DISSERTATION

# INFLUENCES OF ONGOING AND PROJECTED ENVIRONMENTAL CHANGE IN RANGE MARGIN *SEQUOIA SEMPERVIRENS* (COAST REDWOOD) FORESTS

Submitted by

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# ABSTRACT

## INFLUENCES OF ONGOING AND PROJECTED ENVIRONMENTAL CHANGE IN RANGE MARGIN *SEQUOIA SEMPERVIRENS* (COAST REDWOOD) FORESTS

*Overview*: Droughts, warming temperatures, and altered disturbance regimes have placed forest communities of the California Floristic Province under increasing pressure in recent decades. As these conditions are projected to intensify over the next century, forests across the region, including the historically cool and wet conifer forests of the California Coast Range, could be increasingly vulnerable to the effects of rapid environmental change. *Sequoia sempervirens* (coast redwood) is the tallest tree species on earth and also one of the longest living. While the species has been resilient in the face of recent perturbations, the direct and indirect effects of ongoing and projected future environmental change on a conifer species that has persisted *in situ* for millennia have only recently begun to be evaluated. Here, I embark on research across range margin environments of the coast redwood region of California and Oregon to explore the impacts of disturbance, drought, and novel conditions on the species using modeling, experimentation, and observational studies. First, I use species distribution models and climate analog mapping techniques to update climatic suitability projections and create tools that can be used to support conservation decision making, monitoring, and research throughout the range. Next, to determine the response and resilience of an old-growth coast redwood community to a mixed-severity fire event, I analyze postfire data to model the interacting effects of burn severity, stem size, and species biology on survivorship and recovery in a northern range margin redwood community. In the third chapter, I explore the influences of temperature and novel thermal conditions projected at the end of the century in eastern range margin environments on cone and viable seed production in coast redwood, which is unreliable year-to-year. Finally, I provide the first insights available on the impacts and diversity of seed predators in coast redwood forests and track seedling emergence and survival during an extreme drought in the southern portion of the species' range in the Santa Cruz Mountains of California.

*Chapter 1:* Species distribution models and climate analog mapping are valuable tools to evaluate changing suitability for a forest species across time to support conservation decision making and guide future monitoring and research. Here, using best available practices for SDMs, I model current and future climatic suitability for redwood using an ensemble modelling framework, regionally derived climatic and hydrologic data, and systematically collected presence and absence occurrence data spanning the range of the species. The resulting boosted regression tree model accurately (cross-validated AUC = 0.89, sensitivity = .81, specificity = 0.79) identifies the climatic constraints on the species and closely aligns with its known, modern distribution. I apply this model across four end-of-century climate scenarios that collectively represent increases in temperature from 2- 6° C and changes in moisture availability ranging from decreases of 20% to increases of 40%. These projections are used to identify regions that could be effectively conserved and restored to buffer the species from the influences of climate change where it is most likely to continue to thrive, to identify priority research zones, and to explore the potential for natural and assisted migration. Next, I used climate analog mapping techniques to identify geographic changes in seed zones and transfer guidelines under a moderate warming and drying climate change scenario. Identification of analogous seed and clonal material sources can supplement insight provided by SDMs to help communicate climate change impacts and to support

adaptive restoration actions, carry out provenance research, and prepare our forests today for projected climates of the end of the century.

*Chapter 2:* Fire exclusion and suppression in the coast redwood region over the past century has resulted in a lack of understanding as to how fire may benefit or impact these communities. Projections indicate that the coast redwood region will experience more severe fires in the future as conditions become warmer and drier and fog water inputs are potentially reduced. This makes an understanding of the postfire response of these communities to a gradient of burn severities essential to our understanding of their long-term recovery and persistence. A 2017 mixed-severity fire event at the northern range margin of *Sequoia sempervirens* (coast redwood) provided a rare opportunity to analyze early postfire data on the interacting effects of burn severity, stem size, and species biology on survivorship and recovery of coast redwood and three forest community associates (*Pseudotsuga menziesii* var. *menziesii*, “Douglas-fir”; *Notholithocarpus densiflorus,* “tanoak”; and *Rhododendron macrophyllum*, “coast rhododendron”). I employed recursive partitioning to build decision trees that accurately classified (80–88% prediction accuracy) the postfire response of the four primary woody species present in this community. Species specific postfire responses were variable across stem diameters and burn severities, but the ability of three of the four primary woody species to resprout resulted in a resilient postfire community that quickly initiated recovery. Large coast redwood parent stems most typically survived and resprouted from their bole and base, regardless of fire severity, and even the smallest redwood individuals resprouted from their base. Basal sprouting characteristics of coast redwood including sprout presence, growth, and abundance were found to be positively correlated with increasing burn severity. Douglas-fir showed considerable fire resistance at low to moderate burn severities,

but high severity fire killed trees of all sizes. Tanoak and coast rhododendron parent stems typically died and resprouted from the base except where burn severity was very low. I conclude by using my findings to discuss the utility and role of fire in forest management and consider future research avenues that could help to solidify our understanding of the impact and role of fire in these and similar communities.

*Chapter 3:* Coast redwood has unreliable cone production and has low viable seed production (typically 0-15%) for a conifer, but the cause of this low viability is an enigma. As temperatures are projected to rise throughout the coast redwood region over the next century, there is concern that a lack of viable seed production could be one factor contributing to a bottleneck in the regeneration niche of the species in warmer and drier range margin environments. To explore the potential influences of temperature on cone and seed production and viability, I surveyed and collected cones from regions outside of the species' native range that are hotter than existing range conditions and compared them to collections from trees collected in the species native range. My findings showed that coast redwood's ability to produce viable seeds is largely unaffected by average maximum summer temperatures up to 5.2 °C greater than those experienced in any region where the species naturally grows today. This indicates that viable seed production is an unlikely bottleneck in the regeneration niche of coast redwood under projected end-of-century warming, and that temperature alone is not a strong predictor of viable seed production across a 16.2 °C maximum temperature gradient. Timing of cone production and dispersal and basal sprouting were also unchanged across the sampled temperature gradient. While viable seed production is seemingly uncorrelated with maximum temperature, subsequent phases of the regeneration niche, particularly seedling emergence and establishment, are likely more sensitive to the effects of a projected warmer and drier future.

*Chapter 4*: Coast redwood establishment from seed is highly variable across space and time and the causes of this variability have only been partially explained in past research. Here, I conduct a seed sowing experiment in the Santa Cruz Mountains at the southern range margin of the species to explore biotic and abiotic pressures influencing seedling emergence success during an extreme drought event occurring during the 2020-2021 winter, spring, and summer. Using a paired seed sowing experiment with variable predator access, I found that seed predators significantly inhibited the successful emergence of coast redwood seedlings in comparison to treatments that excluded seed predators. The study also represents the first to definitively identify seed predators to coast redwood, including the Dark-eyed Junco and multiple rodent species. I subsequently tracked post-emergence survival of seedlings for a multi-month period and found redwood was highly susceptible to mortality under low moisture conditions post-emergence. The combination of biotic pressures with the lack of the ability to successfully establish in extreme drought conditions helps to partially explain the rarity of seedling establishment in coast redwood forest communities in modern conditions.

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# LIST OF KEYWORDS

coast redwood; *Sequoia sempervirens*; Douglas-fir, coast rhododendron; tanoak; wildfire; burn severity; climatic change; warming; cone production; *in situ* refugia; seed viability; vegetative sprouting; species distribution modeling; climate analogs; seed zones; seed predators; Dark-eyed Junco; drought; seedling emergence; regeneration niche; range margin

# INTRODUCTION

## Background

Forest systems of the California Floristic Province have been under increased environmental pressure during the 21st century (Crockett et al., 2018). Droughts that have occurred throughout the state over the last decade were some of the most intense events in over 1,200 years (Griffin et al., 2014) and drought risks are projected to increase in the future (Diffenbaugh et al., 2015; Mann et al., 2015). Climatic reconstructions have shown that average temperatures of the last 30 years are some of the hottest in at least the last 1,500 years (Trouet et al., 2013), which has amplified already dry conditions. A combination of these warm, dry conditions and high fuel loads and forest densities associated with a century of fire suppression have resulted in wildfires of increased size and severity, trends that are projected to continue in the future (Westerling et al., 2011; Goss et al., 2020; Swain, 2021; Steel et al., 2021). Compounded, these environmental pressures have resulted in rapid environmental change in California's forest communities.

While the most readily observable impacts of these environmental pressures are present in mature mixed-conifer forests of the Sierra Nevada (Fettig et al., 2019a), where millions of acres of forests have died over the past decade, forest systems across California are thought to be vulnerable to climate and environmental change both now and in the future (Thorne et al., 2016). This includes forests of the California Coast Range, which have had relatively lower rates of mortality than other regions of the state (Fettig et al., 2019b). The moderating influences of the Pacific Ocean, including marine fog and cool, mild temperatures, have seemingly buffered forests closest to the coast from the dramatic environmental change observed in neighboring forest systems. The permeability of this buffer, however, remains unclear under future conditions. As such, there has been significant interest in accelerating research in these regions to address knowledge gaps on the potential response of these forests to novel conditions. This is particularly true in forests where the most significant effects of climate and environmental change may have not yet been realized, such as in the iconic *Sequoia sempervirens* (coast redwood) region.

## Coast redwood forests

Coast redwood can live for over 2,500 years and is the tallest tree on earth. The conifer is native to a narrow strip of the California coast that extends c. 700 km north to south and c. 50 km wide. The northernmost stand is located along the banks of the Chetco River in southwestern Oregon, where conditions are wet and humid. The southernmost stands are restricted to a small tributary in the Big Sur Region of Monterey County, CA, where conditions are dry and hot for much of the year, but where fog and access to groundwater may help to support persistence (Noss et al., 2000). The species' range, which suddenly breaks and then continues in locations throughout its distribution, has long puzzled biogeographers and ecologists, which has resulted in considerable debate as to the species climatic constraints and environmental requirements (Noss et al., 2000).

Old-growth coast redwood forests, of which only 5% remain, are renowned for their structural complexity (Iberle et al., 2020). Often growing among other conifers, including *Pseudotsuga menziesii* (Douglas-fir), or in pure stands, the forest type is a critical habitat for a wide variety of endangered wildlife, including the endangered marbled murrelet (*Brachyramphus marmoratus;* Baker et al., 2006). The coast redwood region is also an important contributor to the California economy, supporting a valuable tourist industry and timber market (Stewart, 2007). All of these factors make the conservation, restoration, and adaptive planning for climate change for the species a top priority of managers, policymakers, and scientists (Burns et al., 2018). However, the direct and indirect effects of ongoing and projected future climate and environmental change on a conifer species that has persisted *in situ* for millennia have only recently begun to be evaluated. Recent research has found that redwood growth has generally increased over the last century, suggesting that modern conditions may actually promote growth and biomass accumulation (Sillett et al., 2015). While initially encouraging, it is unknown whether this is a short-term phenomenon, or how coast redwood will respond to other sustained environmental pressures (Burns et al., 2018). Regions just north of the species' modern distribution in southwestern Oregon have been hypothesized as an area of opportunity for the species under climate change (O'Hara et al., 2017). Here, conditions may become suitable for establishment and range expansion as temperatures warm. In contrast, populations along the eastern and southern margins of the coast redwood range, where conditions are the hottest and driest under modern conditions, are thought to be most vulnerable to the pressures of environmental change (Noss et al., 2000).

### Ongoing and projected future influences of environmental change

Moisture availability is projected to decrease in future climates of the redwood region regardless of variability in precipitation (Flint and Flint, 2012). While some have called coast redwood forests drought "tolerant", the most recent research indicates that the species is distributed across a narrow hydrologic niche, primarily on sites close to supplemental water sources or that are foggy (Johnstone et al., 2010) for much of the summer. This provides an initial indication that the species' environment, rather than any known adaptation, is more likely to have contributed to its low rates of mortality in recent droughts (Ambrose et al., 2015; Francis et al., 2020). Given the species considerable water requirements (Noss et al, 2000) and the consistent projections of increasing climatic water deficit throughout the species range (Flint and Flint, 2012), the species has been labeled as "vulnerable" to projected climate change (Soland et al., 2021).

Most research on the response of coast redwood to ongoing and projected climate change has been related to the growth and persistence of mature trees, but mature trees are rarely the most sensitive life stage to altered environmental conditions. As a result, there are significant knowledge gaps on the potential impacts of novel conditions on the phenology, cone and seed production, and successful seedling recruitment in coast redwood forests. The species has long been known to unreliably produce viable seed, the cause for which is unknown (Morrisson et al., 2021). Seedling recruitment in mature forests is also rare (Sillett et al., 2020), particularly at hot and dry sites like growing conditions in southern and eastern range margin environments (Noss et al., 2000). While the species can effectively regenerate vegetatively, sexual reproduction from seed is necessary to support potential range shifts or expansion across time, particularly as conditions are modified in the future (Davis et al., 2001). As such, research that helps to explain the environmental factors that influence seedling establishment via sexual reproduction, as well as those that explore the influence of increased temperature and water availability on coast redwood's regeneration niche, will be critical to our understanding of how projected change may result in long-term compositional shifts in the future.

Finally, the combination of warmer temperatures, lower moisture availability, and increased fuel loads and forest densities as the result of anthropogenic disturbances of the past century could result in increased fire frequency and severity in coast redwood forests (Lorimer et al., 2009), a phenomenon that may have already begun. A series of severe fire events that occurred over a four-year period (2017-2020) brought fire back to the coast redwood range in many areas that had not burned in over a century. While fire is a natural and important part of the disturbance regime in coast redwood forests, the historical fire regime is thought to have been of low to moderate severity (Agee, 1996). A more severe fire regime with greater frequency could impact the species' documented resistance and resilience to fire and impact the persistence of mature trees and regeneration in postfire environments. With the relative rarity of large and severe fire events in the coast redwood range over the last century, the utility of fire in management and response and recovery of these communities to fire remain pressing research topics.

Here, I embark on research across the coast redwood region, with a special focus on range margin environments. Research on the potential impacts of climate and environmental change on forest communities requires a multi-pronged approach that can use a variety of scientific tools and processes. In the four chapters that follow, I use modeling, experimentation, and observational studies to address important knowledge gaps related to the response of coast redwood to a number of environmental pressures. I provide an in-depth exploration of the adaptations that coast redwood has that may benefit the species as environmental conditions are modified, discuss the reproductive bottlenecks the species may experience in potentially warmer and drier conditions, and provide tools that can be used to undertake conservation and adaptation planning for these communities. I provide new insights on the postfire recovery of redwood communities and explore how reproduction and seedling establishment are affected by seed predation and warm and dry conditions during an extreme drought. Findings from my research can be used to help plan conservation and restoration activities and to guide research and monitoring activities in areas where they may be most pressing.

## Dissertation Objectives

### *Chapter 1: Identifying end-of-century habitat suitability and refugia, priority research zones, and climate analogs for Sequoia sempervirens forests under multiple climate change pathways*

- To use the best available practices and data available to create a revised species distribution model for coast redwood that effectively pinpoints the climatic factors that define and constrain the modern distribution.
- Apply this model across multiple end-of-century climate scenarios that span a gradient of change in temperature and moisture to identify portions of the coast redwood range that could be effectively conserved and restored to buffer the influences of climate change (“refugia”) and to identify priority research zones in areas that may experience novel conditions in the future (“marginal habitats”)
- Transparently interpret the results and utility of these models while recognizing their caveats and limitations in climate change adaptation and conservation planning
- Evaluate the potential future suitability and uncertainty associated with implementation of assisted migration of *Sequoia sempervirens* at the species northern range margin
- Explore the use of climate analog mapping to identify geographic changes in seed zones and transfer guidelines under potential climate change to inform adaptive planning and restoration in the region and promote seed provenance research

*Chapter 2 Objectives: Early postfire response of a northern range margin coast redwood forest community*

- Conduct an observational study on the response of a redwood forest community to mixed-severity fire in a region where fire has been absent for over a century.
- Build models that accurately classify the postfire response and survivability of the four primary woody species to mixed-severity fire
- Explore how a gradient of burn severity influences basal regeneration characteristics of coast redwood including sprout presence, growth, and abundance.

- Predict and discuss how mixed-severity fire may influence early recovery and community dynamics in an old-growth coast redwood forest

*Chapter 3 Objectives: Novel maximum temperatures do not impede viable seed production in Sequoia sempervirens*

- Survey and sample coast redwood trees growing inside and outside of the species' range to explore how temperature may influence the species' production of cones, viable seeds, and vegetative sprouts.
- Sample and analyze cone and viable seed production data from trees planted in regions located in considerably warmer environments (>5 °C) than any region of the native coast redwood range
- Compare seed viability data from regions inside and outside thermal conditions in the native region to predict how the species cone and viable seed production may be altered under novel thermal conditions

*Chapter 4 Objectives: Seed predation inhibits Sequoia sempervirens seedling emergence during a Santa Cruz Mountains, CA drought*

- Explore the relative influences of abiotic and biotic pressures on seedling emergence through a paired seed sowing experiment in the Santa Cruz Mountains
- Identify the diversity of avian and mammalian species that feed or may feed upon coast redwood seeds in the post dispersal period
- Identify the potential contribution of seed predators to low seedling establishment rates observed throughout the coast redwood range

- Monitor and track seedling establishment success of coast redwood seedlings during an extreme drought event

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# CHAPTER 1 — IDENTIFYING END-OF-CENTURY HABITAT SUITABILITY AND REFUGIA, PRIORITY RESEARCH ZONES, AND CLIMATE ANALOGS FOR *SEQUOIA SEMPERVIRENS* FORESTS UNDER MULTIPLE CLIMATE CHANGE PATHWAYS

## Introduction

Planning an effective and adaptive response to the potential influences of global climate change on terrestrial ecosystems is one of the most pressing and complex biological conservation issues of the century (Dumroese et al., 2015). While there is considerable uncertainty regarding the magnitude or rate of change (Hausfather and Peters, 2020), environmental conditions across the globe will continue to be altered and the response of most species to these novel conditions remains unknown (Millar et al., 2007). While some mobile species with short-generation times may be able to effectively track suitable climatic conditions across time, immobile organisms that grow and reproduce slowly, such as trees, may have their ability to disperse into newly suitable habitats outpaced by the rate of climatic change (Zhu et al., 2012; Gray and Hamann, 2013). As such, many tree species across the globe will need to migrate, adapt, or be plastic to novel climatic conditions to maintain modern range breadth and long-term population viability (Corlett and Westcott, 2013; Iverson and McKenzie, 2013). In turn, planning and management to promote climate resilience, adaptation, and effective monitoring and research related to the direct and indirect impacts of climate change have become top priorities in forestlands across the globe.

Adaptive conservation planning for climate change in forestlands requires a multi-pronged approach that can use a variety of tools to inform decision making (Millar et al., 2007; Pecchi et al., 2019). Identification of "in situ climatic refugia" (areas of a species range that are currently occupied by a species and are projected to remain suitable under future conditions; Baumgartner et al., 2018) can help prioritize areas for future conservation resources and action (Morelli et al., 2020). Locating areas of a species range considered as novel climatic conditions or unsuitable under future climates can help to pinpoint regions for long-term monitoring and hypothesis-based research on the response of a species to novel conditions (Evangelista et al., 2011). In addition, identifying areas where a species does not currently exist that are currently suitable or may be suitable in the future, known as the “leading edge” (Rehm et al., 2015), can guide conservation of areas that could be important for natural or assisted migration (Vitt et al., 2010) or expanded use in forestry (William et al., 2013). Finally, identification of populations or planting stock that are well-adapted to climatic conditions like those projected for a target area in the future can guide adaptive management and seed and material stock selection from well-suited individuals (Potter and Hargrove, 2013; Pecchi et al., 2019).

While each prong of the spatial conservation planning nexus can be described in simple terms, given the inherent uncertainty in the magnitude of change in future climate projections, successful identification and communication of these conservation priority areas remains challenging (Sofaer et al., 2019). One of the most biologically robust ways to assess the influence of novel conditions is to use information on the physiological response and tolerance of a species to climate (Morin et al., 2009). While conceptually robust, creating a mechanistic understanding of a species’ ability to persist and reproduce under climate change is a complex experimental process that spans the life stages of an organism (Jarnevich et al., 2018). In turn, the physiological response of most species to climate change is just beginning to be explored, leaving those seeking to implement forward-looking conservation and adaptation actions with considerable uncertainty. In turn, in replacement for mechanistic models, most modern conservation assessments use correlative species distribution models (Iverson et al., 2013), which have several advantages and disadvantages in climate change planning (Kearney et al., 2010; Jarnevich et al., 2015; Pecchi et al., 2019).

Correlative species distribution models (SDMs) use spatially explicit observations of a species' presence and absence to build a statistical relationship with environmental variables to predict a species' habitat suitability across environmental space. In climate change planning and research, model developers often use climate data alone to build this relationship. In turn, these SDMs represent a "realized climate niche" of a species, or the climate space that is occupied by a species' modern distribution (but not necessarily all climate space that a species could occupy – the "fundamental niche"; Morin et al., 2013). With recognition of the caveats and limitations inherent in SDMs (Jarnevich et al., 2015), simple SDMs can be projected to future climate scenarios across multiple potential emissions trajectories (Dyderski et al., 2018; Booth et al., 2018) to inform forward looking conservation decision making (Porforino et al., 2014). In some cases, these SDMs have had similar estimates of future projected distributions as the use of process-based or mechanistic models (Coops and Waring et al., 2011), providing encouraging evidence that SDMs and their projections may serve as a suitable proxy for these more complex models (*but see* Sofaer et al., 2018 and Boiffin et al., 2017).

While SDMs are effective tools for use in long-term conservation planning when used and applied appropriately, it is also important to consider implementation of some research and management efforts in the present day that could benefit forest adaptation to future conditions. To grow and establish forests that are best adapted to a particular climate, seed zone and material transfer guidelines have been in use in many of areas of the United States for decades (Buck et al., 1970; Hamann et al., 2011; Pike et al., 2020). These zones provide guidance for the selection of seed or clonal material that are well-adapted to the environmental conditions of a planting site. The general principle underlying these seed zones is that seed or clonal material should be sourced from the same zone and elevation where the planting occurs to prevent maladaptation (Buck et al., 1970; Millar and Libby, 1989). However, as the pace of climate change is likely to accelerate faster than the ability of a species to adapt to new climatic conditions, it is important to identify analogous seed sources within a species range that could be well-adapted to future projected climate conditions (Bradley St. Clair and Howe, 2007). In past research, these analogs have been described as answering the following question: If I want to plant trees that will be best adapted to projected future climatic conditions at a site, where do I go to get the seeds today? (Potter and Hargrove, 2012). In turn, identification of analogous site conditions and seed sources can supplement insight provided by SDMs to help communicate the potential magnitude of change and to support research and adaptive restoration actions.

*Sequoia sempervirens* (coast redwood or redwood) is a long-lived conifer native to the California coast range. It is also the tallest tree species in the world (Sillett et al., 2021). Intensive logging and disturbance in late 19th and early 20th centuries left only a small percentage of old-growth forests intact, and today, most of the species natural distribution is composed of second- and third-growth forestlands (Noss et al., 1999). These forests support a unique and diverse assemblage of species (Sillett et al. 2007) and remain both ecologically and economically important. Millions of tourists visit the region to experience these forestlands annually (Stewart, 2007), and redwood remains a valuable timber product (Henderson et al., 2017). The near and long-term impacts of global climatic change on a species that has endured in-situ for millennia are only just beginning to be explored (Burns et al., 2018). Redwood growth has generally increased over the last century (Sillett et al., 2015), and coast redwood has shown considerable resilience in the face of increased disturbance in the form of logging, more severe and larger fires, and lengthy drought conditions observed in the late 20th and early 21st centuries (Burns et al., 2018). In contrast, moisture conditions known to support redwood forests will likely contract in future climates regardless of variability in precipitation projections (Flint and Flint, 2012), which could be a considerable stressor in range margin environments, where temperatures are relatively warmer and drier. Given the ecological and economic importance of the species, considerable resources are dedicated to its conservation and restoration and in promoting climate resilient forests (Noss et al., 2000; Burns et al., 2018). In turn, detailed and updated models that can support adaptive conservation and restoration actions are needed to predict, monitor, research, and attenuate potential climate impacts in these iconic forestlands.

Here, I used a climatic suitability model framework applied across multiple potential future climate scenarios in combination with seed zone climate analogs to answer the following questions for coast redwood habitats at the end of the 21st century: (1) Which existing habitats will remain most suitable and stable?; (2) which portions of the coast redwood distribution may be most vulnerable and important to monitor and study as climate change intensifies?; (3) which areas of existing range margin environments may be most climatically suitable to support range expansion or migration?; and (4) how could seed or material sourcing and stocking be modified to potentially support well-adapted forests under future climates and where should seed or material be sourced from?

## Methods

### *Species Occurrence Records*

I obtained presence and absence locations for coast redwood from the USDA Forest Inventory and Analysis (FIA) program database (Stanke et al., 2020). The use of systematically collected forest inventory data has several advantages over the use of public occurrence databases, including the availability of true absences and a relatively equal distribution of sampling locations across geographic space (Pecchi et al., 2019). I selected all available plots from the study region, which encompassed an area that extended *c*. 35 km from the northernmost and 50km from the southernmost and easternmost natural populations of *Sequoia sempervirens*. Plots containing *Sequoia sempervirens* were considered presence locations, and all other plots were considered absences. While FIA sampling is systematic (Smith et al. 2002) sampling intensity does vary across land use, time, and space (Gibson et al., 2012). In turn, I standardized plot densities to a maximum of one plot per 3.5 km$^2$. The filtered occurrence dataset contained 183 presences and 1,649 absences.

### *Baseline Climate Data and Predictor Selection*

I selected climatic variables from regionally derived climatic and hydrologic data from the California Basin Characterization Model Dataset (hereafter "BCM"; Flint and Flint, 2012). The BCM couples downscaled climatic data from the PRISM dataset (Daly et al., 2008) with topography, soils, and geology data to derive hydroclimatic variables that, among other applications, are important determinants of vegetation distributions. Predictor variable selection was conducted *a priori* based upon existing knowledge of the species and climatic limitations reported in the literature.

Redwood is spread across a temperate, humid climate space influenced by the Pacific Ocean, where temperatures are mostly characterized as cool and mild throughout the year (average mean annual temperature of 10-16 °C). Temperatures rarely drop below -10 °C anywhere in the range, and snow is only very occasional and short-lived in some of the highest elevation regions (Olson et al., 1990). Although mature redwoods are quite plastic in their ability to persist in temperatures warmer than their modern range (Libby et al., 2017), newly established seedlings are susceptible to heat and moisture stress (Fritz, 1950; Jacobs et al., 1987). Redwoods are also mostly restricted to regions where moisture is available much of the year, usually as a combination of inputs from precipitation, fog, or groundwater (Francis et al., 2020). Changing moisture conditions under a warming climate and in extreme drought conditions are some of the primary concerns of managers for the species under climate change (Burns et al., 2018). Like other conifers, increased minimum and maximum temperatures could also influence phenological progression and timing, and increased temperatures in combination with lower water availability could influence establishment from seed, annual growth, and persistence across time.

Given the known biological considerations for the species, I selected three predictors provided in the BCM dataset *a priori* that I believed to be important determinants of the species distribution: (1) average minimum January temperature (one of the coldest months), (2) average maximum July temperature (one of the warmest months), and (3) the average climatic water deficit for the water year, all averaged across the baseline period (1981-2010). The climatic water deficit is the annual evaporative demand that exceeds available water (Flint and Flint, 2014), and represents an approximation of drought stress on soils and plants. While redwood is a long-lived species that has experienced temperature fluctuations across multiple millennia, the baseline period of 1980-2010 represents one of the warmest periods in recorded history (Trouet et al., 2013) and serves as a suitable reference period for conditions that are known to support redwood persistence and reproduction.

### *Species Distribution Modeling*

I utilized SAHM (Software for Assisted Habitat Modelling; Morisette et al., 2013) to develop species distribution models for coast redwood. I used SAHM's predictor selection feature to ensure that selected climatic variables were correlated ≤ +/-0.50, utilizing the maximum of the Pearson, Spearman and Kendall correlation coefficients. I also used SAHM to resample BCM predictor variables from 270 x 270 m to 1 x 1 km spatial resolution to match the resolution of the occurrence dataset, which provides occurrence locations that are “fuzzed” slightly to protect landowner privacy. These minor offsets have little effect on model performance when an appropriately scaled predictor dataset is employed in analysis (Gibson et al., 2014). Using these predictors in combination with the occurrence dataset, I then utilized SAHM to model baseline period habitat suitability for coast redwood.

Many algorithms are available for species distribution modeling and are suitable for use with presence/absence data (Lawson et al., 2014). I fit initial SDMs utilizing three algorithms: random forests (Breiman, 2001), generalized linear models (Nelder and Wedderburn, 1972), and boosted regression trees (Elith et al., 2008). I first identified overfit models by visually evaluating predictor response curves. Models that are overfit to the occurrence dataset and have unrealistic fluctuations in suitability across a predictor variable are not typically transferable or suitable for projection into future scenarios in space or time (Merow et al., 2012). Once models were pared down to those with biologically plausible response curves, I evaluated model performance utilizing 10-fold cross validation and multiple statistical metrics including the area under the receiving operating characteristic curve (AUC-ROC), AUC-precision recall, sensitivity and specificity. In depth discussion of these accuracy metrics and their interpretation are discussed in Liu et al., (2010) and Sofaer et al., (2019). Where applicable, to discretize predicted suitability as suitable and unsuitable I utilized a threshold equal to the observed prevalence of coast redwood in the observations, a technique appropriate when unbiased occurrence data is used and the occurrence dataset represents the true prevalence of the species on the landscape (Gibson et al., 2014).

### *Future Climate Projections*

As there is considerable uncertainty in the magnitude of future climatic change based upon levels of future global emissions and methodological differences in general circulation models, I utilized a range of climate model projections for the years 2070-2099 (hereafter, 2085) that represent a gradient of future temperature and moisture conditions. I applied the final model into future projected climate space based upon a suite of climate models (IPSL, Dufresne et al., 2013; MIROC-ESM, Watanabe et al., 2010; MPI-ESM, Giorgetta et al., 2013) from the fifth IPCC assessment report (IPCC, 2014) that represent two emissions scenarios (RCP 4.5 and RCP 8.5, moderate and worst case, respectively). RCP 4.5 projections, which have temperature increases of 2 – 3 °C, are currently considered to be plausible future scenarios of warming given current policy, while RCP 8.5 scenarios are currently seen to be unlikely, worst case scenarios (Hausfather and Peters, 2020). The four projections collectively represent increases in temperature from ~2° – 6° C and changes in precipitation ranging from a ~20% decrease to ~40% increase in California's Bay Area (Weiss et al., 2013). While precipitation increases under some selected scenarios, the climatic water deficit increases in BCM projections under all scenarios because the combination of increases in precipitation with warmer temperatures and limited soil water holding capacities results in a reduction of water availability in most regions (Flint and Flint, 2012). To evaluate climatic novelty in future climate projections in comparison to the climatic space represented by the baseline period across the study region, I created bivariate plots of the predictor variables at all occurrence locations for baseline and future periods and identified overlap and divergence between the climate space represented by each of the point clouds.

### *Identifying and Mapping In-Situ Refugia, Priority Research Zones, and Expansion Opportunities*

I analyzed and visualized spatial projections of current and future climatic suitability in multiple ways. We classified predicted values into low, medium, and high bins for locations with predicted suitability values above the prevalence threshold and classified predicted values below the threshold as unsuitable. To identify areas of model agreement regarding future suitability, we discretized and then summed predictions from different GCMs, such that a value of zero represents all four GCM predictions defined unsuitable and four represents complete agreement of suitability across future climate projections. We utilized an existing remote sensing model of the distribution of redwood (California State Department of Forestry and Fire Protection GIS Data, 2016) to define its current distribution and identified areas currently occupied with predicted future unsuitability (i.e. potentially marginal habitats; Sinclair et al., 2010). We also used this information to identify areas predicted as suitable under future climate projections where redwood is currently absent to identify areas of potential interest for natural or assisted migration in future climate conditions.

### *Climate and Seed and Material Transfer Zone Analogs*

To identify locations under modern conditions that will be most similar to climates at 65 reference sites across the redwood range in 2085, I conducted climate analog mapping. I first broke established seed zones (Jones, 1970) into elevation ranges in 152.4 m (500 ft) increments from 0 – 762 m (0 - 2500 ft) to simulate the elevation zones used in the existing California Seed Transfer Zone guidelines (Buck et al., 1970). In total, I identified 14 seed transfer zones and 65 elevational subzones within them relevant to redwood. I distributed a random point within each of the 65 seed subzones to serve as the reference location to calculate climate analogs, or an area in the current known range with a climate similar to the projected climate for the reference location in 2085. I used the same predictor variables as the species distribution models to characterize climate and clipped these layers to an existing range map for redwood buffered by 1 km (California Department of Forestry and Fire Protection GIS Data, 2016). By clipping available climate surfaces to the generalized redwood range, I was able to identify climate analogs in locations where redwood seed has actual potential to be available in the future. While there may be statistically closer climate analogs somewhere on the landscape outside of the redwood range, identifying climate analogs for seed zones requires that there be a nearby population present to obtain seed or clonal material for transfer.

I calculated the 50 closest modern climatic analogs for each seed subzone's future projected climate under a moderate warming and drying scenario (MIROC-ESM, RCP 4.5) in the *BiodiversityR* R package (Kindt et al., 2015). I utilized a moderate climate change projection for discussion and visualization rather than the most extreme projection (RCP 8.5) because temperature projections for the more extreme scenario are largely novel for large areas of the redwood range. Climate analogs were calculated using Mahalanobis distance (De Maesschalck et al., 2000), a unitless distance metric between a reference location and a distribution in multivariate space. Here, the metric calculated can be interpreted as "climatic distance", with a value closer to zero being more climatically similar and larger values being less like the target climate. Accuracy and quality of a selected analog can be evaluated by comparing the analog climate in modern climate space to the projected future climate of the reference location. Here, I compared the differences between the future projected climate for all reference locations and their modern analogs for each of the three climatic variables. Geographic distance and cardinal direction of change between a reference location and its analog were calculated in ArcMap v10.7.1. (ESRI, 2020).

## Results

### *Species Distribution Models*

My post-hoc evaluation of environmental response curves from the test of a three-model ensemble resulted in selection of boosted regression trees (BRT) as the final species distribution modeling algorithm. Early tests with random forests and generalized linear models showed complex or biologically unrealistic response curves that made these algorithms poorly suited for the objectives, particularly for projecting into future potential climate space (Merow et al., 2012). The final BRT model used a learning rate of .0005 and a tree complexity of 2 with all other values set to SAHM defaults. Model performance was excellent, with a cross validated AUC of .89 (Figure 1.1), an AUC-PR of .52, sensitivity of .81, and specificity of .79.

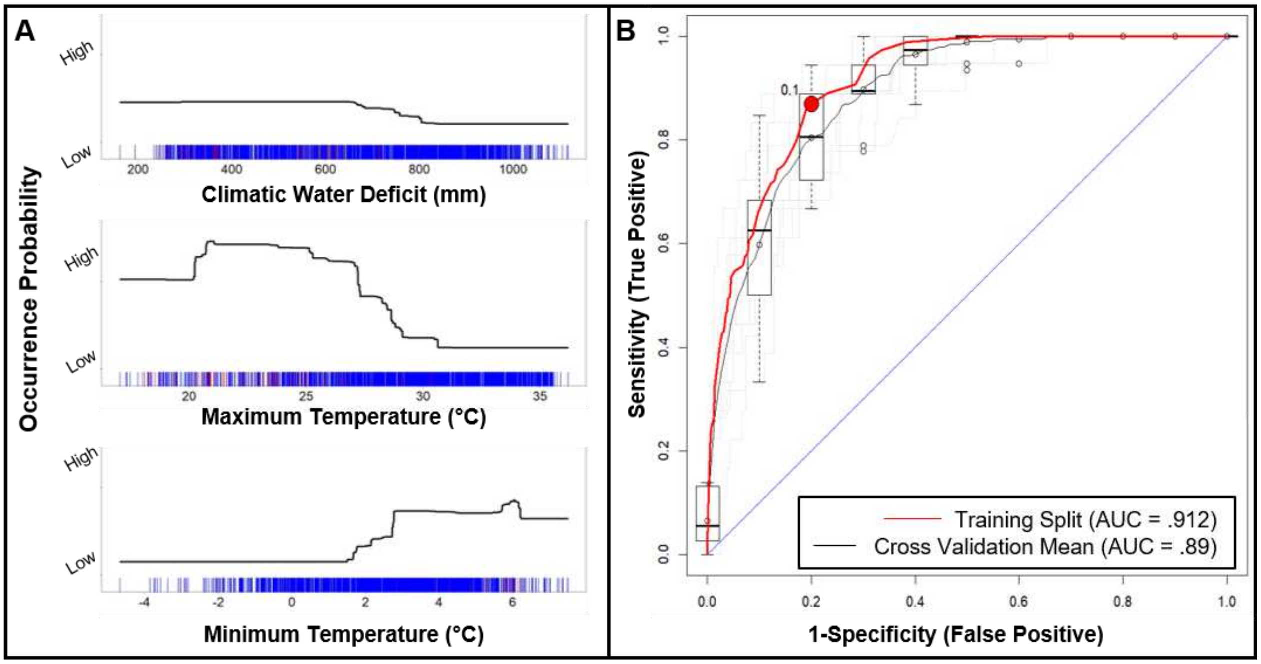

**Figure 1.1:** (A) Environmental response curves showing trends in redwood habitat suitability across the three predictor variables; (B) AUC-ROC curve for the final boosted regression tree model comparing training versus cross validated AUC.

My results show that redwood climatic suitability can be modeled quite effectively in a parsimonious model framework using only three largely uncorrelated variables (maximum correlation = .45). All three of the predictor variables contributed substantially to the model. The relative importance of each variable was as follows: minimum temperature, 43.8%; temperature maximum, 35.8%; and climatic water deficit, 20.2%. Where applicable, the threshold used to distinguish suitable versus marginal habitats was 0.10.

Predictor response curves produced in the BRT model were relatively smooth, interpretable and biologically plausible (Figure 1.1). Habitats most suitable for redwood occurrence are those areas with a climatic water deficit below c. 650 mm. Suitability is gradually reduced between 650 and 800 mm with a sharp drop in suitability in areas with higher water stress. Maximum temperatures in July under 20 °C showed moderate suitability, with a peak in suitability between c. 20 and 27 °C. Suitability gradually decreased as maximum temperatures increased and was largely unsuitable beyond c. 32 °C. Habitat suitability was low in areas with minimum average temperatures below freezing in January, but suitability rises rapidly in areas >1.5°C. The baseline model for the normal climatic period (1980 – 2010) applied across the study region shows close geographic similarity with the species modern range (Figure 1.2A). End-of-century projections of habitat suitability across each of the four climate scenarios are logical identifiers of those regions that will remain suitable and those habitats that will become marginal under varying degrees of warming and drying.

### *Refugia Habitats and Agreement*

Considerable portions of the coastal and northern portions of the redwood range are predicted as “climatic refugia” – areas where multiple model projections show sustained suitability for redwood through the end of the 21st century (Figure 1.3). The northern portion of the modern range (approximately north of Humboldt Redwoods State Park) to the southern border of Oregon

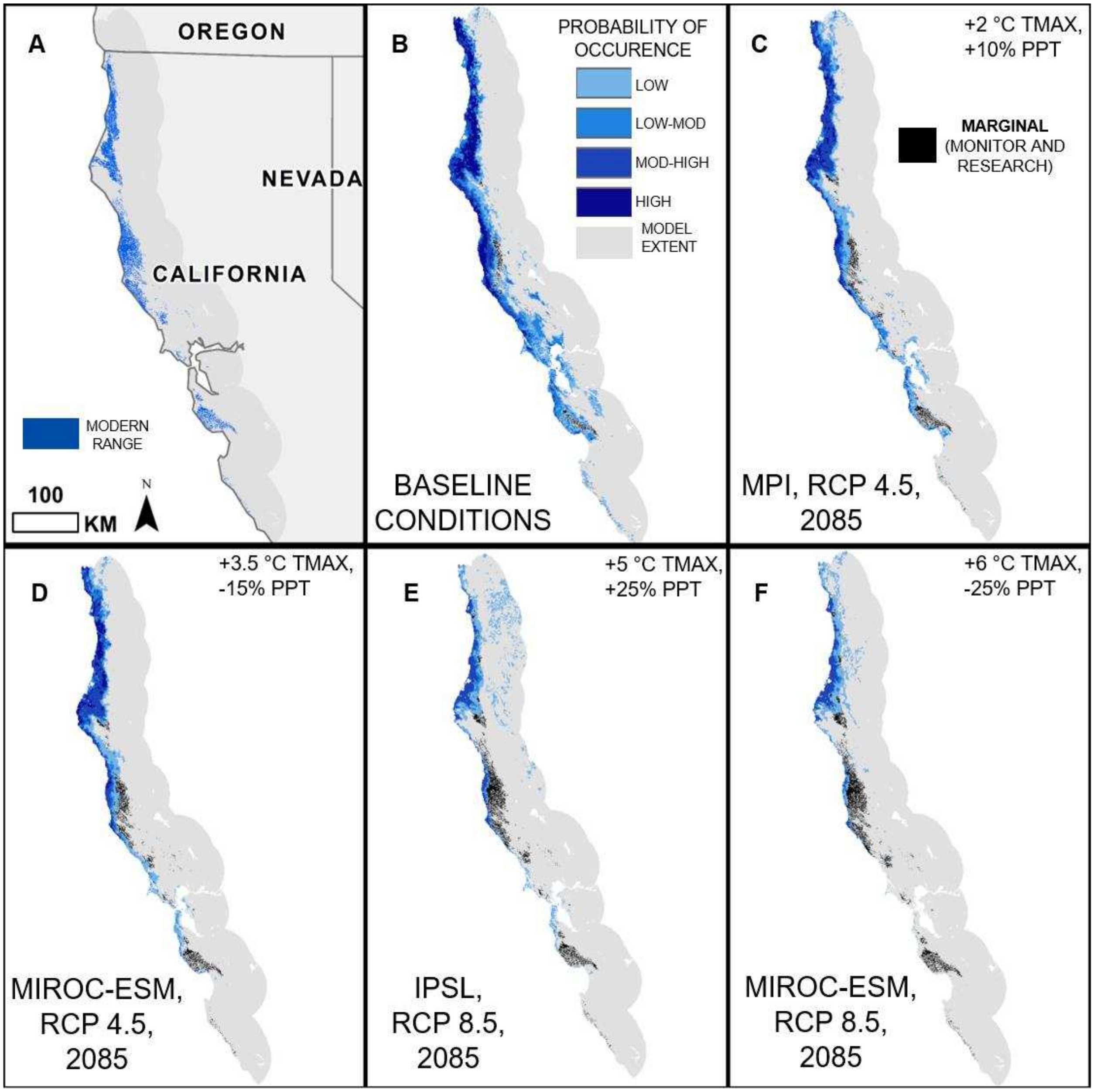

**Figure 1.2:** (A) Generalized range map for Sequoia sempervirens modified from California State Department of Forestry and Fire Protection GIS Data, 2016; (B) Habitat suitability under baseline climate conditions from a Boosted Regression Tree (BRT) model; (C-F) BRT model applied to four individual climate scenarios encompassing a range of future potential temperature and moisture conditions. Approximate average changes in temperature and precipitation values listed are representative of change in the Bay Area of California (Weiss et al., 2013).

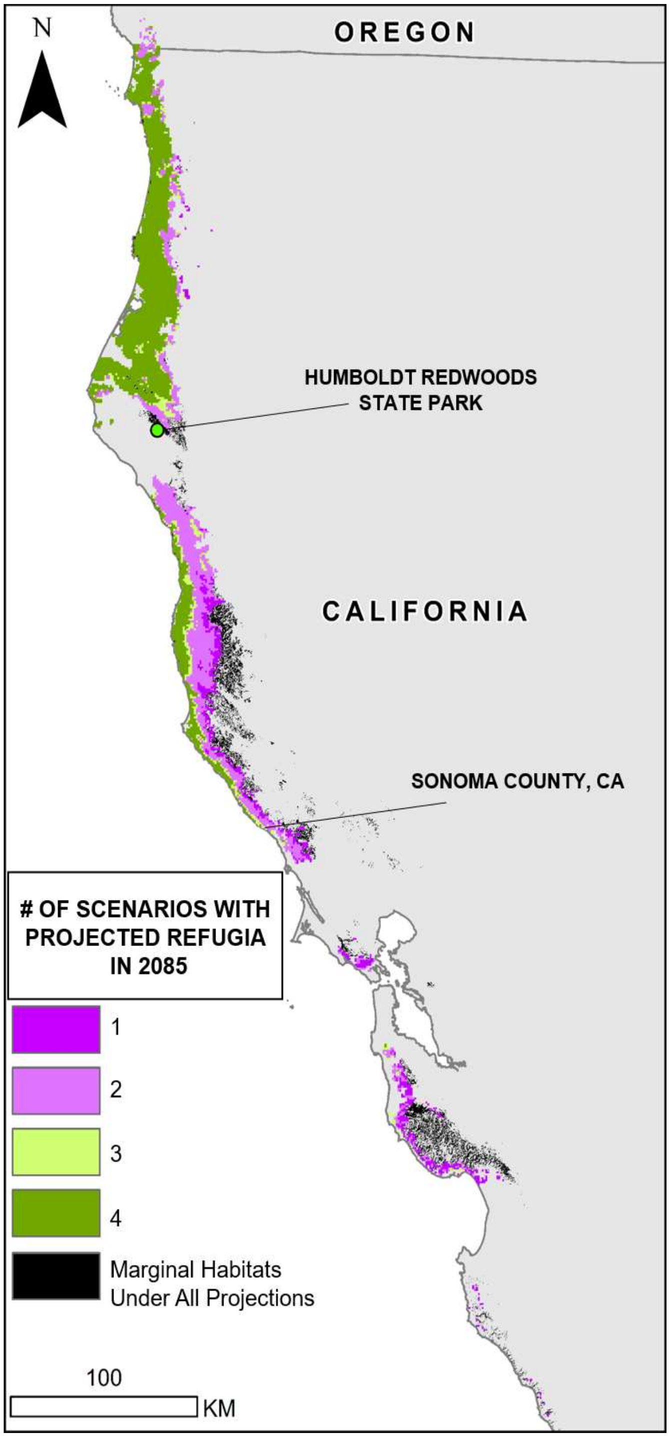

**Figure 1.3**: Spatial predictions of habitat refugia across four climate change pathways for 2085 showing the number of scenarios with projected climatic suitability for coastal redwood. Areas in black show areas where redwood currently exists that the model applied to future climate projections predict to be unsuitable. In this figure, areas outside the modern redwood range are not shown.

(Figure 1.3), is predicted to remain broadly suitable across all climate change scenarios, even those with unlikely magnitudes of warming under the RCP 8.5 emissions scenario. In addition, areas that are closest to the coastline of the Pacific Ocean are predicted to remain climatically suitable habitats in one or both of the RCP 4.5 scenarios (MPI and MIROC) across the latitudinal distribution of redwood. Three to four projections agree on sustained suitability throughout many coastal areas north of Sonoma County, CA to the northern extent of the range in Oregon.

### *Marginal Habitats and Suitable Habitat Expansion in Future Climate Projections*

The baseline model shows considerable areas north of the existing range margin in southwest Oregon to be suitable under baseline climate conditions (Figure 1.4). These are "unfilled" habitats that are climatically suitable under existing conditions, but which have not been colonized by the species. By the end of the century, RCP 4.5 projections show habitats at the northern range margin to remain suitable for range expansion throughout much of southwestern Oregon, but areas further from the coast that connect with the existing range transition to unsuitable under RCP 8.5 projections.

In general, as temperatures and drying increase across future climate scenarios, habitat suitability decreases. Marginal habitats, where model projections no longer predict suitability at the end of the century, are most prevalent in the eastern and southern portions of the range. These range margin environments are distributed across baseline conditions that are some of the hottest and driest regions. Some of these habitats will transition to climates like those where redwood is known to be absent today. Other areas will experience climatic conditions that are entirely novel for the region, meaning that they are not representative of the climatic variability currently found in the study area, and as such, should be considered

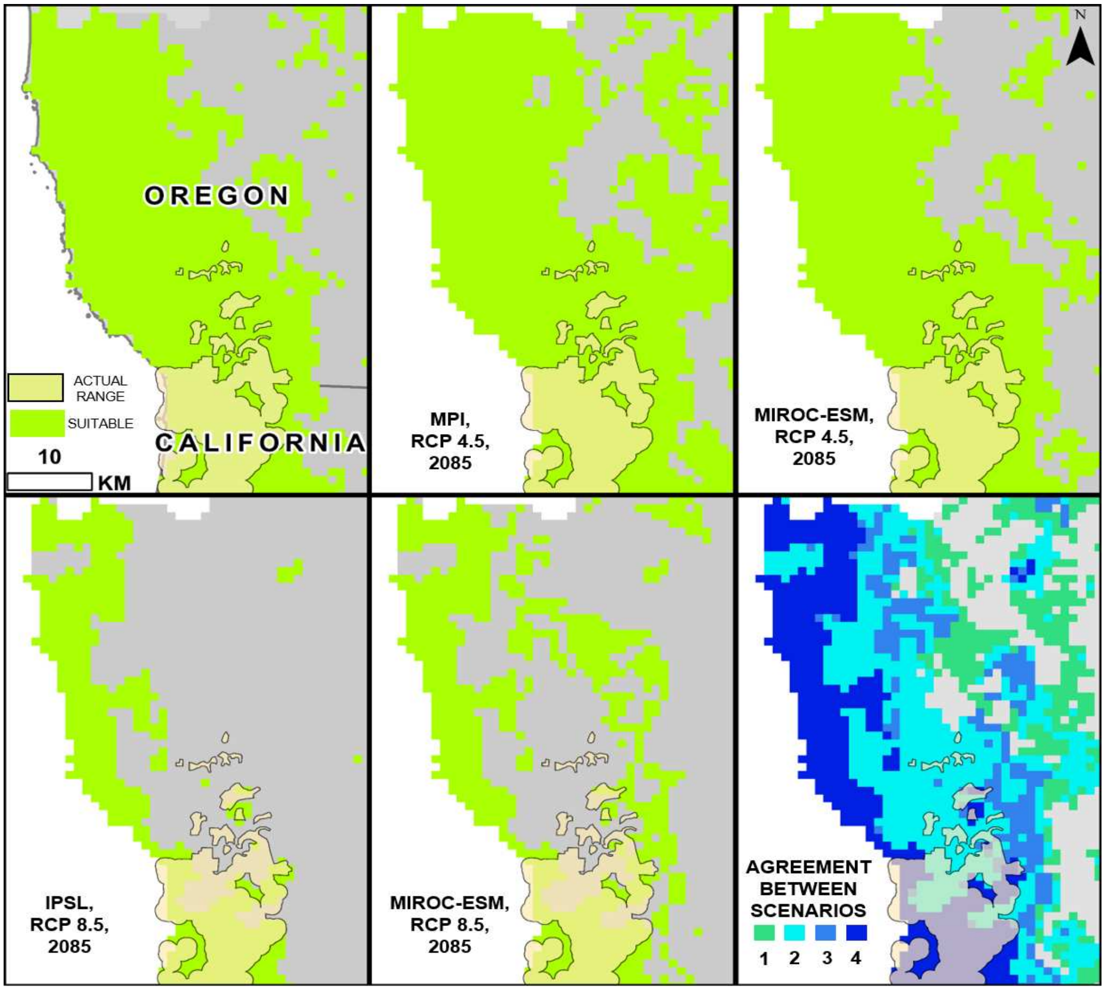

**Figure 1.4:** Projected suitability across four end-of-century emissions scenarios and the actual modern distribution of coast redwood at its northern range margin under modern conditions.

extrapolations (Elith and Graham et al., 2009; Figure 1.5). Projections that are based upon more moderate climate change scenarios (i.e. RCP 4.5) have less divergence into novel climate space than those under higher emissions scenarios (i.e. RCP 8.5). Under RCP 8.5 projections, future temperatures at many of the original presence occurrences are nearly entirely novel (Figure 1.5).

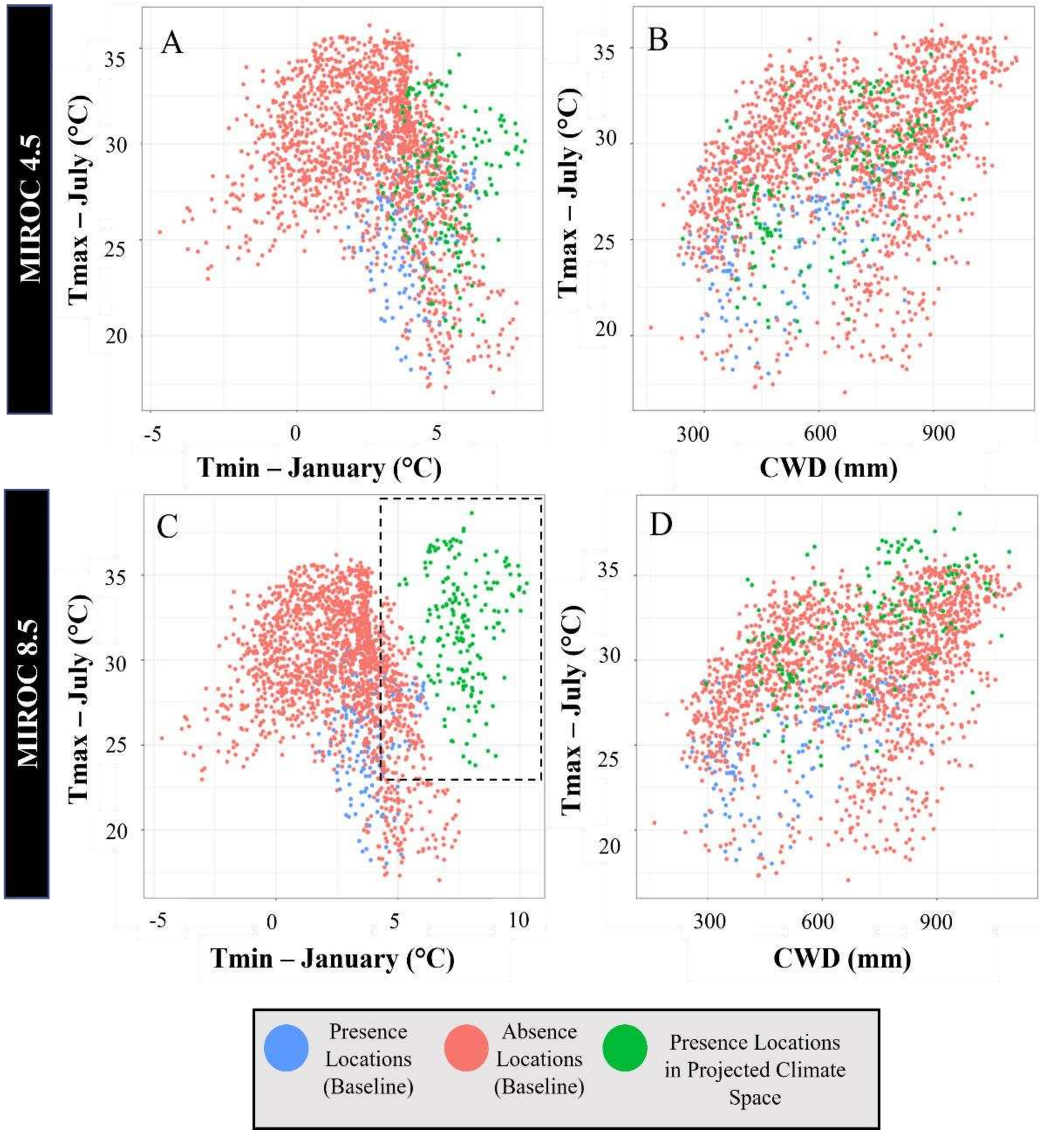

**Figure 1.5:** Existing climatic space of the occurrence locations under baseline conditions (blue - presence and red - absence) compared to the climatic space the presence locations are projected to experience under climate conditions in 2085 in MIROC RCP4.5 and 8.5 models. Areas where the green point cloud diverges from the red and blue point clouds (example in the dashed inset box) represent novel climate space for the study region under future projections. Areas where the green point clouds primarily overlap with the red point cloud are indicative of those climates where redwood occurs today but that will experience conditions in the future that are similar to those where redwood is absent today. Panels A and C show minimum and maximum temperature (tmin, tmax), and panels B and D show the climatic water deficit (CWD) and maximum temperature (tmax).

*Climate and Seed Zone Analogs*

I calculated 2,750 climatic analogs for 65 reference sites across the 14 California seed zones (Figure 1.6). I selected the top analog from each subzone to evaluate analog quality, distance, and cardinal direction (Figure 1.6B). There were only small differences between the best identified analog locations in modern climates and target conditions projected at seed zones for 2085 for temperature minimum (mean difference = .17 °C), temperature maximum (mean difference = .54 °C) and climatic water deficit (mean difference = 29.7 mm).

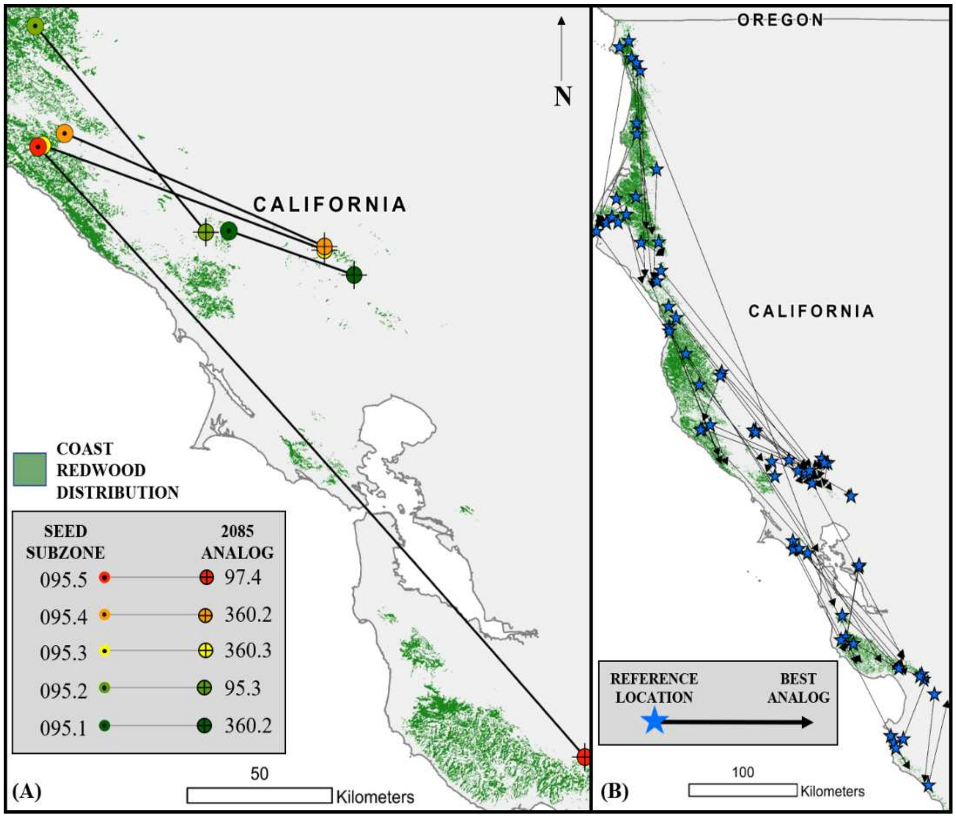

**Figure 1.6:** (A) Seed zone analogs for Sequoia sempervirens for a single seed zone (Zone 95) across 5 bands of elevation (500—2500 ft). All analogs moved southeast in direction in this zone, where conditions are hotter and drier (B) Reference locations and best analogs for all 65 seed subzones.

These small differences indicate that these seed zone analogs are high quality analogs that match closely with projected climate conditions under the MIROC RCP 4.5 projection at the end of the century. Seed zones changed from their baseline zone and elevation in the best matching analog in 63 of 65 cases. In most cases, analog zones were southeast of the existing seed zone (Figure 1.6B). The best matching analog zones were an average of 90 km away from the reference seed zone location (range: 1.0 – 501.3 km, SD= 93.1). The geographic distance between a reference location and its best matching analog becomes inherently smaller as you move to more southern seed zones because analogs are restricted to regions of California where redwood grows as a native species, and most analogs are southeast of their existing seed zone. Southern seed zones in the Santa Cruz Mountains of California and isolated stands along eastern range margins represent the majority of analogs, making these regions important sources of seed and clonal material under ongoing climate change.

## Discussion

While the direct and indirect influences of future projected climate change on the persistence, growth, and reproduction of redwood communities remain unknown, the climate suitability model, projections, and seed zone analogs created in this research are valuable conservation and restoration planning tools that can aid decision making and guide research regarding the effects of ongoing climate change. The model and associated projections can be used to pinpoint areas of stability across climate change projections and areas where more mechanistic climate change research is necessary to better understand how redwood may respond to new and novel climatic conditions. The seed zone analogs are some of the first available for a California conifer species and can be used by managers and researchers to test appropriate provenances in new climates, prioritize seed collections, and to implement climate adaptive restoration actions.

In comparison to projections of future habitat suitability produced in past research (Fernandez et al., 2011; DellaSala et al., 2015), the projections produced here are relatively encouraging for coast redwood's climatic suitability under climate change, particularly in RCP 4.5 projections. Methodologies and best practices for applying species distribution models to future climate conditions have advanced considerably since a climate conservation assessment was performed for the species. I believe the use of a parsimonious model with uncorrelated predictor variables, regionally derived climatic data and projections from the IPCC 5th Assessment, and the use of presence/absence occurrences rather than presence-only data are likely accountable for the differences observed between my models and previous SDMs.

My model projections identify end of century refugia for redwoods that we can more confidently project will be areas where the species can effectively persist. In turn, these regions may be particularly suitable portions of the species range to prioritize conservation and restoration actions over the next century, potentially helping to build an effective buffer for the species to ongoing climate change. Still, the modern distribution of coast redwood is limited and there is inherent uncertainty in future climate projections. As such, continued monitoring, conservation, and restoration actions across the species range, including those habitats determined to be marginal in future climates, should remain a priority for managers and policymakers whenever resources are available.

When SDMs are applied to future climate projections and areas enter a realm of "unsuitability", these projections are sometimes interpreted as a reflection of the biological ability of a species to persist *in situ*. I believe this is misguided for a long-lived tree species like coast redwood. Here, I stress that those areas which transition from suitable to marginal in the model projections are not an indication of the species abrupt contraction but instead are areas where expanded mechanistic and physiological research on the influences of climate change on all life stages of redwood should be carried out. As a long-lived conifer species, mature coast redwood individuals are likely to display an unknown degree of plasticity and adaptability to persist in novel climatic conditions.

Established coast redwood in plantation and ornamental environments sometimes thrive in temperatures like those projected to be unsuitable by my models, particularly when sufficient moisture is available. This could be an indication that redwood's niche breadth is wider than expressed by its natural range (Sax et al., 2013; Booth et al., 2017). It remains unclear, however, how novel thermal conditions or sustained reductions in moisture may influence the species phenological progression or its ability to produce and establish from seed or recover from intensive disturbance in future conditions. In turn, the early life stages, from seed and sprout, may be particularly important stages to study in marginal environments. Those future research efforts could elicit how the regeneration niche of the species may be altered under novel climate conditions. While mature trees are likely less sensitive to the direct effect of increased temperature, broad swaths of forestlands projected as marginal under multiple climate scenarios could be effectively monitored using remote sensing or aerial surveys. Those same projected marginal habitats could also be representative of those portions of the redwood range that could be at most risk during extreme events, such as multi-year droughts or particularly severe fires. However, these types of extreme events are more difficult to consider in SDMs.

Assisted migration, the intentional relocation of a species to previously uncolonized areas projected to be suitable under future climates, has been discussed as a potential mechanism to establish a climate change buffer for coast redwood and several other conifer species (O'Hara et al., 2017; McLachlan et al., 2007). My model projections extend only 35 km north of the existing northern range margin for redwood, but the projections indicate that restoring and conserving existing habitats in the northern reaches of coast redwood comes with less uncertainty than establishing new populations just north of the species range. While sustained suitability is projected under moderate climate change scenarios in habitats just north of the existing northern range margin in southwestern Oregon, under the hottest and driest scenarios suitability wanes. In contrast, sustained suitability is projected across all four future climate scenarios in broad swaths of the northernmost reaches of the species existing range, where there is considerable potential to restore and conserve habitats that have been degraded from a legacy of intensive timber extraction (Noss et al., 1999) and fire exclusion (Woodward et al., 2020).

The climate and seed zone analogs identified herein provide a valuable tool for communication of climate change impacts, restoration projects and research in the coast redwood region. First, climatic conditions of any given redwood stand across the region will be, on average, more climatically similar in 2085 to conditions 90 km southeast of its present location under a moderate warming and drying scenario. As species composition, growth, and reproductive dynamics gradually change in the redwood region from north to south, analog forests can be used to provide initial insights as to how climate change may alter community dynamics across these communities. Next, most seed zone analogs are located in the southern portion of the species range and in comparatively isolated easterly stands in and around Napa County, CA. These same regions are those that the SDM projections classify as transitioning from suitable to marginal across multiple future climate scenarios. As such, in preparation for the potential impacts of climate change, collection of seed from these regions should be prioritized.

Existing research into the growth or comparable resilience of different provenances to warmer and drier conditions should be continued to determine whether various seed sources are better adapted to these conditions than others (Ambrose et al., 2015; Dagley et al., 2017; Morrison et al., 2021). Seedlings from these populations should also be made readily available for use in restoration and research. In future planting or reseeding projects within the redwood region, managers could consider conducting trials by introducing seedlings or cloned individuals from analog zones, thereby effectively mixing provenances to potentially support genetic diversity and potential resilience to climatic change (O'Hara et al., 2017).

While logistically complicated, the utilization of seed zone analogs as a climate adaptation strategy follows the same principles of silviculture that resulted in the creation and utilization of seed zones in the first place: individuals best adapted to their localized climatic conditions are most appropriate in planting projects (Buck et al., 1970). As such, sourcing seed from populations that are known to persist and successfully regenerate in warmer, drier, or more fire frequent environments could help prevent climate change driven maladaptation. If hypotheses underlying the creation of seed zones are correct, by the time these trees have matured at the end of the century, their offspring will be well-suited to the projected climatic conditions of the future, which could result in more successful natural regeneration from seed, stronger patterns of growth, and greater tolerance of warmer and drier conditions.

While SDMs and seed zone analogs can be effective tools for use in climate change conservation and adaptation planning and to guide future research, caveats in the use of these models and their predictions remain. First, SDMs assume that a species is in equilibrium with its climate, meaning that a species natural distribution can serve as an effective proxy for their climatic requirements and constraints (Booth et al., 2018). While I have shown that habitat suitability can be modeled quite effectively using only climatic variables, I also recognize that there are many non-climatic factors that could result in redwood's absence at a location where it is otherwise a suitable habitat. These include soil characteristics, the effects of competition (Mpakairi et al., 2017), disturbance (Moretti et al., 2006), and biological and topographic barriers to dispersal

(Monsimet et al., 2020). SDMs are also a broad scale planning tool. At a resolution of 1 km², microclimatic drivers, such as hydrologic factors (Francis et al., 2020), soils, and competition with other species are not considered, but may play an important role in persistence and establishment of redwood across the species range. In addition, uncertainty regarding future climate space is an important consideration when using seed zone analogs and SDMs. Analog zones could be altered substantially based upon the magnitude and rate of climate change that occurs across the next century. In addition, whether there are benefits in adaptive seed sourcing for redwood remains largely unknown, and evaluating this question requires long-term research and proactive planning.

## Conclusions

Coast redwood dominated forestlands spread across coastal regions of northern California and southern Oregon are predicted to experience new and novel climatic conditions over the next century that pose a conservation planning challenge. The SDMs and seed zone analogs produced in this research can play an important role in guiding decision making and management of the species as ongoing climate change modifies environmental conditions. The model and spatial predictions of agreement across future climate projections identify considerable portions of the species modern range that can be prioritized for conservation, restoration, and adaptive management to create a buffer to the potential effects of climate change. Range margin environments at the species southern and eastern boundaries are the most likely to experience climatic conditions outside the range of current redwood occurrence or that are novel combinations of climate variables where we do not know how redwood will respond. Expanded monitoring of these marginal habitats and mechanistic research that elicits the response of the species to these novel conditions should be carried out across all life stages. Considerable uncertainty remains as to the future suitability of redwood outside of its existing range at its northern range margin. As such, protection and restoration of existing redwood habitats, particularly those in the northern reaches of the species range, should be prioritized over implementation of an assisted migration program if conservation resources remain limited. The existing seed zone and material transfer guidelines for the region must be revisited as temperatures warm and moisture availability potentially declines. Many southern and eastern areas of the range have the potential to be particularly important for seed and material collection in support of adaptive management that could help to establish individuals that may be most resilient to future climatic conditions. As more refined climatic and occurrence data become available and methods in species distribution modeling improve, the model produced here should be updated to reflect these improvements. Finally, continued research on the degree to which redwood from different provenances tolerate warming and drying will help to elicit the benefits of the use of climate analogs in seed sourcing.

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# CHAPTER 2 — EARLY POSTFIRE RESPONSE OF A NORTHERN RANGE MARGIN COAST REDWOOD FOREST COMMUNITY[1]

## Introduction

Abundant fire scars and cavities on large trees reveal the historical presence of fire in many northern range margin coast redwood communities (*Sequoia sempervirens*; hereafter "redwood"). Over the last century, however, wildland fire has been rare, often attributed to increased suppression activities, annual precipitation that can exceed 2,500 mm (100 in), and an infrequent lightning regime (Agee, 1993; Lorimer et al. 2009). Recent compounded fire events in neighboring forest communities in the Klamath-Siskiyou Mountains of northern California and southern Oregon (Donato et al., 2009), and projected increases in fire frequency and severity in the western United States (Rogers et al., 2011; Westerling, 2016), have added a sense of urgency to the exploration of the biological response of these forest systems to mixed severity fire (Lorimer et al., 2009). In 2017, the Chetco Bar Fire in southwestern Oregon burned portions of one of the northernmost contiguous old growth redwood communities that remained extant, providing a unique opportunity to explore postfire response after what is thought to be nearly a century without fire (Dyrness et al., 1973).

Postfire recovery of a coniferous forest species to high severity fire often hinges upon the presence of refugia or a viable cone-seed bank (Heinselman, 1981; Stark et al. 2006; Stephens et al., 2013). Subsequent seedling recruitment can then support the recovery of coniferous forest species over time and across disturbance events (Larson and Franklin, 2005). Redwood forest communities have several characteristics that add complexity to this typical postfire trajectory.

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First, redwood has the uncommon ability as a coniferous species to sprout basally and epicormically (O'Hara et al., 2017). This occurs most often when individuals are injured, making stand replacement extremely rare (Lorimer et al., 2009). Next, in the northern portion of the range of the species, many redwood communities are characterized as mixed coniferous-evergreen forests (Franklin and Dyrness, 1988) where a non-sprouting conifer (*Pseudotsuga menziesii* var. *menziesii*, "Douglas-fir"), a sprouting hardwood (*Notholithocarpus densiflorus,* "tanoak"), and a large sprouting shrub species (*Rhododendron macrophyllum*, "coast rhododendron") coexist with redwood in a multi-layered canopy. This complicates our understanding of the impacts of fire, the appropriateness of typical postfire management actions (e.g., timber salvage; Lazzeri-Aerts and Russell, 2014), and the successful prediction of postfire forest structures, species compositions, and potential for community recovery.

Most postfire studies in coast redwood communities have been conducted on sites characterized as alluvial flats in the central and southern portion of the species range and it is unclear how well the results of those studies apply to forests on the more rugged topography at the northern range margin (Lorimer et al., 2009; Ramage et al., 2010). Nevertheless, those other studies provide insight into the potential response of similar communities located in the northern portion of the species range. In the south-central range, Lazzeri-Arts and Russell (2014) found that redwood had the lowest rate of mortality of all tree species and the greatest basal sprout density of all sprouting species following fire. All redwood trees larger than 7.5 cm diameter at breast height (DBH) survived in some form, while Douglas-fir and tanoak mortality rates were nearly 75% and 30%, respectively (Lazzeri-Arts and Russell, 2014). In a study of the Mendocino Lightning Complex Fires on a commercial redwood timberland in central California, low levels of mortality were observed in redwood, the sole study species. While there was a concern that merchantable sized trees would die in the high severity fire, they did not observe bole mortality of any trees larger than 34 cm. Resprouting occurred across all size classes, but most vigorously in small, top-killed trees (Douglas and Bendurel, 2009). In contrast, Metz et al. (2013) observed high rates of redwood mortality following wildfire in its southern range, which was attributed to standing dead fuels associated with a pathogen that impacted tanoak individuals present in the redwood understory prior to burning. Next, in a multi-fire study, surveys in redwood forests burned in 2008 lightning events spanned from Mendocino County, CA in the north to Monterey County, CA in the south (Ramage et al., 2010). While this study focused on competitive dynamics of coast redwood and tanoak in burned and unburned environments, fire increased redwood abundance and induced basal sprouting, with high severity fire favoring redwood over tanoak (Ramage et al., 2010). The variable response of redwood to fire across its distribution highlights the potential for environmental conditions to alter postfire trajectories. Given the rarity of fire at the northern range margin over the last century, we lack an adequate understanding of how previous research findings transfer to this portion of the range.

To evaluate the role and impacts of wildfire and the utility of fire management in northern range margin communities, forest managers need simple models that can be used to assess how fire modifies community trajectories across a range of species, burn severities, and tree sizes. Here, field data were collected after a recent fire with four primary objectives: 1) to characterize and model patterns of postfire survivorship of coast redwood, tanoak, coast Douglas-fir, and coast rhododendron across a gradient of burn severities; 2) to evaluate the postfire basal sprouting response of fire-affected coast redwood; 3) to describe how mixed-severity fire may influence forest development in this old-growth forest system; and 4) to consider the potential role of fire in forest management in this and similar northern range margin redwood-Douglas-fir forest communities.

## Methods

### *Study Area*

The Wheeler Creek Research Natural Area (WCRNA) was established in 1972 to set aside one of the last old-growth redwood forest communities in Oregon for research and preservation (Dyrness et al., 1973). The site represents one of the northernmost contiguous redwood communities, located eight km south of what is thought to be the absolute northern range margin of the species distribution (Figure 2.1). The southern boundary of the natural area is a ridgetop, but much of the WCRNA is a north-facing slope. The northern boundary follows a dense riparian area along Wheeler Creek. Elevations range onsite from 540 m at the ridgetop to 170 m along Wheeler Creek. Climatic models show the site has received an average of 2,362 mm (93 in) of precipitation annually over the previous 30 years with some extremely moist years exceeding 3,500 mm (137 in). Average temperatures were 12.2 °C (54 °F), with a mean minimum of 6.1 °C (43 °F) and a maximum of 18.3 °C (65 °F) (PRISM Climate Group, 2019). Weather conditions often produce fog, which flanks the site on late summer

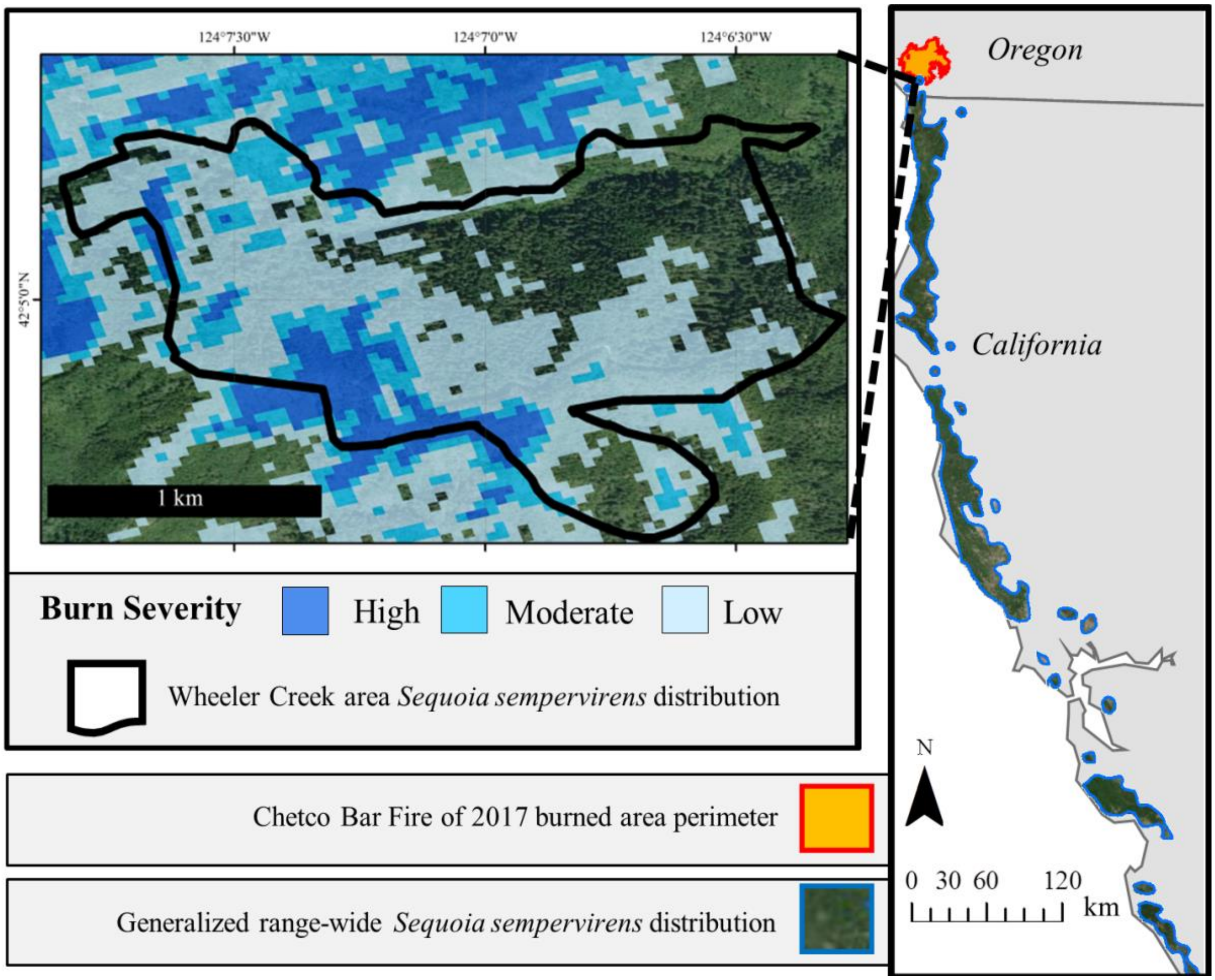

**Figure 2.1**: The general study region in and around the Wheeler Creek Research Natural Area, Rogue River - Siskiyou National Forest, Oregon, USA, compared to the entire distribution of the *Sequoia sempervirens*. The region was burned in the Checto Bar Fire of 2017. Fire perimeter and burn severity measurements are classified using Monitoring Trends in Burn Severity (MTBS) data for visualization of fire extent and heterogeneity of burn severity across the site. In the study, field based burn severity measurements were collected independently using the Composite Burn Index.

mornings and evenings. The upper canopy is dominated by mature coast redwood and coast Douglas-fir, while pole-sized trees of the same species occupy the middle story. Tanoak and coast rhododendron dominate the understory. The forest community is mixed-age with multiple cohorts of redwood and Douglas-fir ranging from saplings to old-growth individuals. The largest old-growth redwoods are thought to be 200 to >500 years in age (Dyrness et al., 1973), and many exceed 150 cm in diameter. There is no history of logging on the site. In 2017, the Chetco Bar Fire burned in and around the WCRNA. Publicly available remotely sensed data (Eidenshink et al., 2007) show a burn severity range from very low to high (MTBS Project, 2019; Figure 2.1 and 2.2). With the exception of a small area burned by an incendiary bomb during World War II (Hoff, 1999), the Chetco Bar Fire is thought to have been the first fire in the WCRNA in c. 100 years (Dyrness et al., 1973); however, a quantitative fire history for the natural area has not yet been completed. Evidence of previous fire events is visible in the form of fire cavities and scars on old-growth redwood individuals (Woodward, *Personal observation*; Figure 2.2).

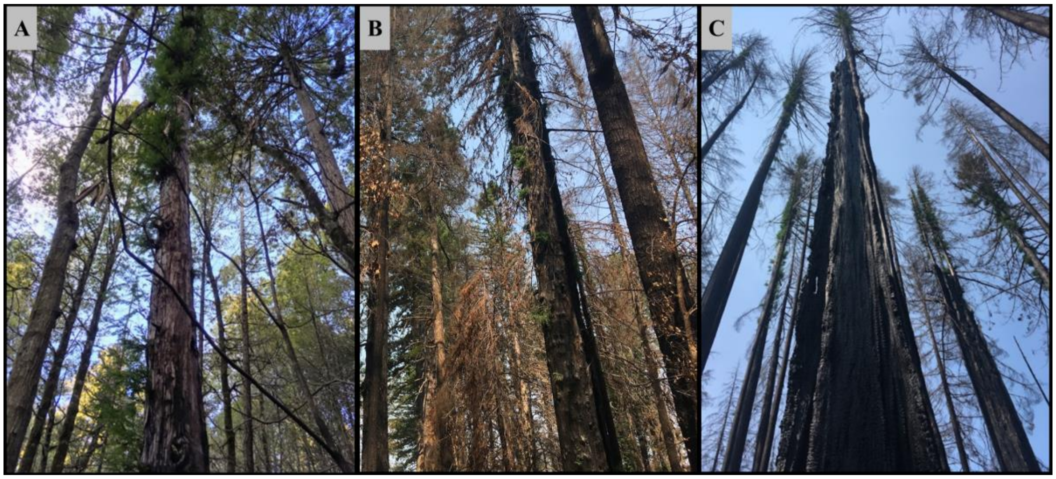

**Figure 2.2:** Site photos representative of low (A), moderate (B), and high (C) burn severity in the middle and upper stories. Panel C includes an old growth redwood individual with deep fire scarring from previous fire event(s) and multiple individuals sprouting epicormically following the Chetco Bar Fire of 2017.

### *Data Collection and Analyses*

In the late summer and early fall of 2018, we conducted a site survey in and around the WCRNA in areas observed to be broadly dominated by mixed coast Douglas-fir and coast redwood forest types. We used roads, trails, and natural features to survey burned portions of the Natural Area to delineate accessible sampling boundaries and to visually estimate and record relative burn severity estimates (i.e., Low, Medium, or High). Based upon time and resources, these initial survey data were used to randomly stratify seven to eight sampling locations within each estimated burn severity category. In the field, we used a high precision global positioning system (GPS; Model: Trimble GeoExplorer) to locate and mark the center of each randomly distributed plot. Within each plot, we measured 1) burn severity, 2) tree and shrub species composition and size, 3) postfire survivorship, and where applicable, postfire recovery and growth of individual coast redwood sprouts, and 4) the number of tree seedlings by species. We installed variable radius (10-20 m) circular sampling plots. 18 plots had a radius of 10 m, while four plots were expanded incrementally until three redwood individuals were sampled (Ramage et al., 2010), for a total of 22 plots. For every tree species and coast rhododendron with DBH ≥2.5 cm encountered in the first 10 m, we recorded the species, DBH to the nearest 1/10 of a centimeter, and postfire status of each tree. Between 10 and 20 m radius, the same information was collected but only for redwood. Stems and snags that appeared to have died prior to the Chetco Bar Fire were excluded from further analyses. For each redwood encountered, we counted the number of basal sprouts and measured the maximum basal sprout height (cm) and aerial sprout cover ($m^2$). We defined aerial sprout cover to be the ground area covered by basal sprouts when looking down upon the sprouts from above. Finally, a 5 m diameter circular subplot was positioned from plot center, where we searched for postfire seedling regeneration of tree species.

We used the Composite Burn Index (CBI; Key and Benson, 2006; Kasischke et al., 2008; Chen et al., 2011) to measure burn severity at each plot. We selected the CBI over other measures of burn severity in an effort to create continuity with similar postfire redwood research (Scanlon et al., 2006; Metz et al., 2011) and to evaluate burn severity at the community scale. The CBI is a field-collected measure that considers fire effects on five individual strata across the entire plot, broadly characterizing the “degree of environmental change caused by fire”, which represents “the magnitude of environmental change from prefire conditions” (Key and Benson, 2006). At the

WCRNA, the five strata evaluated across the CBI are fairly discretely represented by the present community (Table 2.1).

**TABLE 2.1**: Dominant forest community element represented by each stratum measured in the Composite Burn Index (CBI) in and around the Wheeler Creek Research Natural Area (WCRNA) in the Rogue River-Siskiyou National Forest, Oregon, USA.

| CBI STRATA | DOMINANT COMMUNITY ELEMENT |
|---|---|
| **Substrates** | soils, duffs and down-dead woody fuels |
| **Herbs and Shrubs < 1 m** | western sword fern (*Polystichum munitum*) and evergreen huckleberry (*Vaccinium ovatum*) |
| **Tall shrubs and trees < 5 m** | coast rhododendron, Evergreen huckleberry, small tanoak, and saplings of coast redwood and Douglas-fir |
| **Intermediate Trees (subcanopy, pole-sized trees)** | mature tanoak and pole-sized Douglas-fir and coast redwood, and more rarely, Pacific madrone (*Arbutus menziesii*) |
| **Big Trees (upper canopy, dominant, and codominant trees)** | coast redwood and Douglas-fir, including a significant element of trees considered to be old-growth. Occasionally large tanoak. |

Following traditional methods for CBI data collection (Key and Bernson, 2006), all relevant postfire effects factors (e.g. duff char, percentage of foliage altered, percentage of canopy mortality) were evaluated at each plot. For each factor, a score of 0 – 3 was assigned based upon visual evaluation, with 0 being unburned and 3 being the highest severity. To obtain a final CBI, we averaged the resulting scores from each stratum to obtain a single “composite” burn severity rating. A detailed description of each of the post-fire effects factors and the standardized data collection template for the CBI are provided in Key and Benson (2006).

All statistical analyses were conducted using Program R’s Software for Statistical Computing (R Core Team, 2019). To visualize species-scale response to fire, we first plotted our field data by species on bivariate plots. We subsequently employed recursive partitioning (Breiman et al., 1984) to build individual classification models of postfire mortality and survivorship of four community species (coast redwood, coast Douglas-fir, tanoak, and coast rhododendron) using two variables: 1) burn severity as measured by the CBI and 2) stem DBH. We selected recursive partitioning because of its non-parametric nature, simplicity in interpretation through decision tree plotting, and its successful application in studies exploring ecological questions with similar data structures (Dobbertin and Bigging, 1999; De'ath et al., 2000; Leonard et al., 2014; Hart et al., 2014). Potential postfire outcomes that were classified through recursive partitioning were variable depending on the potential biological response of each tree species and the data collected. For redwood, the potential classifications included 1) live canopy/parent stem, no epicormic sprouting response, 2) primary stem survived, resprouting epicormically or 3) dead primary stem, regenerating from basal burl. For coast Douglas-fir, 1) live or 2) dead. For tanoak, 1) primary stem survival, 2) primary stem mortality, resprouting from base, or 3) absolute mortality. For coast rhododendron, 1) live primary stem(s), 2) dead primary stem(s), regenerating from base, or 3) absolute mortality. Stem survival and mortality were defined by the presence or absence of live leaves in the canopy or sprouts along the bole, and absolute mortality was defined as an individual with a dead bole or stem that had biological potential to resprout from the base but did not. Where applicable, all live categories were inclusive of individuals that also sprouted from the base. We used the "rpart" package in the R Software for Statistical computing to conduct recursive partitioning to build a classification tree for each species of interest (Therneau et al., 2019). We initially grew a classification tree for each species with a minimum complexity parameter of 0.0001 and employed the package's default 10-fold cross-validation routine. The final model selected for each species was the most simplistic tree that minimized cross-validated error rates. Each tree was pruned by selecting the best model based upon the above criteria (Hothorn and Everitt, 2014). Misclassification and prediction accuracy were calculated independently for each model and scaled to 0-100%. Outcomes were plotted as decision trees and reviewed to ensure logical ecological outcomes based upon our knowledge of the study system. We used the Spearman's rank sum test to evaluate the correlation between postfire redwood sprout characteristics (average sprout height, sprout area, number of sprouts, and proportion of redwood sprouting) and the field measured CBI (n = 22).

## Results

Our sampling captured the wide range of burn severities present at the WCRNA following the Chetco Bar Fire. Composite Burn Index measurements were well distributed, ranging from low to high (.71 – 2.77, Figure 2.3) at the 22 plots sampled across our study area. While we anticipated encountering unburned areas among our distributed plot locations, all sites visited were affected by the fire to some degree, and as such, no unburned plots were collected. Our recursive partitioning models applied postfire response data for each species in combination with two predictor variables (CBI and DBH) and accurately classified individual species response to fire (Figure 2.4). Cross-validated prediction accuracies were 88% for redwood, 87% for coast Douglas-fir, 86% for tanoak, and 80% for coast rhododendron (Figure 2.4).

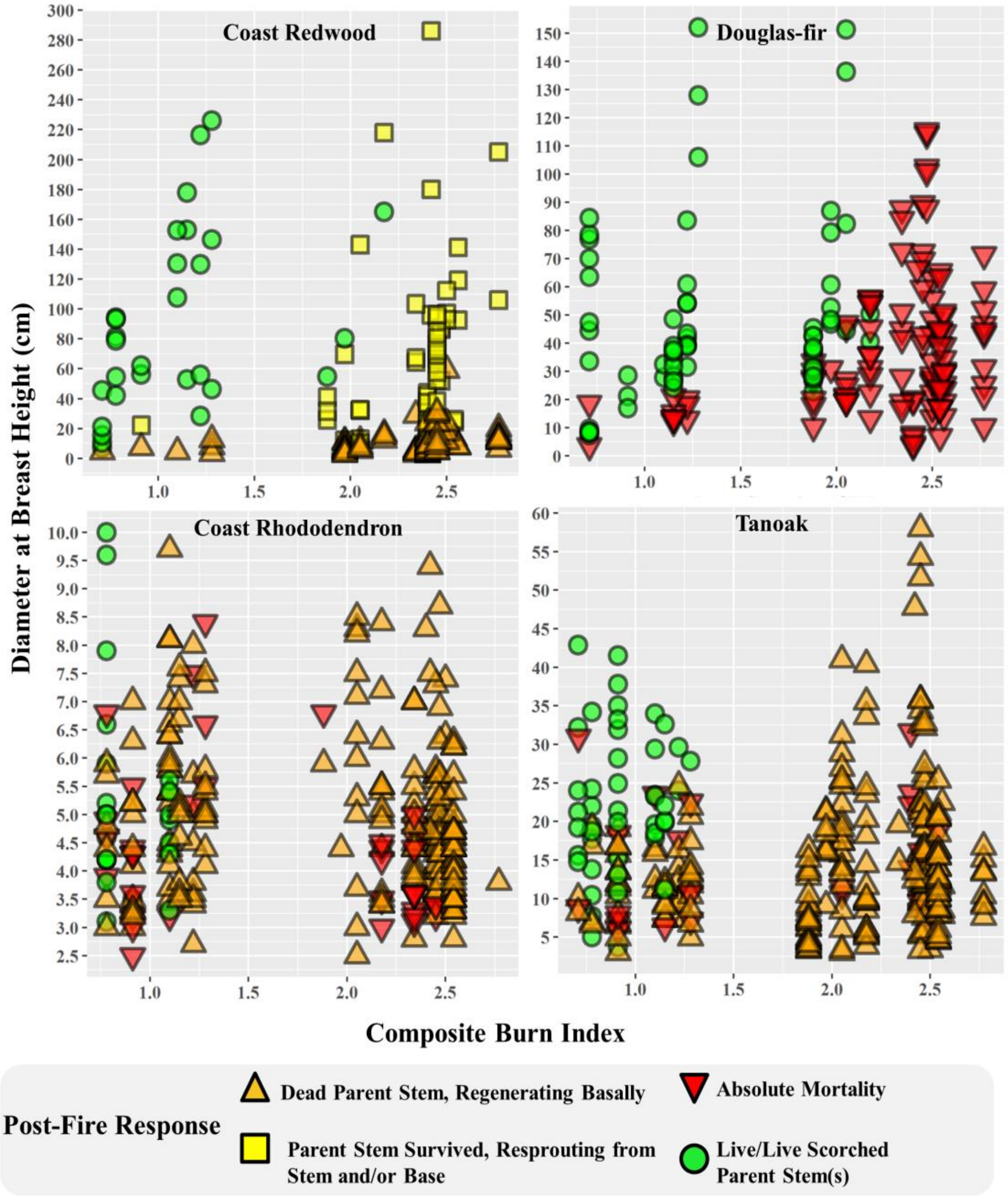

**Figure 2.3:** The postfire response of four community species across the range of sampled diameter at breast heights (DBH) and burn severities assessed by the Composite Burn Index (CBI) at the Wheeler Creek Research Natural Area, OR, USA.

Nearly all fire-affected redwoods lived through the event in some form. Larger redwoods that experienced lower to moderate burn severities were largely unaffected by the fire. Small trees, however, showed little resistance to fire at any level of burn severity, but remained highly resilient, resprouting from the basal burl in the event of parent stem mortality. As tree size and burn severity increased, the scorched primary stems of redwood typically lived and responded by sprouting epicormically and in many cases, the basal burl. This was typical of canopy dominant redwoods ranging in size from 30 to over 200 cm DBH, the primary response to fire by mature redwood individuals. Our recursive partitioning models (Figure 2.4) were effective in classifying these trends by showing that individuals <18 cm DBH were top-killed and regenerated from the basal burl regardless of burn severity. When burn severity was ≥1.6 CBI and trees were between 18 and 31 cm DBH, redwoods similarly died and regenerated from the basal burl. Trees ≥31 cm that experienced burn severity of ≥1.6 CBI were scorched but lived through the fire, responding by resprouting along the primary stem and in many cases, from the basal burl. Trees larger than 18 cm that experienced fire severities less than 1.6 had live canopies/stems and did not epicormically sprout.

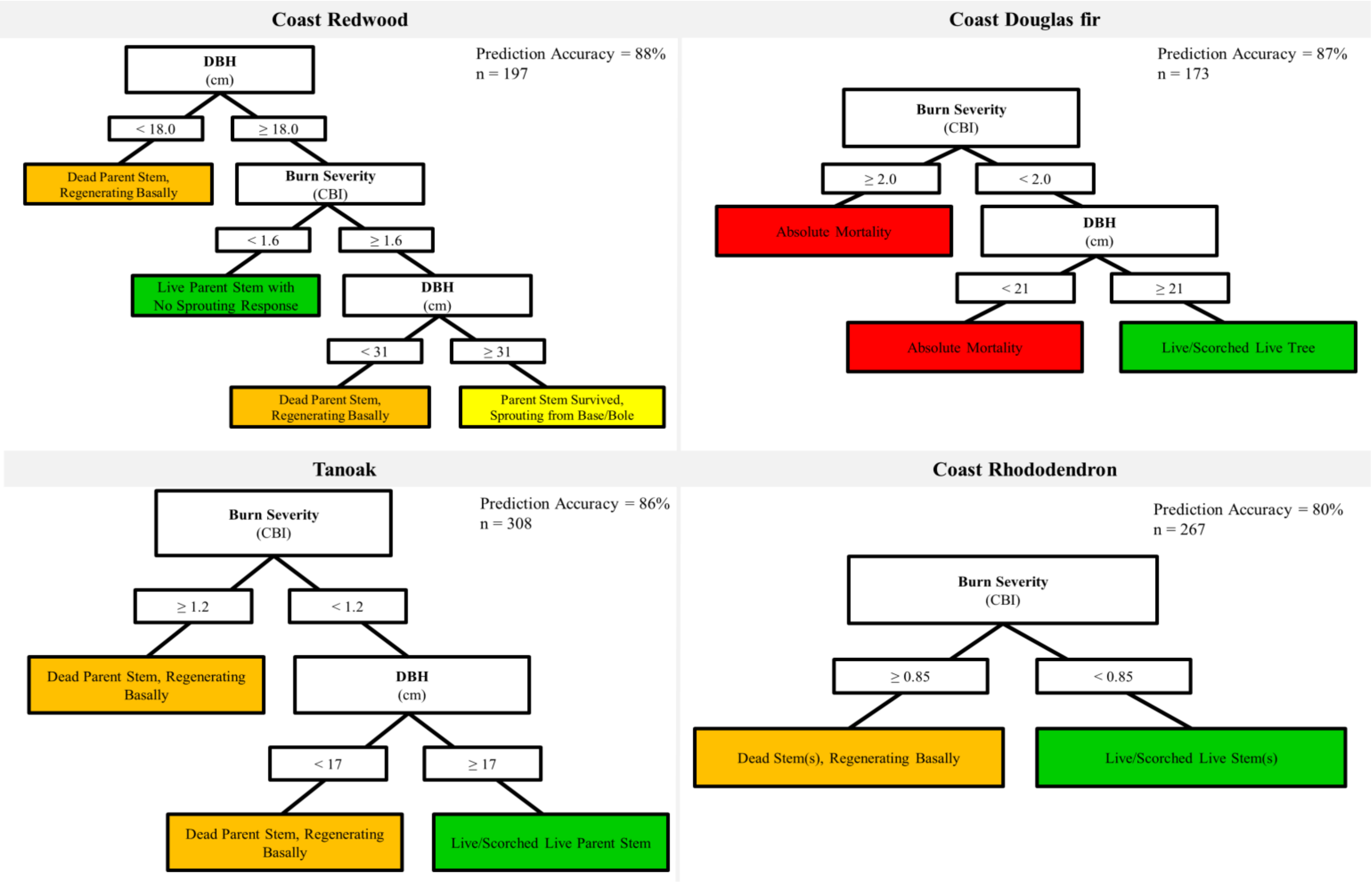

**Figure 2.4:** Recursive partitioning models displayed as decision trees for each of the four primary study species. Box colors correspond with those displayed in Figure 2.3.

The response of coast Douglas-fir individuals to fire was more simplistic. Large individuals were resistant to low to moderate levels of burn severity, but as burn severity increased, nearly all individuals died, regardless of size. Smaller trees were not resistant to any degree of burn severity. Our model for Douglas-fir (Figure 2.4) showed that at burn severities >2.0, trees died regardless of their size. When a tree was ≥21 cm DBH and burn severity was <2.0, these larger trees lived, but trees <21 cm DBH died.

Tanoak was resistant to fire at very low levels of burn severity, but as burn severity increased, trees were nearly always top-killed and regenerated basally. Absolute mortality did occur in tanoak but with no discernable trend (Figure 2.3), and absolute mortality was an unused category in our recursive partitioning model for the species. This model (Figure 2.4) showed that tanoak experienced primary stem mortality regardless of size at fire severities ≥1.2 and at burn severities < 1.2 when the tree was <17 cm DBH. In low severity fire (<1.2 CBI) trees survived if they were ≥17 cm DBH.

Coast rhododendron had little resistance to fire. At very low levels of burn severity, some individuals remained unaffected, but in nearly all cases, rhododendron stems died and vigorously resprouted from their root collar. While absolute mortality was shown to occur in some individuals, it also did not occur with a discernable trend and was an unused category in our recursive partitioning models. This model (Figure 2.4) showed that coast rhododendron parent stems died and regenerated basally regardless of stem size when CBI was ≥ 0.85 and lived if burn severity was <0.85, making it the least fire-resistant species in the Wheeler Creek community, but highly resilient.

Postfire redwood basal sprouting response was positively correlated with burn severity (Figure 2.5). As burn severity increased, redwoods were more likely to sprout ($R^2$ = .44, p <.001, n=22), sprouts were more numerous ($R^2$ =.61, p <.001, n = 22), grew taller ($R^2$=.60, p <.001, n = 22), and covered a larger ground area ($R^2$ = .74, p<.001, n = 22). One year following the fire, we encountered no seedlings of any of the primary study species at our plot locations, regardless of burn severity, but this is likely attributable to the late season nature of the fire event.

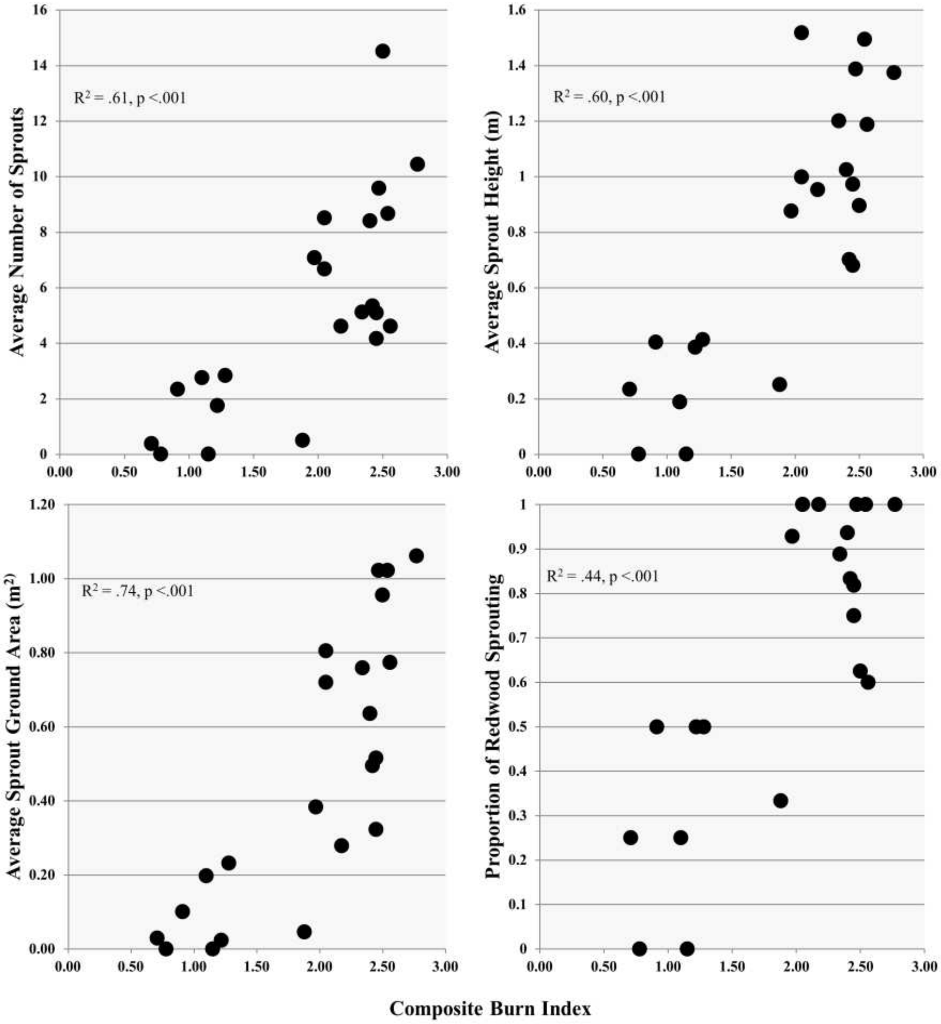

**Figure 2.5:** Plot wide average postfire basal sprouting characteristics and proportion of basally sprouting redwood individuals across a burn severity gradient following the Chetco Bar Fire at Wheeler Creek Research Natural Area, Rogue River-Siskiyou National Forest, Oregon, USA.

## Discussion

The 2017 Chetco Bar Fire provided us the rare opportunity to gather early postfire data on the interacting effects of burn severity, stem size, and species biology on survivorship and recovery in a northern range margin coast redwood forest community. Here, we applied these data to build simple predictive models that can be used to evaluate the potential effects and utility of fire. We found the impact of fire on the four primary forest species to be heterogeneous across the community, yet relatively predictable within each species, with burn severity, stem size, and sprouting ability acting as key drivers in the early structural and compositional modifications observed at Wheeler Creek. While our findings are from a single fire event, they provide important insights into postfire dynamics that were not previously available for this portion of the range, in a community type that has shown variable response and survivorship in previous studies spanning the range of coast redwood. We believe our findings are therefore applicable to similar upper slope redwood communities at the northern margin of the community type in southwestern Oregon and northwestern California.

### *Species and Community Response to Mixed Severity Fire*

Low to moderate severity fire regimes are thought to be most typical in coast redwood forests (Agee, 1993). At Wheeler Creek, sites affected by low burn severity saw the most significant effects in the understory, with the middle to upper canopy layers left lightly scorched or intact (Figure 2.2). As such, low severity fire had the most intensive impacts on coast rhododendron, which nearly always died and regenerated from the base regardless of stem size, and on small redwood parent stems <18 cm DBH, which died and regenerated basally regardless of burn severity. The three tree species showed increasing resistance to low severity fire as stem sized increased. On plots burned with moderate severity, fire more significantly altered size diversity of the forest community, as Douglas-fir < 21 cm DBH typically died and redwood <31 cm DBH and tanoak of all sizes were most typically top-killed and “reset” to regenerate basally. The propensity of these small to medium sized tanoak, rhododendron and redwood to die and regenerate basally shows a lack of fire resistance but a high degree of resilience (Ramage et al., 2010). Larger Douglas-fir (≥21 cm DBH) and redwood were both more resistant to the effects of moderate severity fire, but high burn severities resulted in the most variable response among the coniferous species. While redwood individuals were often crown scorched in high burn severity areas, individuals ≥ 31 cm DBH typically responded by sprouting from axillary buds along larger branches, with dense ‘fire columns’ of sprouts present along many parent boles. The ability of crown-scorched redwood to resprout from their bole and burl made stand-replacement absent on even the most severely burned sites, and likely provides redwood an advantage in postfire recovery and persistence over less fire resistant or shade tolerant species (Ramage et al., 2010; Lazzeri-Aerts and Russell., 2014; Brousil, 2016). In contrast, high severity fire considerably impacted co-dominant and old-growth coast Douglas-fir individuals of all sizes.

While Douglas-fir is considered fire resistant at low to moderate burn severities (Wright and Bailey, 1982) and sometimes reliant upon occasional fire to reach stand dominance (Sillett et al., 2018), nearly all Douglas-fir individuals died at our plots where burn severity was high. This makes an initial species composition shift in the upper canopy layer of our site likely and canopy gaps pronounced. Here, redwood individuals in the upper canopy hold a significant advantage over Douglas-fir in their ability to resprout epicormically, and tanoak and redwood of all sizes hold an initial competitive advantage in their ability to regenerate basally. These patterns are not distinct from those described by Thornburgh (1982), who predicted existing hardwoods to initially outcompete Douglas-fir in postfire environments because of their ability to resprout from their root collar. How the presence of regenerating, canopy dominant redwood individuals will affect long-term Douglas-fir recruitment on these sites is unknown, but we can infer that seed-dependent coast Douglas fir may be initially excluded from the upper canopy on high severity burn sites, where tanoak and redwood may subsequently release into gaps formed by dead Douglas-fir through advanced basal regeneration. Future Douglas-fir recruitment would then depend on seed availability and sufficient canopy gaps for the light-dependent species to germinate and maturate across time (Viers, 1980). Still, the mixed severity nature of the burn across our site left viable individuals of each of the primary forest species at Wheeler Creek, making potential compositional changes described likely to occur only at localized scales.

### *Seedling Regeneration and Coast Redwood Basal Sprouting*

Seedling regeneration was absent on our site regardless of burn severity one year following fire, but we believe this was a short-lived phenomenon likely as a result of the timing of the Chetco Bar Fire itself. While studies have shown vigorous seedling regeneration of redwood and associate species one year following fire in similar communities (i.e., Lazzeri-Aerts and Russell, 2017), the Chetco Bar Fire burned the WCRNA in mid-September, months later in the year than most reported research accounts. We hypothesize that the late season fire and postfire environment likely prevented seed germination at Wheeler Creek in the first postfire year. Indeed, observational accounts on our site two years following fire have confirmed vigorous seedling regeneration in many burned areas of the WCRNA. Long-term monitoring is now planned to understand seedling survivorship and composition across time, but the lack of seedling recruitment one year following fire highlights the importance of advanced basal regeneration in this early post fire environment.

The ability of a tree species to resprout from the base offers a considerable advantage in recovery from intensive disturbance (Del Tredici, 2001). Redwood basal sprouting ability is well established (Cole, 1983) and is reviewed extensively in O'Hara et al (2017), but the influence of burn severity on sprout presence and growth has been largely unexplored at the northern range margin. We were surprised to find such a strong correlation between burn severity and plot wide basal sprouting characteristics. As burn severity increases, heat and charring affect the lignotuber more significantly (Sawyer et al., 2000) and as a result, it seems that more buds are activated to sprout. Higher severity fire also creates more extensive canopy gaps, allowing more light to reach the forest floor. Therefore, these environments may enhance sprout growth (Cole, 1983), both in height and area, in postfire environments. While it has been inferred in early postfire research, it is largely unknown whether greater basal sprout density or sprout height results in a higher potential for redwood to outcompete associate species or to maturate over longer time periods successfully. Long-term research is warranted to quantitatively track redwood sprout development, self-thinning, and growth across time to confirm this inferred relationship.

### *Management Considerations*

Determining the role of fire in management or the appropriateness of exclusion of wildfire in the remaining old-growth and mixed age coast redwood communities like those at Wheeler Creek must be carefully considered based upon prescribed objectives for the managed area. The long-term outcomes and utility of prescribed or wildland fire is highly dependent upon pre-fire forest structure and the potential to project and/or control burn severity. Our simple decision tree models can be used in pre-fire scenario planning at sites similar to the Wheeler Creek Research Natural Area to project species survivability and system trajectory across a range of potential burn severities and tree sizes. We offer the following management considerations from our observations in the post-fire environment at the northern range margin of the species.

In the estimated century of fire absence on the WCRNA prior to the Chetco Bar Fire, coast rhododendron had developed into relatively tall, dense thickets in the understory of many of our sites, likely limiting light and resource availability for the recruitment of new individuals of each of the primary tree species. It appears that fire of nearly any severity will at least temporarily reduce rhododendron cover, which may provide an opportunity to recruit new individuals of other species in stands where natural upper canopy gaps exist. Therefore, low severity fire may have the most utility in management on sites dominated by larger, more fire-resistant redwood and Douglas-fir that lack size and age diversity as the result of fire exclusion and corresponding dense understory cover. Next, the reduction of tanoak has been cited as a management priority in some protected redwood communities (O'Hara et al., 2017), but we believe fire is an unlikely avenue to effectively exclude the species over long periods, as basal regeneration at WCRNA was robust one year after fire, and the species is highly shade tolerant (Tappeiner et al., 1984). Next, on sites where the understory is naturally free of vegetation, the utility of fire may lie in stimulating new clonal development of redwood on and around existing parent stems. This can create age diversity for the species and promote site persistence (Douhovnikoff et al., 2004), but would likely require at least moderate burn severity to successfully initiate sprouting in large redwood trees, which could result in undesired old-growth Douglas-fir mortality (Figure 2.4). Our findings are in agreement with recent research that suggests caution in salvage logging redwood individuals in an early postfire environment (Lazzeri-Aerts and Russell, 2014) if post-fire management objectives include retaining viable individuals. Since salvage logging is often carried out quickly following a fire event, it would be challenging to discern which individuals will epicormically resprout based upon visual evaluation alone. If salvage logging is prescribed and a manager's goal is to extract only dead redwood stems, we would recommend against extracting trees larger than 30 cm in diameter, as trees of this size lived through fire of any severity observed at Wheeler Creek. Finally, it is important to note that charred individuals in burned forest communities can sometimes experience delayed mortality. While we carefully evaluated the postfire status of each tree in our sampling to prevent misclassification, future studies should consider revisiting fire-affected sites in subsequent postfire years to assess the degree of delayed mortality and/or recovery.

## CONCLUSIONS

High severity fire was well tolerated by large coast redwood individuals and Douglas-fir showed considerable fire resistance in low and moderate severity fire. In addition, the biological ability of three of the four primary woody species at Wheeler Creek to resprout resulted in a highly resilient postfire community that quickly initiated recovery. Still, fire has significant potential to modify community structures at localized scales and has potential to promote stand dominance of sprouting species over Douglas-fir in early postfire environments. Longer-term monitoring across a range of redwood communities and continued fire history research would help to solidify our broader understanding of the utility and role of fire, but insight from early postfire studies like these provide valuable management guidance in the consideration of system recovery, postfire stand management, and to stimulate new growth and reduce mortality in prescribed and natural fire events. While fire of any severity did not result in mortality of old-growth redwood at Wheeler Creek, large redwood trees have been known to die in high severity fires in the past (Agee, 1993; Metz, 2013). Further research is needed to understand an old growth redwood's survivability in the face of compounded severe fire events, which is critical to our understanding of the utility or risk of fire in old-growth systems in a region that is projected to experience more frequent and intensive fires in the face of global climatic change.

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# CHAPTER 3 — NOVEL MAXIMUM TEMPERATURES DO NOT IMPEDE VIABLE SEED PRODUCTION IN *SEQUOIA SEMPERVIRENS* (COAST REDWOOD)

## Introduction

By the end of the 21st century, mean maximum temperatures in California, USA are anticipated to increase between c. 1° C and 6° C under low and high trajectories of potential warming, respectively (Weiss et al., 2013). Increased temperatures across the growing season of coniferous tree species can alter historical phenological patterns (Saxe et al., 2000; Richardson et al., 2013, Prevéy et al, 2018) and effect cone and seed production, germination, and establishment (Kroiss and HilleRisLambers, 2015; Kramer et al., 2020). If warmer temperatures modify any one of these processes, there is potential that a species' regeneration niche could be out of equilibrium with its environment in the future (Grubb 1977).

While it is common to explore the influence of novel environmental conditions on seedling establishment and growth in forest systems, the earliest stages of the regeneration niche, including the production of cones and viable seeds, have received far less research attention. In some conifer species, warming temperatures have been negatively correlated with cone production (Redmond et al., 2012) and have altered the timing of seed dispersal and germination (Liu et al., 2015). Warmer temperatures across populations have also been shown to reduce seed viability in some species (Gruwez et al., 2014) and increase viability in others (Daubenmire, 1960; Roland, 2013). As such, further exploration of the degree to which modified thermal conditions will influence successful cone and seed production in conifer species will be critical to our understanding of a species ability to successfully reproduce under future projected temperatures (Brown et al., 2018).

Exploring the influence of warming temperatures on the reproductive capacity of terrestrial plants has traditionally been a logistically difficult experimental process (Hurteau and North, 2008;

Hansen and Turner, 2019), which is often carried out through long-term studies or warming experiments (Kueppers et al., 2017; Hanninen et al., 2019). While these experiments can be carried out quite effectively for annual plants that quickly mature and reproduce (Quan et al., 2020), they are particularly difficult to conduct with long-lived tree species which may not reproductively mature for decades after establishment. In addition, the high costs required to effectively simulate projected thermal conditions on large and mature trees are often prohibitive (Wu et al., 2020). These factors have hampered our ability to effectively explore the influence of warming and novel temperatures on the reproductive processes of well-established and mature individuals of long-lived tree species, such as *Sequoia sempervirens* (coast redwood). Recently, however, interest has grown in the utilization of trees planted outside of their modern range in thermal conditions that may be more similar to those of the future, in an effort to understand some of the potential impacts that increased warming may have on a species reproductive processes, phenology, and growth (Sax et al., 2013; Booth, 2017; Primack et al., 2021).

Viable seed production in coast redwood is not reliable (Morrison et al., 2021). Within the species' native range in California and Oregon, USA, cone and viable seed production is highly variable across environments and time (Rydelius and Libby, 1993; Griffis, 2009; O'Hara, 2017; Morrison et al., 2021). This phenomenon and its causes are not well studied or understood (McBride and Jacobs, 1977; Noss et al., 1999). In some years, coast redwood individuals produce cones abundantly (Boe et al., 1968), and at least a small number of cones are produced in most years (Olson, 1990; Morrison et al., 2021). The cones, however, often contain a high percentage of seeds that are not viable (typically 0-15% viability when unprocessed; Lott et al., 1923; Olsen et al, 1990) because they are empty (lacking an embryo), resin filled, or more rarely, pathogen infected (Hansen and Muelder, 1963). Observations from a number of plantation environments have also found that cone and seed production of coast redwood may be influenced by its environment. In some areas of Hawaii and Australia, for example, where coast redwood otherwise thrives in plantation environments, well-established trees reportedly completely fail to produce ovulate cones or pollen at some sites, making reproduction by seed impossible (Libby et al., 2017; Roger Smith, *personal communication*, March 2020).

Because of the relative rarity of coast redwood seedlings in old growth habitats and in hotter, drier portions of the species range, some have hypothesized that the seed regeneration niche of coast redwood is out of equilibrium with its environment. Under this scenario, the species' long-term persistence in these areas is largely attributable to a combination of its long-lived nature and ability to sprout, with seed reproduction playing little or no role in the hottest and driest portions of the range (Reid, 1996). While rare, seedling establishment does occur in warmer and drier range margin environments but is more likely in moist years or following a disturbance event (Noss et al., 1999). A number of studies have explored factors that influence seedling survival in coast redwood forests in central and southern portions of the redwood range (Jacobs et al., 1989), but the influence of viable seed production as a potential bottleneck in the regeneration niche of the species has never been explored, particularly in the context of novel thermal conditions.

In California, USA, where nearly the entire modern distribution of coast redwood lies, the species has been planted extensively over the past century. It can be found in plantations, parks, botanical gardens, at century-old homesteads, along highways, and in neighborhoods throughout coastal, central, and southern California. Many of these regions have considerably warmer average and maximum temperatures and longer growing seasons than any area where coast redwood naturally grows today. This makes these established plantings a unique resource for exploring how the species' production of cones and viable seeds may be altered under novel thermal conditions projected for the future. Given the uncharacteristically low seed viability of redwood in its native range and its apparently unreliable production of cones and seeds in new environments, we asked: how is seed viability influenced by temperature, and how could increases in maximum temperature projected for the end of the century influence cone, viable seed, and sprout production in coast redwood? To answer this question, we utilized surveys and cone collections from plantings of coast redwood both inside and outside of the native range to explore how the production of cones, viable seeds, and basal sprouting may change over a 16.2 °C maximum average temperature gradient, including increases of c. 1 – 5.2 °C over any existing conditions known to occur in the native range.

## Methods

We first located the site with the hottest maximum average temperature for July (hereafter "maximum temperature") in the native range of coast redwood using occurrence locations from the USDA Forest Inventory and Analysis program (Smith, 2002; McRoberts et al., 2005; Tinkham et al., 2018; Stanke et al., 2020). Maximum temperatures are projected to increase up to c. 6 °C in the coast redwood region by the end of the century (under MIROC-ESM, RCP 8.5; Watanabe et al., 2011), so we sought out regions of California where coast redwood is known to be planted that had average maximum temperatures for July that were 1 – 6 °C warmer than the hottest site in the redwood region in the present day (hereafter, "novel conditions"). We subsequently located established coast redwoods planted outside of the species' native distribution in these novel thermal conditions in Lake, Yolo, Sacramento, Sutter, Butte, Glenn, and Shasta counties. Our selection of trees in these regions as proxies for projected future thermal conditions is consistent with results from existing climate analog research, which showed that there is considerable projected climatic similarity between cities at the eastern edge of the redwood range margin in the future and areas of the northern Central Valley in the present (Fitzpatrick et al., 2014). We compared trees growing in these novel conditions to a baseline group of established, planted redwoods growing within areas of Santa Cruz, Sonoma, and Napa Counties across a range of thermal conditions where the species is native (hereafter "baseline conditions"; Figure 3.2). All baseline and projected climate data were obtained from the Basin Characterization Model (Flint et al., 2013), which downscales PRISM climate data as its reference climate dataset (Daly et al., 2000).

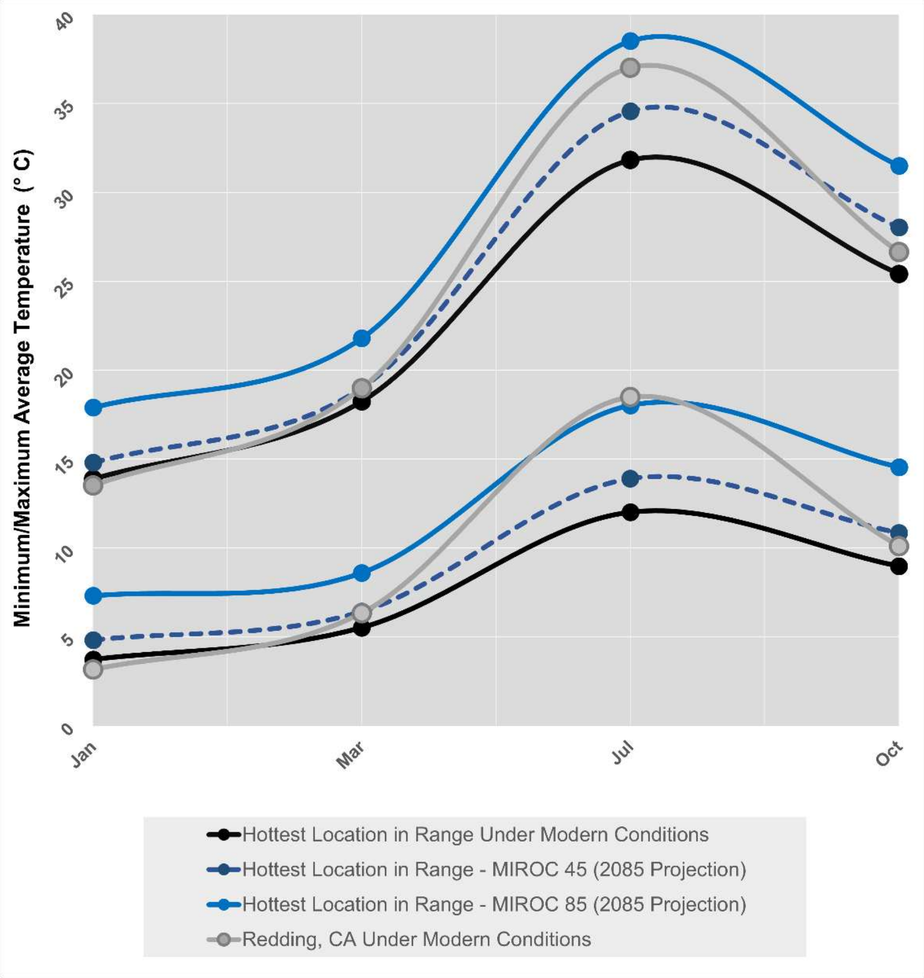

**Figure 3.1:** Annual temperature variability in the hottest region of the redwood range in baseline conditions compared to future temperature for 2085 under MIROC RCP 4.5 and MIRCO RCP 8.5 projections. Modern temperature conditions in Redding, CA (shown here) and many areas of the California Central Valley and Coast Range serve as suitable proxies for future projected thermal conditions in the redwood range for much of the year.

Cone collections were conducted across a c. 400 km latitudinal gradient over a 17-day period in October 2020 (Figure 3.2). In the native range, October typically represents a period when cones have begun to ripen but have yet to disperse seeds (Roy, 1966; Olson et al., 1990, Sloan and Boe, 2008). We sampled cones from individuals on as many different sites as possible in each region to encompass the range of ages, provenances, and conditions that existed across sites which could influence seed viability. We recorded the location of each tree with a GPS unit, measured its height using a hypsometer, and estimated the abundance of cones (light, medium, heavy) on each tree. Coast redwood can produce many thousands of cones in dense clusters, so exact quantification of the number of cones was not possible (Table 3.1). We also observed and noted cone ripeness by photographing trees and recording the presence of cones that were other than green to greenish yellow in color. We also noted the presence or absence of basal sprouting for each tree.

**TABLE 3.1:** Description of characteristics of trees with light, medium, and heavy cone production.

| **Estimated Cone Abundance** | **Definition** |
|---|---|
| Light Cone Production | Trees where cones were difficult to locate without close inspection. |
| Medium Cone Production | Cones could be easily seen but were scattered intermittently across the tree. Few large clusters of cones |
| Heavy Cone Production | Trees that had cones as a prominent visual feature throughout the tree. Large clusters of cones. |

Cones were collected by hand and with a 3 m cone rake from all aspects where cones were present (whenever available). They were then placed together into a paper bag, stapled loosely closed, returned to the laboratory and left to dry at room temperature (c. 20 °C) for three weeks. During this period, the bags were lightly shaken on occasion to promote airflow. By the end of the drying period, the cone scales had opened and many of the seeds had already dispersed into the bag. The

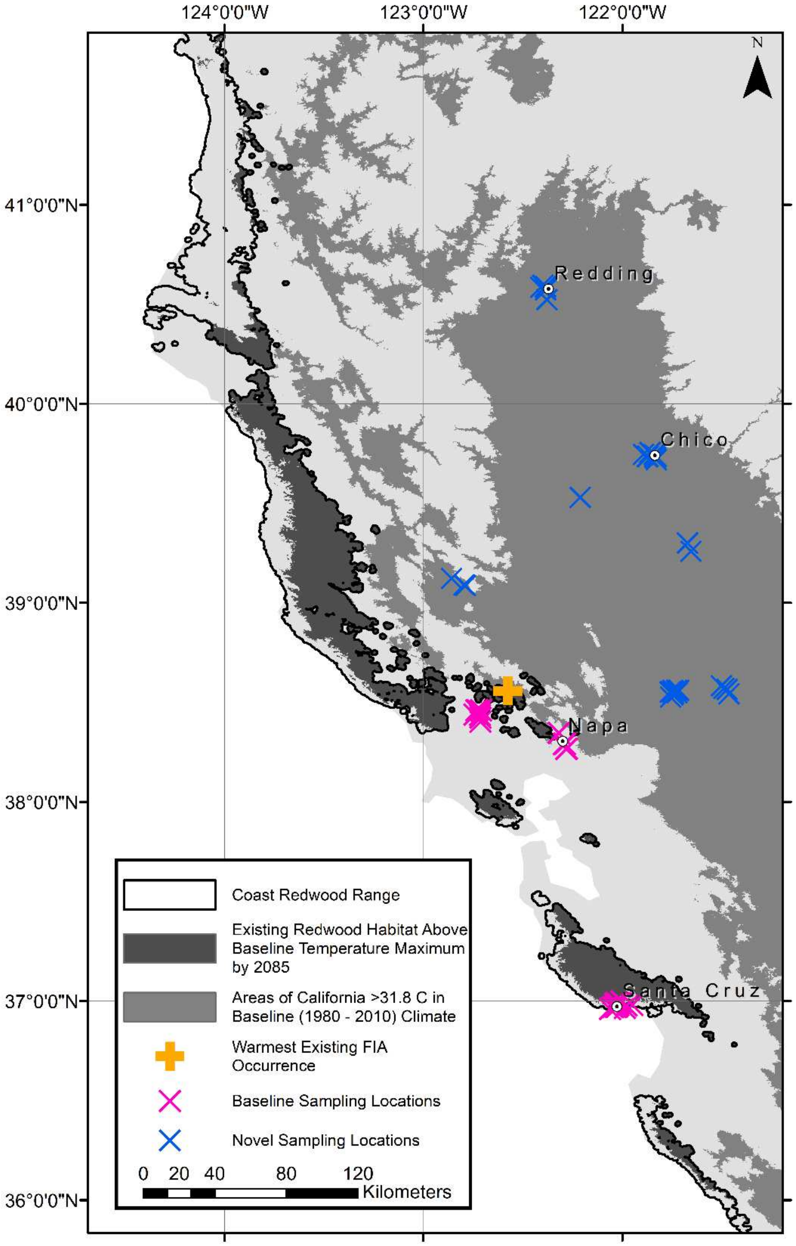

**Figure 3.2:** Map depicting baseline conditions in California that are suitable proxies for projected maximum temperatures in 2085, and the portion of the redwood range that would exceed those temperatures under the RCP 8.5 scenario.

bags were shaken for a final time, resulting in the mixing of seeds from all cones collected from a single tree. Seeds were sieved through a #12 mesh to exclude resin and chaff and to remove the very smallest seeds, which have been shown to be largely ungerminable in previous research (Lott et al., 1923). Discarded material consists primarily of red tannins in crystalline form (Davidson, 1971). Following sieving, all remaining non-seed detritus was removed.

There are no special germination requirements for redwood other than moisture (Boe et al., 1974, Sloan and Boe, 2008); however, we used conditions that were consistent with successful germination testing in the past (*summarized in* Jacobs et al., 1987). We counted two sets of 50 seeds from each parent tree to create two replicates for germination testing. In the rare event (n=3) that less than 50 seeds were available for each replicate, all available seeds were divided equally. Seeds for each replicate were placed on a three-thick layer of paper cloth in a 100 mm diameter plastic petri dish and moistened with 5 mL of distilled water. Plastic film was used to seal the petri dishes, and each sample was placed in a dark cabinet at room temperature (c. 20 °C).

Seeds were checked twice weekly for 52 days to track germination. We considered any seed with a radicle extending >2 mm from the seed shell to be a viable seed and any seed not germinated by this period to be unsound. After 52 days, the experiment was terminated because few, if any, seeds are known to germinate following this length of time (Lott et al., 1923). Percent seed viability for each of the 66 trees was defined as the average number of germinated seeds in both replicates divided by the total number of seeds tested. We allowed a subset of the samples to continue growth in petri dishes with moist paper following emergence. After the 52-day germination experiment, we counted the number of germinants in these samples that had successfully grown into seedlings, here defined as visible emergence of cotyledons (with or without the seed shell remaining), and growth of a root/shoot.

Statistical tests were implemented with Minitab software (v19.0) and $P < 0.05$ was used to determine significance in relevant tests We compared seed viability between the baseline and novel groups using a series of two sample t-tests. We analyzed correlations between temperature and seed viability and seed viability and tree height on a continuous scale using simple linear regression. To explore the potential that intra-annual temperature variability influenced rates of viable seed production, we used multiple regression and mean maximum and minimum temperatures of July and December (which represent some of the warmest and coldest months in the region, respectively) as independent variables. Qualitative data, such as cone production, ripening, and sprout production, were collated and reported.

## Results

The highest maximum July temperature at an FIA plot with coast redwood presence during the baseline climate period was 31.8 °C at a Napa County, CA site (38°33'21.6"N 122°34'33.6"W) where some of the easternmost natural redwood groves exist in isolated patches amongst mixed conifer, oak woodland, and agriculture (Figure 3.2). Under MIROC ESM RCP 8.5 projections, maximum July temperatures at this site are projected to be 38.5 °C in 2085, a 6.7 °C increase over baseline conditions. The site is projected to remain the hottest site where native redwood stands exist in 2085. Maximum temperatures in 2085 are projected to exceed 31.8 C under the MIROC-ESM RCP 8.5 scenario in a majority of the southern and eastern portions of the redwood range (Figure 3.2), making our findings broadly applicable to these regions under a worst-case warming scenario.

In the present study, we conducted sampling at sites outside of the native redwood range with novel maximum temperature conditions ranging from 33.7° C (Lake County, CA) to 37.0 °C (Shasta County, CA). Trees sampled in Redding, CA, the hottest novel sampling location, represent a 5.2 °C increase in maximum temperature over modern conditions in the hottest known site with native coast redwood presence. Samples extracted within the normal temperature gradient had maximum temperatures for the baseline period ranging from 20.8 °C (Santa Cruz County) to 30.2 °C (Napa County). In total, we sampled trees across a maximum temperature gradient of 16.2 °C.

Cones were collected from a total of 66 trees (39 in the novel group and 27 in the baseline group). Overall, 96% of the trees in the baseline group produced viable seeds and 92.3% of the trees in novel group produced viable seeds, although germination percentages varied widely within both groups. Seed viability for both groups was typical for unsorted coast redwood seed (Olsen et al., 1990): for the baseline group viability ranged from 0-28% (mean +/- S.D. = 9.30 +/- 7.64), and for the novel group 0 – 24% (mean +/- S.D. = 7.2 +/- 5.75). There was no significant difference between the mean percentage of viable seeds present in the baseline or novel groups (Figure 3.4; t=1.17, p = .250, DF= 45).

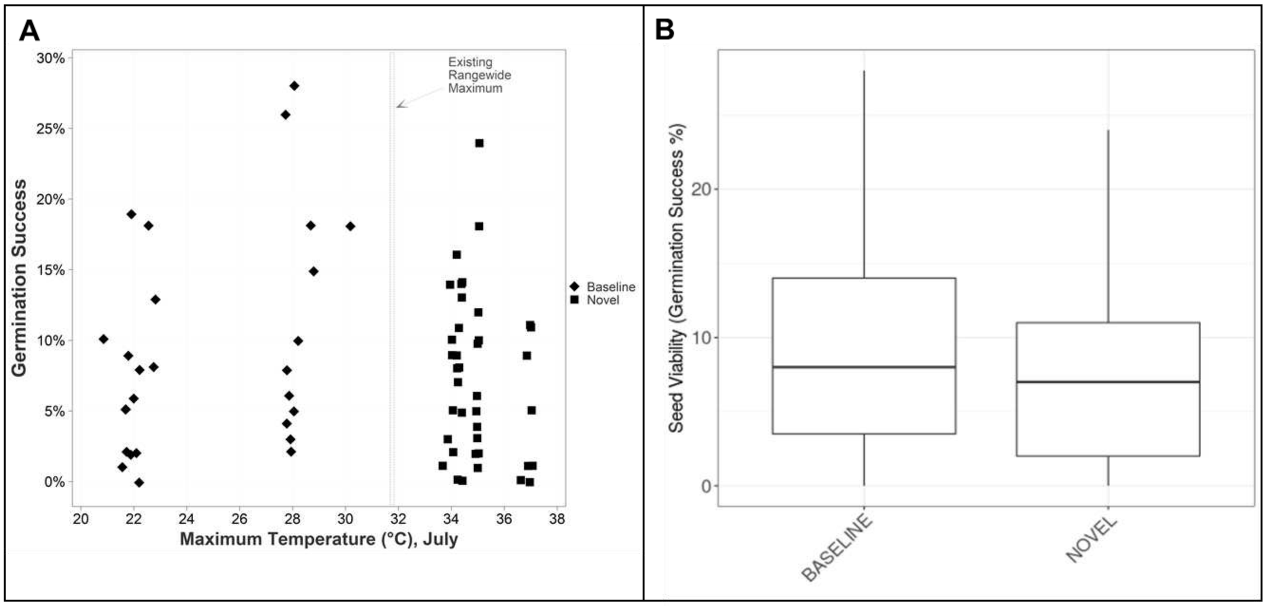

**Figure 3.3:** (**A**) Seed viability of 66 redwood trees in relation to mean maximum temperature in July. (**B**) Seed viability grouped between baseline and novel maximum temperature groups.

Scatterplots of these data show a spread of seed viability across temperature gradients consistent with those observed within the baseline group (Figure 3.3). Multiple regression also showed that average annual variation in temperature at our sites did not explain the variability in seed viability that we observed (adjusted $R^2 = .00$, $p = 0.680$). Most of the seeds that met our criteria for successful germination (>2 mm radicle emergence) subsequently developed into seedlings (93% in the baseline group and 91.2% in the novel group) suggesting that radicle emergence is a strong predictor of successful seedling development under ideal conditions.

Trees within the baseline group ranged in height from 12.8 m to 39 m (average = 24.6 m) compared to a novel group range of 10.4 m – 39.6 m (average = 23.5 m). No relationship was found between tree height (which may be correlated with tree age) and seed viability (adjusted $R^2 = .00$, $p = .321$). The tree with the highest viability (28%) in the normal group was a 15 m tall individual located in a public park in Napa. It was in a dense cluster of planted coast redwood. The individual with the highest viability in the novel group (24%) was a 24.4 m tall tree in a Chico neighborhood pocket park, which was also planted amongst other coast redwood individuals. The five individuals that produced no viable seeds were in Santa Cruz (1), Davis (2), and Redding (2). All of these trees were in proximity to other redwoods.

There was little variability in estimated cone production between the two groups. Most sampled trees had heavy cone production (59% for baseline, 59% for novel), followed by medium (33% for baseline, 26% for novel) and then light (7% for baseline and 15% for novel). Cone ripeness was highly variable within both the baseline and novel groups. Most trees had a range of ripeness from green to greenish yellow. In some cases, cones had already dried and begun dispersing seeds in both the baseline and novel groups. Many trees had some empty cones that had remained on branchlets from previous years. The proportion of trees that produced sprouts was similar between groups, with 77% of baseline trees and 67% of novel trees producing at least one basal sprout.

## Discussion

The goal of this study was to determine the influence of novel projected temperature conditions on cone and viable seed production in coast redwood. Coast redwood displayed considerable plasticity in its ability to produce cones and viable seeds across our sampled temperature gradient, providing an initial indication that increases in temperature alone may not impinge upon their development. Our findings also suggest that patterns of viable seed production under projected maximum temperatures will be similar to those observed under modern baseline conditions: highly variable amongst individuals, but low overall. While the majority of seeds produced were unsound in all trees, the vast majority of trees (>90%) produced at least some viable seeds. The lack of a significant correlation between temperature and viable seed production indicates that other environmental or genetic factors are responsible for differences known to occur across regions and environments.

While some studies have focused upon cone or seed production to determine the influence of increasing temperatures on conifer reproductive capacity, our tests of seed viability ensured not only that seeds were produced but that they were sound. This is an important consideration in a species with low seed viability under modern environmental conditions. Coast redwood strobilli develop into woody cones and produce many sterile seeds even in the absence of pollination (Berrill and Libby, 2017), making cone and seed production alone a poor indicator of seed viability. Our results show that redwoods grown under considerably hotter average temperature conditions than those observed today still exhibit successful male and female cone production, pollen transfer, and embryogenesis, which are all important components of the regeneration niche (Grubb et al., 1977; Rosbakh et al., 2018). In contrast, we cannot be sure that warmer conditions do not alter fecundity of an individual across time, as our study entails only a single year and used average climatic data, and cone and seed viability and production could vary across time and interannual variation in temperature.

Regardless of the location or environment of collection in our study, seed viability of coast redwood was low overall. The species expends substantial resources to produce many cones that are filled mostly with empty or sterile seeds. The cause of this consistently low viability remains an enigma, even though this phenomenon was first documented a century ago (Lott, 1923; Metcalf, 1924). A small portion of the sterile seed production is attributable to pathogenic infection, but most seeds are simply empty or filled with resins (Davidson, 1971). Weather conditions during pollen shedding have previously been observationally noted as a factor that could influence successful pollination, and therefore viable seed production (Roy et al., 1966). Other hypotheses for low viable seed production include genetic limitations on fecundity (Bonner et al., 2008), inbreeding depression (Libby et al., 1981), tree age and height (Lott, 1923; Roy, 1966), and proximity to other trees (Boe et al., 1968). Quantitative evaluations of the influence of these factors have not yet been explored. Conversely, low viable seed production may be advantageous for coast redwood. In other conifers, low seed viability and high seed production confers an evolutionary advantage against seed predators, which may not allocate their own energetic resources to locate viable seeds amongst the many seeds which would provide no nutritional value (Perea et al., 2013). Given the large quantities of cones and seeds produced by many redwoods, particularly in "mast" years (Morrison et al., 2021), low seed viability may be compensated for by the sheer number of seeds that are available and dispersed.

Our observations on cone ripening indicate that coast redwood will likely ripen in warmer futures at a similar time of year as those observed in the past (Boe, 1968). In early October, we saw trees with cones from green, to greenish-yellow, to just beginning dispersal across both baseline and novel environments. Basal sprouting was also a common occurrence in trees across both groups, indicating that sprouting will continue to serve as an alternative reproductive pathway in warmer climates. Cone ripening and sprout production under climate change both deserve further quantitative evaluations in future studies.

Planted redwoods growing in novel temperature conditions have potential to serve as valuable experimental resources that can be used to better understand how one of the tallest and most iconic conifers in the world may respond to environmental change over the next century, but caveats in their use remain. First, we were unable to control for the potential influence of covarying climatic factors other than temperature, such as moisture availability, on viable seed production. Because the sampled trees were growing in managed systems, we assumed they had ready access to moisture throughout the year, and therefore did not explore the potential influence of varied precipitation across sites. While warming temperatures alone did not seem to influence the early phases of redwood reproduction, interactions between moisture availability and temperature may be important and should be explored in future research. Next, all sampled individuals were of unknown provenance, and while experiments which tested variabilities in the growth and function of redwoods of different origin in new environments have been conflicting (Thimmappa et al., 1994; Ambrose et al., 2015), there is evidence that redwoods in the central portion of the region seemingly produce cones less often than other portions of the range (Rydelius and Libby, 1993). Finally, exact analogs for future maximum temperature conditions, particularly under the RCP 8.5 climate change pathway, are not available in California throughout the entire year (Fitzpatrick et al., 2014), but the areas we collected cones serve as suitable proxies for much of the year (Figure 3.1).

While our findings suggest that patterns of viable seed production are unlikely to be significantly modified by warmer temperatures alone, this does not indicate that the subsequent stages of the regeneration niche are resilient to future warming, and most quantitative evidence and observational accounts indicate that coast redwood will have trouble regenerating from seed in warmer and drier regions (Jacobs et al., 1987; Noss et al., 1999). Even in optimal environmental conditions, redwood rarely establishes by seed in undisturbed environments or old growth forests (Libby and Rydelius, 1993; Sillett et al., 2020). Most of the trees we sampled were likely planted as established, cultivated seedlings, rather than grown directly from seed on site. This has allowed many redwoods growing outside of their range to exist, persist, and sometimes flourish in very warm environments. Trees planted in Chico, CA in 1890 (Metcalf, 1924) have since grown into an impressive stand that has the feel of many older second growth redwood forests within the species' range. There is little evidence, however, that new individuals of seed origin have matured on the site over the past century, although some accounts do suggest that seedlings have established there for short periods in the recent past (Kuser et al., 1981). While cone and viable seed production seem plastic to warmer temperatures, subsequent stages of the regeneration niche, including germination and seedling establishment, may be less flexible. Therefore, a natural progression of this work would be to explore how effectively redwoods can establish from seed in much warmer environments than their native range, which has been shown to result in dramatic declines in seedling establishment in other conifer species (Hansen and Turner, 2019).

## Conclusions

Our results indicate that coast redwood's ability to produce viable seeds is largely unaffected by average maximum temperatures up to 5.2 °C greater than those experienced in any region where the species naturally grows today. This indicates that viable seed production is an unlikely bottleneck in the regeneration niche of coast redwood under projected end-of-century warming. While viable seed production seems unlikely to be hindered by projected future maximum temperatures, seed production between individuals was highly variable across a 16.2 °C temperature gradient and overall seed viability was low for a conifer. Cone production was frequent in novel environments and cones ripened at a similar time of year. Basal sprouts were also a common occurrence in novel temperature conditions and will likely continue to serve as an alternative reproductive pathway under warmer temperatures. Given the importance of seed regeneration in maintaining genetic diversity and expanding from range edges, all phases of the coast redwood seed regeneration niche deserve renewed research interest as the global climate warms. Planted individuals growing in novel conditions could therefore play an important role in researching and projecting the potential effects of warming temperatures and climate change on coast redwood.

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# CHAPTER 4 — SEED PREDATION INHIBITS *SEQUOIA SEMPERVIRENS* (COAST REDWOOD) SEEDLING EMERGENCE DURING A SANTA CRUZ MOUNTAINS, CA DROUGHT

## Introduction

Successful seedling recruitment in forest communities is a phenomenon dependent upon the spatial and temporal alignment of complementary environmental factors which support seed development, dispersal, germination, and establishment (Grubb et al., 1977; Romme et al., 1997; Kramer et al., 2020). For some species, such as *Sequoia sempervirens* (coast redwood or redwood), these factors rarely align to result in significant seedling recruitment, particularly in mature and old growth forest communities (Lorimer et al., 2009; Sillett et al., 2020). Redwood has the uncommon ability as a conifer to regenerate through vegetative reproduction (Ramage et al., 2010; Woodward et al., 2020), a regeneration strategy which has allowed the species to effectively recover much of its historical range following intensive extraction in the 19th and 20th centuries. Reproduction by seed, however, is an important mechanism to maintain genetic diversity (Douhovnikoff et al., 2004) and to support potential range shifts or range expansion across time, particularly as environmental conditions continue to be altered under global climate change (Davis et al., 2001).

A number of factors potentially contribute to a lack of seedling establishment in coast redwood forests. The biological characteristics of coast redwood seeds themselves are one potential factor limiting successful recruitment. The seeds have a short period of viability, germinating in the same year as dispersal (Olson et al., 1990). In addition, the majority of seeds produced by coast redwood are not viable, with typical viability ranging from 0 – 15% under optimal germination conditions (Roy, 1966). Site conditions may also limit the ability of viable seeds to successfully germinate and establish. Seedlings emerge most readily on moist and bare mineral soil in partial shade (Griffith et al., 1992), but these seedbed conditions can be scarce in undisturbed redwood forests, where a thick duff-layer is a common feature. Even when suitable seedbed conditions are available, which can be facilitated by disturbance events such as root-wad exposure, landslides, or wildfire, seedling recruitment has been reported to be highly variable in space and time (Lorimer et al., 2009).

In a study of competitive dynamics in redwood forests, Ramage et al., (2010) called seedling regeneration "scarce" across multiple disturbed sites throughout a significant portion of the species range, even in postfire conditions that ostensibly should be environmentally suitable for seedling recruitment. Woodward et al., (2020) found no seedlings in postfire environments one year following fire but observed seedling regeneration of seed origin at many sites in the second year following fire. Lazzeri-Aerts and Russell (2014) found that redwood seedling recruitment success varied significantly across a number of disturbed sites, but that abiotic factors, such as slope, aspect, and soil moisture, did not explain these differences in recruitment. Lazzeri-Aerts (2011) hypothesized that, among other factors, some of the differences in seedling regeneration success could be attributable to post-dispersal seed predation rather than site conditions alone. This potential "top-down" effect has never been explored in coast redwood forests.

Seed predation is an important factor influencing seedling recruitment success in a number of mixed conifer systems. In one study, seed predation of *Pinus sylvestris* (scots pine), assumed to be by birds and rodents, inhibited seedling emergence by up to 92% (Dulamsuren et al., 2012). In Zwolak et al., (2010), predation by deer mice nearly eliminated emergence and establishment success of *Pinus ponderosa* (Ponderosa pine) and *Pseudotsuga menziesii* (Douglas-fir; a coast redwood community associate), and also eliminated the beneficial effects of the postfire environment on supporting recruitment success when predator access was available. Similarly, vertebrate seed predators in the post seed dispersal period significantly reduced recruitment success of *Picea glauca* (white spruce) in logged forests of central Alberta (Peters et al., 2004). In combination, these studies highlight the potential for biotic pressures to considerably limit recruitment success in coniferous forest systems.

Given that no studies exist on coast redwood seed predation, little is known about the diversity of potential seed predators or their potential impact on seedling emergence, but limited observational accounts do exist. In a spot-wise direct seeding trial for redwood, Fritz (1950) noted that rodents may find and consume redwood seed both before and after germination. He noted that squirrels and rats likely only consume established seedlings. To the contrary, Boe (1975) reported that redwood seeds were an unlikely food source for deer mice and Roy (1966) hypothesized that although rodents may consume redwood seed, they are unlikely to significantly alter the effectiveness of seed fall. These conflicting accounts on seed predation and limited information on seed predator diversity leave their impacts on coast redwood seedling emergence and establishment an open question.

The primary goals of this study were to evaluate the influence of seed predators on seedling emergence potential in a mature coast redwood forest located in the Santa Cruz Mountains of California. In addition, we sought to identify mammalian and avian predators that may consume coast redwood seeds to improve our understanding of biotic pressures in these forest communities. To answer these questions, we deployed a network of paired seed sowing experiments with exclosures that offered variable access to seed predators, and deployed camera traps in front of redwood seeds to capture seed predator diversity. We subsequently tracked seedling survival and establishment of all emerged seedlings over 133 days during an extreme drought event that occurred throughout California in the winter, spring, and summer of 2020-2021 and compared site characteristics in the absence of seed predation that promoted seedling emergence.

## Methods

### *Site and Climatic Description*

The study was carried out in the southern portion of the *Sequoia sempervirens* (coast redwood) range on the University of California Santa Cruz Campus Natural Reserve. The Reserve is located in the Santa Cruz Mountains, ~ 6 km northwest from Santa Cruz, CA. Temperatures on site average 14.6 °C and annual precipitation averages 1225 mm. Our study system was located on a flat ridge at c. 350 m in elevation in a mature mixed evergreen forest that extends to the edge of a coastal prairie. The system is dominated by coast redwood, with *Pseudotsuga menziesii* (Douglas fir), *Arbutus menziesii* (Pacific madrone), *Quercus* spp. (oak) and *Notholithocarpus densiflorus* (tanoak) as primary associates. The largest conifers in an adjacent forest with a similar disturbance history were measured to be approximately 30 - 49 m in height and 90 – 124 years of age (Gilbert et al., 2010).

### *Seedling Emergence and Establishment Experiment*

Our seedling emergence and establishment experiment was carried out in the winter, spring, and summer of 2021 across 16 plots. Eight of the plots were distributed throughout a mature forest canopy. An additional eight plots were distributed on the edge of the mature forest in areas where tree density and canopy cover were comparably lower overall. Our seed predation exclosures and site preparation for seed sowing were modified from Zwolak et al., (2010) and Gray et al (1996). At each of the 16 plots, two patches spaced *c.* 0.75 m. apart from one another and covering 0.1 m² of the forest floor were cleared of duff and debris and roughened with a gardening hoe (Gray et al., 1996). This process was conducted to create matching seed bed conditions across sites and to serve as a proxy for natural ground disturbances within a redwood forest that expose bare mineral soil and that are thought to promote seedling establishment under natural conditions (Davidson, 1971; Lorimer et al., 2009). At each of the cleared ground surfaces, 200 redwood seeds were evenly rained by hand across the soil surface in an effort to mimic natural dispersal. Two-hundred seeds represents the approximate total number of seeds that are dispersed by three to four cones (Sloan and Boe, 2008). In some years, redwoods are capable of producing many thousands of cones per tree, but seeds do not disperse far from their parent trees, often accumulate in high densities following dispersal, and have low seed germination rates under natural conditions. The seeds were obtained from the same seed zone and elevation as our study site and were processed by the LA Moran Reforestation Center and tested to be 64% viable under optimal conditions (in laboratory germination testing). Seeds were spread in February, which coincides with the natural dispersal period of coast redwood.

Two thimble shaped wire mesh cages, one that allows seed predator access and one that does not, were randomly assigned to each seeded patch at each plot. The first cage was fully covered in wire mesh to exclude all mammalian and avian predators. The second cage was identical except for a c. 15 cm gap that was cut from 330° of the base of the circular cage to allow access to seed predators. Both cages were staked tightly to the ground. The cages were fit with diamond shaped mesh that did not prevent water entry and that did not considerably shade the ground below them.

### *Tracking Emergence and Survival*

The plots were initially visited on a biweekly basis to check for germinants. Any stray duff was occasionally removed and any non-redwood germinants were plucked. When the first coast redwood germinant was observed, we started to track emergence and survival on a weekly to biweekly basis. Seedlings were considered emerged if they were erect and a radicle was observed in the soil surface (Gray et al., 1996). All emerged seedlings were marked with a toothpick and tracked at each visit. As new seedlings emerged, these were added to the maximum total emerged, and as emerged seedlings died this was noted. When possible, the potential cause of mortality was also recorded. We also occasionally searched across treatments visually to inspect for the presence of broken seed shells or scat (signs of seed predation). Seedlings were considered "established" if they remained at the end of the 133-day study period. Over the course of the study, the sum of all emerged seedlings represents maximum total emergence, which includes both those seedlings that died and those seedlings that were alive at the end of the study period.

### *Identifying Potential Seed Predators*

To identify potential seed predators that may feed on coast redwood seeds prior to establishment, we deployed camera traps in and around the same forest stands as our seedling establishment experiments in 2020 and 2021. The camera traps were arranged in front of petri dishes (Zwolak et al., 2010) or on bare soil that were spread with coast redwood seeds. The camera traps were positioned 3-5 inches off the ground on a flexible tripod pointed directly at the seed offering. The cameras were set to take motion activated images and up to a 15 second video. If a potential seed predator was present in any image or video, we documented the species whenever possible (if identification was possible). Given that camera trap identification of small mammals can be unreliable where similar species ranges overlap (Meek et al., 2013), we selected to not make definitive identifications of individuals and instead estimated the genus, or if unidentifiable, the order, and provided our best approximation of the species identification. We also documented whether the individual(s) were captured consuming redwood seeds from the offering or left other indicators of predation, such as scat or broken seed shells (*high confidence* predators) or rather were in the direct vicinity of the seed offering without consumption observed or other indicators left behind (*potential* seed predators). We also tallied the number of individual observations of each predator, here defined as a unique image captured of a predator that occurred greater than one hour from the previous observation. As our goal was to document seed predator diversity, not abundance or rate of consumption, we did not attempt to track individuals or number of seeds consumed.

### *Site Factors and Statistical Analyses*

We collected canopy cover and soil moisture measurements at each plot to determine whether conditions that could influence emergence varied between the edge of the forest and the forest center. Gravimetric soil moisture was analyzed the first week a germinant was observed, following methods detailed in Black et al., (1965). A 10 cm soil core was extracted from each of the plots, with the sample being taken at a single location between the two treatments. The wet soil sample was weighed to the nearest 1/10 of a gram, placed in an oven at 55 ° C and dried until the dry weight did not change after multiple measurements. Soil moisture was calculated as the difference between the wet weight and the dry weight of the soil sample. Percent canopy cover was calculated using hemispheric photography and image analysis. At each plot, a hemispheric photograph was taken upwards towards the canopy from in between the two treatments. Each image was analyzed using *ImageJ* software to calculate percent cover.

All statistical analyses were conducted using the Statistical Package for Social Science Software (“SPSS”, version 28; IBM Inc.) and $P < 0.05$ was used to determine significance in relevant tests. Variables used in the statistical tests were tested for normality. When variables were found to be non-normal, nonparametric methods were utilized. We compared total seedling emergence success between treatments with and without predator access ($n = 16$ treatment pairs) using a paired sample non-parametric Wilcoxon signed rank test. We compared differences in soil moisture and canopy cover and emergence success in treatments that excluded seed predators by plot type (forest edge versus forest center) using the Mann-Whitney U test. We tracked seedling survival throughout the study and reported survivorship across time and compared this to observed drought conditions in the text. Climatic normals from 1980-2010 and daily climate data for the study period were obtained from the PRISM network (Daly et al., 2000). We used reports of the Palmer Drought Severity Index (Alley, 1984) from the NOAA National Centers for Environmental Information to report the status of drought conditions in the study region as the study progressed.

## Results

### *Seed Predation*

Seedlings successfully emerged at 50% of the treatments exclosed to predators and at 0% of the paired treatments with predator access (Figure 4.2). The average number of seedlings that emerged in exclosures was 3.94 (range: 0 – 27) versus zero at the paired treatments with predator access. The difference in the number of emerged seedlings between these two groups varied significantly (Z= -2.5, p = 0.01), indicating that seed predators reduce the number of seedlings that are able to successfully emerge. Signs of seed predation were found at all patches open to seed predators. The most common indicator that seeds had been predated upon included cracked seed shells, followed by the presence of scat. No cracked seed shells were observed at our paired treatment patches exclosed to predators, indicating that our exclosures were effective in removing access to seed predators.

Two species were confirmed, either directly or indirectly, to consume coast redwood seeds with high confidence (Table 4.1 & Figure 4.1). *Junco hyemalis* (Dark-eyed Junco) was observed on eight separate occasions consuming seeds. The species was observed consuming seeds both alone and in pairs. In video captures, the birds can be seen cracking seed shells open, consuming the embryo, and sometimes leaving the seed shell behind. On several occasions, Dark-eyed Juncos can be seen transitioning from feeding on the seed offering placed in this study to what appears to be naturally dispersed seeds in the surrounding forest duff layer. A rodent species, likely a *Peromyscus* spp. (deer mouse) individual, was also observed in a nighttime video over a sample dish apparently consuming the seeds. This was confirmed by the presence of mouse scat that was left on the same dish with broken seed shells.

**TABLE 4.1**: A listing of potential seed predators observed at the University of California Upper Campus Reserve in the study, confidence in predation, and a description of the observation.

| **Predator Observed** | **Predation Confidence** | **# of Unique Observations** | **Description** |
|---|---|---|---|
| *Junco hyemalis* (Dark-eyed Junco | High confidence seed predator | 8 | (A) Observed directly consuming redwood seeds in images and videos. Scat resembling that of a seed eating bird was regularly found at sites where the Junco was observed. |
| Rodent 1: probable *Peromyscus* spp. (deer mouse) | High confidence seed predator | 1 | (B) Observed apparently feeding on seeds in a nighttime video. Scat resembling that of a mouse was observed at the seed station within the petri dish. |
| *Sciurus* spp. (gray squirrel) | Potential seed predator | 2 | (C) Captured in images with head above seed offerings. |
| Rodent 2: probable *Neotoma* spp. (woodrat) | Potential seed predator | 2 | (D) Captured in images with body and head on and above seed offering. |

Two additional species were observed in the vicinity of the seed offering in images or videos but were not captured consuming the seeds directly or indirectly through remnant scat. A *Sciurus* spp. (gray squirrel) individual was observed with its head over the seed tray on one occasion and in direct vicinity of the seed offering on another occasion. In addition, a rodent species, which appears to be a species of woodrat (*Neotoma* spp.), was observed on two occasions in the direct vicinity of the seed offering. On one occasion, it was observed in an image directly on top of the seed offering.

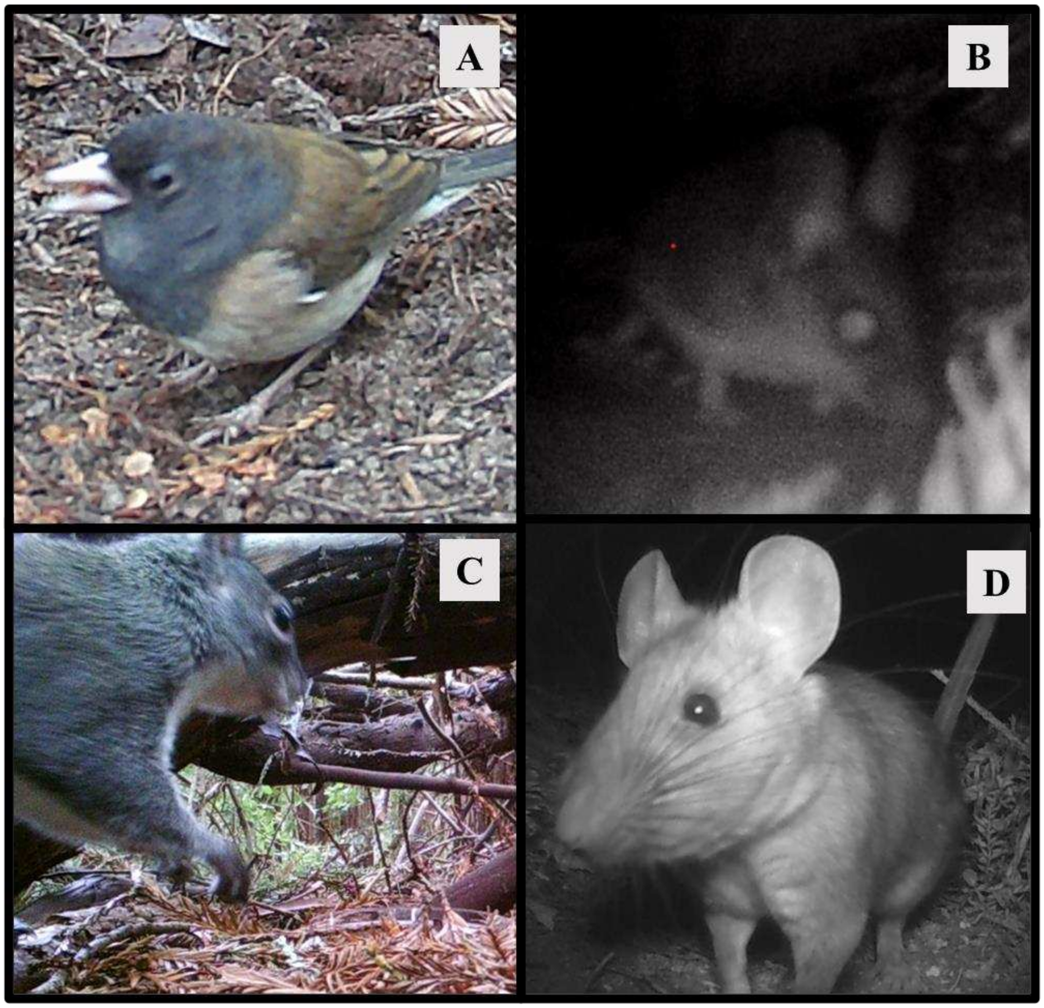

**Figure 4.1:** The four species captured by our camera traps confirmed or suspected of consuming coast redwood seeds and contributing to a lack of emergence of seedlings in sites open to predators. The letters align with the descriptions offered in Table 4.1.

### *Emergence and Survival Across Conditions and Time in Absence of Predation*

Since no seedlings emerged in our treatments with predator access, our analyses on seedling emergence across site characteristics were carried out using only the treatments which excluded predators (n = 16) which allows for an evaluation of environmental factors that may support seedling emergence and survival in absence of the pressures of seed predation. Treatments located on the forest edge (n = 8) had significantly lower canopy cover (Mann–Whitney *U*= 0.5, p = <.001) and soil moisture (Mann–Whitney *U*= 0.0, p = <.001) than sites in the forest center. Average canopy cover on the forest edge was 56% (+/- S.D. = 9.6) and 73.4% in the forest center (+/- S.D. = 1.5). Average soil moisture content on the forest edge was 16.4% (+/- S.D.= 5%), and 50% (+/- S.D. = 9.5%) in the center of the forest. While half of our sites had seedlings successfully emerge, 75% of those sites were located in the forest center, and 25% were located on the forest edge. The mean number of seedlings emerged was higher in the center of the forest (mean = 7.0; median = 5.0) than on the forest edge (mean = 0.875, median = 0) and the difference in seedling emergence between these two groups was significant (Mann–Whitney *U*= 12.0, p = 0.04).

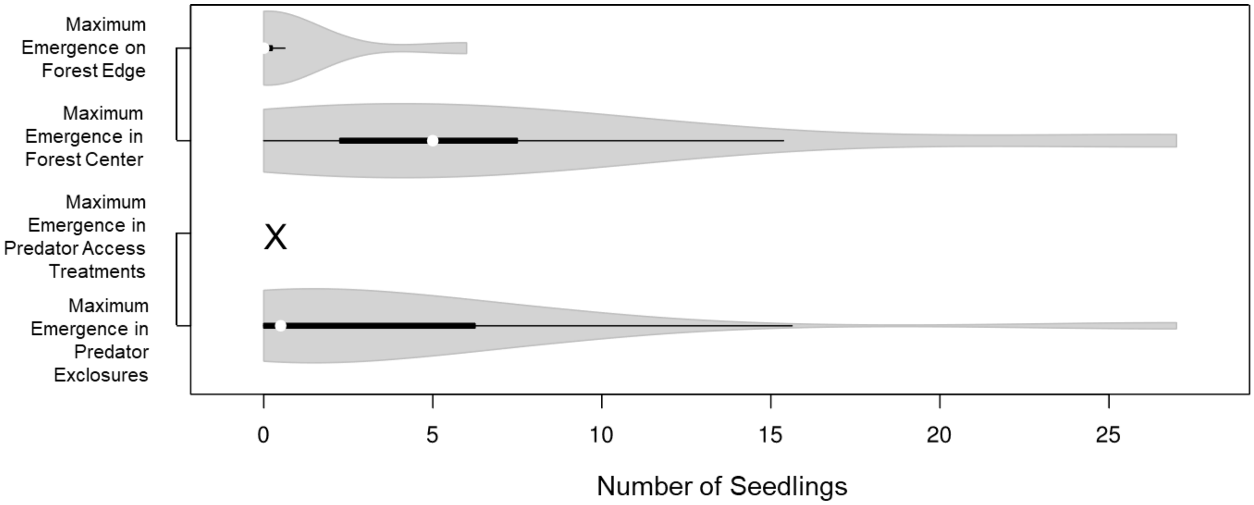

**Figure 4.2:** Violin plots depicting maximum emergence of seedlings throughout the study period across site conditions in absence of predation (forest edge vs. forest center) and maximum seedling emergence compared between sites with and without predator access. The white dot represents the median, the thick black bar represents the interquartile range (IQR)., the thin line represents the 1.5 x IQR, and the gray shows the distributional shape of the data. The X indicates that no seedlings emerged at these sites.

Seedlings were first observed emerging 53 days following sowing (Figure 4.3). Two precipitation events that exceeded 25 mm likely facilitated initial germination and emergence of the seedlings. Less than 4 mm of additional precipitation fell at the site for the remainder of the study period. At the beginning of our study in February of 2021, the study site was categorized as experiencing a moderate drought by the Palmer Drought Severity Index. By March, severe drought conditions

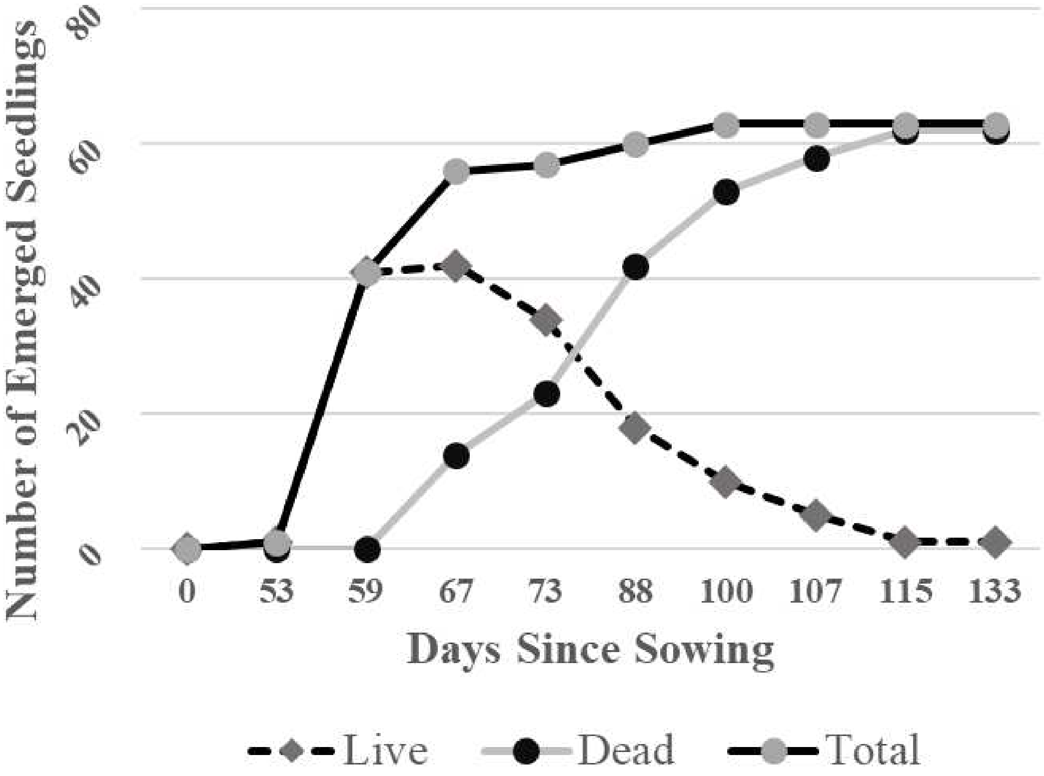

**Figure 4.3:** Total seedling emergence, survival (live), and mortality (dead) across time at 16 sites at the UC Upper Campus Reserve, Santa Cruz, CA. All seedlings that emerged were located in predator exclosures.

were present. By May, extreme drought conditions had initiated and remained to the end of the study. From the beginning of the seed sowing experiment to its end, the study area received 87 mm of precipitation. In contrast, total average precipitation from the 1980 – 2010 normal period for the same three-month period was c. 290 mm.

The first seedlings that emerged started dying approximately two weeks after initial emergence (Figure 4.3) and by the end of the study, only one seedling remained alive. Desiccated seedlings indicated that moisture availability was the primary cause of mortality. One seedling appeared to die as the result of damping off. The only seedling that survived was in a plot located in the forest center; no seedlings that successfully emerged were successful in establishing in the drier forest edge sites with lower canopy cover.

## Discussion

Our results indicate that seed predators have been an overlooked environmental factor that can inhibit successful seedling emergence in mature coast redwood forests. While low seed viability and lack of suitable sites have often been suggested as primary factors limiting successful coast redwood seedling recruitment, the seeds used in this experiment had high viability in laboratory conditions and our seedbeds were prepared to promote establishment. Still, no seedlings successfully emerged in treatments accessible to seed predators, and signs of predator activity were found at all treatments with predator access. As many as four species, including three rodents and one avian species, were found to potentially feed on coast redwood seeds. While rodents have been suspected of consuming redwood seeds in past planting trials (Fritz et al., 1950), this is the first study to successfully identify and document an avian species, *Junco hyemalis,* as a predator of coast redwood seeds.

Dark-eyed Juncos are known to consume seeds as a primary staple of their diet (The Cornell Lab, 2021). They are also well-documented as predators of *Pseudotsuga menziesii* (Douglas-fir) seeds, a coast redwood forest community associate. Hagar (1960) conducted a study in the inner coast ranges of northern California and found that the Dark-eyed Junco was the most abundant avian species in the Douglas-fir community. The same study reported that Douglas-fir seeds were a primary portion of the species' diet and that "the birds obviously influence forest regeneration." As a year-round resident of coast redwood forests, Dark-eyed Juncos may predate on seeds throughout the entire duration of seed dispersal (Boe et al., 1968). The Dark-eyed Junco is also a resident or migratory species in coniferous and mixed forests throughout North America. As such, their role as a potential seed predator, particularly their preference for various seed sources and their rates of consumption, deserves continued research attention in these and similar forest systems.

While we have effectively confirmed that the Dark-eyed Junco is a coast redwood seed predator, it was not possible to confirm that the species consumes redwood seeds at a greater rate than the other seed predators observed in our study. Small mammals, such as mice, which are often most active during night and move across the forest floor rapidly, are very difficult to effectively capture using camera traps (Glen et al., 2013). In contrast, Dark-eyed Juncos stayed in the vicinity of the seed offerings for 15+ second periods, making them easier to capture in images and video. Future studies could try to elucidate the relative contribution of each seed predator by tracking seed removal and consumption (Zwolak et al., 2010) and by placing camera traps coincident with seed sowing experiments for the duration of the study period.

Rates of seed predation vary as a function of seed predator diversity and abundance, which have been shown in a number of studies to fluctuate across time and space (Zwolak, 2010; Whelan et al. 1991). This may partially explain why some disturbance events in coast redwood forests result in considerable seedling recruitment while others do not. Coast redwood also has variable seed production patterns across time (Norman et al., 2009). In some years, trees produce only a small cone crop or no cone crop at all, and in other years the species produces crops that have been estimated to produce many thousands of cones per tree (Olson et al. 1990). As such, it is plausible that in "mast" years (Morrison et al., 2021), the supply of seeds on the forest floor may outstrip consumption potential by seed predators. Masting has been proposed as a defense against seed predators in past research in other conifer systems (Lobo, 2014), and it is plausible that this holds true for coast redwood.

Coast redwood's production of many empty seeds may serve as another line of defense against seed predators when a large seed supply is available. If the majority of seeds a predator seeks to consume are empty, past research in other conifers has shown that those seeds could be less appealing as a food source due to the energetic requirements of seed searching (Fuentes et al., 1998). Our use of seeds with relatively high viability may have resulted in higher rates of seed predation than may occur with seeds that are mostly empty, a characteristic that also varies across the species range and across time (Olson, 1990). Given the low moisture conditions during our study period, the seeds may have also taken longer to germinate than under optimal forest floor conditions, which may have also given the seed predators a longer period of time to locate and consume the seeds than may occur during wetter years that can promote more rapid germination.

While a significantly higher number of seedlings emerged under the forest canopy, where soil moisture conditions were initially higher, as the drought intensified into the spring and summer with little to no precipitation, even those seedlings in the forest center eventually died. Given insights from past research on the importance of fog to coast redwood (Dawson, 1998), we had initially hypothesized that seedlings under the forest canopy may fare better than those on the forest edge in drought conditions because alternative water inputs from fog drip may be available in these environments. Given the rapid decline of the seedlings, the contribution of fog drip was apparently not sufficient at our study site to sustain growth and further development of the emerged seedlings, but the topic deserves further research attention.

Finally, our results highlight the difficulty that coast redwood has in successfully establishing via sexual reproduction in hot, dry conditions that are becoming increasingly frequent at the species' southern range margins in California (Diffenbaugh et al., 2015). As drought conditions are projected to occur with more frequency under projected global climatic change, the already narrow window of opportunity to establish via sexual reproduction may further narrow in the future. As such, the coincidence of suitable seedbed conditions, seed availability, weak predation pressures, and suitable climates, which in combination can result in successful seedling recruitment, may also reduce in frequency.

## Conclusions

Our results serve as the first example that the biotic pressures of seed predation can significantly inhibit seedling emergence in coast redwood forest communities. While abiotic factors eventually led to a total lack of establishment of coast redwood seedlings at our study site, even in the absence of predation, the strong and early influence of seed predation may significantly alter regeneration dynamics in mature coast redwood communities when climatic conditions are more suitable for establishment. The combination of biotic pressures with the lack of ability to successfully establish in extreme drought conditions helps to partially explain the rarity of seedling establishment in coast redwood forest communities. As such, the "window of opportunity" for seedling establishment in these forests may become less frequent in years with higher predator abundance or as conditions throughout the coast redwood range become drier as climate change intensifies.

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# CONCLUSIONS

In this dissertation, I have provided new insights on the current and potential response of coast redwood forest communities to environmental pressures and change, with a special focus on range margin communities. I used models, observational studies, and experiments to explore the species' response to environmental perturbations across life stages (from seed to sprout to old growth trees) including wildfire, increased temperatures, regeneration from seed in drought, and the influences of the biotic pressures of seed predation on seedling emergence. I have built valuable tools and models and developed incremental knowledge on the resistance and resilience of coast redwood to environmental perturbations that can be expanded upon in the future as conditions continue to change and updated as new tools and resources become available.

In Chapter 1, I created new spatial climate change planning and adaptation tools for coast redwood. I demonstrated the utility of well-constructed, parsimonious species distribution models in climate change research and clearly reported their utility, caveats, uncertainty, and potential for improvement in the future. These projections can be used to identify regions that can be effectively conserved to buffer the species from the influences of climate change where it is most likely to continue to thrive, to identify priority research zones, and to explore the potential for natural and assisted migration. In addition, I conducted the first seed zone analog mapping for a California tree species, helping to answer the question: *If I want to plant a redwood tree here that will be well-adapted to future conditions, where could I go to get the seeds today*? These findings will hopefully stimulate researchers to evaluate whether different seed sources of coast redwood establish, grow, and persist better than others across environments and inspire California's forest managers to consider alterations and innovations to their existing seed sourcing program to support climate adaptation.

In Chapter 2, I reported findings on the early postfire response of an old-growth coast redwood forest community to a mixed severity fire event at the northern range margin of the species. Insights from this study help to identify the role and utility of fire in these communities and support the concept that high severity fire can result, at least in the system's early recovery phase, in the dominance of coast redwood. The resistance and resilience of coast redwood to fire in comparison to Douglas-fir and other community associates is attributable to its ability to sprout from its bole and base. The models that I created in this study can be used to help to predict the response and survivability of trees across species, stem sizes, and burn severities. Today, these insights are increasingly valuable following the occurrence of a number of large and severe fire events in coast redwood forest communities that started in the summer and fall of 2020.

In Chapters 3 and 4, I explore the sensitivity of two phases of the regeneration niche (viable seed production and seedling emergence and establishment) to biotic and abiotic environmental pressures. Researchers have been searching for the causes of low viable seed production and the rarity of seedling establishment in coast redwood forests for over a century. Through use of a novel sampling network of over 30 trees planted outside of the species range, I showed that coast redwood's ability to produce viable seeds is largely unaffected by average maximum temperatures up to 5.2 °C greater than those experienced in any region where the species naturally grows today, and that temperature and temperature variability are not strong predictors of viable seed production. While there are caveats in using planted trees in environmental research, creativity is and will continue to be necessary to begin creating an understanding of how long-lived species may respond to conditions that are well outside of those experienced in their natural distributions. My findings provide an initial positive indicator that warmer temperatures projected for the future are unlikely to significantly alter viable seed production in coast redwood. Instead, other environmental factors, such as suitable site conditions and moisture availability, will likely determine seedling establishment success in the warm and dry conditions present in the central and southern range margin environments of the species. In Chapter 4, I found that seed predators significantly alter regeneration dynamics in mature coast redwood communities and that a number of native species prey upon coast redwood seeds in the post-dispersal period. In addition, I found that establishment of coast redwood seedlings in hot, dry conditions like those present in the drought event occurring in the Santa Cruz Mountains in 2021 are unlikely to result in seedling establishment, even when viable seed is available and biotic pressures are eliminated. The combination of these pressures may make seedling establishment of coast redwood growing in hot and dry communities of the southern and eastern range margins of the species even less frequent in the future.

Coast redwood forests have been resilient to environmental changes that have occurred over the past two or more millennia, but it is imperative that we do not become complacent as researchers and managers working in these iconic ecological communities. Research across the coast redwood range may be more imperative today than potentially ever before as environmental pressures continue to alter California’s forest systems. Given the lengthy amount of time it takes to build insights on the response of a long-lived tree species to environmental change, we must continue to conduct incremental research to supplement long-term data. Collectively, these efforts will lead to a better understanding of how coast redwood and the forests of California’s coast range should be best managed to persist and adapt in the face of novel environmental conditions.