree density also strongly increased at high elevations where historical fire return intervals were much longer and fire suppression is less likely to have impacted forest structure. Van Mantgem and Stephenson (2007) found increases in mortality of both *Abies* and *Pinus*, the dominant taxonomic groups in the Sierra Nevada, in all but the highest elevation classes, consistent with temperature driven increases in water deficit. While acute physiological stress alone does not explain patterns of mortality among size classes experienced by different species in the Sierra Nevada, these patterns are consistent with host-tree selection preferences of different beetle species, suggesting the combination of drought stress and bark beetle attack as an explanation for increased mortality (Stephenson et al. 2019).

Annual growth of living trees is affected by inter-annual variability in climate over multiple years, especially conditions associated with drought. 235 ring-width index (RWI) chronologies from the southwestern United States show a strong positive correlation with total annual precipitation, and a strong negative correlation with early season daily maximum temperature, two drought related climate variables (Williams et al. 2010). Gebregeorgis et al. (2020) found that historical drought years corresponded to narrow rings in *Juniperus procera* in Ethiopia, but that narrow rings

also occurred in years without drought, indicating a possible time lag in drought impacts. In a study of six subalpine species in the western Sierra Nevada, Dolanc et al. (2013), found radial growth was positively correlated with cool temperatures prior to the growing season, warmer temperatures during the early growing season, and wetter conditions the previous year. Despite the relatively large range of latitudes and elevations represented by the sites, there was high synchrony in the chronologies of all six species, suggesting a strong response to variation in macroclimate (Dolanc et al. 2013). In contrast, Hurteau et al. (2007) found growth responses to time lagged Palmer Drought Severity Index (PDSI) in a Sierra Nevada mixed-conifer forest were species specific, with white fir (*Abies concolor*) responding most strongly. Annual growth in whitebark pine in the eastern Sierra Nevada was also strongly correlated to climatic water deficit and precipitation in the previous year (Millar et al. 2012). Tree growth is very responsive to drought associated climate variables, especially at drier sites (Williams et al. 2010), but responses are strongly influenced by conditions the previous year, consistent with greater growth declines over multi-year periods of elevated CWD (Millar et al. 2012).

Physiological responses to climate often differ across a species' range corresponding to local temperature and precipitation regimes and may reflect both genetic adaptation and/or phenotypic plasticity (Buechling et al. 2017, Duputié 2015). In a common garden experiment, variation in climatic sensitivity between populations of *Pinus strobus* was significantly correlated with mean annual temperature of the

provenance (Housset et al. 2018). Southern most populations were more vulnerable to late spring or early fall freezes but benefited from a warm fall in the year preceding ring formation and were less sensitive to summer drought (Housset et al. 2018). Montwé et al. (2018) found populations of lodgepole pine from colder regions were less vulnerable to fall frost damage, but more vulnerable to frost damage in the late spring, possibly due to their adaption to a shorter growing season (Montwé et al. 2018). In contrast, De Rose et al. (2015) found no relationship between variability in ring growth and elevation for the widespread species Douglas fir. While variability decreased with elevation for three pine species, this relationship disappeared when elevation was corrected for changes in latitude and longitude (De Rose et al. 2015).

California is expected to experience increased inter-annual variability in precipitation over the coming century, including a greater occurrence of extreme wet and dry years (Berg and Hall 2015, Swain et al. 2018). Coupled with warming, this is likely to increase the incidence of drought conditions and reduce winter snowpack in the Sierra Nevada (Diffenbaugh et al. 2015, Berg and Hall 2017). Tree species sensitivity to these changes will influence mortality, growth, and ultimately distribution, with potentially striking consequences for forest structure. Moreover, between 2012 and 2015 California experienced a drought representing one of the most severe events over the past 1200 years, driven by a combination of unusually low precipitation and record temperatures (Griffin and Anchukaitis 2014). To assess species sensitivity to historical variation in climate including the recent drought, I

compared the annual ring-growth of four dominant conifer species at four elevations to an 88-year record of April 1st snow water content, which approximates total water year precipitation. These sites spanned the lower extent of conifer species at the Sierra Nevada - Great Basin ecotone. In addition, I examined size and age structure across elevations to determine if current populations show patterns consistent with distributional shifts expected under climate warming. I hypothesized that:

(1) Age and size structure of study species would be consistent with upslope migration in response to climate warming. Populations are expected to be skewed toward younger and smaller individuals at all sites, but this would be more extreme at higher elevations, and there would be relatively fewer old and large trees.

(2) Ring growth and inter-annual sensitivity would be greater at lower elevations, reflecting greater limitation from water availability but longer growing season length due to warmer temperatures.

(3) RWI and mean annual ring growth would be correlated with changes in total water year precipitation over multiple years across species and sites, but this relationship would be stronger at lower elevations.

Materials and Methods

Study Sites and Species

This study was conducted along an elevation gradient extending through approximately 500 m of the lower portion of a desert-to-forest ecotone, from the Great Basin Desert sagebrush steppe to the subalpine forest of eastern California,

USA. I selected four study sites in the area around Mammoth Lakes, CA based on their elevation and accessibility. These sites are at approximately 2290 m, 2510 m, 2700 m, and 2800 m; the linear distance between the farthest two sites is approximately 12 km. The soils at all four sites are derived from geologically recent volcanic deposits, primarily well-drained rhyolitic pumice (Rinehart and Ross 1964, Huber and Rinehart 1965). Six conifer species from the family Pinaceae occur at these sites. *Pinus contorta* subsp. *murrayana* (Balsf.) Critchf. is present at all four sites; *P. jeffreyi* Balf. at the lowest two; *Abies magnifica* A. Murray at the highest three; and *P. albicaulis* Engelm. occurs at the highest two sites. *A. magnifica* and *P. contorta* are abundant where they occur. *P. albicaulis* is abundant at the highest site, but rare at the 2700 m site. Similarly, *P. jeffreyi* is abundant at the lowest site, but rare at the 2510 m site. A few scattered individuals of *P. monitcola* Douglas ex. D. Don and *Tsuga mertensiana* (Bong.) Carrière are present at the highest two sites. The lowest site represents the lower distributional edge of conifers in this area, while the highest site is below the upper range limit for the two pine species, but near the reported upper elevational limit of *A. magnifica* in the southern Sierra Nevada (Laacke et al. 1990).

Meteorology

The eastern Sierra Nevada has historically received the majority of its precipitation between the months of October and March, when much of it falls as snow. The growing season begins when the snow has melted, usually between March

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and May, though this occurs later at higher elevations and the timing varies considerably between years. Historical meteorological information for Mammoth Pass, near the highest site, was obtained from the California Data Exchange Center of the California Department of Water Resources (cdec.water.ca.gov). Snow water content on or near April 1st was available starting in 1929. This variable primarily serves as a proxy for total water year precipitation, as it is measured when most of the annual snowfall for the season has accumulated, but before warmer temperatures have started the spring melt. However, it is also affected by winter temperatures, especially unusually warm periods that bring winter rain or cause melting.

Daily and/or monthly minimum, maximum, and average air temperature, and incremental and accumulated precipitation were available over a shorter time period. Starting dates differed at Mammoth Pass, but all variables were recorded after 2005. Records for Crestview CA, near the lowest site, were obtained from the Western Regional Climate Center (wrcc.dri.edu) and started in November 1993. Trends in snow water content, total water year precipitation, and temperature over time were assessed with a simple linear regression over the time period available for each variable and site.

Size, Age, and Ring Width

In August of 2016, four points within each site were randomly selected and located with a GPS. The area within a 10 m radius around each point was considered a plot, with each plot totaling 314.15 m². All trees taller than 10 cm within each plot

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were identified by species and the distance and angle (where north is 0˚) from the plot center were recorded. In addition, the height, diameter at base, and diameter at 1.37 m (breast height, DBH) were measure for each tree.

Stem density was calculated as the number of stems of all species within the 314.16 m² area of each plot. Basal area was measured as the total stem area of trees at breast height in each plot. For both, a simple linear regression was used to examine changes across elevation and a Tukey's post hoc test was used to compare pairs of elevations. Size within species was compared using a one-way ANOVA across elevations for *A. magnifica* and *P. contorta,* the only species to occur at three or more sites. Base diameter and height were log-transformed to meet assumptions of normality. Post hoc Tukey tests were used to compare pairs of elevations.

At least two cores were taken for all trees with DBH > 5 cm, one near breast height (approximately 1.3 m) and one as close to the ground as feasible (between 20 and 50 cm). The height and cardinal or inter-cardinal direction was recorded for each core. In sloped plots, cores were taken perpendicular to the slope to avoid compression wood, unless the presence of branches, other trees, or geographic features made this impossible (Speer 2010). All cores were taken with a 5-mm-diameter Haglof increment borer. All fieldwork was completed in August and September of 2016 except for cores taken from four trees in a single plot at the 2700 m site. At that time a yellow jacket's nest made these trees inaccessible. I returned to the site and obtained cores from these trees in 2018.

Cores were mounted and sanded with progressively finer sandpaper, starting with 220 grit and proceeding to 600 grit, until a smooth surface was visible under a microscope. Cores were cross-dated using standard skeleton plots (Stokes and Smiley 1968), and the total number of rings was recorded for each core. Black and white scans at a resolution of 4800 dpi were made of each core using an HP Scanjet G4050 scanner. Raw ring-widths were measured from scanned images with ImageJ (Version 2.0.0-rc-43/1.52i) open source imaging software. Cross-dated tree-ring series were checked for possible errors using COFECHA (Holmes 1983, Grissino-Mayer 2001).

All trees taller than 10 cm, but with a DBH less than 5 cm were considered saplings. At the lowest site, eight *P. contorta* saplings and eleven *P. jeffreyi* saplings had been destructively harvested and aged in 2007. At each of the other sites ten off-plot saplings of *P. contorta* and *A. magnifica* were haphazardly selected, and ten saplings of *P. albicaulis* were selected at the highest site only. Base diameter and height were recorded before these individuals were destructively harvested. Entire rounds from the base of the saplings were sanded with progressively finer sandpaper as described above. Harvested saplings were aged by counting the number of rings in the round visible under a microscope at magnification of 40 power.

Two simple linear regressions for each species and site were created to predict sapling age (estimated as the number of rings at the base) from the measured height and base diameter using the harvested saplings. The age of all on-plot saplings (DBH < 5 cm) was estimated as the mean of the ages predicted by the height and the base

diameter. The age of mature trees (DBH ≥ 5 cm) was estimated using the core from that tree that included or was closest to the pith, as judged by visual comparison of the inner most rings. If one was not clearly closer or both included the pith, the longer series was used. Age was estimated as the number of rings in the core, corrected for the species and site predicted age of the tree at the height the core was taken. Four individuals of *A. magnifica* and four of *P. contorta* could not be aged because cores from these trees were missing or could not be cross-dated. These individuals were removed from further analysis. Generalized linear models with a negative binomial error structure and a log link function were used to examine the relationship between estimated ages and elevation for *A. magnifica* and *P. contorta.* A Tukey's test for post hoc analysis was used to compare pairs of elevations.

The relationship between tree age and size was compared across elevations for *A. magnifica* and *P. contorta* using DBH and the estimated age for all trees with a DBH > 0. The effect of age and elevation on DBH was tested using an ANCOVA. Estimated marginal means of the linear trends for age at each elevation were calculated using the 'emmeans' package in R (Lenth 2020). A post-hoc Tukey test was used to compare slopes and intercepts of the trends between pairs of elevations.

Cross-dated ring-width series were analyzed using the Dendrochronology Program Library in R ("dplR") (Bunn 2008, Bunn 2012). Descriptive statistics for raw ring-width series were calculated using the "rwl.stats" function (Bunn 2008, Bunn 2010). The effect of elevation on series mean raw ring-width was examined

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with a linear mixed-effects model for each species, with individual tree as a random factor. To account for elevational differences in age, this analysis was repeated with tree age as a predictor, and again on subsets of the data restricted to the range of ages overlapping between sites. For *A. magnifica,* this included all trees younger than 126 years, the maximum age at 2800 m. For *P. contorta,* this was 55-85 years for the sites at 2290 m, 2510 m, and 2800 m and 85-150 years for the higher three sites. Cores at the 2290 m and 2700 m sites had no overlap in tree age. Post hoc Tukey tests were used to compare pairs of elevations within species.

Ring-Width Indices

Raw ring-widths were converted to ring-width indices (RWIs) using Friedman's super smoother in the 'detrend' function in "dplR" (Bunn 2008, Bunn 2010, Friedman 1984). This removes low-frequency variability in tree ring-widths resulting from reduced growth rates as trees age, but preserves high-frequency variability due to climate and other drivers. Descriptive statistics for detrended series included the Gini coefficient, a measure of series variability that can account for growth sensitivity across all time lags (Biondi and Qeadan 2008), and first order autocorrelation, a measure of the relationship with the previous years' growth. The Gini-coefficient and first order auto-correlation of ring-width indices were compared between elevations for *P. contorta* and *A. magnifica* with a linear mixed-effects model, with plot and individual tree as nested random factors.

The effect of April 1st snow water content on RWI over the 88-year period was assessed for each species using a linear mixed-effects model with individual tree as a random factor and snow water content for the three consecutive years ending at the year of ring growth as fixed effects. For the two species that occur at multiple sites, elevation was also included as a fixed effect. To reduce the effect of non-independence between cores from the same tree, only the core taken farthest from the ground for each tree was used.

The effect of temperature and precipitation variability on RWI was examined for the highest and lowest elevations from 2006-2016 and 1996-2016, respectively, corresponding to availability of meteorological data from nearby weather stations. The effect of average maximum summer temperature, average minimum winter temperature preceding the growing season, and total water year precipitation for the three consecutive years ending with the year of ring growth were determined using a linear mixed effects model for each species, with individual tree as a random effect. Only one core per tree was included in the analysis.

Chronologies

Mean value chronologies for each elevation were constructed using robust means of detrended series with the 'chron' function in "dplR" (Bunn 2008, Bunn 2010). Both a standard chronology and a residual chronology were constructed. In the residual chronology an autoregressive model is run on each series to account for autocorrelation through time before ring-widths are averaged (Bunn 2010). These

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chronologies were used to assess the relationship between mean annual growth and April 1st snow water content for the concurrent year and the previous 2 years over the 88-year period between 1929 and 2016 using a simple linear regression. Snow water content was standardized by subtracting the mean from each value and dividing by the standard deviation to allow easier interpretation of coefficient estimates. This analysis was completed for both the standard chronologies and the residual chronologies. The chronologies for the 2290 m site begin in 1951, the first year for which the sample depth to construct the chronology was greater than one series.

All analyses were done in R version 3.6.2 (R Core Team 2019). Data organization and manipulation was done using the 'tidyverse' package (Wickham et al. 2019). Linear mixed-effects models used the 'nlme' package (Pinheiro et al. 2018). All figures were produced using 'ggplot2' (Wickham 2016).

Results

Meteorology

Long-term total water year precipitation for the study site was approximated with records of April 1st snow water content, which showed considerable year-to-year variation (Figure 2-1). Between 1929 and 2016, mean snow water content was 924.2 mm and ranged from a maximum of 2197 mm in 1969 to a minimum of 38.1 mm in 2015, with a coefficient of variation of 43.6%. In three years, 1969, 1983, and 1995 snow water content was more that 1987 mm or two standard deviations above the long-term mean. 2015 was the only year that snow water content was less than 138.6

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mm, two standard deviations below the mean. In fact, in this year it was only 17% of the next lowest measured snow water content of 218.4 mm from 1931. A simple linear regression showed no significant increasing or decreasing trend in snow water content over the 88-year period.

Average summer temperatures decreased with elevation consistent with the adiabatic lapse rate. From 2006 to 2016, average summer air temperature (between June-September) was 14.9˚C (±2.24) at 2315 m and 11.7˚C (±2.19) at 2835 m. By contrast, winter air temperatures (December-February) were similar at both sites, averaging -2.62˚C (±1.92) and -2.74˚C (±1.94) for the lower and higher stations, respectively. Precipitation was greater at the higher elevation over the same time period. Mean total annual precipitation (by water year 1 October - 30 September) was 443 (±348) mm at the lower site and 1235 (±379) mm at the higher site. Both sites experienced considerable between-year variation, but total annual precipitation varied more at the lower site, which had a coefficient of variation of 80.0% compared to 30.7% at the higher site. At the 2835 m station, there was a marginally significant (p = 0.0983) increasing trend in average winter (December-February) temperature between 2005 and 2016. There was no trend in average temperature, summer temperature, or total water year precipitation. No significant trends were evident in any of the measured variables over the 23-year period from 1994-2016 at the lower elevation station.

Stem Density, Size, and Age

In total, 746 individual trees were identified. Individuals of *P. contorta* and/or *A. magnifica* dominated the plots at all four elevations (Figure 2-2). *P. jeffreyi* was found only in plots at the 2290 m site, although individuals were observed off plot at the 2510 m site. Stem density varied across elevations; it was highest (0.252 stems m^{-2}) at the 2510 m site, and lowest (0.0414 stems m^{-2}) at the 2290 m site. There was a high density of small trees across elevations, with the majority of trees measuring less than 10 m in height and 30 cm in base diameter. However, the largest tree at the lowest elevation (height = 15.8 m, base diameter = 72.1 cm) was considerably smaller than the largest tree sampled (height = 31.1 m, base diameter = 161.5 cm) at the 2700 m. Mean basal area per plot, was significantly lower at the 2290 m site compared to the other three sites (Table 2-1). Basal area was also highest at the 2510 m site, but this difference was only significant compared to the lowest elevation site.

Across all species and elevations, the size distribution was skewed toward small trees (Figure 2-3). Median DBH was less than 10 cm for all species and elevation combinations, except for *P. albicaulis* at the 2700 m site, where there were only two individuals of this species within the plots, and for *P. contorta* at the 2800 m site, where median DBH was 10.1 cm. For *A. magnifica,* median DBH was 0 cm at all elevations, meaning more than 50% of trees were shorter than breast height.

Comparisons across elevations were possible only for *A. manifica* and *P. contorta*, which had more than a few individuals at multiple elevations. Base diameter and height of *A. magnifica* were significantly smaller at 2800 m compared to 2510 m

($p<0.001$ for both) and 2700 m ($p<0.001$ for base and $p = 0.0083$ for height, Figure 2-4a and 2-4b). Base diameter and height of *P. contorta* also differed across elevations. Height of sampled trees was greater at 2510 m ($p = 0.0061$) and 2800 m ($p = 0.0092$) compared to 2700 m, and base diameter was greater at 2800 m ($p = 0.0011$) and 2290 m ($p = 0.0168$) than at 2700 m (Figure 2-4c and 2-4d).

Age was estimated for 730 individual trees across the four species and elevations. Similar to size, the age distribution tended to be skewed toward younger individuals, though not as strongly (Figure 2-5). The oldest individuals of both *A. magnifica* and *P. contorta* occurred at the 2700 m site, estimated at 270 and 433 years respectively. The oldest individual of *P. albicaulis* was estimated to be 263 years old; the oldest of *P. jeffreyi*, 54.

I compared the age of trees at different elevations for *A. magnifica* and *P. contorta*. Individuals of *A. magnifica* were significantly younger at the 2800 m site compared to the 2510 m site and the 2700 m site ($p<0.001$ for both) and were marginally younger at the 2510 m site compared to the 2700 m site ($p = 0.057$). For *P. contorta*, individuals at the lowest site were significantly younger than all other sites ($p <0.001$ for all three comparisons), but none of the other three elevations differed significantly from each other.

The relationship between DBH and age across elevations was also compared for the same two species. For *P. contorta,* this trend differed between elevations (Figure 2-6). The estimated coefficient for age was greatest at 2290 m ($b = 0.561$),

though this was only significantly greater than the coefficient at 2700 m ($p = 0.008$). The coefficient at 2700 m was also significantly lower than at 2150 m ($p<0.001$) and 2800 m ($p = 0.0025$), consistent with the observation that trees at this elevation were on average smaller but not younger than the other three sites. The coefficient at 2510 m was significantly greater than at 2800 m ($p = 0.0385$). While the coefficients did not differ between 2290 m and 2150 m, the intercept at 2290 m was significantly greater ($p = 0.0033$), suggesting that for trees at a given age, DBH at 2290 m is expected to be larger. Neither the coefficients nor intercepts differed significantly between any two elevations for *A. magnifica.*

Ring-Width

Raw ring-width was measured for 538 cores representing 294 trees. Of these, 15 series were from *P. albicaulis,* 14 were from *P. jeffreyi,* 151 were from *A. magnfica,* and the remaining 358 were from *P. contorta.* Rings of *P. contorta* were significantly wider at the 2290 m elevation compared to the higher three elevations ($p < 0.001$ for all three comparisons), and were thinner at the 2700 m site compared to 2510 m ($p < 0.001$) and 2800 m ($p = 0.0011$). As individuals at the 2290 m site were younger, this could have been an artifact of the expected decrease in growth rates as trees age. However, the patterns of significance in these relationships remained when age was included in the model as a predictor, and when the analysis was conducted on subsets of the data where age overlapped between elevations. For *A. magnifica*, rings were significantly wider at the 2800 m site compared to the 2510 m site ($p = 0.0371$)

and the 2700 m site ($p = 0.0146$). Trees at the highest site were similarly younger than the other two sites, but the direction and significance of these relationships remained when age was included as a predictor and when the analysis was restricted to trees younger than 126 years, the maximum age at 2800 m.

For *P. contorta,* the Gini-coefficient was significantly higher at 2700 m ($p = 0.0157$) and 2800 m ($p = 0.0141$) compared to 2290 m. It was marginally higher ($p = 0.0861$) at 2510 m than 2290 m. No other elevations differed from each other. The Gini coeffcient did not differ between any pair of elevations for *A. magnifica.* First Order Autocorrelation for *P. contorta* was significantly lower ($p < 0.001$) at 2290 m compared to the three higher elevations, but none of the other elevations differed from each other. For *A. magnifica,* first order autocorrelation was significantly lower at 2800 m ($p = 0.0208$) and marginally lower at 2510 m ($p = 0.0863$) than at 2700 m, but did not differ between 2510 m and 2800 m.

For *A. magnifica,* April 1st snow water content of the concurrent year had a highly significant, positive effect on RWI. The effect of the previous two years' snow water content and the interaction between elevation and the concurrent year's snow water content were also highly significant (Table 2-2). The effect of the concurrent year's snow water content and that of the previous year were highly significant for *P. contorta,* with RWI increasing with higher snow water content from both years. The interaction of elevation and concurrent year snow water content was also highly significant (Table 2-2). For *P. jeffreyi,* snow water content of the concurrent year was

significantly and positively related to RWI. The effect of the snow water content 2 years prior was also significant, but in the opposite direction (Table 2-2). For *P. albicaulis*, which only occurs at the highest elevation, the only significant effect was previous year's snow water content. This effect was also positive (Table 2-2).

Sensitivity to more recent variability in temperature and precipitation also differed between elevations. At the 2290 m site, where data were available since 1995, RWI for *P. contorta* significantly increased with total water year precipitation from the concurrent year ($p = 0.0011$) but decreased with greater average minimum winter temperature ($p = 0.0026$). For *P. jeffreyi*, only total water year precipitation from the concurrent year was significant ($p = 0.0010$) and this relationship was positive. At the highest elevation, RWI for *P. contorta* increased significantly with total water year precipitation of the concurrent year ($p < 0.001$) and the previous year ($p = 0.0035$) since 2005. Higher average maximum summer temperature and higher minimum winter temperature were also significantly related to higher RWI ($p < 0.001$ and $p = 0.0013$ respectively). For *P. albicaulis*, the total water year precipitation of the previous year was significantly and positively correlated with RWI, but no other effect was significant. None of the tested variables had a significant effect on RWI of *A. magnifica* at the 2800 m site.

Chronologies

Mean value chronologies for each elevation showed considerable inter-annual variability in ring-width over the 88-year period (Figure 2-7). The relationship

between mean annual ring width and snow water content differed between elevations, but patterns of significance were largely consistent between both standard and residual chronologies (Table 2-3). At the lowest elevation, mean ring-width increased with the snow water of the concurrent year, but this effect was only marginally significant ($p < 0.1$). At the 2510 m and 2700 m sites, average ring-width increased with the previous year's snow water content for both chronologies, though this was only marginally significant for the residual chronologies (Table 2-3). The effect of snow water content was strongest at the highest elevation, where mean ring-width was significantly and positively correlated with the previous year's snow water content. The relationship with the concurrent year was highly significant, but in the opposite direction, with mean ring-width decreasing with greater snow water content (Table 2-3). Despite these relationships, the most extreme years in terms of snow water content did not result in the most extreme mean-ring widths. Of the five years with the least snow (1931, 1977, 2007, 2014, and 2015), only 2015, the last year of a severe multi-year drought, was among the smallest five ring-widths for all three of the lower elevations. At the highest site, only 1931 was among the five widest rings, while none of the five heaviest snow years corresponded to the five years with thinnest average ring-widths.

Discussion

In general, snow water content of the concurrent and previous years had strong positive effects on RWI across species. However, the effects of snow water

content were not consistent across elevations. There was no impact of the 2012-2015 drought was evident in tree rings at the highest elevation. Reduced ring growth emerged at the lower elevations only in the later years of the drought, suggesting that multiple years of drought were necessary to impact ring widths. Trees generally appeared to be less sensitive to an extreme drought event than expected.

The positive effect of concurrent year's snow water content was not exhibited for *P. albicaulis,* which was only analyzed for the highest site. For both the narrowly distributed *A. magnifica* and the widespread *P. contorta,* the interaction of concurrent year's snow water content and elevation was highly significant, likely because the direction of the effect at the highest elevation was reversed. Similarly, the mean chronologies for this elevation show that greater snow water content was associated with reduced growth. Heavy snow years likely delay the start of the growing season, an effect that is more pronounced at the highest elevation, which appears to have the consequence of reducing overall growth. The apparent reversal of this relationship for *P. contorta*, and disappearance for *A. magnifica* in comparisons with shorter term climate variability may be because the last heavy snow year (where snow water content exceeded two standard deviations above the mean) was in 1995, well before the records for temperature and precipitation at the highest elevation are available (starting in 2005). While concurrent water year precipitation was important in limiting growth for trees at the lowest elevation, growth was also reduced by warmer

winter temperatures, suggesting water limitation at this site is also mediated by the extent and duration of the winter snowpack.

For three of the four species, ring-width increased with the prior year's snow water content, supporting the idea that growth is impacted by antecedent conditions (Olge et al. 2015). For *P. albicaulis*, the positive association with total precipitation the previous year was the only significant effect, a pattern consistent between both the long-term snow water content and the shorter records of temperature and precipitation. This is in agreement with results from Millar et al. (2012) who found time-lagged total water year precipitation and climatic water deficit were the variables most strongly correlated with growth for this species throughout the eastern Sierra Nevada.

Mean ring-width chronologies, which pool across species, but examine elevations separately, largely corroborated the relationships between species' RWI and snow water content, especially at the highest elevation. At the lowest elevation, the relationship was only marginally significant, but was consistent in type and direction. For the middle two elevations, only the effect of previous year's snow water content was significant for mean ring-width, an effect that was also significant on RWI for the both species present at these sites. This supports the conclusion that the effect of water year precipitation on tree growth is not consistent across elevations. The positive influence of the current year's snow water content is greatest at the lowest elevation but declines and even reverses as elevation and total snowfall

increase. Similarly, Buechling et al. (2017) found radial growth in conifers in the Rocky Mountains was positively correlated with annual precipitation in the drier parts of their ranges, but that this relationship disappeared or reversed above a certain threshold of growth year precipitation. The stronger effect of snow water content on mean ring-width at the highest elevation could be influenced by this site's closer proximity to the station (at 2835 m) where this variable was measured. Furthermore, the lack of correspondence between extremes in snow water content and extremes in the mean chronologies suggests that while precipitation affects ring-width, other factors are important in driving inter-annual variability, both between elevations and between individuals at the same site.

On the whole, trees at the lowest site were less sensitive to inter-annual differences in snow water content, despite receiving less precipitation and experiencing higher growing season temperatures. Inter-annual sensitivity in ring-growth, as measured by the Gini-coefficient was lower for *P. contorta* at the lowest elevation compared to other sites, contrasting with the prediction of hypothesis 2. This relative lack of sensitivity at the lowest elevation could indicate genetic adaptation to drier conditions. For *P. ponderosa*, sensitivity to water year precipitation generally increased as annual mean precipitation declined across the western United States, but some populations at the southern range edge were less sensitive compared to populations that received similar average amounts of precipitation, suggesting local adaptation (McCullough et al. 2017). It is also possible that trees at the lowest

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elevation have to access groundwater that partially decouples their responses from the snow water content of that year.

Growth was greater at the lowest site, both in terms of mean annual ring-width, and as illustrated by size and age comparisons (Figure 2-6), supporting hypothesis 2. For a given age, trees at the 2290 m site tend to be larger than those at higher elevations. In contrast, the elevation with the slowest growth was 2700 m, as evidenced by average raw ring-width and the relationship between DBH and age. Even compared to the highest elevation, *P. contorta* individuals at this site are not larger, despite the fact it contains the oldest individual trees. Reed and Loik (2016) found significant differences in soil organic matter, total exchange capacity, and nitrogen availability between elevations for soils in this region, which could also influence growth. More detailed meteorological data and information about soil properties from this site would be necessary to determine what might be driving this pattern.

The age and size structure for *P. contorta* is not consistent with an upslope distributional shift, contrary to hypothesis 1. In fact, the individuals at the lowest elevation are both younger and smaller, suggesting that if anything this species has shifted downslope over the past century, or begun "filling-in" at this site due to elevated CO_2 or changing patterns of land use.   In contrast, the size and age structure for *A. magnifica* are consistent with upslope migration, particularly between the highest two sites. Individuals at the highest site are both smaller and younger, with

only a single individual estimated to be older than 100 years. This may be because this site is close to the reported upper elevational limit for this species (Laacke 1990), suggesting that it may be in the process of increasing its abundance in the high elevation part of its range or even expanding its upper range boundary.

Although I did not measure mortality directly, my field research followed a massive mortality event throughout the Sierra Nevada in 2015 (Fettig et al. 2019). However, I was surprised to observe that most of my plots had few or no standing dead trees, and I did not see widespread mortality off-plot at most of the sites. The exception was at 2510 m, where all of the plots had multiple standing dead trees and off plot mortality was quite evident. This elevation also had much higher stem density (Table 2-1), which has been associated with higher drought-induced mortality (Jump et al. 2017). This was also the only site where I observed evidence of bark beetle activity, which also contributes to mortality under drought conditions (Stephenson 2019). Moreover, the area around Mammoth Lakes suffered highly patchy tree mortality after the drought that was not evident in my plots.

The recent California drought exposed trees at these study sites to multiple years of below average precipitation coupled with unusually high temperatures (Griffin and Anchukaitis 2014), culminating in the record low April 1st snow water content of 2015. Despite these conditions, 2015 was the only year from the drought that was consistently narrow across cores (a "marker year"), and only in cores from the lowest three elevations. In the mean ring-width chronologies, only 2014 and 2015

were noticeably thinner at 2290 m and 2510 m, while for 2700 m it was only 2015, suggesting that even for low elevations, multiple years of dry conditions were necessary to significantly impact average growth. This also suggests that at 2700 m there was still sufficient snow in 2014 to avoid the growth reducing impacts seen at the lower elevations, but 2015 was so dry that only the highest elevation avoided these effects. Increasing climate variability will likely subject these trees to new extreme events in the future, but they have demonstrated an unexpected capacity to tolerate considerable meteorological variability, including extended record drought conditions.

Table 2-1. Tree density and species composition by elevation. Data for basal area and stem density are means across four plots (±standard deviation). Species counts are the total number of stems in all four plots.

Elevation (m)	Basal Area (m²)	Stem Density (stems m⁻²)	Species	Count
2290	0.288 (±0.305)	0.0414 (±0.0224)	*P. contorta*	37
			P. jeffreyi	15
2510	2.06 (±0.373)	0.252 (±0.0763)	*A. magnifica*	186
			P. contorta	131
2700	1.61 (±0.427)	0.177 (±0.0609)	*A. magnifica*	140
			P. albicaulis	2
			P. contorta	81
2800	1.75 (±0.767)	0.118 (±0.0740)	*A. magnifica*	42
			P. albicaulis	13
			P. contorta	93

Table 2-2. Effect of elevation and three consecutive years of April 1st snow water content (SWC - current ring year, SWC1 - previous year, SWC2 - 2 years before) on RWI for the four study species. Estimates and *p*-values are from a linear mixed effects model with tree as a random factor. Significant effects ($p < 0.05$) are in bold.

Species	Effect	Estimate	*t* - value	*p*-value
A. magnifica	Elevation	-0.000019	-0.6095	0.5438
	SWC	0.5810	**7.203**	**<0.001**
	SWC1	0.0268	**8.826**	**<0.001**
	SWC2	0.0140	**4.473**	**<0.001**
	Elevation*SWC	-0.00022	**-7.050**	**<0.001**
P. albicaulis	SWC	-0.0086	-0.8616	0.3892
	SWC1	0.03447	**3.470**	**<0.001**
	SWC2	0.01089	1.064	0.2875
P. contorta	Elevation	-0.00001	-0.7651	0.4452
	SWC	0.3544	**9.699**	**<0.001**
	SWC1	0.0132	**6.348**	**<0.001**
	SWC2	-0.0022	-1.015	0.3101
	Elevation*SWC	-0.00013	**-9.450**	**<0.001**
P. jeffreyi	SWC	0.0636	**3.910**	**<0.001**
	SWC1	0.00068	0.0430	0.9658
	SWC2	-0.0352	**-2.079**	**0.0388**

Table 2-3. Relationship between mean annual ring-width from standard and residual chronologies and April 1st snow water content over three years for each elevation. Estimates and *p*-values are from a simple linear regression. Significant effects (*p* < 0.05) are in bold.

Elevation (m)	Chronology	Years before measured ring	Estimate	t - value	*p*-value
2290	Standard	0	0.0187	1.782	0.0797
		1	0.0074	0.711	0.4795
		2	-0.0064	-0.586	0.5603
	Residual	0	0.0169	1.712	0.0919
		1	0.0067	0.674	0.5027
		2	-0.0071	-0.691	0.4919
2510	Standard	0	0.0139	1.642	0.1044
		1	0.0215	**2.630**	**0.0141**
		2	0.0107	1.251	0.2146
	Residual	0	0.0098	1.224	0.2244
		1	0.0146	1.837	0.0698
		2	0.0059	0.762	0.4698
2700	Standard	0	0.00563	0.625	0.5336
		1	0.0217	**2.434**	**0.0171**
		2	0.0043	0.832	0.4080
	Residual	0	0.0061	0.682	0.4973
		1	0.0157	1.800	0.0756
		2	-0.00073	-0.081	0.9358
2800	Standard	0	-0.037	**-4.272**	**<0.001**
		1	0.0179	**2.084**	**0.0403**
		2	0.002	0.271	0.7868

Residual				
	0	-0.0345	**-4.070**	**<0.001**
	1	0.0194	**2.311**	**0.0234**
	2	-0.0017	-0.196	0.8448
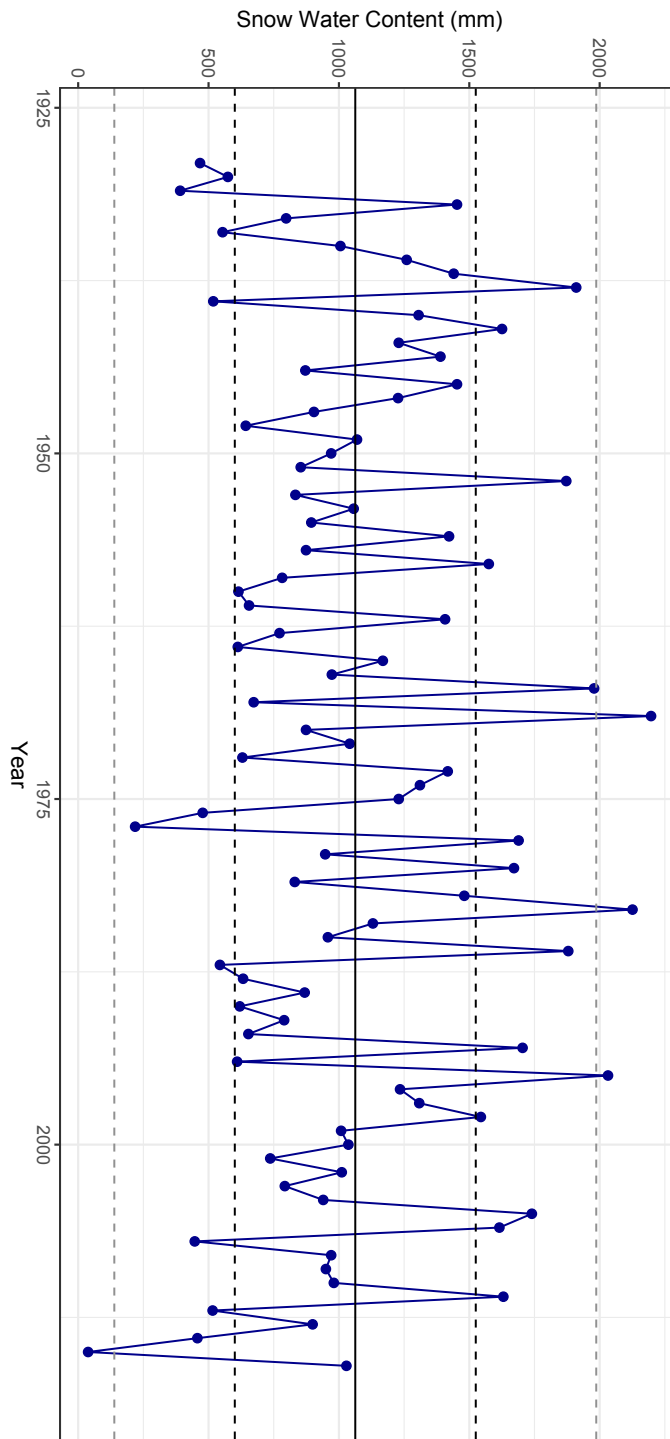
Figure 2-1. April 1st snow water content from Mammoth Pass from 1929-2016. The solid black line is the mean. Black and gray dotted lines are one and two standard deviations, respectively, above and below the mean.
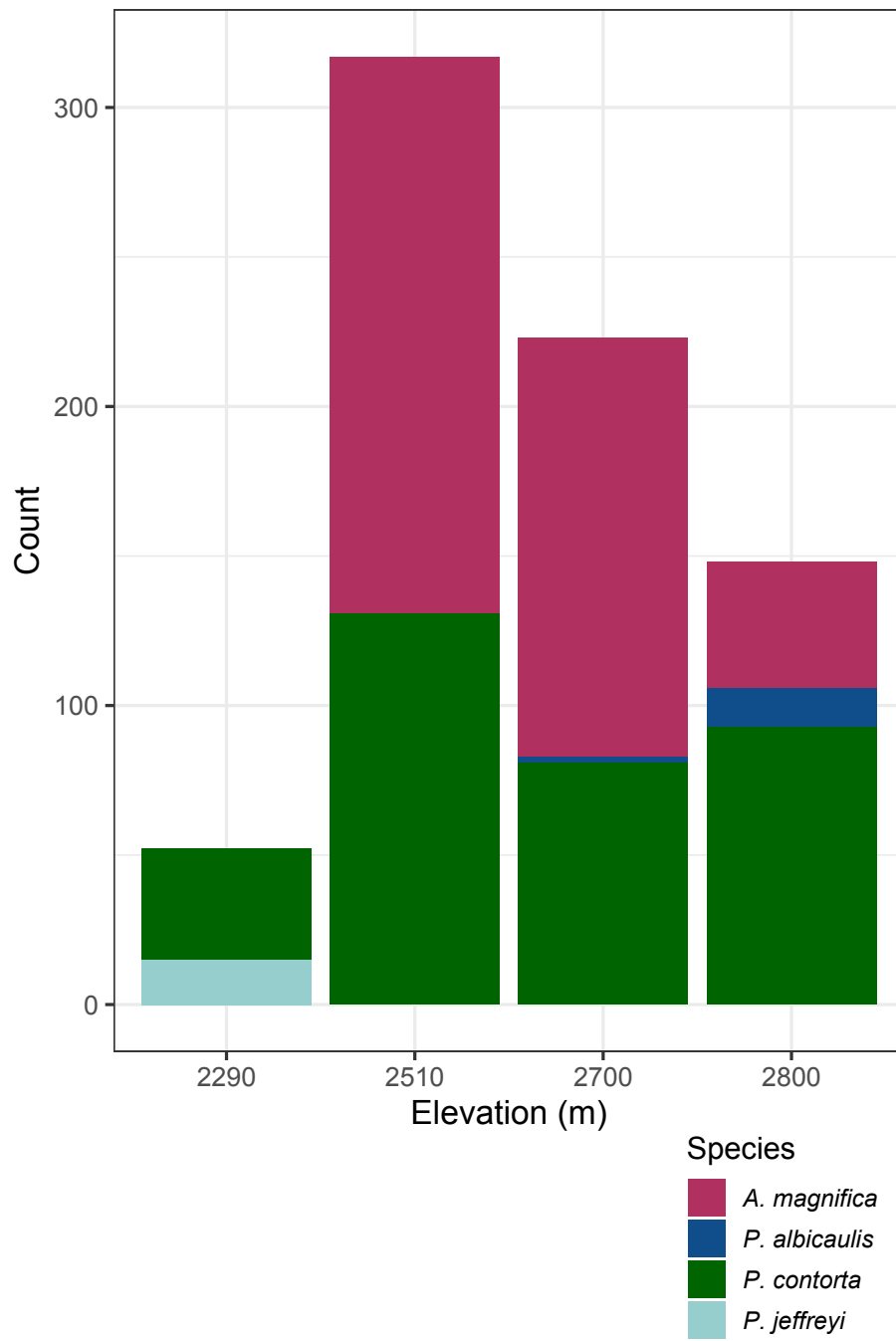
Figure 2-2. Number of individuals of each species at each elevation.
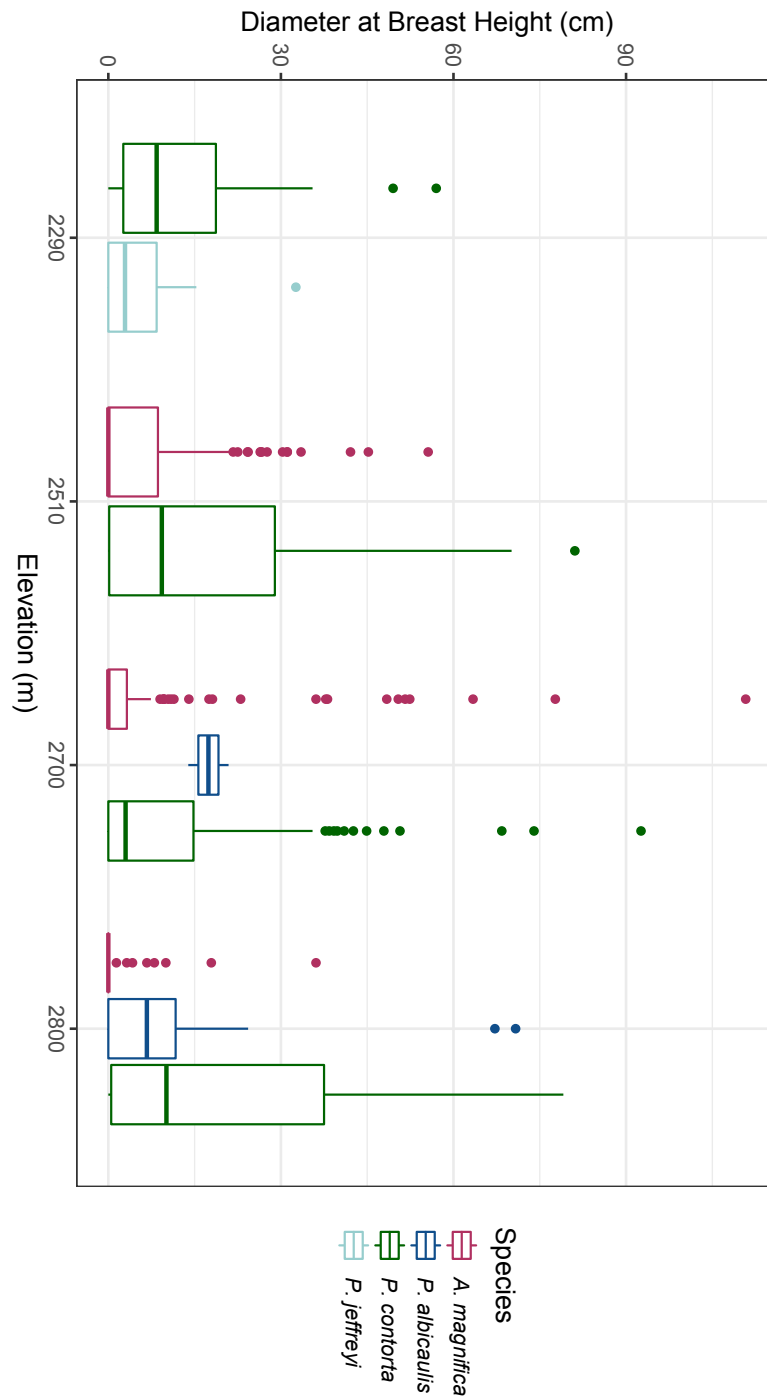
Figure 2-3. Diameter at breast height for all measured trees by elevation and species. Boxes represent the first and third quartiles, the dark line represents the median, whiskers extend to minimum and maximum values with distance of 1.5 times inter quartile range above or below the box, and dots represent outliers.
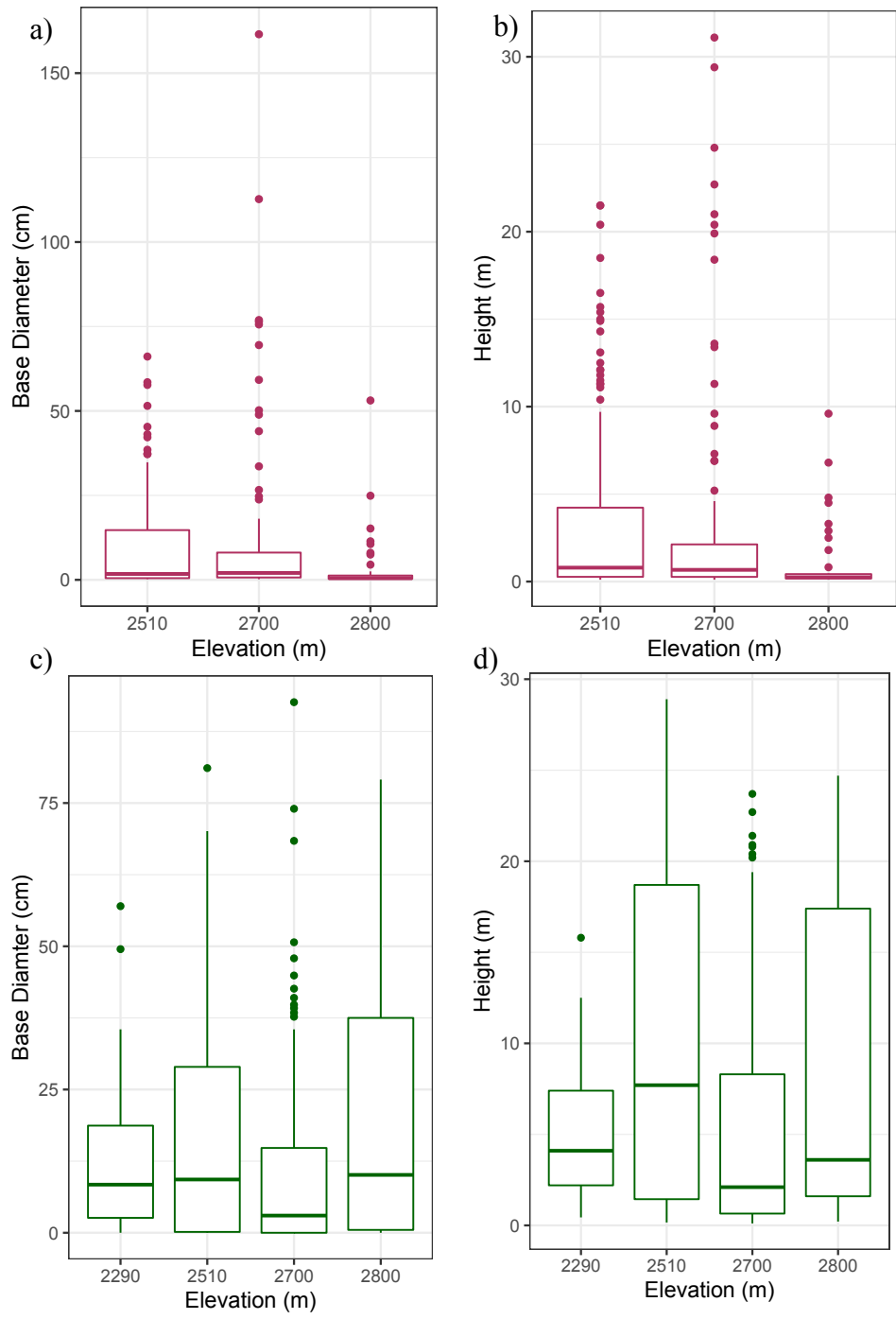
Figure 2-4. Distribution of individual tree base diameter and height by elevation for *A. magnifica* (a and b) and *P. contorta* (c and d). Boxes represent the first and third quartiles, the dark line represents the median, whiskers extend to minimum and maximum values with distance of 1.5 times inter quartile range above or below the box, and dots represent outliers.
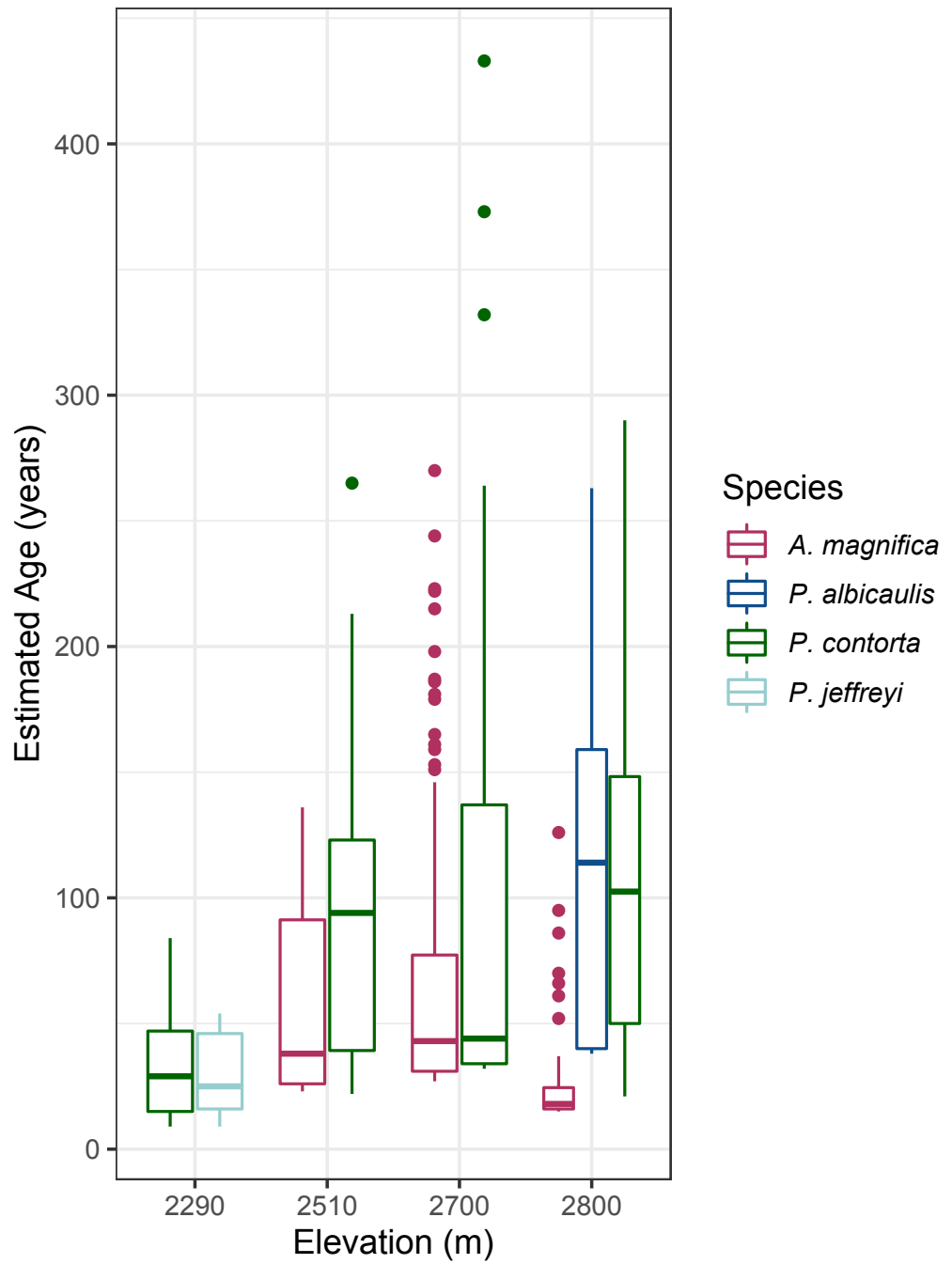
Figure 2-5. Estimated age by species and elevation. Boxes represent the first and third quartiles, the dark line represents the median, whiskers extend to minimum and maximum values with distance of 1.5 times inter quartile range above or below the box, and dots represent outliers.
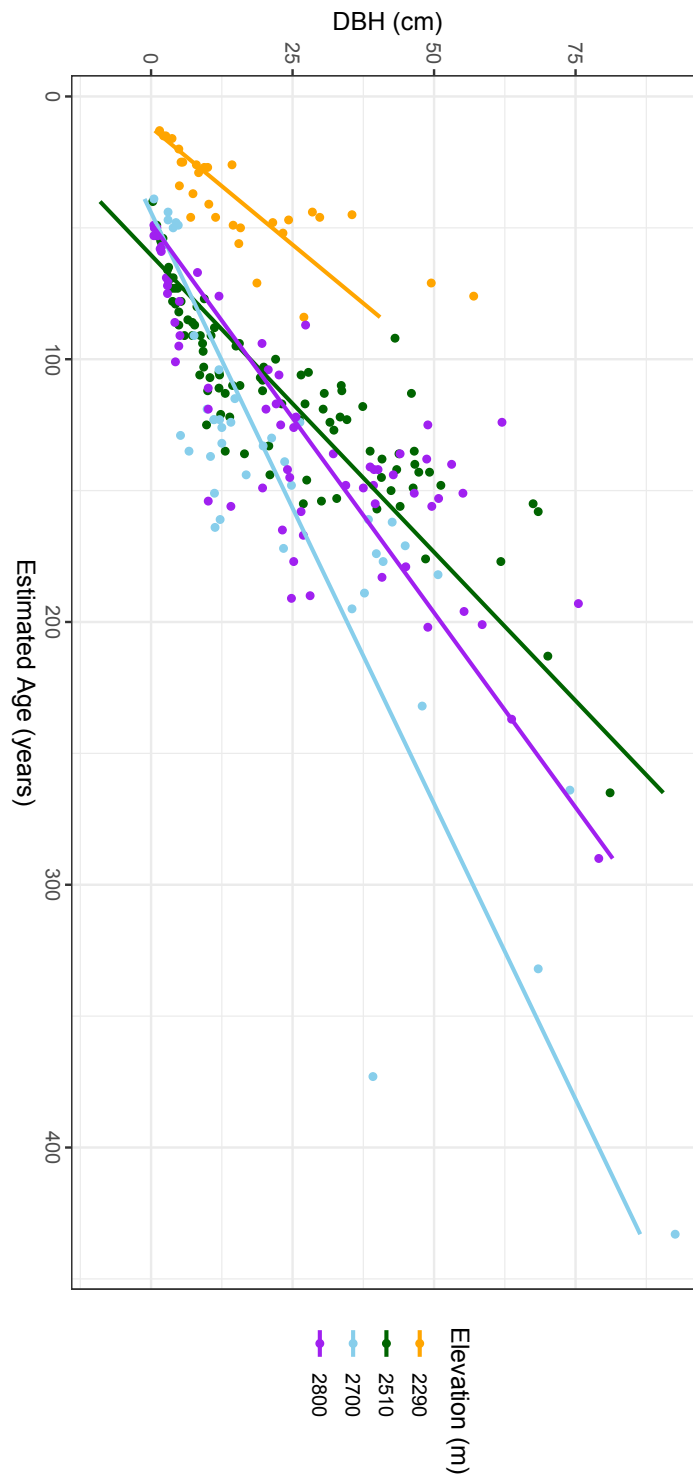
Figure 2-6. Diameter at Breast Height compared to tree age for *P. contorta* across the four elevations. Lines are linear models of the relationship for each elevation.
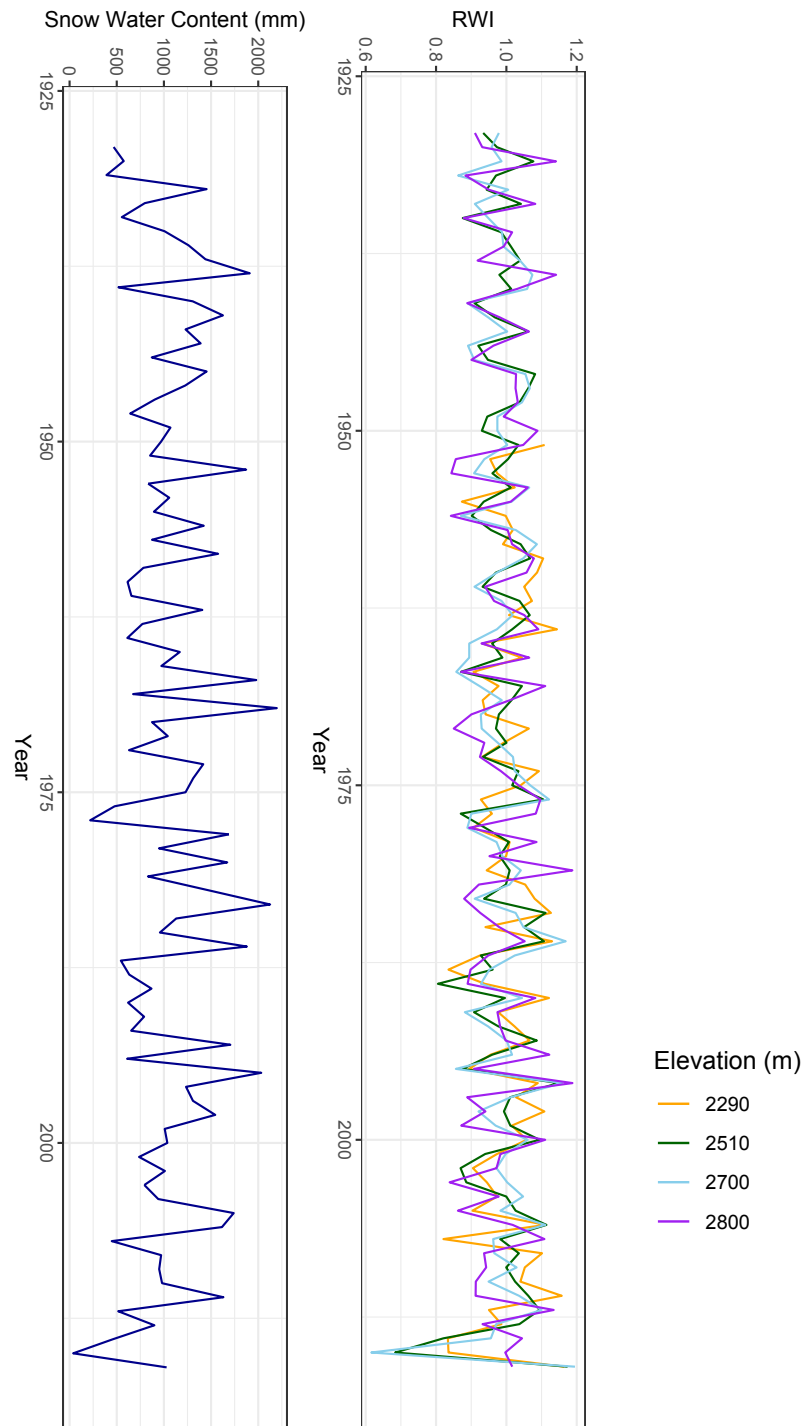
Figure 2-7. Standard mean value chronologies for each elevation and snow water content from 1929-2016. The chronology for the 2290 m elevation site (in orange) begins in 1951, the first year for which the sample depth to construct the chronology was greater than one.

Chapter 3:

Cultural attitudes and climate change beliefs in the Inyo and Sierra National Forests

Introduction

The Inyo and Sierra National Forests are located in the central part of the Sierra Nevada mountains of California. Both Forests include substantial wilderness areas and provide habitat for at-risk species, including the California Spotted Owl, the Sage-Grouse, and the Sierra Marten. They are also gateways to neighboring National Parks and provide recreational opportunities for both local residents and visitors, and recreational services have become an increasingly important part of the economies of the surrounding communities (Inyo National Forest 2017; Sierra National Forest 2017). These Forests have also historically supported uses such as livestock grazing, mineral prospecting, and timber production, which are much more limited today.

The United States Forest Service (USFS) and other federal agencies develop rules and regulations meant to implement federal legislation, including the National Forest Management Act (NFMA), the Multiple Use Sustained Yield Act (MUSY), the National Environmental Policy Act (NEPA), and the Endangered Species Act (ESA), which govern the management of national forests. The USFS is primarily responsible for implementing NFMA, which requires a three-tiered approach to forest management. At the national level, the 2012 National Forest Planning Rule is the current regulation interpreting NFMA and providing explicit direction for compliance

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with the law. At the Forest level, this national rule guides the development and revision of a land management plan (LMP), which identifies desired conditions and management objectives for the Forest, but neither authorizes nor requires specific actions. At the local level, site-specific management actions or projects, such as a timber sale or a controlled burn, should carry out the goals of LMP.

All Forests in the USFS system developed LMPs during the 1980s and early 1990s, following the passage of NFMA in 1976, but most Forests have not updated these plans since that time. The Inyo and Sierra National Forests were among eights forests selected as "early adopters" for revising their current LMPs in accordance with the 2012 Planning Rule, and published draft revisions and environmental impact statements (EISs) in 2016 (Inyo, Sequoia, and Sierra Forest Plan Revisions 2017). In August 2018, the Inyo National Forest submitted a revised plan, final EIS, and draft record of decision. The Sierra National Forest is still revising its LMP, and released newly revised draft EIS in the summer of 2019 and the public comment period for this draft ended September 26, 2019 (Sierra National Forest 2019, USFS Pacific Southwest Region 2019). These comments will be reviewed before the final EIS, final plan, and draft record of decision are submitted.

In the coming century, climate change may threaten conservation and livelihood goals in these Forests. Despite the substantial body of literature exploring climate change impacts on forests, US land management agencies, including the USFS, have only gradually been incorporating climate change science into their

planning. Actual implementation and evaluation of methods is rare (Littell et al. 2012, Bierbaum et al. 2013). The draft revisions for both the Inyo and the Sierra LMPs make numerous references to climate change and managing Forests for resilience to climate change is a stated goal of the 2012 National Forest Planning Rule (National Forest System Land Management Planning 2012), but both the rule and the plan revisions are quite vague in their guidance. The Rule identifies climate change as a stressor that will impact Forests and suggests a "strategic framework for adaptive management" that will "assess conditions on the ground using readily available information, build plan components recognizing that conditions may be changing, and monitor to determine if there are measurable changes related to climate change and other stressors on the plan area" (National Forest System Land Management Planning 2012, 21176). But it is unclear how this information will be evaluated or what "consideration" of these changing conditions practically entails. Moreover, the plan explicitly recognizes climate change as a "[factor] outside the Agency's control" and therefore as a constraint in its ability to achieve other goals such as the maintenance and restoration of ecological conditions suitable for native species (National Forest System Land Management Planning 2012, 21212). Similarly, the Draft Record of Decision for the INF identifies three climate change monitoring indicators—health, extent, and regeneration of white pines; changes in flow regimes for specific waterways; and changes in fire return interval or severity—but provides little to no guidance on how the target of improved resilience of the Forest's ecosystems to this

stressor should be achieved (Randall-Parker 2018). It is unclear how climate change science will affect specific management decisions in these Forests or how managers will balance climate concerns with other management priorities.

Beliefs and attitudes held by the local community may affect forest management decisions. Depending on the salience and proximity of the issue, public opinion can be both a resource and an obstacle for actors advocating specific policies or decisions, and in some cases may lead to substantial shifts in institutional arrangements (Jones & Jenkins-Smith 2009). After the passage of the National Forest Management Act in 1976, individual Forests in the US National Forest system engaged in the lengthy process of developing a plan to guide forest management over the next several decades. In investigating potential factors influencing USFS decision making, Sabatier et al. (1995) conclude that actors seeking to protect environmental and recreational values, either interests groups and agencies with environmental goals and/or employees within the Forest Service sympathetic to these goals, were the most influential factor in determining the final plan, especially with respect to timber harvesting and livestock grazing. As the process is repeated in these two Forests more than two decades later, community belief systems may impact the development and implementation of the land management plan. Characterizing these belief systems can help forest managers in framing management actions and policies addressing the new situations caused by climate change to better appeal to these citizenries.

Cultural Theory

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Cultural theory posits that individuals in any society subscribe to one of four[1] "ways of life" that support mutually reinforcing patterns of social relationships and systems of values and beliefs (Thompson et al. 1990). These types can be described along two independent dimensions: (1) Group, measuring "the extent to which individuals value group membership" and (2) Grid, measuring the extent to which external prescriptions regulate individuals (Jones 2011). This results in four worldviews—(1) hierarchy (high group, high grid), (2) egalitarianism (high group, low grid), (3) individualism (low group, low grid), and (4) fatalism (low group, high grid)—that broadly explain the belief system that determines an individual's understanding of his or her role in society and the way society ought to be structured (Jenkins-Smith et al. 2014). Hierarchs believe humans are flawed, requiring strong institutions and well-defined rules to keep them in check. They value authority, stability, and order, and prefer to trust experts and those in authority in decision-making (Ripberger et al. 2014). In contrast, egalitarians view humans as basically good, but corrupted by institutions (making them distrustful of authority). They value equality and believe in collective decision making through deliberation and consensus (Ripberger et al. 2014). Individualists view humans as self-seeking and value personal liberties above other values. They believe individuals directly affected by an issue should negotiate in decision making and that the market will offer the best

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[1] Thompson et al. allow a fifth way of life, "autonomy" or "the hermit", who does not participate in "coercive social interactions" (but it will be ignored in this analysis).

solutions, especially when unrestricted by institutional rules and regulations

(Ripberger et al. 2014). Fatalists see themselves as unable to control their own lives.

They are bound by external constraints and random chance, but remain outside social

groups. They believe decision-making is largely futile because events in life are

beyond human ability to control (Ripberger et al. 2014). Cultural types are also

associated with characteristic "myths" about nature and social institutions that

connect these underlying values and belief systems to policy preferences (Thompson

et al. 1990, Jenkins-Smith et al. 2014), making the cultural types potentially useful in

predicting attitudes on a variety of issues.

Jones (2011) examined the relationship of people's identification with these

cultural types with their attitudes toward climate change. This survey sought to move

beyond the liberal/conservative divide in understanding people's beliefs about climate

change by comparing responses to five questions (scale 0 to 10) assessing belief

about climate warming, anthropogenic causes, personal and social risk, and the need

for action with political ideology and the four cultural types, or "ways of life"

identified in cultural theory (Jones 2011). As expected, political ideology was a strong

predictor, with higher levels of conservatism significantly and negatively related to all

five climate change beliefs. However, including the cultural types paints a more

complex picture. Hierarachism and Egalitarianism were both associated with greater

belief in climate change and higher estimation of climate change risk and the need for

action, though presumably for different reasons (Jones 2011). Conversely,

Individualism, which views nature as resilient and resists the regulation of individual choices that addressing climate change would entail, was significantly and negatively associated with four of the five factors (Jones 2011).

Global Warming's Six Americas

Starting in 2008, the Yale Program on Climate Change Communication began conducting a survey to segment the adult population in the United States based on their beliefs about and engagement with the issue of global warming and what should be done to address it to inform climate change communication strategies (Leiserowitz et al. 2009). By identifying specific audiences within the larger American public, including certain policies or behaviors they were likely to support, the program was intended to increase the effectiveness of public engagement on climate change issues by institutions, including government agencies (Maibach 2011b). Six distinct audiences were identified that varied in (1) their certainty about the reality of climate change, (2) their level of concern, (3) their beliefs about primary causes, (4) their opinions about actions to address it, and (5) their assessment of their own knowledge about the issue (Leiserowitz et al. 2009). These audiences form a continuum ranging from the people convinced of the seriousness of climate change who already engage in individual actions to address it to the people convinced climate change is not happening and actively oppose efforts to combat it. These six categories, from most to least concerned with climate change are described as: Alarmed, Concerned, Cautious, Disengaged, Doubtful, and Dismissive (Leiserowitz et al. 2009). Subsequently, a 15-

item survey instrument and linear discriminant function were developed to allow other researchers to categorize respondents for new samples of the US population into the identified segments, correctly classifying 84% of a sample (Maibach et al. 2011b).

The survey has been repeated annually since 2010, and while there was an initial drop in the percentage of American's that believe global warming is happening and caused by human actions, it has since risen to the levels observed in 2008 (Ballew et al. 2019). Moreover, risk perception related to climate change has been rising, with 73% of Americans believing global warming will cause harm to future generations and plants and animals (Ballew et al. 2019). The distribution of the US adult population into the six categories has also shifted since 2008. In the most recent survey in December 2018, 29% were classified as Alarmed, 30% as Concerned, 17% as Cautious, 5% as Disengaged, 9% as Doubtful, and 9% as Dismissive (Yale Program on Climate Change 2019). While this represents an overall increase in belief in and concern about climate change, the proportion of people classified as Doubtful and Dismissive has remained relatively unchanged, which were 11% and 7% respectively in 2008 (Leiserowitz et al. 2009).

Survey Methods

The underlying belief systems and attitudes towards climate change expressed by local community members near the Inyo and Sierra National forest were quantified using the combinations of these two previously developed survey instruments. To assess respondents' identification with the four cultural types proposed by cultural

theory (Thompson et al. 1990), participants were asked to indicate their level of agreement with a set of 12 statements. Three of these statements represent views consistent with each of the four cultural types (Jones 2011). To assess respondents' attitudes towards climate change, participants were asked 15 questions from the Global Warming's Six Americas survey instrument from the Yale project on climate change communication (Maibach et al. 2011a). In addition, participants were asked to report their age, gender, ethnicity, highest level of education, the number of years they had lived near the Forest, and whether that was their primary address. Lastly, participants were asked to identify their political ideology on a seven point scale, with one being strongly liberal and seven strongly conservative. Surveys were printed and mailed with a stamped, self-addressed envelope in November of 2018.

A random sample of 300 addresses near each forest was selected using ArcGIS (CITE). The basemap and the Inyo and Sierra National Forest boundaries were collected from ArcGIS online. Geolocated addresses from Fresno, Inyo, and Mono counties were downloaded from the county websites and added as a layer to the basemap. From these addresses we created a sub-selected layer of valid mailing addresses within approximately 25 kilometers of the forest boundaries. From this layer, 300 points were randomly chosen from both Fresno County and Inyo and Mono Counties.

Because of the rural nature of the areas being sampled, mail delivery is not available to many residents. To account for this, a random sample of 300 post office

boxes was also selected near each forest. Post offices within the same distance of the forest boundaries were identified in Fresno and Madera Counties, near the Sierra National Forest, and Inyo and Mono Counties near the Inyo National Forest. 18 were identified for the Sierra National Forest and 10 were identified near the Inyo. For each forest, half of the post offices were randomly selected to be sampled: nine near the Sierra and five near the Inyo. The total number of post office boxes at each post office was obtained from the United States Postal Service website, and this was used to determine the proportion of post office boxes represented by each post office. 300 post office boxes were randomly selected for each forest so that the proportion from each post office was the same as its proportion of the total. For example, Mammoth Lakes, which has over 4000 post office boxes, was sent 201 surveys, while Lee Vining, which has less that 300 post office boxes, was sent only 12.

Surveys were collected between November 2018 and March 2019. Responses to the Global Warming's Six America's survey were coded according to Maibach et al. (2011a). All analyses were done using R version 3.5.1 (R core team 2018). All figures were produced using 'ggplot2' (Wickham 2016).

Survey Respondents

A total of 194 surveys were returned, 57 from mailing addresses and 47 from post office boxes near the Inyo National Forest, and 56 from mailing addresses and 34 from post office boxes near the Sierra National Forest. This represents an overall response rate of 16.2%. The respondents were primarily older and white. Though the

ages of respondents ranged from 14 to 90, the mean and median ages were 57.6 and

60 years respectively (Figure 3-1). 139 of the respondents (71.6%) listed their

ethnicity as white; the next largest response group was 'Decline to State' at 26

(13.4%). Respondents were more evenly divided in terms of gender, with 90 (46.4%)

responding 'Female,' 85 (43.8%) responding 'Male,' and 19 (9.8%) responding

'Decline to State' (Figure 3-2).

More than 40% of the respondents had lived near the Forest for more than 30

years, while only 11 individuals (5.7%) had lived there 2 years or less. The remaining

responses were more evenly distributed among the middle three categories, with 34

(17.5%), 36 (18.6%), and 28 (14.4%) individuals reporting 3-10 years, 11-20 year,

and 21-30 years, respectively. More than 90% of respondents indicated the survey had

come to their primary address (Figure 3-3). Respondents represented all education

levels, though only two (1%) and ten (5.2%) respondents reported 'Some High

School' or 'High School' respectively. Forty-eight (24.7%) had attended 'Some

College' and the remaining 128 (66%) had at least an Associate's degree and 51

(26.3%) reported holding a postgraduate degree (Figure 3-4). In terms of political

ideology, both sides of the political spectrum were represented. On the seven-point

scale, the mean and median political ideology were 4.1 and 4, the center of the scale.

Moreover, with 42 responses (21.6%), 4 was also the most common response,

meaning many participants view themselves as neither liberal nor conservative

politically (Figure 3-4).

Chi-square tests were used to compare the populations of respondents between the two Forests and address types in terms of gender, ethnicity, level of education, and length of time living near the Forest. Differences were not significant for any of these factors at the level of $p = 0.05$. Age and political ideology were compared between these populations using an ANOVA. Age did not differ between forests ($p = 0.6872$) or address type ($p = 0.8884$), but political ideology did, with respondents from the Sierra National Forest ($p < 0.001$) and from mailing addresses ($p = 0.01995$) reporting significantly more conservative views (Figure 3-5).

Despite the overall similarity in the demographic characteristics of these populations, their political attitudes are quite different. Respondents from the two Forests did not differ in terms of age, gender, ethnicity, education level, or how long they had lived near the Forest, nor did these attributes differ among respondents who received mail at their home address compared to those that had post office boxes. However, political ideology differed significantly along both of these dimensions: residents near the Sierra National Forest reported significantly more conservative views than those near the Inyo National Forest, and respondents with post office boxes reported significantly more liberal views than those with mailing addresses in both Forests (Figure 3-5).

Cultural Types

Participants' level of agreement across the three statements corresponding to each cultural type were summed creating a composite score for that type. Some

respondents provided no response to one or more of the statements. For each participant, composite scores for each cultural type were only reported if all three statements had been answered. As a result, 188 individuals (96.9%) could be assessed on their level of individualism, 192 (99%) on their level of egalitarianism, 189 (97.4%) on their level of hierarchism, and 193 (99.5%) on their level of fatalism. The cultural type with the highest composite score was assigned as a respondent's dominant cultural type. For example, if an individual's composite scores were 19, 4, 10, and 6 for individualism, egalitarianism, hierarchism, and fatalism respectively that, that respondent was considered an individualist. After tied composite scores were removed, 157 respondents (80.9%) could be classified according to their dominant cultural type. Of these, 82% were Individualists (71 respondents) or Egalitarians (58 respondents).

Mean composite scores for each of the four cultural types were compared between Forests and address types using a two-way ANOVA (Table 3-1). Adherence to the four cultural types did not significantly differ between address types (at $p = 0.05$), but did differ between forests. Levels of individualism and hierarchism were higher in the Sierra National Forest, while levels of egalitarianism were higher in the Inyo National Forest (Figure 3-6a). Similarly, Egalitarian was the dominant cultural type for 43 respondents (43%) in the Inyo National Forest, but only for 15 (17.9%) in the Sierra (Figure 3-6b).

Consistent with the expectations of cultural theory, respondents' political ideology was related to their level of agreement with the three 'strong' cultural types: individualism, hierarchism, and egalitarianism. The effect of each of the four cultural types on political ideology was assessed using simple linear regression. More conservative views were associated with higher levels of individualism ($p < 0.001$) and hierarchism ($p = 0.01762$) and lower levels of egalitarianism ($p < 0.001$). When address type and Forest were included as predictor variables, the relationship between political ideology and levels of individualism and egalitarianism remained highly significant, while that with hierarchism did not. Controlling for differences in cultural type, living near the Sierra National Forest was still related to identifying as more conservative ($p = 0.0196$).

Global Warming's Six Americas

Responses to the 15-question survey were coded and classified into the six categories of attitudes towards climate change following Maibach et al. (2011a). For respondents who declined to answer three or fewer questions, the missing answers were replaced with the mean answer from their Forest and address type. Respondents who skipped more than three questions were removed from the analysis. This left 184 (94.8%) of the original respondents.

During the coding process it was discovered that in transcribing Question 4 an error was made, so that this question had to be removed from our initial analysis. The question, which should have read, "How much do you think global warming will

harm you personally?" was mistakenly stated as " "How much do you think about global warming?" Question 4 had five possible answers: (1) "Not at all," (2) "Only a little," (3) "A moderate amount," (4) "A great deal," and (5) "Don't know." Not including this question compromised the ability of the discriminant analysis used to correctly classify respondents. To address this problem, the discriminant analysis was done five times, assuming each time that all of the respondents had answered Question 4 the same way. This allowed us to examine all the possible ways respondents could have been classified and assess the sensitivity of the classification to the possible answers to Question 4. I compared the distributions of the respondents in the six categories based on the answer to Question 4 using a Chi-square test. Regardless of the answer to Question 4, the greatest number of respondents were classified as "Alarmed" followed by "Concerned" (Figure 3-7). However, the distributions across the six categories differed (χ^2 = 38.621, p = 0.007429), which was driven by the distribution associated with answer "Not at all."[2]

Examining the classification of individual respondents across all five answers revealed that the classification of 132 participants did not change according to the answer to Question 4. The distribution of these respondents across the six categories is shown in Figure 3-8. While all six categories are represented, respondents belonging to the more extreme categories were less likely to change in response to the

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[2] A Chi-square test of the remaining four possible answers showed no differences between the distributions (χ^2 = 18.102, p = 0.2573).

answer to Question 4. For the 'Alarmed' category, 65 respondents out of a maximum of 85, did not change. Similarly, 18 of the maximum of 19 respondents classified as 'Dismissive' were in this category regardless of the answer to Question 4. In contrast, only 12 individuals were classified as 'Cautious' for all answers, compared to a maximum of 32 individuals, and only six individuals were always classified as 'Disengaged', compared to maximum of 23. Of the 52 individuals whose classification would have changed depending on their answer to Question 4, only 4 were classified in the most extreme categories for more than one answer (Figure 3-9).

Despite the greater chance of respondents from the less extreme categories to be classified differently in response to the answer to Question 4, the overall distribution differed only marginally from those of four of the five possible answers ($\chi^2 = 31.048$, $p = 0.05456$)[3]. This subset of individuals whose classification was consistent for all possible answers to Question 4 (the "no change" group) combined with the classifications for each of the five possible answers created six cases that were considered in further analyses. I compared the distribution of individuals into the six categories between the two Forests and address types, as well as with the national survey. I also analyzed the relationship between an individual's classification and their political ideology, demographic characteristics, and cultural type.

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[3] That is comparing the distributions omitting that for the answer "Not at all," which differed from the others.

For all six cases, the distribution of respondents into the categories was compared to the results of the national survey using a Chi-square test (Yale Program on Climate Change 2019). The distributions did not differ ($p > 0.05$) from the national survey for the answers "Not at all," "Only a little," or "A moderate amount." However, for the answers "A great deal" and "Don't Know" as well as for the no change group the distributions were significantly different, with a larger proportion of individuals classified as "Alarmed" for the "A great deal" answer and the no change group, and larger proportion classified as "Disengaged" for the "Don't Know" answer (Table 3-2).

The distribution of respondents into the six categories differed between Forests and address types, consistent with the higher levels of conservatism, individualism, and hierarchism observed in the Sierra National Forest. A majority of respondents who lived near the Inyo National Forest were classified as "Alarmed" and "Concerned," while the distributions for the Sierra National Forest were less skewed. Respondents with post office boxes were classified as "Alarmed" at greater rates in both Forests, and the highest number of respondents classified as "Doubtful" or "Dismissive" were from mailing addresses near the Sierra Forest (Figure 3-10). While the exact number of responses varied with different responses to Question 4, the overall patterns and significant differences between the four populations remained the same (Table 3-3). Compared with the national survey respondents, the distribution of responses in the Inyo National Forest differed for four of the six cases,

all except the answers "Not at all" and "Only a little." In all of the cases where the distributions differed, more respondents were classified as 'Alarmed' or 'Concerned' and fewer as 'Doubtful' or 'Dismissive' than would be expected based on the national distribution of responses. For the Sierra National Forest, the distribution differed from the national responses in three cases: the no change case and the answers "A great deal" and "Don't Know." For the no change case and the answer "A great deal" a higher proportion of respondents were classified as 'Alarmed' compared to the national survey, but more were also classified as 'Doubtful' and Dismissive.' For the answer "Don't Know," smaller proportions were classified as 'Alarmed' and 'Concerned' and higher proportions as 'Doubtful' and 'Dismissive' compared to the national survey (Table 3-4).

Relationship with Cultural Theory

Generalized Linear Models with a multinomial error distribution and a logit link function were used to assess the influence of an individual's adherence to the different cultural types on their classification in the Global Warming's Six America's survey. The association was tested for each of the five answers to Question 4, as well as on the subset of respondents whose classification did not change. In all six cases, an individual's level of egalitarianism was highly significant ($p < 0.001$) in predicting their classification. The level of individualism was also an important predictor, and was highly significant in three cases, for Question 4 answers "Only a little," "A moderate amount," and "A great deal" and significant ($p < 0.01$) for the other three

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cases. Again, the overall patterns were consistent across the six cases, with an individual's level of egalitarianism and individualism strongly related to their beliefs about climate change.

When demographic factors were added as predictors, the effect of individualism disappeared but that of egalitarianism remained. Age, gender, education, residence time, Forest, address type, political ideology and level of agreement with the four cultural types were included in the model. Because an overwhelming majority of respondents were white, ethnicity was excluded as a predictor. For all six cases (the five possible answers and the no change group), address type, level of egalitarianism, and political ideology were significant ($p < 0.05$) or highly significant ($p < 0.001$) predictors (Table 3-5). For the no change group, level of fatalism was also marginally significant ($p = 0.06179$). For the answers "Not at all," "Only a little," "A moderate amount," and "Don't Know," gender was significant ($p < 0.05$) or marginally significant ($p < 0.1$), with the Decline to State group more evenly split between all six categories compared to male and female respondents, which both had higher proportions classified 'Alarmed' and 'Concerned.' For the answer "Don't Know" and the no change group, residence time, specifically living near the forest 21-30 years, was marginally significant.

This strong relationship between an individual's level of egalitarianism and their classification in the Global Warming's Six America's survey was also apparent when looking at dominant cultural types. All six categories were represented among

99

the individualists and the hierarchs (though there were fewer hierarchs overall), but all the egalitarians were classified as 'Alarmed,' 'Concerned,' or 'Cautious,' for all five answers to question 4 and the no change case (Figure 3-11). While some Individualists are greatly concerned about climate change, as many are 'Dismissive,' 'Doubtful,' or 'Disengaged,' no Egalitarians fell into these three categories. [4]

Discussion

Despite the demographic similarities between the two Forests, their populations do differ in important ways. Near the Inyo National Forest, the overwhelming majority of residents believe climate change is happening and are concerned about its effects, while near the Sierra National Forest attitudes are more evenly mixed. The attitudes held by residents near these forests also differed from those of residents nationally for three and four of the six cases in the Sierra and Inyo Forests, respectively. In the Inyo this was driven by larger proportion of respondents being 'Alarmed' and 'Concerned' and fewer being 'Dismissive' and 'Doubtful' for all four cases. In the Sierra National Forest this was pattern for the answer "A great deal," but the opposite was true for the answer 'Don't Know.' For the no change group, the proportion of 'Alarmed,' 'Dismissive,' and 'Doubtful' respondents was higher, but 'Concerned was much lower. Thus, in the Inyo National Forest, local residents are at least as concerned about climate change as would be expected from

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[4] Only 4 respondents had Fatalism as their dominant cultural type.

the national survey, and probably more.[5] In contrast, residents near the Sierra

National Forest may be less concerned about climate change than the nation as a

whole. Forest managers working with the local community near the Sierra would be

more likely to encounter individuals who hold 'Dismissive' or 'Doubtful' attitudes.

These differences in climate change attitudes are reflective of underlying

belief systems. As might be expected, the more climate doubtful respondents in the

Sierra are more conservative politically, consistent with their lower levels of

egalitarianism and higher levels of individualism and hierarchism. However, the

observations utilizing cultural theory offer two helpful points. The higher levels of

individualism apparent in the Sierra National Forest suggest that framing

management actions in ways that appeal to individualist values may increase support,

or at least reduce opposition to these measures. Even individuals who deny climate

change is a threat may not oppose actions to mitigate or adapt to this threat (Jones

2011). Second, respondents holding egalitarian views are already concerned about

addressing climate change, so it is not necessary to convince them. While appeals to

equity or responsibility to the global community are more likely to be constructive in

the Inyo National Forest, even in this situation, they are unlikely to convince the

residents who are mostly likely to oppose actions. At the same time, individualists do

not universally reject the reality or seriousness of climate change. Engaging with

individualist values is more likely to broaden support. Indeed, institutional structures

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[5] This pattern was consistent even where it was not significant.

that allow space for voices representing all of the cultural types to be heard are most likely to result in cooperative behavior needed for climate change mitigation and adaptation (Verweij et al. 2006, McNeeley and Lazrus 2014).

As individual Forests move through the process of developing their LMPs, accounting for differences in attitudes among local residents and framing their desired actions in ways that appeal to these attitudes is crucial. Relying on national surveys may result in unexpected opposition at the local level, or conversely, prevent Forests from taking advantage of local concern about climate change. Similarly, public comments, which tend to typify extreme views, may mask widespread support for policies from the less engaged. At the same time, USFS policies at the national level need to account for how local residents' views differ from or are consistent with other USFS stakeholders, including non-local residents and interest groups.

Table 3-1. Two-way ANOVA comparing composite level of agreement with each Cultural Type by Forest and Address type. Participants that provided responses for all three questions associated with a cultural type were included for that type, resulting in $n = 188$, 192, 189, and 193 for individualism, egalitarianism, hierarchism, and fatalism, respectively.

Cultural Type	Factor	Degrees of Freedom	F-value	*p*-value
Individualism	Forest	1	**11.3205**	**<0.001**
	Address Type	1	3.2499	0.0730574
Egalitarianism	Forest	1	**6.6473**	**0.01069**
	Address Type	1	1.2045	0.27383
Hierarchism	Forest	1	**14.7381**	**<0.001**
	Address Type	1	1.3507	0.2466488
Fatalism	Forest	1	0.1388	0.7099
	Address Type	1	0.1274	0.7215

Table 3-2. Pearson's chi-squared tests with simulated p-values comparing the distribution of respondents in the the six categories from each of the six cases (5 possible answers to question 4 and the no change group) with that of the national survey (Yale Program on Climate Change 2019). For each of the 5 answers, $n = 184$, and for the no change group $n = 132$.

Case	χ^2	p-value
"Not at All"	6.4678	0.2729
"Only a little"	5.3082	0.3863
"A moderate amount"	10.218	0.07096
"A great deal"	**23.321**	**0.0004998**
"Don't Know"	**16.04**	**0.005997**
No Change	**19.542**	**0.001999**

Table 3-3. Pearson's Chi-squared tests with simulated *p*-values comparing the distributions of respondents in the the six categories between forests and address types for each of the six cases. For each of the 5 answers, $n = 184$, and for the no change group $n = 132$.

Case	Factor	χ^2	*p*-value
"Not at All"	Forest	**19.608**	**0.0004998**
	Address Type	**28.563**	**0.0004998**
	Forest × Address Type	**18.75**	**0.000995**
"Only a little"	Forest	**20.62**	**0.0004998**
	Address Type	**27.543**	**0.0004998**
	Forest × Address Type	**18.496**	**0.001499**
"A moderate amount"	Forest	**22.075**	**0.0009995**
	Address Type	**27.684**	**0.0004998**
	Forest × Address Type	**18.101**	**0.0009995**
"A great deal"	Forest	**21.615**	**0.0004998**
	Address Type	**23.794**	**0.0004998**
	Forest × Address Type	**15.54**	**0.004498**
"Don't Know"	Forest	**22.101**	**0.000995**
	Address Type	**27.101**	**0.0004998**
	Forest × Address Type	**16.603**	**0.003498**
No Change	Forest	**22.481**	**0.0004998**
	Address Type	**25.196**	**0.0004998**
	Forest × Address Type	**14.876**	**0.004998**

Table 3-4. Pearson's chi-squared tests with simulated p-values comparing the distribution of respondents in the the six categories for each Forest and each of the six cases (5 possible answers to question 4 and the no change group) with that of the national survey (Yale Program on Climate Change 2019). For each of the 5 answers, $n = 100$ and 84 for the Inyo and Sierra National Forests, respectively, and for the no change group $n = 71$ for the Inyo National Forest and 61 for the Sierra National Forest.

| Forest	Case	χ^2	p-value
Inyo	"Not at All"	7.4659	0.1894
	"Only a little"	8.3127	0.1334
	"A moderate amount"	**12.568**	**0.02499**
	"A great deal"	**18.528**	**0.002499**
	"Don't Know"	**16.579**	**0.003998**
	No Change	**14.124**	**0.01299**
Sierra	"Not at All"	10.275	0.07246
	"Only a little"	8.4332	0.1259
	"A moderate amount"	9.5976	0.08696
	"A great deal"	**17.091**	**0.004498**
	"Don't Know"	**11.644**	**0.030989**
	No Change	**16.322**	**0.007496**

Table 3-5. P-values from Generalized Linear Model assessing effect of Forest, Address Type, levels of Egalitarianism, Individualism, Hierarchism, and Fatalism, Political Ideology, Gender, Age, and Residence Time on an individual respondents classification according to the Global Warming's Six America's survey for each of the possible answers to Question 4 ($n = 184$) and the no change group ($n = 132$).

| Factor	Case					
	"Not at all"	"Only a little"	"A moderate amount"	"A great deal"	Don't Know	No Change
Forest	0.61086	0.859421	0.859421	0.88131	0.730244	0.49483
Address Type	**<0.0001**	**0.000116**	**0.000116**	**0.000787**	**0.000114**	**0.00666**
Egalitarianism	**0.00228**	**0.003098**	**0.003098**	**0.21777**	**0.003810**	**0.00511**
Individualism	0.27066	0.245372	0.245372	0.439143	0.260973	0.55871
Hierarachism	0.15231	0.176192	0.176192	0.62283	0.242144	0.30222
Fatalism	0.24688	0.158282	0.158282	0.901716	0.165657	0.06179
Political Ideology	**<0.0001**	**0.000102**	**0.000102**	**<0.0001**	**0.000113**	**0.00140**
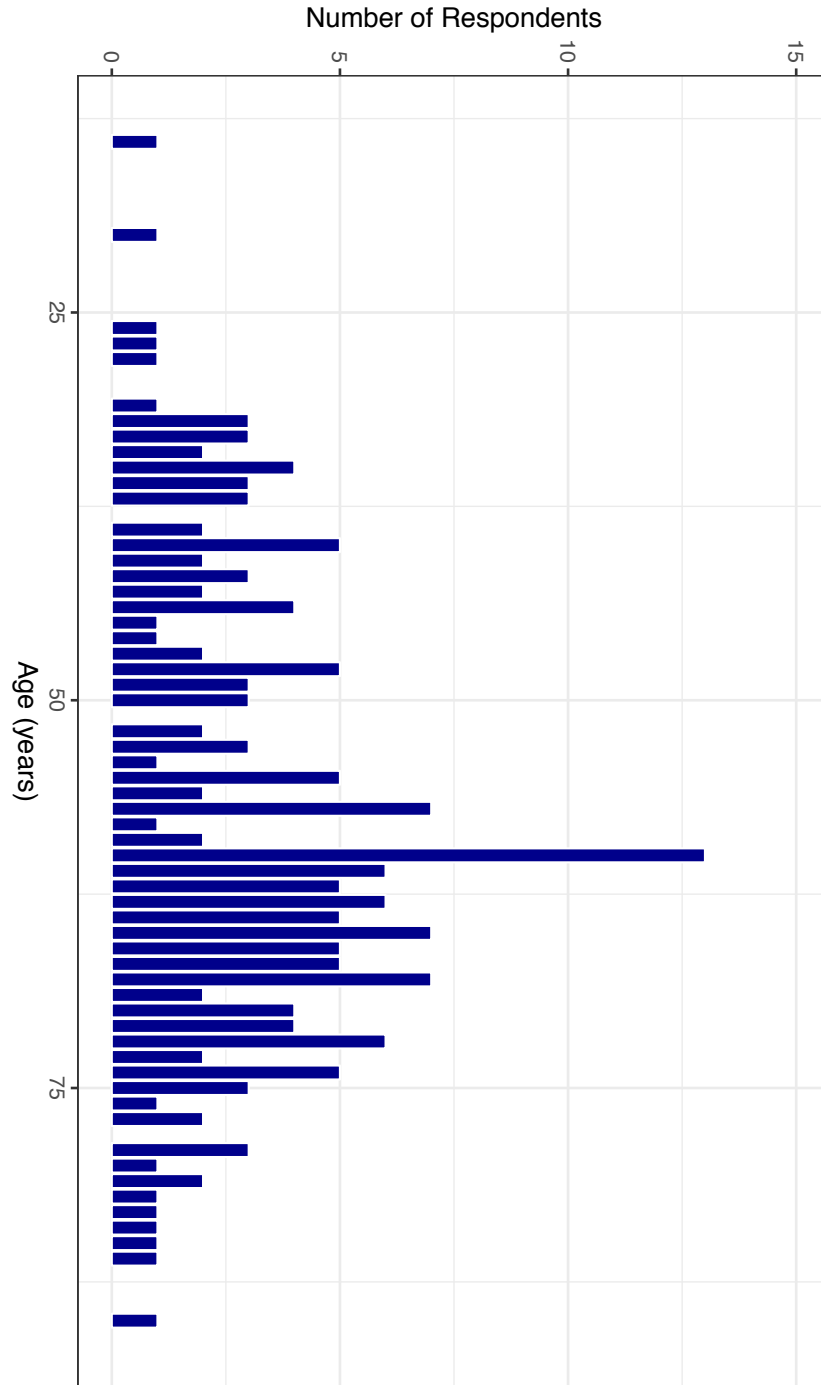
Figure 3-1. Age of survey respondents (*n* = 180).
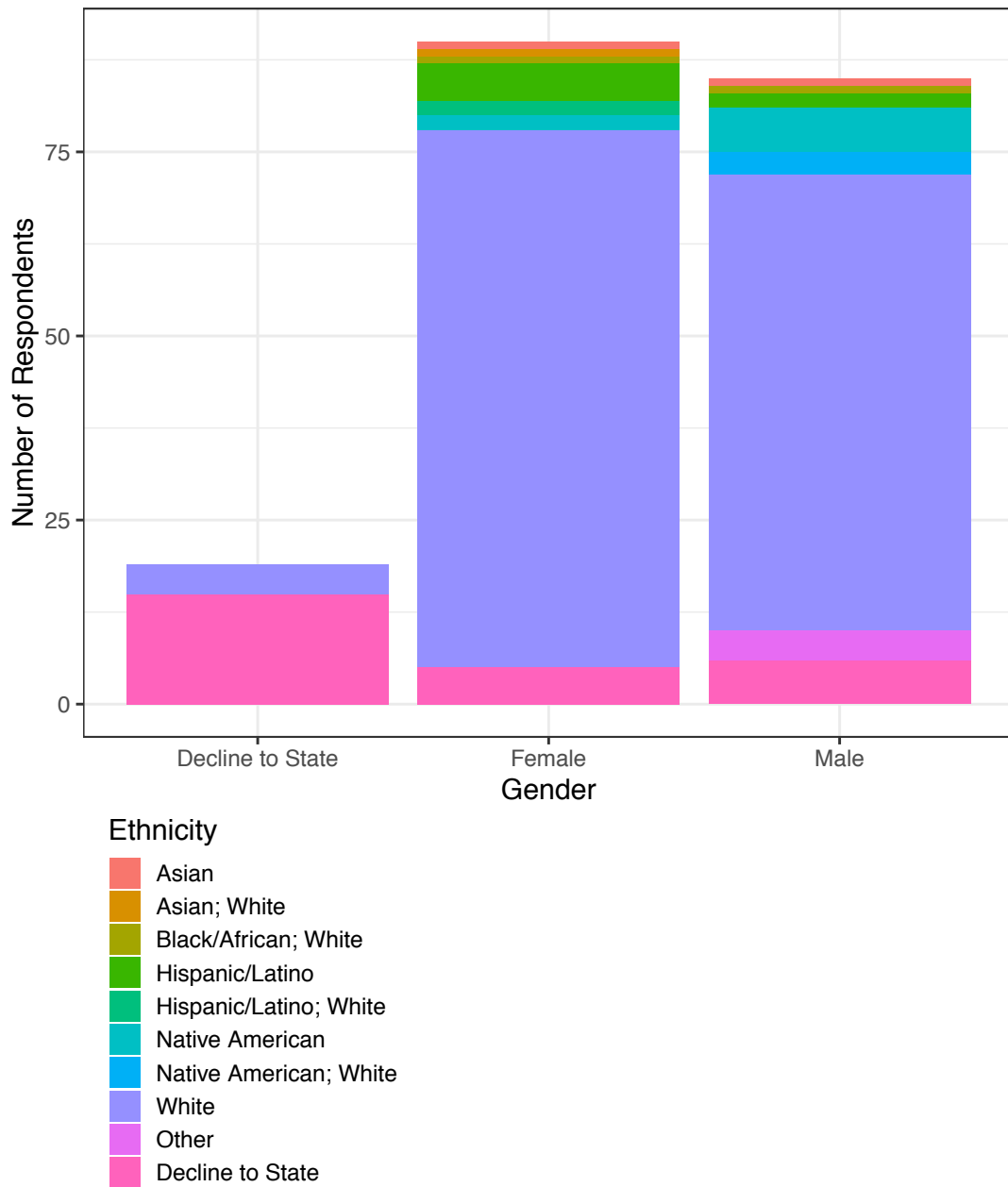
**Figure 3-2.** Gender and ethnicity of survey respondents (*n* = 194).
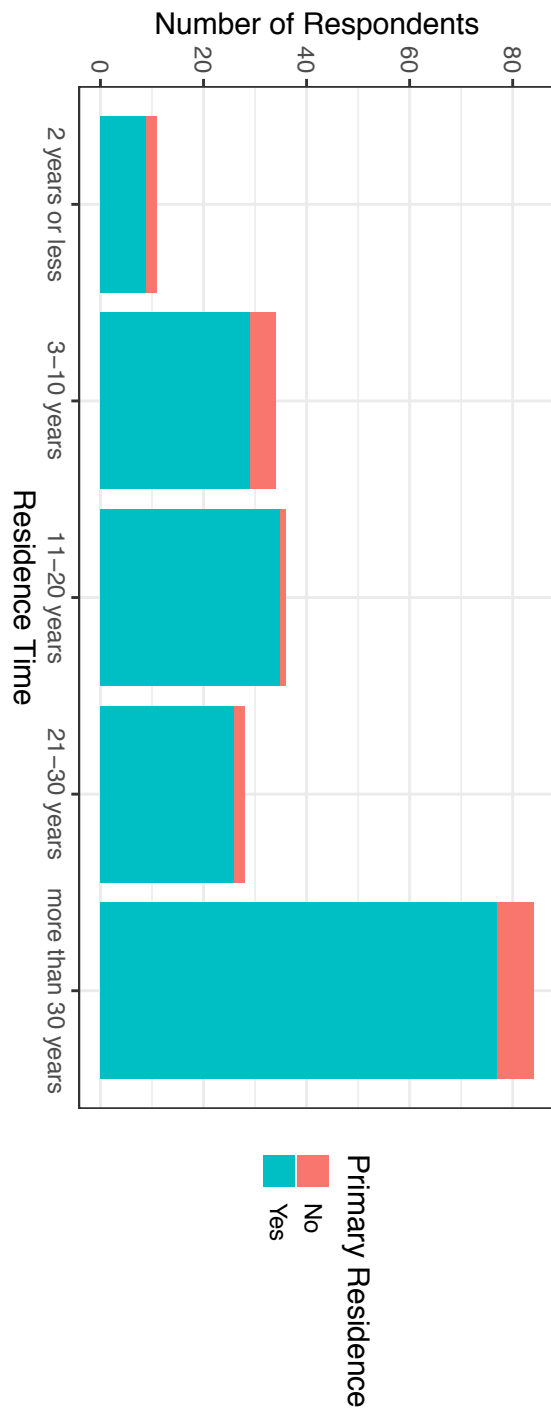
Figure 3-3. Number of years respondents have lived near the Forests, and whether the address that received the survey is their primary residence (*n* = 194).
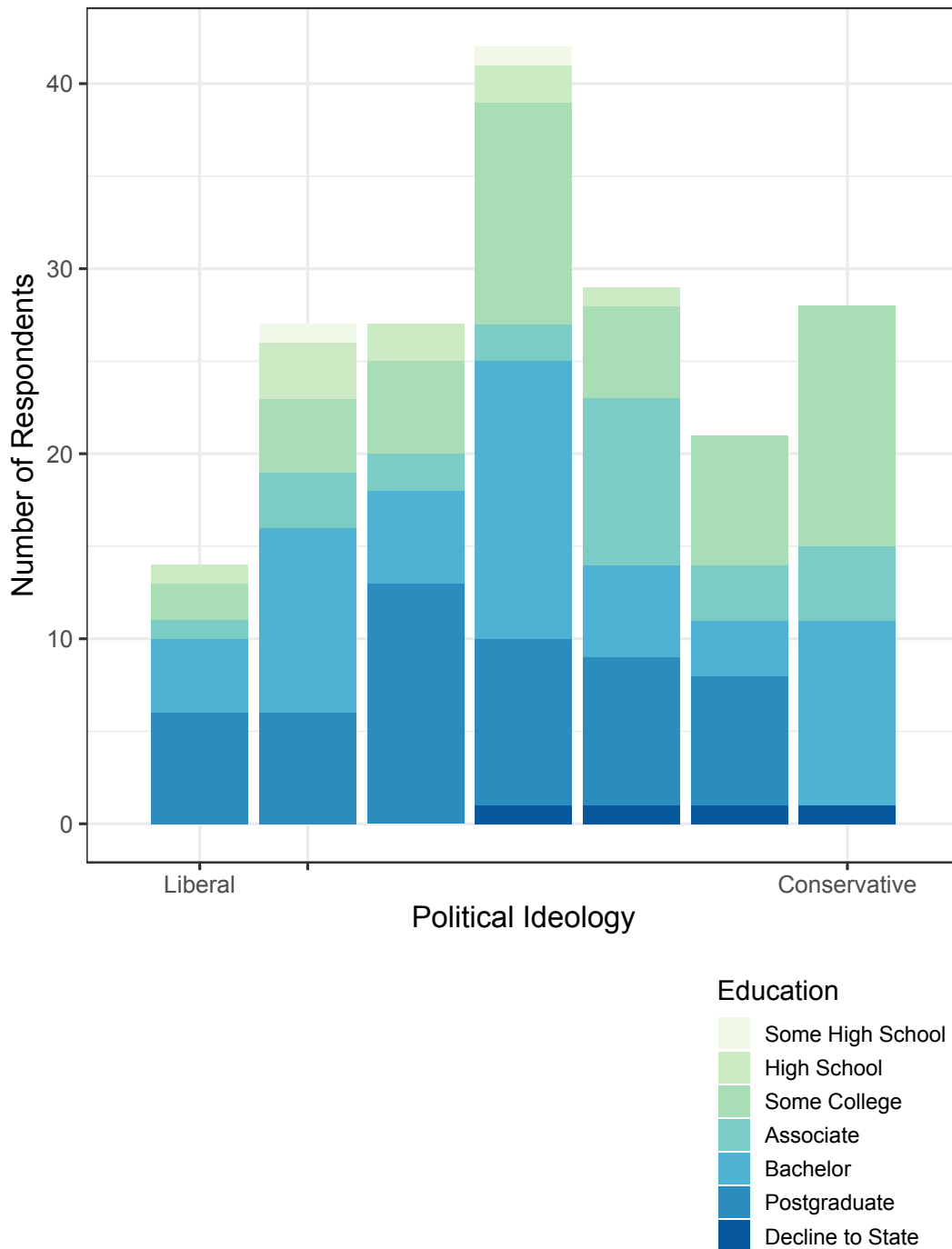
Figure 3-4. Political ideology and level of education of respondents. Respondents were asked to report their political ideology on a seven point scale, with one being liberal and seven conservative (*n* = 188).
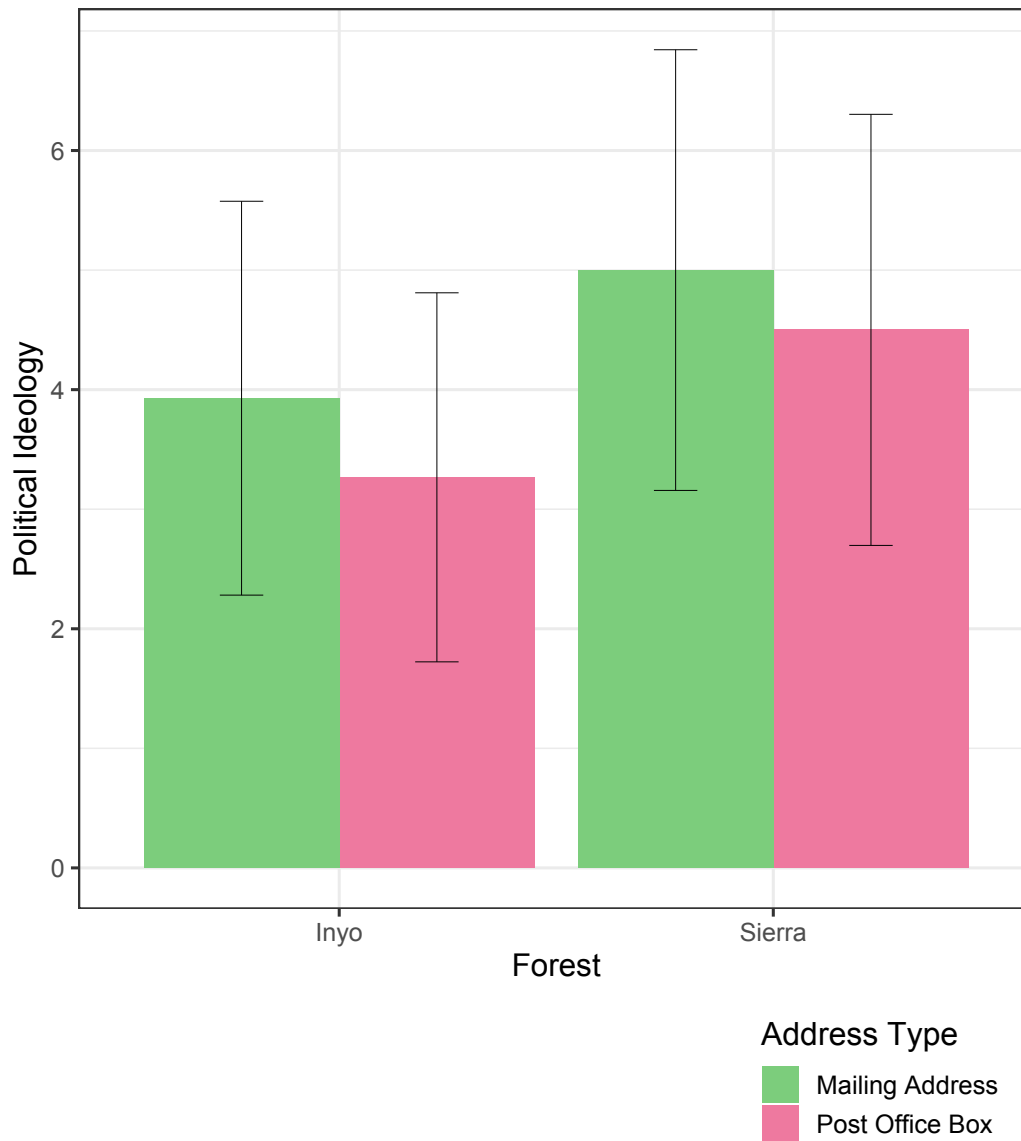
Figure 3-5. Political Ideology, on a seven point scale, by Forest and address type. Higher numbers correspond to a more conservative ideology. Error bars represent one standard deviation from the mean (*n* = 188).

a)

b)
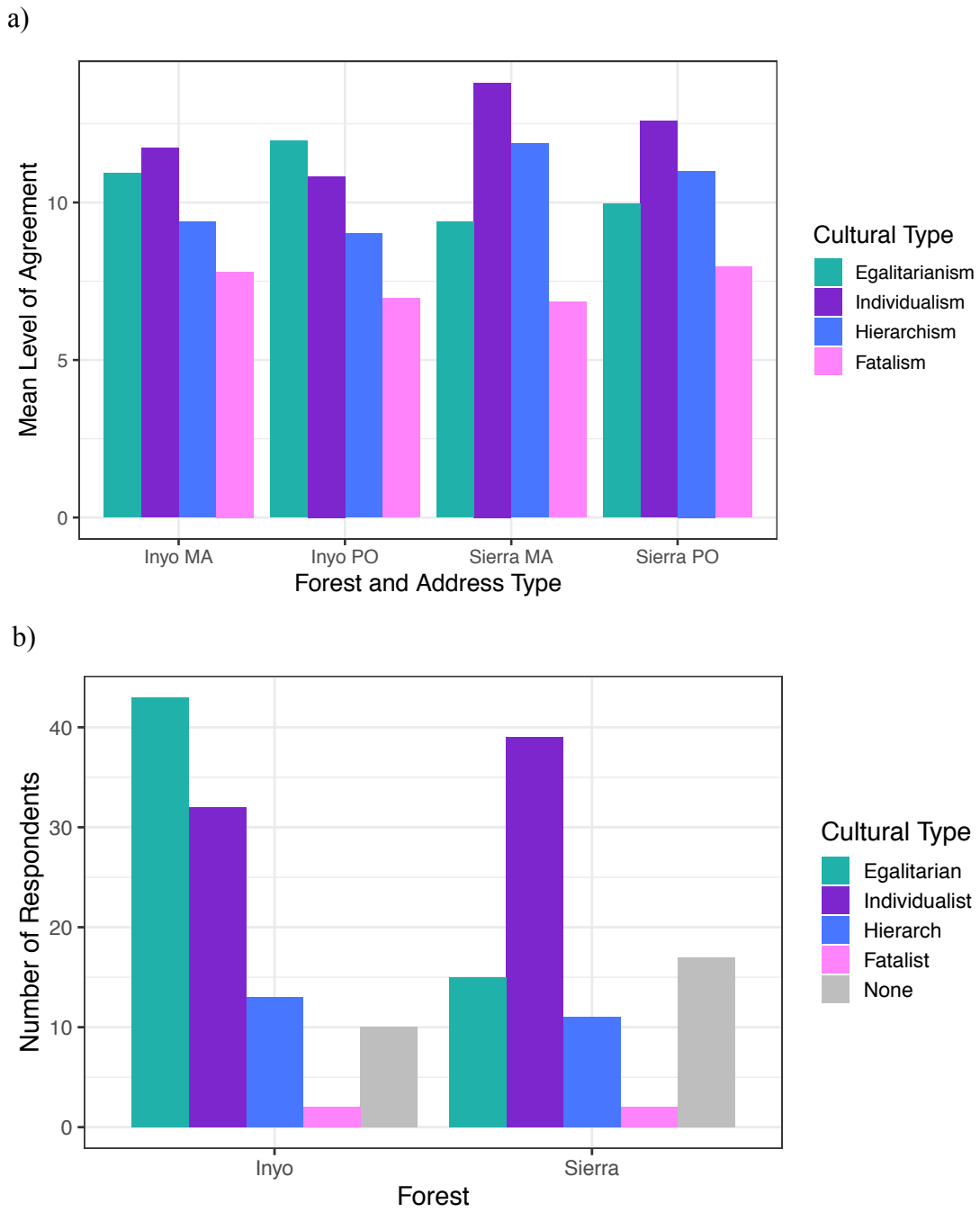
**Figure 3-6**. a) Mean composite scores for the level agreement with each of the four cultural types by Forest and address type (n = 192, 188, 189, and 193 for egalitarianism, individualism, hierarchism, and fatalism, respectively), and b) dominant cultural type by Forest (n = 194).
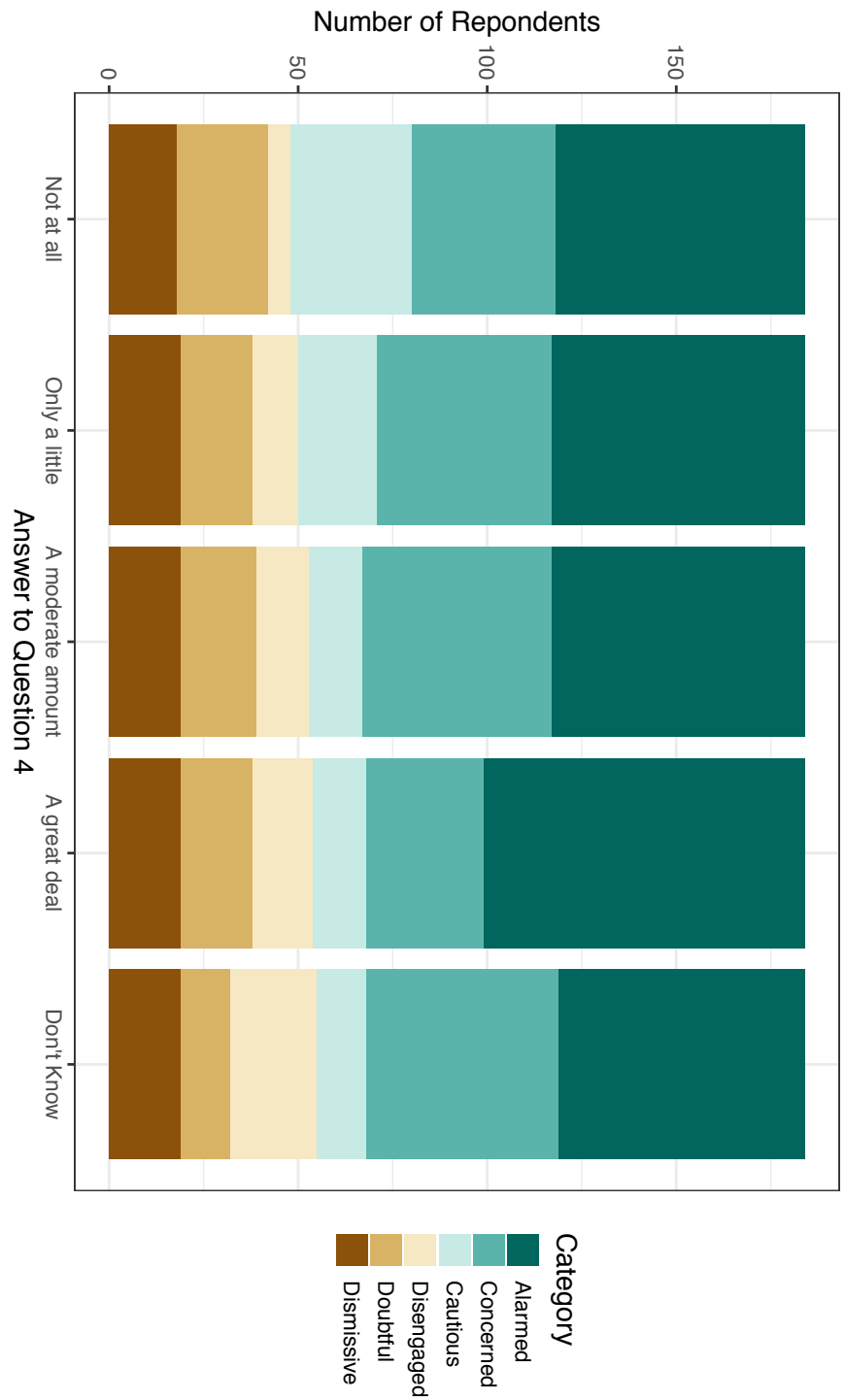
Figure 3-7. Results of discriminant analysis for each of the possible answers to Question 4 (*n* = 184).
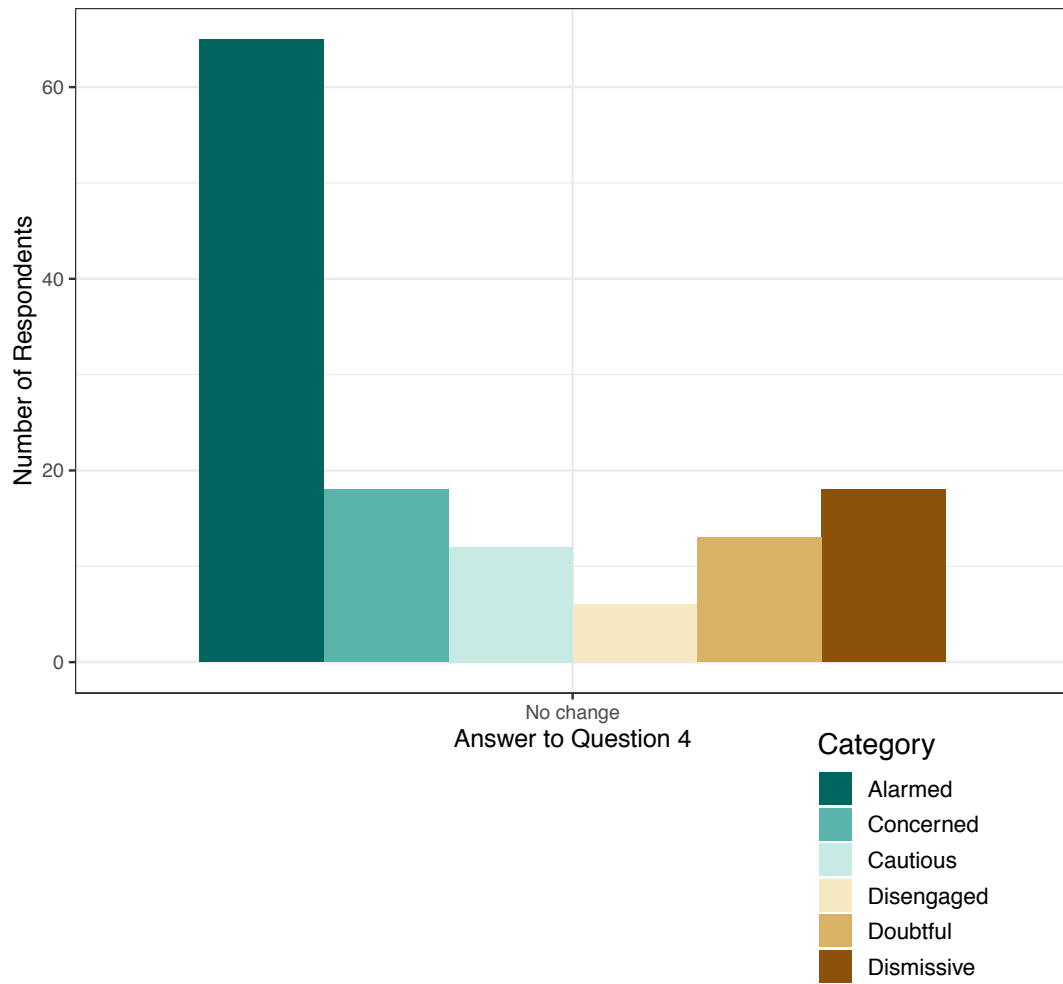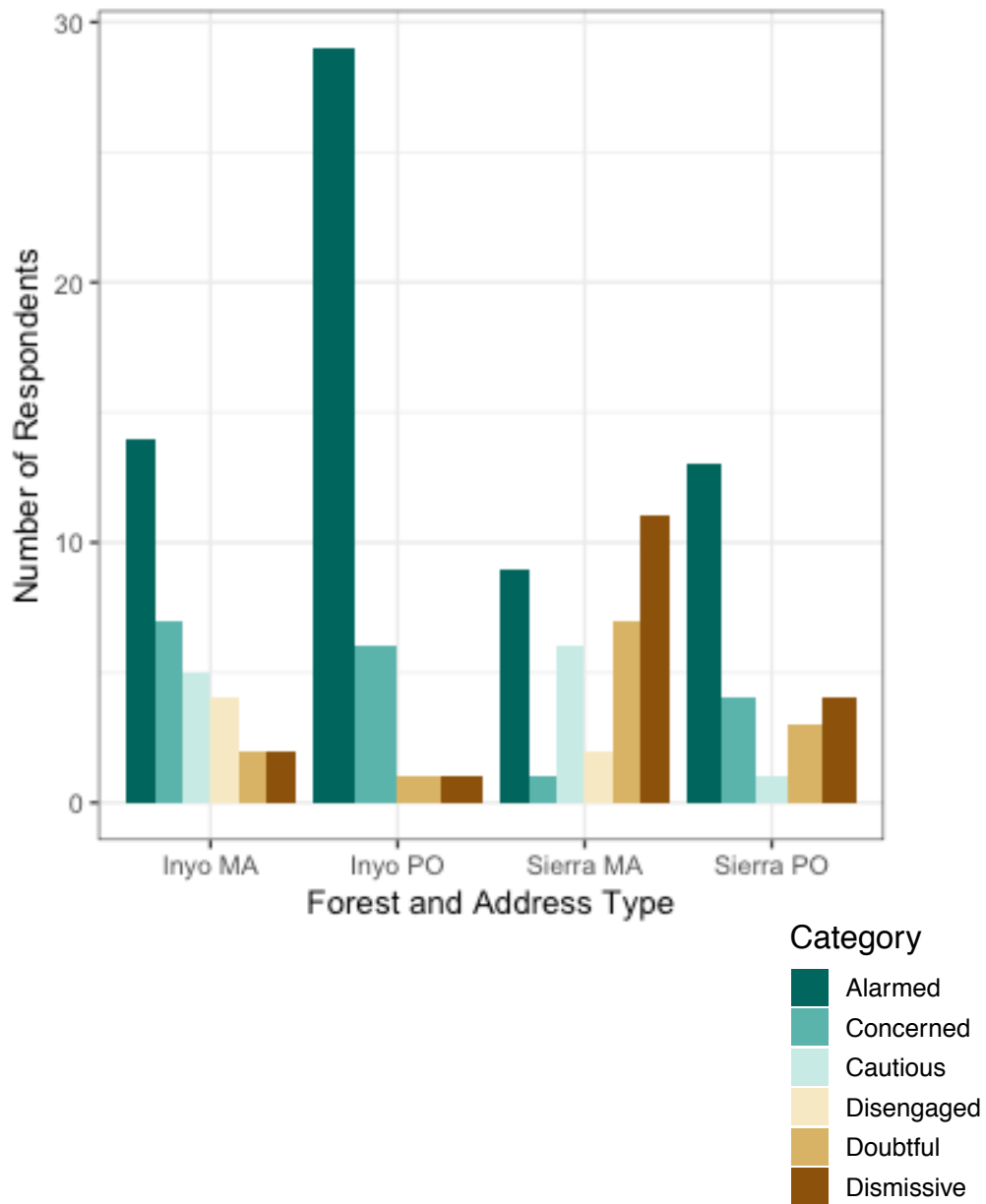
Figure 3-8. Distribution of respondents whose classification did not change with different answers to Question 4 (*n* = 132).
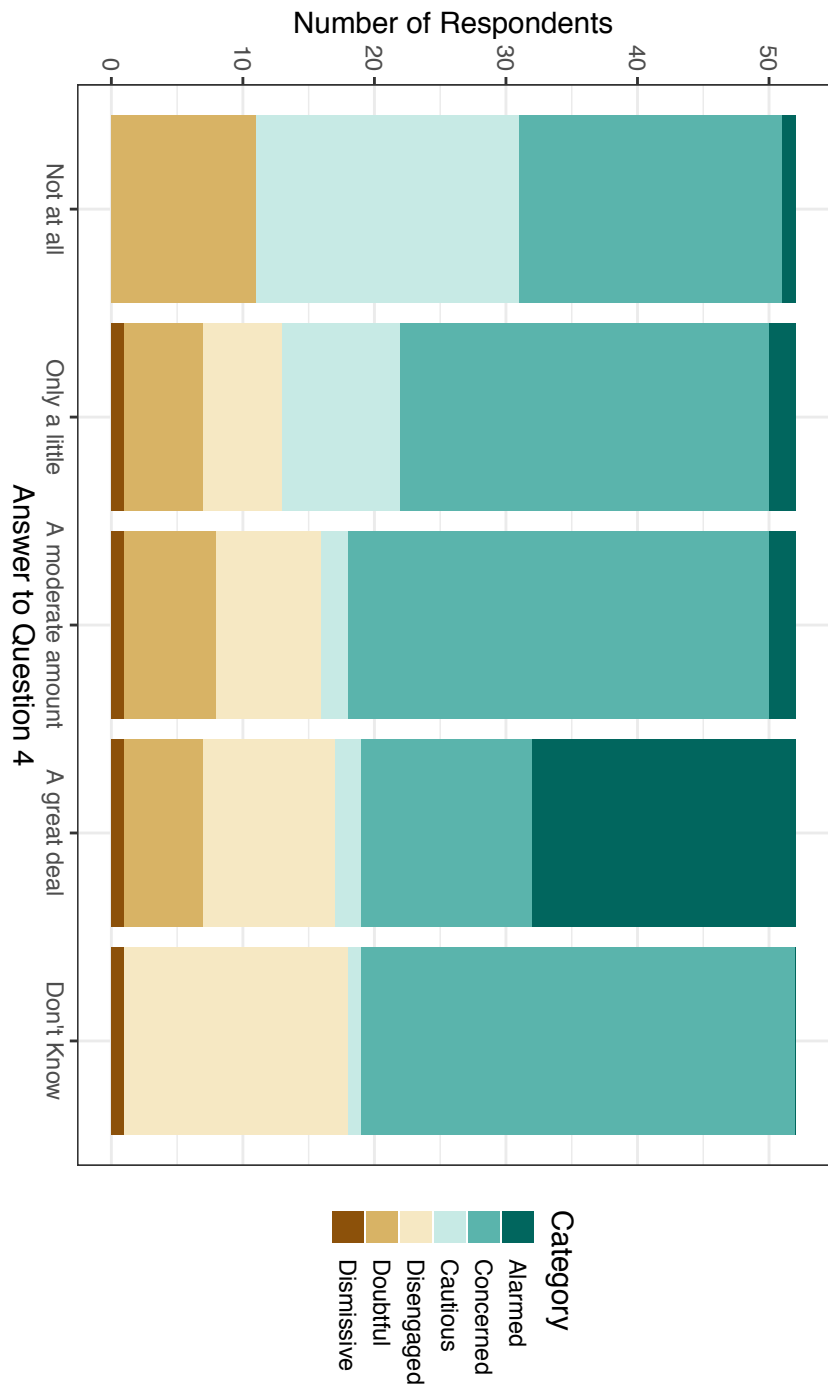
Figure 3-9. Classification of respondents that changed in response to question 4, for each possible answer (*n* = 52).

Figure 3-10. Respondents whose classification did not change in response to Question 4, by Forest and Address Type (*n* = 132).
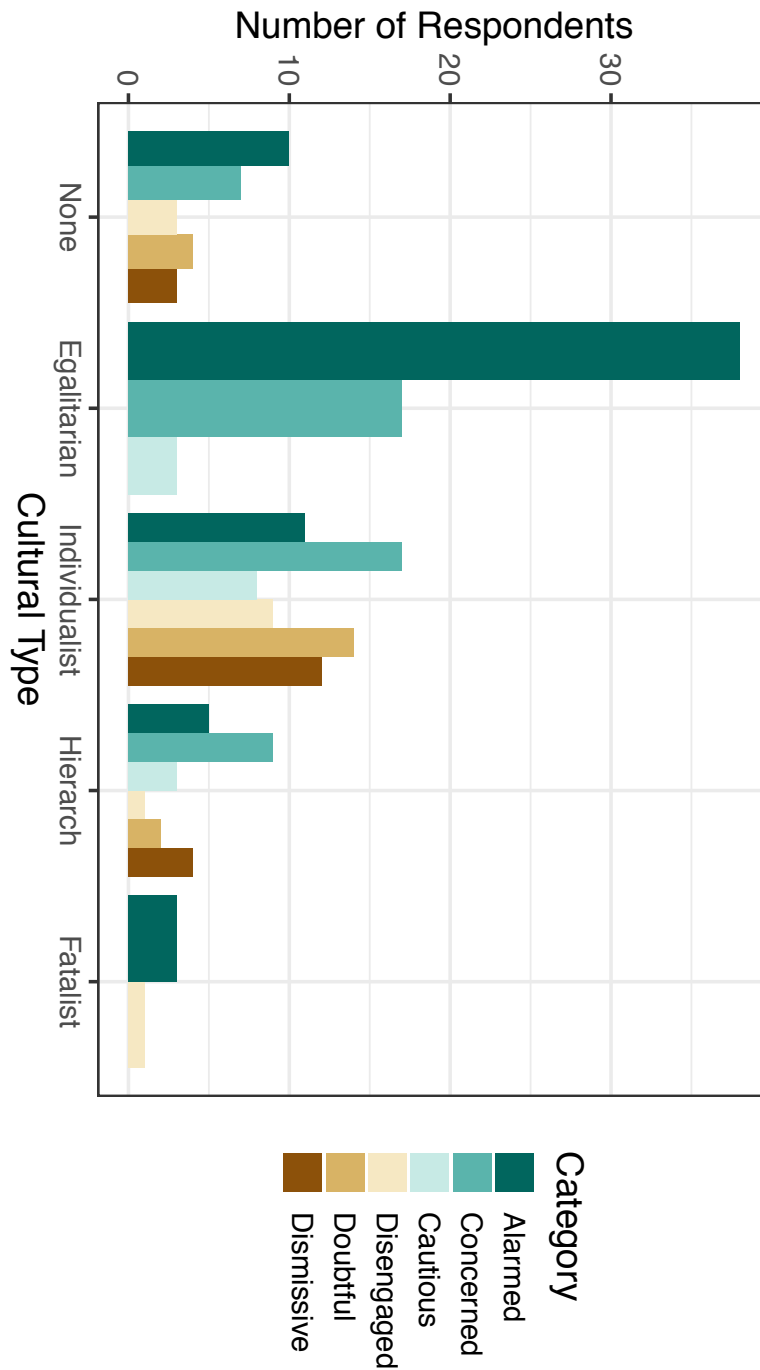
Figure 3-11. Respondents classified by dominant cultural type and Global Warming's Six America's category, as if they had answer "A moderate amount" to Question 4 (*n* = 184). While the number of respondents in individual columns changed slightly for the different cases, the overall patterns did not.

REFERENCES

Adams, H. D., C. H. Luce, D. D. Breshears, C. D. Allen, M. Weiler, V. C. Hale, A. Smith, and T. E. Huxman. 2012. Ecohydrological consequences of drought–and infestation–triggered tree die–off: insights and hypotheses. Ecohydrology **5**:145-159.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, and E. T. Hogg. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management **259**:660-684.

Anderegg, W. R., J. M. Kane, and L. D. Anderegg. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change **3**:30-36.

Ballew, M. T., A. Leiserowitz, C. Roser-Renouf, S. A. Rosenthal, J. E. Kotcher, J. R. Marlon, E. Lyon, M. H. Goldberg, and E. W. Maibach. 2019. Climate Change in the American Mind: Data, Tools, and Trends. Environment: Science and Policy for Sustainable Development **61**:4-18.

Berg, N., and A. Hall. 2015. Increased interannual precipitation extremes over California under climate change. Journal of Climate **28**:6324-6334.
Berg, N., and A. Hall. 2017. Anthropogenic warming impacts on California snowpack during drought. Geophysical Research Letters **44**:2511-2518.

Bierbaum, R., J. B. Smith, A. Lee, M. Blair, L. Carter, F. S. Chapin III, P. Fleming, S. Ruffo, M. Stults, and S. McNeeley. 2013. A comprehensive review of climate adaptation in the United States: more than before, but less than needed. Mitigation and adaptation strategies for global change **18**:361-406.

Biondi, F., and F. Qeadan. 2008. Inequality in paleorecords. Ecology **89**:1056-1067.

Breshears, D. D., T. E. Huxman, H. D. Adams, C. B. Zou, and J. E. Davison. 2008. Vegetation synchronously leans upslope as climate warms. Proceedings of the National Academy of Sciences **105**:11591-11592.

Borick, C.P., 2010. American public opinion and climate change. Pages 24-57 *in Greenhouse governance: addressing climate change in America.* Rabe, B.G., editor. Brookings Institute Press, Wasthington, D.C.

Buechling, A., P. H. Martin, and C. D. Canham. 2017. Climate and competition effects on tree growth in Rocky Mountain forests. Journal of Ecology **105**:1636-1647.

Bunn, A. G. 2008. A dendrochronology program library in R (dplR). Dendrochronologia **26**:115-124.

Bunn, A. G. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia **28**:251-258.

Carroll, C. J., A. K. Knapp, and P. H. Martin. 2017. Dominant tree species of the Colorado Rockies have divergent physiological and morphological responses to warming. Forest Ecology and Management **402**:234-240.

Chevin, L. M., S. Collins, and F. Lefèvre. 2013. Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. Functional Ecology **27**:967-979.

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A.J. Weaver and M. Wehner, 2013: Long-term climate change: projections, commitments and irreversibility. Pages 1039-1136 *in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley, editors. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Cubasch, U., D. Wuebbles, D. Chen, M.C. Facchini, D. Frame, N. Mahowald, and J.-G. Winther, 2013: Introduction. Pages 119-158 *in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley, editors. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Das, A. J., N. L. Stephenson, A. Flint, T. Das, and P. J. Van Mantgem. 2013. Climatic correlates of tree mortality in water-and energy-limited forests. PloS one **8**:e69917.

DeRose, R. J., J. D. Shaw, and J. N.Long. 2015. Spatiotemporal Patterns of Ring-width Variability in the Northern Interior West. Wasatch Dendroclimatology Research. Paper 8. https://digitalcommons.usu.edu/wadr/8.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Sciences **112**:3931-3936.

Dolanc, C. R., H. D. Safford, J. H. Thorne, and S. Z. Dobrowski. 2014. Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s. Ecosphere **5**:art101.

Dolanc, C. R., J. H. Thorne, and H. D. Safford. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. Global Ecology and Biogeography **22**:264-276.

Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species adapt to climate change. Global change biology **21**:3062-3073.

Duursma, R. A. 2015. Plantecophys-an R package for analysing and modelling leaf gas exchange data. PloS one **10**.

Farquhar, G. D., S. v. von Caemmerer, and J. A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta **149**:78-90.

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. Forest Ecology and Management **432**:164-178.

Fotelli, M. N., E. Korakaki, S. A. Paparrizos, K. Radoglou, T. Awada, and A. Matzarakis. 2019. Environmental Controls on the Seasonal Variation in Gas Exchange and Water Balance in a Near-Coastal Mediterranean Pinus halepensis Forest. Forests **10**:313.

Friedman, J. H. 1984. A variable span smoother. Stanford Univ CA Lab for Computational Statistics.

Gebregeorgis, E. G., I. Robertson, M. Koprowski, L. Zhou, P. Gao, A. Williams, Z. Eshetu, and T. Wils. 2020. Historical droughts recorded in extended Juniperus procera ring-width chronologies from the Ethiopian Highlands. International journal of biometeorology:1-15.

Google Maps. https://www.google.com/maps/@37.4674649,-120.2705946,8z. Accessed June 8, 2020.

Griffin, D., and K. J. Anchukaitis. 2014. How unusual is the 2012–2014 California drought? Geophysical Research Letters **41**:9017-9023.

Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA.

Grulke, N. 2010. Plasticity in physiological traits in conifers: implications for response to climate change in the western US. Environmental Pollution **158**:2032-2042.

Guarín, A., and A. H. Taylor. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. Forest Ecology and Management **218**:229-244.

Hartmann, D.L., A.M.G. Klein Tank, M. Rusticucci, L.V. Alexander, S. Brönnimann, Y. Charabi, F.J. Dentener, E.J. Dlugokencky, D.R. Easterling, A. Kaplan, B.J. Soden, P.W. Thorne, M. Wild and P.M. Zhai, 2013: Observations: Atmosphere and Surface. Pages 159-254 *in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley, editors. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring bulletin **43**:69-78.

Housset, J. M., S. Nadeau, N. Isabel, C. Depardieu, I. Duchesne, P. Lenz, and M. P. Girardin. 2018. Tree rings provide a new class of phenotypes for genetic associations that foster insights into adaptation of conifers to climate change. New Phytologist **218**:630-645.

Huber, N. K. and C. D. Rinhart. 1965. Geologic map of the Devils Postpile quadrangle, Sierra Nevada, California. U.S. Geological Survey. https://ngmdb.usgs.gov/Prodesc/proddesc_319.htm.

Hurteau, M., H. Zald, and M. North. 2007. Species-specific response to climate reconstruction in upper-elevation mixed-conifer forests of the western Sierra Nevada, California. Canadian journal of forest research **37**:1681-1691.

Inyo National Forest. USFS. https://www.fs.usda.gov/inyo. Accessed June 3, 2017.

Inyo, Sequoia and Sierra Forest Plan Revisions. USFS. http://www.fs.usda.gov/detail/r5/landmanagement/planning/?cid=STELPRDB5444003. Accessed June 3, 2017.

Jenkins‒Smith, H., C. L. Silva, K. Gupta, and J. T. Ripberger. 2014. Belief system continuity and change in policy advocacy coalitions: Using cultural theory to specify belief systems, coalitions, and sources of change. Policy Studies Journal **42**:484-508.

Jones, M. D. 2011. Leading the way to compromise? Cultural theory and climate change opinion. PS: Political Science & Politics **44**:720-725.

Jones, M. D., and H. C. Jenkins‒Smith. 2009. Trans‒Subsystem Dynamics: Policy Topography, Mass Opinion, and Policy Change. Policy Studies Journal **37**:37-58.

Jump, A. S., P. Ruiz‒Benito, S. Greenwood, C. D. Allen, T. Kitzberger, R. Fensham, J. Martínez‒Vilalta, and F. Lloret. 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought‒induced forest dieback. Global change biology **23**:3742-3757.

Kahan, D. M., E. Peters, M. Wittlin, P. Slovic, L. L. Ouellette, D. Braman, and G. Mandel. 2012. The polarizing impact of science literacy and numeracy on perceived climate change risks. Nature Climate Change **2**:732-735.

Laacke, R. J. 1990. *Abies magnifica* A. Murr. Page 654 *in* Burns, R. M., and B. H. Honkala. Silvics of North America. Vol. 1. Conifers. US Department of Agriculture Agricultural Handbook.

Leiserowitz, A., Maibach, E., and Roser-Renouf, C. 2009. Global Warming's Six Americas 2009. Yale University and George Mason University. Yale Project on Climate Change Communication, New Haven, CT. Available at http://climatecommunication.yale.edu/publications/global-warmings-six-americas-2009/.

Lenth, R. (2020). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.6. https://CRAN.R-project.org/package=emmeans.

Littell, J. S., D. L. Peterson, C. I. Millar, and K. A. O'Halloran. 2012. US National Forests adapt to climate change through Science–Management partnerships. Climatic Change **110**:269-296.

Loik, M. E., A. B. Griffith, and H. Alpert. 2013. Impacts of long-term snow climate change on a high-elevation cold desert shrubland, California, USA. Plant ecology **214**:255-266.

Long, S., and C. Bernacchi. 2003. Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. Journal of Experimental Botany **54**:2393-2401.

Lutz, J., J. Van Wagtendonk, and J. Franklin. 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. Forest Ecology and Management **257**:2296-2307.

Maibach, E.W., Leiserowitz, A., Roser-Renouf, C., Mertz C.K., & Akerlof, K., 2011a. Global Warming's Six Americas screening tools: Survey instruments; instructions for coding and data treatment; and statistical program scripts. Yale University and George Mason University. Yale Project on Climate Change Communication, New Haven, CT. Available at http://climatechangecommunication.org/ SixAmericasManual.cfm.

Maibach, E. W., A. Leiserowitz, C. Roser-Renouf, and C. Mertz. 2011b. Identifying like-minded audiences for global warming public engagement campaigns: An audience segmentation analysis and tool development. PloS one **6**:e17571.

McCullough, I. M., F. W. Davis, and A. P. Williams. 2017. A range of possibilities: Assessing geographic variation in climate sensitivity of ponderosa pine using tree rings. Forest Ecology and Management **402**:223-233.

McIntyre, P. J., J. H. Thorne, C. R. Dolanc, A. L. Flint, L. E. Flint, M. Kelly, and D. D. Ackerly. 2015. Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. Proceedings of the National Academy of Sciences **112**:1458-1463.

McNeeley, S. M., and H. Lazrus. 2014. The cultural theory of risk for climate change adaptation. Weather, climate, and society **6**:506-519.

Millar, C. I., R. D. Westfall, D. L. Delany, M. J. Bokach, A. L. Flint, and L. E. Flint. 2012. Forest mortality in high-elevation whitebark pine (Pinus albicaulis) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. Canadian journal of forest research **42**:749-765.

Montwé, D., M. Isaac-Renton, A. Hamann, and H. Spiecker. 2018. Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. Nature communications **9**:1-7.

Myhre, G., D. Shindell, F.-M. Bréon, W. Collins, J. Fuglestvedt, J. Huang, D. Koch, J.-F. Lamarque, D. Lee, B. Mendoza, T. Nakajima, A. Robock, G. Stephens, T. Takemura and H. Zhang, 2013: Anthropogenic and Natural Radiative Forcing. Pages 659-740 *in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley, editors. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

National Forest System Land Management Planning, Final Rule. Forest Service, USDA. 2012. 77 Federal Register 68: 21162-21276.

Ogle, K., J. J. Barber, G. A. Barron‒Gafford, L. P. Bentley, J. M. Young, T. E. Huxman, M. E. Loik, and D. T. Tissue. 2015. Quantifying ecological memory in plant and ecosystem processes. Ecology letters **18**:221-235.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. **37**:637-669.

Pierce, D. W., T. Das, D. R. Cayan, E. P. Maurer, N. L. Miller, Y. Bao, M. Kanamitsu, K. Yoshimura, M. A. Snyder, and L. C. Sloan. 2013. Probabilistic estimates of future changes in California temperature and precipitation using statistical and dynamical downscaling. Climate Dynamics **40**:839-856.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2018). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137, https://CRAN.R-project.org/package=nlme.

Potts, D., R. Minor, Z. Braun, and G. Barron-Gafford. 2017. Photosynthetic phenological variation may promote coexistence among co-dominant tree species in a Madrean sky island mixed conifer forest. Tree physiology **37**:1229-1238.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Randall-Parker, T. 2018. Draft Record of Decision for the Inyo National Forest Land Management Plan. USDA Forest Service.

Rapacciuolo, G., S. P. Maher, A. C. Schneider, T. T. Hammond, M. D. Jabis, R. E. Walsh, K. J. Iknayan, G. K. Walden, M. F. Oldfather, and D. D. Ackerly. 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global change biology **20**:2841-2855.

Reed, C. C., and M. E. Loik. 2016. Water relations and photosynthesis along an elevation gradient for Artemisia tridentata during an historic drought. Oecologia:1-12.

Reyer, C. P., S. Leuzinger, A. Rammig, A. Wolf, R. P. Bartholomeus, A. Bonfante, F. De Lorenzi, M. Dury, P. Gloning, and R. Abou Jaoudé. 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. Global change biology **19**:75-89.

Rinehart, C. D. and D. C. Ross. 1964. Geology and mineral deposits of the Mount Morrison quadrangle, Sierra Nevada, California. U.S. Geological Survey. https://ngmdb.usgs.gov/Prodesc/proddesc_447.htm.

Ripberger, J. T., K. Gupta, C. L. Silva, and H. C. Jenkins−Smith. 2014. Cultural theory and the measurement of deep core beliefs within the advocacy coalition framework. Policy Studies Journal **42**:509-527.

Sabatier, P. A., J. Loomis, and C. McCarthy. 1995. Hierarchical controls, professional norms, local constituencies, and budget maximization: an analysis of US Forest Service planning decisions. American Journal of Political Science:204-242.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits.

Sierra National Forest. USFS. https://www.fs.usda.gov/sierra/. Accessed June 3, 2017.

Sierra National Forest. USFS. https://www.fs.usda.gov/sierra/. Accessed September 24, 2019.

Speer, J. H. 2010. Fundamentals of tree-ring research. University of Arizona Press.

Stephenson N. L. and A. J. Das. 2011. Comment on "Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum Elevations." Science **334**:177.

Stephenson, N. L., A. J. Das, N. J. Ampersee, B. M. Bulaon, and J. L. Yee. 2019. Which trees die during drought? The key role of insect host−tree selection. Journal of Ecology **107**:2383-2401.

Stokes M.A. and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, IL, USA.

Storer, T. I., and R. L. Usinger. 1963. Sierra Nevada natural history: an illustrated handbook. Univ of California Press.

Swain, D. L., D. E. Horton, D. Singh, and N. S. Diffenbaugh. 2016. Trends in atmospheric patterns conducive to seasonal precipitation and temperature extremes in California. Science Advances **2**:e1501344.

Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first-century California. Nature Climate Change **8**:427.

Thompson, M., R. Ellis, and A. Wildavsky. 1990. Cultural Theory. Westview Press, Boulder, CO, USA.

USFS Pacific Southwest Region. Planning: Forest Plan Revision Documents–Inyo, Sierra, Sequoia. https://www.fs.usda.gov/detail/r5/landmanagement/planning/?cid=STELPRD3802842. Accessed June 9, 2019.

Van Mantgem, P. J., and N. L. Stephenson. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecology letters **10**:909-916.

Verweij, M., M. Douglas, R. Ellis, C. Engel, F. Hendriks, S. Lohmann, S. Ney, S. Rayner, and M. Thompson. 2006. Clumsy solutions for a complex world: the case of climate change. Public administration **84**:817-843.

Wertin, T. M., M. A. McGuire, and R. O. Teskey. 2012. Effects of predicted future and current atmospheric temperature and [CO2] and high and low soil moisture on

gas exchange and growth of Pinus taeda seedlings at cool and warm sites in the species range. Tree physiology **32**:847-858.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, USA.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, and J. Hester. 2019. Welcome to the Tidyverse. Journal of Open Source Software **4**:1686.

Williams, A. P., C. D. Allen, C. I. Millar, T. W. Swetnam, J. Michaelsen, C. J. Still, and S. W. Leavitt. 2010. Forest responses to increasing aridity and warmth in the southwestern United States. Proceedings of the National Academy of Sciences **107**:21289-21294.

Williams, A. P., R. Seager, J. T. Abatzoglou, B. I. Cook, J. E. Smerdon, and E. R. Cook. 2015. Contribution of anthropogenic warming to California drought during 2012–2014. Geophysical Research Letters **42**:6819-6828.

Yale Program on Climate Change Communication. Global Warming's Six Americas. https://climatecommunication.yale.edu/about/projects/global-warmings-six-americas/. Accessed June 13, 2019.

Zhang, J., and B. M. Cregg. 2005. Growth and physiological responses to varied environments among populations of Pinus ponderosa. Forest Ecology and Management **219**:1-12.