Serotinous forest resilience in a warmer and more fire-prone world

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Abstract

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Warming climate and increased fire activity are expected to lead to decreased capacity of woody plant-dominated ecosystems to recover following fire (i.e., the erosion of resilience) in ecosystems globally. Systems characterized by stand-replacing fire regimes and dominated by serotinous plants (plants that release seeds from cones when heated by fire) may be particularly at risk. Two key conditions for resilience to fire in systems dominated by serotinous species are the sufficient production of cones following one fire and prior to the occurrence of subsequent stand-replacing fire (reburn) and climate conditions suitable for recruitment in the first post-fire year. Expected increases in fire frequency, hot and dry conditions during the inter-fire period, and occurrence of post-fire drought may lead to significant decreases in serotinous plant population persistence (interval squeeze). While the interval squeeze has been demonstrated for some serotinous species (e.g., *Banksia* spp. in Western Australia), key knowledge gaps exist

regarding resilience mechanisms of serotinous species in North American forests and how populations may respond in a warmer future with more fire.

My dissertation used closed-cone pine (*Pinus attenuata* and *P. muricata*) forests of California, USA as a study system to empirically test for evidence of the interval squeeze. Specifically, I assessed the developmental trajectories of fuels and cones over a chronosequence of three decades since stand-replacing fire to understand how reburn and population self-replacement potential develop over time. Building on these trajectories, I assessed the effects of fire interval and post-fire climate on *in situ* post-fire recruitment within the first two years post-fire, using a plot network of stands that burned in 2018, on intervals from 6 - 31 years. I found that 1) fuel development occurs rapidly in these forests, with fuels available to support a high severity reburn by ~10 years post-fire, 2) canopy seed bank development to support stand self-replacement occurs by ~15 years post-fire, 3) *in situ* post-fire recruitment was present following all fire intervals, and reaches stand self-replacement for fire intervals ≥15 years on average, but under harsh post-fire climate conditions, fire intervals must be ≥20 years to reach stand self-replacement. Collectively, these results suggest that closed-cone pine forests are resilient to relatively frequent stand-replacing fires and warming that has occurred thus far. However, if fire recurs on an interval of <15 years, or post-fire growing seasons co-occur with severe drought conditions, resilience may be eroded. Combined with a review of the literature on the environmental conditions that have given rise to serotiny as a trait and variability in trait expression, this work provides a framework for understanding how coniferous forests dominated by serotinous species may respond to future climate and changing fire activity in ecosystems across North America, with significant implications for forest and fire management in rapidly changing environmental conditions.

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Chapter 1. INTRODUCTION

Evidence from terrestrial ecosystems globally indicates that climate change is eroding resilience to disturbance (IPCC 2022) – defined as an ecosystem's capacity to experience disturbance and reorganize without transitioning to an alternative state (Walker et al. 2004). Direct effects of warming climate, including increased occurrence of drought and heatwaves, as well as persistent increases in moisture stress, are contributing to increases in tree mortality and forest die-offs (van Mantgem et al. 2009, Williams et al. 2013, Allen et al. 2015, Matusick et al. 2018). Increasing disturbance activity can also erode forest resilience (an indirect effect of climate change) by decreasing the capacity of an ecosystem to recover following a disturbance event (Seidl et al. 2017). Understanding how direct and indirect effects of climate change combine to affect forest resilience is critical to anticipating vulnerability to plant population loss or non-forest conversion (Coop et al. 2020, Falk et al. 2022).

Resilience of serotinous plant populations – those that accumulate seeds within a canopy seed bank for multiple years for release following fire – may be particularly at risk as the climate continues to warm (Enright et al. 2015). Serotinous plants are typically well-adapted to predictable stand-replacing fire regimes (Lamont and Enright 2000), given their capacity to release seed *en masse* and establish at high densities in a post-fire environment (Turner et al. 1999, Harvey and Holzman 2014). However, this capacity is dependent on enough time between fires to accumulate a canopy seed bank sufficient for population persistence (Enright et al. 1998, Tonnabel et al. 2012) as well as favorable climate conditions for post-fire seedling establishment (Enright et al. 2014). These resilience mechanisms are likely to erode through an "interval squeeze" (Enright et al. 2015), by which direct and indirect effects of climate change combine to

constrain serotinous population persistence. Increasing fire activity attributed to climate change is already apparent (Abatzoglou and Williams 2016), with further increases likely. As fires overlap past fire activity, short-interval fires may burn young serotinous populations, facilitating a "fire interval shift" and decline in serotinous population density or localized extinction (Keeley et al. 1999, Brown and Johnstone 2012). Direct effects of warming may also lead to decreased reproductive capacity of serotinous populations (Redmond et al. 2012, Clark et al. 2021), leading to a "demographic shift" that reduces seed availability at the time of fire. Compound effects (*sensu* Paine et al. 1998) of post-fire drought, an increasingly common occurrence with climate warming (Stevens-Rumann et al. 2018), can lead to a "post-fire recruitment shift" that reduces seedling establishment post-fire. The overarching objective of this dissertation is to build understanding of the mechanisms of serotinous plant population resilience to increasing fire activity and warming climate by empirically testing for evidence of the interval squeeze in North American forests. Specifically, my work builds new insight into the potential for increased fire frequency (fire interval shift), drivers of cone production leading to seed availability at the time of fire (demographic shift), and how short-interval fires and post-fire climate combine to affect post-fire regeneration (fire interval and post-fire recruitment shifts), using California closed-cone pine forests as a model system.

The closed-cone pine forests of California, USA are an ideal model system to test for evidence that interval squeeze is occurring in forested systems. Structurally, California closed-cone pine forests are relatively simple as they are typically dominated by even-aged cohorts of a single tree species – bishop pine (*Pinus muricata*) or knobcone pine (*Pinus attenuata*). Both species are strongly serotinous (i.e., they retain seeds within closed cones for decades during the inter-fire period), forming a canopy seed bank. In general, both forest types are characterized by

a stand-replacing fire regime, with mean fire return intervals varying from ~30 to 90 years (Sugnet 1985, van de Water and Safford 2011). Cones open with heat from fire and most seedling recruitment occurs within one year following fire (Harvey and Holzman 2014), with little inter-fire recruitment (but see Fry et al. 2012). Stands rapidly proceed through the stages of development – initiation of reproductive maturity, density-dependent mortality due to intraspecific competition, stand mortality through fire or senescence – compared with other coniferous forest types in North America (Keeley et al. 1999, Holzman and Folger 2005). Testing mechanisms that govern serotinous forest resilience to warming climate and increased fire activity across the inter-fire period using field data has greater feasibility in these systems than in most other serotinous forests in western North America [e.g., lodgepole pine (*Pinus contorta),* black spruce (*Picea mariana*)] where fire return intervals and time to closed cone production are considerably longer (i.e., decades vs. centuries; Romme 1982, Turner et al. 2007, Johnstone et al. 2010, Viglas et al. 2013). For forests governed by analogous processes (i.e., high-severity fire regime, dominance by a single cohort of a serotinous tree species immediately following fire), findings from California closed-cone pine forests may illuminate mechanisms driving species persistence in forests in which these processes occur on a longer temporal scale.

First, in Chapter 2, I review published literature on serotiny as a fire-adapted trait. The literature review builds understanding of the adaptive advantages and disadvantages as well as evolutionary history of serotiny as a trait, which arose independently across millions of years and several continents during periods characterized by high intensity fire (Lamont et al. 2020). I then examine the nature of variation in serotiny across taxa at multiple spatial scales (species, population, individual plant, cone), and temporally. Through examination of variation that exists in the expression of serotiny and the biological consequences of each scale of variation, this

work expands on previous work (Lamont et al. 1991, Buma et al. 2013) to deepen understanding of how serotiny – and variable serotiny – may be adaptive or maladaptive under projected future climate and altered disturbance regimes.

Fire activity is increasing across many forested regions (Jolly et al. 2015, Abatzoglou and Williams 2016, Boer et al. 2020) and with such increases, fire will inevitably overlap recently burned forest (i.e., short-interval reburn). Short-interval severe reburns can cause immaturity risk (Keeley et al. 1999, Buma et al. 2013) in serotinous populations when they burn through areas that lack a canopy seed bank. Fuel limitation following severe fire is a critical negative feedback on the occurrence of short-interval severe reburns, but the duration of fuel limitation varies across ecosystems (Parks et al. 2015, Harvey et al. 2016b, Buma et al. 2020). In Chapter 3, I conducted a study that quantifies surface and canopy fuel accumulation over time since stand-replacing fire in California closed-cone pine forests to understand the duration of fuel limitation in this system, and when fuels could support a subsequent severe reburn. To achieve this objective, I measured surface and canopy fuel loads in 79 forest stands over a 33-year chronosequence of time since fire. This analysis reveals that the duration of fuel limitation is likely brief (< 10 years), indicating high potential for increased fire activity in these forests as weather conditions favorable for fire continue to increase in occurrence. Such an increase in fire activity may erode resilience of serotinous populations where fire intervals become misaligned with demographic rates governing seed availability.

Although serotiny is thought to be an adaptation to severe (stand-replacing) fire (He et al. 2016, Causley et al. 2016, Lamont et al. 2020), serotinous populations require the accumulation of a sufficient canopy seed bank to self-replace and persist following such fires (Enright et al. 2015). However, the drivers of canopy seed bank production, and how demographic rates may

shift with warming climate (Clark et al. 2021), remain poorly understood in many systems. To understand the consequences of increasing fire activity and warming climate on potential for resilience loss of serotinous populations, in Chapter 4, I tested how several biotic and abiotic drivers constrain seed availability and potential for population self-replacement at various stand ages. To achieve this objective, I assessed two demographic processes – reproductive capacity and mortality – at individual tree and stand levels over time since stand-replacing fire using data from a chronosequence of 69 forest stands ranging from 5 – 33 years. Stand age was the dominant driver of reproductive capacity, but a lower magnitude effect of high moisture stress was associated with increased mortality and decreased reproductive capacity. Collectively, these results suggest potential for resilience loss where fire occurs in stands < 20 years old, and that direct effects of climate change are already apparent.

Post-fire recruitment is a key indicator of resilience following severe disturbance in forests that do not resprout. Previous work suggests that fire followed by drought can have compounding effects on post-fire recruitment (Stevens-Rumann et al. 2018, Kemp et al. 2019, Whitman et al. 2019, Rodman et al. 2020), leading to the erosion of forest resilience with climate warming. Findings from Chapters 3 and 4 suggest a window of vulnerability to resilience loss for California closed-cone pines during which susceptibility to reburning has recovered but the canopy seed bank has not yet accumulated. However, these trajectories do not encompass dynamics following canopy seed bank release, such as post-fire climate and microsite, which are important controls on seedling establishment (Harvey et al. 2016a, Stevens-Rumann et al. 2018, Littlefield 2019). In Chapter 5, I capitalized on an opportunity to test the framework suggested by the previously developed trajectories by establishing a plot network in recently burned knobcone pine forests. I assessed post-fire regeneration across a range of fire intervals (i.e., stand

age at the time of fire) and post-fire climate conditions to understand how indirect (shortened fire intervals) and direct effects (harsh post-fire climate conditions) of climate change combine to constrain *in situ* tree regeneration. Fire interval – the primary control on seed availability at the time of fire – had the strongest effect on post-fire regeneration, while post-fire climate had a minor but detectable effect, likely to be important especially near thresholds of seed availability. Climate change impacts are likely to be catalyzed by increasing disturbance activity in serotinous forests with compounding effects of post-fire climate increasing as post-fire droughts become more frequent and severe.

The effects of increasing fire activity and warming climate are already apparent in many forest and woodland ecosystems globally. Collectively, this work builds on the interval squeeze hypothesis (Enright et al. 2015) to provide a framework for understanding how coniferous forests dominated by serotinous tree species may respond to future climate and changing fire activity in ecosystems across North America. This framework guides understanding of when and where resilience of serotinous populations may erode, with significant implications for forest and fire management in rapidly changing environmental conditions.

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Chapter 2. VARIABILITY IN SEROTINY OF FIRE-PRONE SPECIES

2.1 ABSTRACT

Fire is the dominant disturbance in terrestrial ecosystems globally and is important for regulating processes in many ecosystems. Fire-prone plant populations typically persist through adaptations to a specific fire regime and plant resilience to fire may erode as traits become misaligned with shifting fire regimes. While variation in flammability strategies at the community level can be important for post-fire resilience, variation within individual fire-adapted traits has rarely been considered. Serotiny is a common fire adaptation associated with stand-replacing, predictable fire regimes. Given complete serotiny at individual and populations levels, as fire activity increases in areas with warming and drying climates, serotinous plant populations may face increases in immaturity risk, causing serotiny to become a maladaptive trait for population persistence. However, there is evidence of variation in serotiny at multiple levels of organization, and how such variation may impact plant persistence through time is poorly understood. Here, we review the conditions associated with variation in serotiny at levels of organization from cone to species to understand how serotinous population resilience may differ where serotiny is variable. While loss of serotinous populations due to increased fire frequency and warming climate is a concern in some areas, invasions by serotinous conifers in novel environments suggest that serotinous species may be poised to persist or even expand with warming temperatures and increased fire activity. Additional research to understand relative effects of biotic and abiotic drivers of serotinous cone production and viable seed availability are needed to integrate with empirical and modeling studies investigating the interval squeeze in serotinous plant-dominated systems around the world. Increased understanding of these mechanisms will

contribute to the ability to predict when and where serotinous populations may be susceptible to loss due to warming climate and a shifting fire regime.

2.2 INTRODUCTION

There is mounting evidence globally that climate change is eroding resilience across many ecosystems and scales of organization (IPCC 2022). Phenomena including the deterioration of coral reefs (Hughes et al. 2017), increased morality of large trees (van Mantgem et al. 2009), and tree regeneration failures following disturbance (Stevens-Rumann et al. 2018) represent evidence of such losses. Understanding resilience of individuals, populations, species, and ecosystems is of paramount importance during this period of rapid global environmental change (IPCC 2022). A common definition of ecosystem resilience identifies it as the ability of a system to return to a pre-disturbance state, rather than transitioning into an alternative state following a disturbance (Gunderson 2000). As the climate continues to become warmer, and in many regions also drier, the resilience of terrestrial ecosystems is predicted to decrease, with state transitions (e.g., conversion of forest to shrubland) likely (Johnstone et al. 2016, Coop et al. 2020).

Changes in resilience in woody plant-dominated ecosystems are predicted to result from both direct and indirect effects of climate change. Direct effects of climate change, including increased temperature and decreased moisture availability are projected to continue to intensify in the form of more frequent droughts and heatwaves (Allen et al. 2015). At spatial scales from individual plants to populations, increased temperature and moisture stress can result in increased mortality of established plants, decreased regeneration success, increased time to reproductive maturity and decreased seed production (van Mantgem et al. 2009, Redmond et al. 2012, Williams et al. 2013, Enright et al. 2015, Stevens-Rumann et al. 2018, Clark et al. 2021).

Indirect consequences of climate change include potential increases in insect attacks (Raffa et al. 2008) and susceptibility to pathogens (Agne et al. 2018), as well as increases in fire activity (Abatzoglou and Williams 2016), and decreased capacity to recover post-disturbance (Seidl et al. 2017) which may have influences at spatial scales from individual plants to ecosystems. Direct and indirect impacts of climate change may combine to severely restrict the environmental space in which certain woody plant-dominated ecosystems, particularly those that are fire-prone, can exist (Enright et al. 2015).

Fire is the dominant disturbance that shapes terrestrial ecosystems globally (Bowman et al. 2009). Therefore, changes in fire regimes have the potential to result in shifts to alternative ecosystem states (Coop et al. 2020). Increasing fire activity is apparent in terrestrial ecosystems around the globe with evidence of increased annual area burned (Boer et al. 2020, Abatzoglou et al. 2021), proportion area burned with high severity (Parks and Abatzoglou 2020, Collins et al. 2021), and an extended fire season (Jolly et al. 2015). Ecosystems that are characterized by predictable stand-replacing fire regimes (i.e., trees are killed and stand regeneration depends on recruitment from seed) may be particularly vulnerable to climate-mediated changes in ecosystem resilience. Most ecosystems are fuel-limited immediately following stand-replacing fire, initially limiting the potential for short-interval reburns (Parks et al. 2015). However, in systems in which fire activity is generally climate-limited (*sensu* Littell et al. 2009), the temporal window of fuel-limitation following fire is brief (Parks et al. 2015, Harvey et al. 2016, Buma et al. 2020). As fire activity continues to increase with warming climate (Westerling 2016, Abatzoglou and Williams 2016), this climate limitation will decrease (i.e., climatic conditions allowing for stand-replacing wildfire will occur more frequently), increasing the likelihood of short-interval fires following the window of fuel-limitation (Westerling et al. 2011). Conversely, fuel-limited ecosystems are

not dependent upon climate as a limiting factor and may be better adapted to warming and decreased fire intervals (Holden et al. 2007), further indicating the necessity of understanding the impacts of climate warming in climate-limited systems. Questions remain regarding the potential of systems to absorb impacts from altered fire regimes. Evidence from systems globally suggests that increases in fire frequency may already be contributing to shifts in forest composition and conversions to non-forest (Brown and Johnstone 2012, Coppoletta et al. 2016, Fairman et al. 2019, Baltzer et al. 2021, Hoecker and Turner 2022). However, fire frequency must be considered simultaneously with reproductive capacity and regeneration dynamics to understand the capacity of a population to respond to an altered fire regime.

The capacity of a population to maintain its size through sufficient reproductive capacity from one generation to the next is a key feature of resilience at the population level. Sufficient reproductive capacity refers to the point in time at which a stand has enough available propagules to ensure approximate self-replacement following a stand-replacing disturbance (Enright et al. 2015). Important components of reproductive capacity include time to seed production, total seed production, total seed bank and seed viability. In ecosystems that are adapted to predictable stand-replacing fire regimes, some species store seed within woody fruits or cones (hereafter, cones) in a canopy seed bank (Lamont and Enright 2000). This habit, typically referred to as serotiny, is further defined as the retention of mature seeds on a plant for at least one year (sensu Lamont 1991) so that there are at least two years of seed production held on the plant at the same time. Other strategies for fire resilience include resprouting, soil seed bank storage, fire-stimulated flowering, seed release, or germination, and long-distance seed dispersal (Agee 1993, Keeley et al. 2011, Lamont and He 2017), and plants often employ multiple strategies (Newton et al. 2021).

In serotinous species, a population will persist on a given site following stand-replacing fire only if it has accumulated a canopy seed bank of sufficient size at the time of fire. Stand density will vary from generation to generation depending on the size of this seed bank, which is a function of inter-fire time available for seed accumulation plus suitability of post-fire conditions for recruitment (Esler and Cowling 1990). Although the largest fitness benefit of serotiny is achieved by holding two years of seeds within the canopy seed bank, development of sufficient seed for self-replacement often takes much longer (Enright et al. 1998). Warming and drying climate has been shown to increase time to seed production in water-limited ecosystems, leading to decreased total viable seed at a given point in time as compared with cooler and wetter climatic conditions (Redmond et al. 2012, Enright et al. 2015). However, this is not a consistent pattern, suggesting complex drivers of seed production and species-specific responses to changing climate (Wright et al. 2021). Further, this trend may reverse in energy-limited ecosystems where water is not limiting (Buechling et al. 2016, Clark et al. 2021). As time to accumulate a canopy seed bank and frequency of fire increase in tandem in water-limited systems, the ability of forests to persist in their current states is of considerable concern.

Serotiny occurs in at least 1200 plant species globally and is prominent in species that experience predictable stand-replacing fire regimes (Lamont et al. 1991). Here, I explore the conditions under which serotiny evolved as a trait, review variability of serotiny at multiple spatial and temporal scales and evaluate the utility of serotiny as an adaptive trait within the context of a world characterized in some regions by warming and drying climatic conditions and increased fire frequency.

2.3 EVOLUTIONARY CONDITIONS LEADING TO THE RISE OF SEROTINY AS A TRAIT

There is strong evidence from both paleoecological and empirical research that serotiny evolved as an adaptation to stand-replacing fire (Lamont et al. 2020). Paleoecological records indicate that early conifers, which evolved approximately 332 million years ago, were generally serotinous, suggesting that that period was also characterized by intense crown fires (He et al. 2016). Serotiny evolved separately, and during distinct time periods, within various regions of the world, arising at least eleven times in the past 110 million years (Lamont et al. 2020). The evolution of serotiny in the genus *Pinus* (Pinaceae) in North America co-occurred with a period characterized by high intensity crown fire and increased probability of burning during the mid-Cretaceous period, approximately 89 million years ago (He et al. 2012). Fossil evidence from New Zealand suggests that serotiny evolved within Gondwanan Cupressaceae taxa nearly contemporaneously, 90-99 million years ago (Mays et al. 2017). Oxygen concentrations were well above contemporary levels during this time, which led to increased combustion (Belcher et al. 2010). Atmospheric CO2 was also elevated during this time, leading to increased primary productivity (LaMarche et al. 1984). The combination of these factors likely resulted in increased probability of burning (He et al. 2012). It has been suggested that the evolution of serotiny within the genus *Pinus* may predate the Cretaceous period, given the high concentration of oxygen in the atmosphere during the Carboniferous period, but further macroevolutionary research is needed to provide support for this link (Pausas 2015).

The earliest noted occurrence of evolution of serotiny in angiosperms was in the Proteaceae in South Africa approximately 71 million years ago (Lamont and He 2012). Serotiny in Australian *Banksia* spp. appears to date to 61 million years ago, coinciding with the approximate establishment of this taxon, suggesting that fire was likely prominent in the

landscape prior to this time (He et al. 2011). Conversely, speciation leading to relative increases in non-serotinous species has been linked to relatively low fire activity associated with a period of low global temperature and atmospheric oxygen (Lamont 2022). Fire was notably infrequent in the Mediterranean Basin prior to about 780,000 years ago, but serotiny also occurs in several *Pinus* spp. in this region (Ne'eman et al. 2004). Despite the relatively recent increase in fire, it has been estimated that the dominant strongly serotinous species in the region, *Pinus halepensis*, has completed at least 6,240 generations over this time-period, a plausible time within which the species may have evolved this adaptation to fire (Ne'eman et al. 2004), given the high level of heritability of the trait in this species (Hernández-Serrano et al. 2014).

Empirical studies in systems characterized by serotinous species globally provide additional evidence that serotiny evolved as an adaptation to stand-replacing fires. Within the genus *Pinus*, serotiny is correlated with traits associated with increased flammability (e.g., dead lower branch retention), suggesting that these species evolved an overall "fire embracing" strategy in response to increased crown fires (Schwilk and Ackerly 2001). Furthermore, there is evidence from closely related groups of *Pinus* spp. and *Callitropsis* spp. in Mexico that species exposed to stand-replacing fire are more likely to be serotinous, while those from relatively fire-free environments are likely to be non-serotinous (Rodríguez-Trejo and Fulé 2003, Garcillán 2010). Cupressaceae in the southern hemisphere demonstrate a similar pattern, in which species from low severity frequent fire regimes or unpredictable stand-replacing fire regimes are nearly always non-serotinous (Ladd et al. 2013).

Although the hypothesis that serotiny evolved as an adaptation to fire is the most widely supported, other hypotheses have been proposed. It has been suggested that serotiny may have evolved as an adaptation to drought or low soil nutrient availability (Axelrod 1980, Hopper 2009,

Bradshaw et al. 2011), rather than to stand-replacing crown fire. Canopy seed storage may be a benefit under resource-limited conditions, as annual seed production may be insufficient for population self-replacement (Bradshaw et al. 2011). It is difficult to determine the relative contribution of each factor to the evolution of serotiny as a trait, and selection for serotiny was likely driven by a combination of these factors (Keeley et al. 2011). However, experimental comparisons of seven serotinous *Banksia* spp. and *Hakea psilorrhyncha* (Proteaceae) germination and recruitment following drought mortality and fire mortality in SW Australia showed that regeneration success is much higher following fire (Causley et al. 2016). This provides experimental evidence suggesting that serotiny evolved as an adaptation to fire rather than drought within *Banskia* spp. and *Hakea* spp. Furthermore, a review of 134 speciation events associated with the evolution of fire-adaptive traits (including fire-stimulated seed release from serotinous cones, fire-stimulated germination, and fire-stimulated flowering) provided no examples of speciation events that selected for these traits in the absence of a fire-prone environment, providing further evidence that serotiny is an adaptation rather than an exaptation to fire (Lamont and He 2017).

2.4 SELECTIVE FORCES AGAINST SEROTINY AS A TRAIT

Although there are strong adaptive advantages associated with serotiny in fire-prone systems, selective forces against serotiny must be accounted for when considering the advantages of this trait under various climate change scenarios. Serotiny is selected against by fire regimes characterized by either high frequency fires that recur prior to plant maturity or infrequent fires that exceed plant longevity as few seeds would be stored at the time of fire (Lamont et al. 2020). Two additional mechanisms that may select against serotiny are metabolic costs of serotinous cone production (Cramer and Midgley 2009) and high susceptibility to seed

predation (Smith 1970). The importance of each of these mechanisms is likely to interact differently with the selective force of fire to influence the relative adaptive advantage of serotiny in various species.

Cone formation and cone maintenance both have a higher metabolic cost for serotinous cones than for non-serotinous cones. Increased resource allocation to cone production can result in lower seed counts within serotinous cones as compared with non-serotinous cones of the same species (Muir and Lotan 1985) or of related non-serotinous species (Cramer and Midgley 2009). Furthermore, serotinous cone maintenance requires increased water and carbon allocation in many species (Cramer and Midgley 2009, Harris and Pannell 2010). Evidence from *P. halepensis* in Spain indicates that serotinous cones open in both lab and field settings when water becomes limiting, suggesting serotiny may become a maladaptive strategy for population self-replacement as the climate becomes warmer and drier and seeds are increasingly released into stressful conditions (Martin-Sanz et al. 2016, Martín-Sanz et al. 2017). If these effects scale up to the stand level (i.e., serotinous trees do not produce more cones than non-serotinous trees to compensate for the decreased number of seeds contained within a cone), overall propagule availability over the lifespan of stands could be substantially dampened where serotiny exists. However, it should be noted that fewer seeds are required to sustain a stand of serotinous plants as compared with non-serotinous plants (Enright and Lamont 1989, Enright et al. 1998), due to tendencies of serotiny to maximize and stabilize seed supply for subsequent generations and maximize post-fire seedling establishment in the post-fire environment (Lamont et al. 1991).

Pre-dispersal seed predation has a strongly negative impact on serotinous species and is associated with a decreased canopy seed bank in several serotinous species (Bond 1984, Nathan and Ne'eman 2004). Where serotinous plants and seed predators have coevolved, some seed

predators have developed the ability to select food sources based upon energy content, suggesting that serotinous cones should be preferentially selected by granivores (Smith 1970). Serotinous plant species often have adaptations to protect against seed predation, such as protective scales (Leslie 2011), cones that are reflexed on plant branches to prevent removal (Keeley and Zedler 1998), or leaf spinescence (Lamont et al. 2016). However, seed predation pressure on certain species has been strong enough to have selected against serotiny in populations of plants that substantially overlap a seed predator's range. For example, American red squirrel (*Tamiasciurus hudsonicus*) abundance is strongly negatively associated with percent serotiny in *P. contorta* forests characterized by stand-replacing fire (Benkman and Siepielski 2004, Talluto and Benkman 2013). This indicates that the selection pressure against serotiny by a seed predator competes with the opposing pressure from stand-replacing fire regimes, resulting in variation in serotiny, and subsequently stand structure and composition, at fine spatial scales (Talluto and Benkman 2014). However, there is recent evidence that red squirrels preferentially predate non-serotinous cones (due to lower defenses against predation) where both morphologies coexist, thereby lessening selection against serotiny (Parker and Benkman 2020).

Although seed predation can select against serotiny, there is evidence of a wide range of interactions between serotinous species and seed predators. Despite potential for considerable cone damage from squirrel predation in *P. coulteri*, the weakly serotinous *P. coulteri* may rely on animal caching of seed for seedling establishment during inter-fire periods (Borchert et al. 2003, Johnson et al. 2003). This suggests that seed predation may confer an adaptive advantage for some weakly serotinous species. *Pinus halepensis* also demonstrates a complex relationship with seed predators; as a proportion relative to the overall canopy seed bank, seed predation rates are lowest at the stand level when the seed bank is large, suggesting that predator satiation limits

seed predation at high seed densities (Nathan and Ne'eman 2004). Strongly serotinous *Hakea* spp. are less likely to be attacked by cockatoo granivores than weakly serotinous *Hakea* spp., suggesting that large woody fruits serve as a protection against seed predation in this case (Lamont et al. 2016). Mast seeding, defined as the synchronous intermittent production of seed crops within plant populations, is another seed production strategy employed by some plant species (Kelly 1994). Species that employ this strategy are hypothesized to satiate seed predators in mast years, while starving them between mast years (Silvertown 1980). Mast seeding species' highly variable seed availability deters seed predators (Kelly 1994), while serotinous species' relatively stable seed availability may either attract or satiate seed predators (Benkman and Siepielski 2004, Nathan and Ne'eman 2004). Therefore, canopy seed storage may increase the risk of maintaining a large population of pre-dispersal seed predators, but mass release following fire may be useful in saturating the post-fire predation impact. Furthermore, increased canopy seed bank density does not facilitate increased seed predation across all species assemblages, suggesting that seed predation may not act as a strong selection pressure against serotiny in all systems.

2.5 SEROTINY – ONE SIZE DOES NOT FIT ALL

In the broadest sense, serotiny refers to the habit of seed retention on a plant for at least one year following maturity (Lamont et al. 1991). However, serotiny is typically referred to specifically as an adaptation to fire, although there are several mechanisms by which seed may be released from serotinous cones that are unrelated to fire activity (Lamont 1991). Here, I focus primarily on serotinous cones that release seed following heat from fire (pyriscence), but also consider seed release with warm and dry conditions in the absence of fire (xeriscence), as these mechanisms of seed release co-occur within many serotinous species (Nathan et al. 1999).

2.5.1 *Varying definitions of serotiny*

A difficulty in synthesizing research on serotiny is that there is no single standard index of serotiny (Lamont 2021). Furthermore, this trait can be measured at multiple spatial and temporal scales despite common application of definitions in a binary manner at the species scale (Table 2.1). Few studies have explicitly addressed the multiple spatial scales at which serotiny operates (Tinker et al. 1994, Hernandez-Serrano et al. 2013). Spatially, individual cones, individual trees, stands, regions, subspecies, and species may be either broadly categorized as serotinous or non-serotinous (Figure 2.1). Furthermore, serotiny exists on a continuum from weakly to strongly serotinous (Cowling and Lamont 1985). The individual cone level is the most clearly defined level with respect to serotinous (closed cone containing mature seed) versus non-serotinous (open cone which has released seed upon ripening) cones. However, even at the individual cone level, partial opening of cones is common, complicating this perceived binary description. Although for the most strongly serotinous species, nearly 100% of cones are closed (e.g., *Pinus attenuata*; Keeley and Zedler 1998), for many serotinous species, individual plants have a combination of open and closed cones.

Table 2.1. Processes hypothesized to drive variation in serotiny across scales.

Scale of variation	Processes hypothesized to drive variation
Spatial variation among species	Natural selection, atmospheric and environmental conditions occurring on evolutionary timescales
Spatial variation within species among populations	Climate and fire severity gradients select for different degrees of serotiny
Spatial variation within populations	Frequency dependent selection responding to mixed severity fire regime
Spatial variation within individuals	Bet hedging related to fire regime - open and closed cones produced where fire frequency is unpredictable
Temporal variation within individuals	Bet hedging related to fire regime - serotiny is strongest at historical mean fire return interval
Temporal variation within cones	Opening with cone age, earlier opening related to environmental conditions such as drought or extreme heat

Therefore, a threshold of the percentage of serotinous cones contained on an individual plant to be considered serotinous must be chosen, and often varies among researchers and species of interest (e.g., Muir and Lotan 1985, Gauthier et al. 1993). Similar categorizations can be made at each of the higher levels of spatial organization (Figure 2.1), potentially leading to disparate definitions of serotiny at various levels. Although a quantitative assignment of percent serotiny can aid in clarifying these designations, it remains important to understand at which spatial scale this percentage has been assigned.

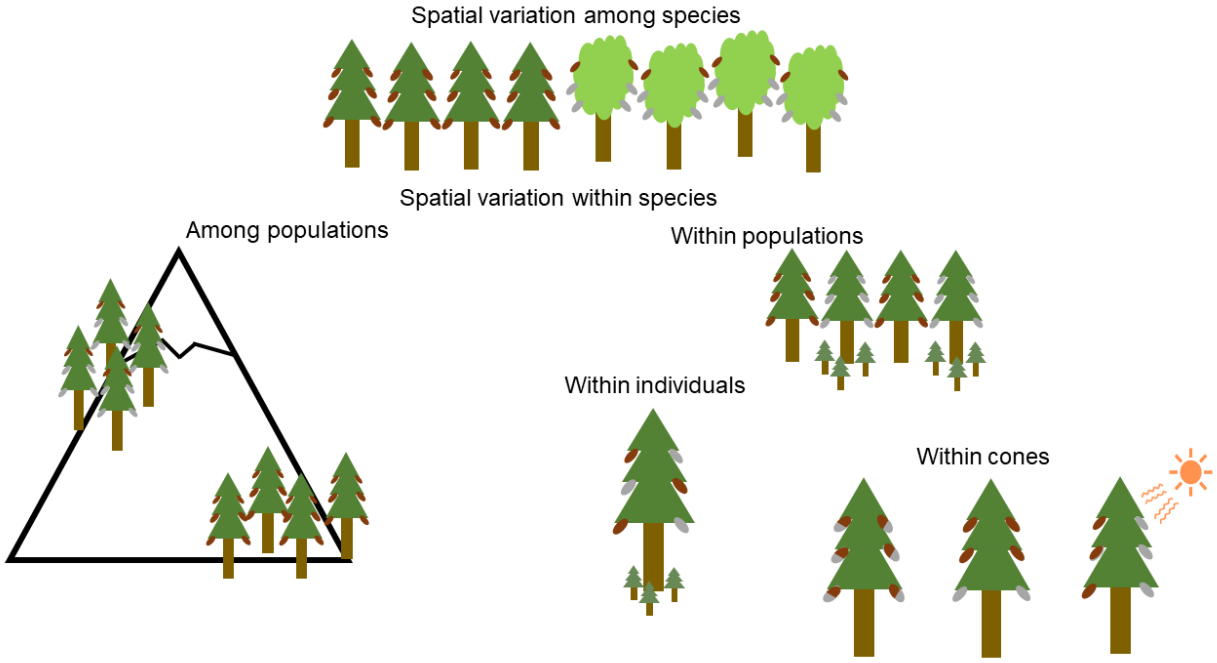

Figure 2.1. Conceptual diagram of variation in serotiny at multiple spatial scales. Note: Brown ovals represent closed serotinous cones and gray ovals represent open and/or non-serotinous cones.

2.5.2 *Variability of serotiny among species*

Levels of serotiny vary widely among serotinous species. Serotinous species are broadly separated into those characterized by “strong” versus “weak” serotiny. Strongly serotinous species are defined by their ability to retain mature seed within cones for five years to several

decades, depending upon the species (Vogl 1973, Cramer and Midgley 2009). Weakly serotinous species conversely retain mature seed within cones for at least one year, and release seed within three years of maturity in the absence of fire (Midgley 2000). Although there is clearly variability within each of these broad categories, separate mechanisms for the evolution of strong versus weak serotiny have been proposed. There is evidence from serotinous species globally that strong serotiny has been selected for over evolutionary timescales by predictable stand-replacing crown fire (Perry and Lotan 1979, Cowling and Lamont 1985, Rodríguez-Trejo and Fulé 2003, Goubitz et al. 2004, Tapias et al. 2004, Radeloff et al. 2004). Additional evidence from recently established non-native *Pinus radiata* populations suggests serotiny strength at the population level can increase even following a single severe fire (Ripa et al. 2020). Strong serotiny is selected for in systems with predictable stand-replacing fire regimes because plants are killed by fire, and fire occurs frequently enough that the canopy seed bank is likely to remain viable until the next fire event. Therefore, natural selection should favor strategies other than serotiny in species that experience either low intensity surface fires or infrequent and unpredictable stand-replacing fire (Keeley and Zedler 1998).

Several explanations for the selection of weak serotiny as an adaptive trait have been proposed. It has been suggested that due to high metabolic costs of maintaining serotinous cones, weakly serotinous cones open without exposure to fire during periods of water stress (xeriscence), particularly for *Pinus* species (Nathan et al. 1999, Martín-Sanz et al. 2017). This suggests that weak serotiny is a maladaptive consequence of serotiny, rather than an adaptive trait. However, this mechanism has been disputed as an explanation for weak serotiny within the Australian and Cape Proteaceae species, for which the maintenance costs of serotinous cones are low compared with maintenance costs of leaves (Cramer and Midgley 2009). Weak serotiny has

been proposed in these systems as an adaptive trait that allows for inter-fire recruitment in addition to the presence of a canopy seed bank to be released following stand-replacing fire, as the benefits of serotiny (i.e., post-fire recruitment) are obtained quickly as serotiny level increases (Enright et al. 1998). Weak serotiny is associated with species in habitats in which inter-fire resource availability (particularly with respect to soil nutrient content) is not limiting and fire regimes are relatively unpredictable or burn with mixed severity, resulting in an increased requirement to utilize multiple methods of regeneration (Cramer and Midgley 2009, Clarke et al. 2013).

2.5.3 *Variability of serotiny within species*

2.5.3.1 Variability among populations

Serotiny varies widely within species, often occurring along environmental gradients. Strong relationships between serotiny and environmental gradients have been noted for distributions of *Banksia attenuata*, *B. menziesii*, and *B. prionotes* in Western Australia (Cowling and Lamont 1985), *Leptospermum scoparium* in New Zealand (Battersby et al. 2017), *Pinus banksiana*, *P. contorta*, and *P. muricata* in the USA (Zedler 1986, Tinker et al. 1994, Schoennagel et al. 2003, Radeloff et al. 2004), *Hesperocyparis forbesii* in Mexico (de Gouvenain and Delgadillo 2012), *P. halepensis* in Spain (Moya et al. 2008), and *Protea repens* in South Africa (de Gouvenain et al. 2019). Serotiny increases at more xeric sites for each of these species. Within-species variation in serotiny is also closely related to fire regime for many weakly serotinous species. Evidence of stronger serotiny in *P. banksiana* in Canada is associated with populations that experience stand-replacing crown fire (Gauthier et al. 1996, Briand et al. 2015), *P. pinaster* (Tapias et al. 2004, Gil et al. 2009) and *P. canariensis* (Climent et al. 2004) in Spain, *P. halepensis* in Israel and Spain (Goubitz et al. 2004, Hernandez-Serrano et al. 2013), *P.*

coulteri (Borchert 1985) and *P. rigida* (Givnish 1981) in the United States, and *L. scoparium* in New Zealand (Bond et al. 2004). For each species, serotiny is strong where populations experience relatively predictable stand-replacing crown fire, and weak to non-existent where populations are exposed to either infrequent fire or low severity surface fire. Additionally, germination trials from *P. halepensis* have shown that under high heat and high soil pH, conditions that simulate the post-fire environment, seeds from serotinous cones germinate at higher rates than seeds from non-serotinous cones (Goubitz et al. 2003). This result suggests that there are seed-level traits, in addition to cone-level traits, associated with serotiny, which confer an adaptive advantage within a post-fire environment. Associations between serotinous species and stand-replacing fire regimes worldwide provide strong support for the hypothesis that serotiny as a trait evolved in response to fire (He and Lamont 2017).

Pinus contorta is a species characterized by strong differences among populations in North America with respect to serotiny. Although *P. contorta* is often classified as a strongly serotinous species, serotiny varies widely between its subspecies (Keeley and Zedler 1998, Figure 2.2). While serotiny in *P. contorta* ssp. *latifolia* varies over a climatic gradient and with topography within its range in the Rocky Mountains (Lotan 1967, Schoennagel et al. 2003), serotiny is absent from *P. contorta* ssp. *murrayana* throughout its range in the Cascade Mountains and Sierra Nevada Mountains and *P. contorta* ssp. *contorta* along the coast (Mowat 1960, Keeley and Zedler 1998). The difference in life-history is largely attributed to differences in site productivity and fire regime. *Pinus contorta* ssp. *murrayana* typically establishes in uneven-aged stands on low productivity sites (Parker 1986, Stuart et al. 1989), while *P. contorta*

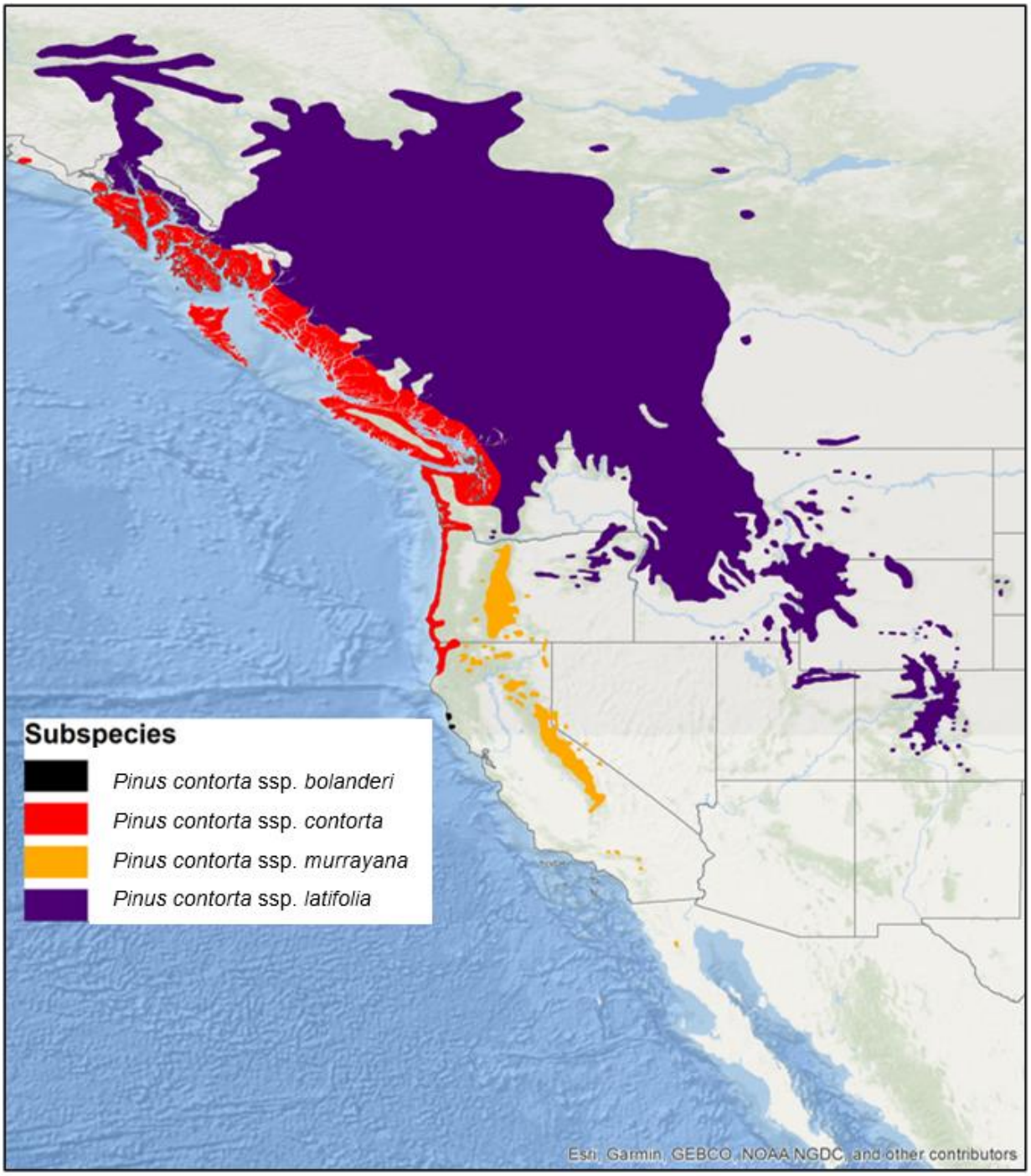

Figure 2.2. Species distribution map of lodgepole pine (*Pinus contorta*) subspecies. Note: Range map from "Atlas of United States Trees" by Elbert L. Little, Jr. (US Geological Survey 1999).

ssp. *latifolia* establishes in even-aged stands over a wider range of site conditions (Arno 1980).

Differences in site productivity are related to differences in fuel accumulation in both the

understory and the canopy; *P. contorta* ssp. *murrayana* stands historically experienced a mixed-severity fire regime (Parker 1986, Heyerdahl et al. 2014), *P. contorta* ssp. *contorta* experienced infrequent fire, and *P. contorta* ssp. *latifolia* stands experienced a stand-replacing fire regime (Romme 1982). Furthermore, relatively stable climatic conditions are required for the evolution of serotiny as a trait (Lamont et al. 1991); the Cascade Mountain Range developed more recently and was characterized by more variable climate over the past 3-4 million years than the Rocky Mountain Range (Mustoe and Leopold 2014). This suggests that a non-stand-replacing fire regime and variable climatic conditions exerted selection pressure for open cones in *P. contorta* ssp. *murrayana* (Heyerdahl et al. 2014, Figure 2.3A) while a stand-replacing fire regime selected for varying proportions of closed cones and open cones in *P. contorta* ssp. *latifolia* (Muir and Lotan 1985, Tinker et al. 1994, Schoennagel et al. 2003, Figure 2.3B-C).

Further complicating the relationship between serotiny and canopy seed storage in *P. contorta* is that between fire events mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) outbreaks cause high levels of mortality in *P. contorta* (Raffa et al. 2008). Widespread outbreaks throughout western North America since the mid-1990s prompted concern regarding subsequent reproductive capacity of *P. contorta* in attacked stands (Astrup et al. 2008; Figure 2.3D). Some opening of serotinous cones occurs immediately following a mountain pine beetle outbreak, and nearly half of the canopy seed bank is lost by six years following the outbreak (Teste et al. 2011a). However, *P. contorta* seed viability within serotinous cones remains high following an outbreak both within the canopy seed bank retained on dead trees and within serotinous cones buried on the forest floor for at least 15 years, before declining to 30-50% viability over the subsequent decade (Teste et al. 2011b, Aoki et al. 2011). Furthermore, serotinous cones from MPB-killed trees have increased time to opening with heat than those

from live trees, indicating that cones from MPB-killed trees are likely to release viable seed following fire (Sharpe and Ryu 2015). This suggests that mountain pine beetle outbreaks should not significantly limit the canopy seed bank in *P. contorta*. However, biotic disturbances can have significant impacts and should be considered when evaluating propagule availability.

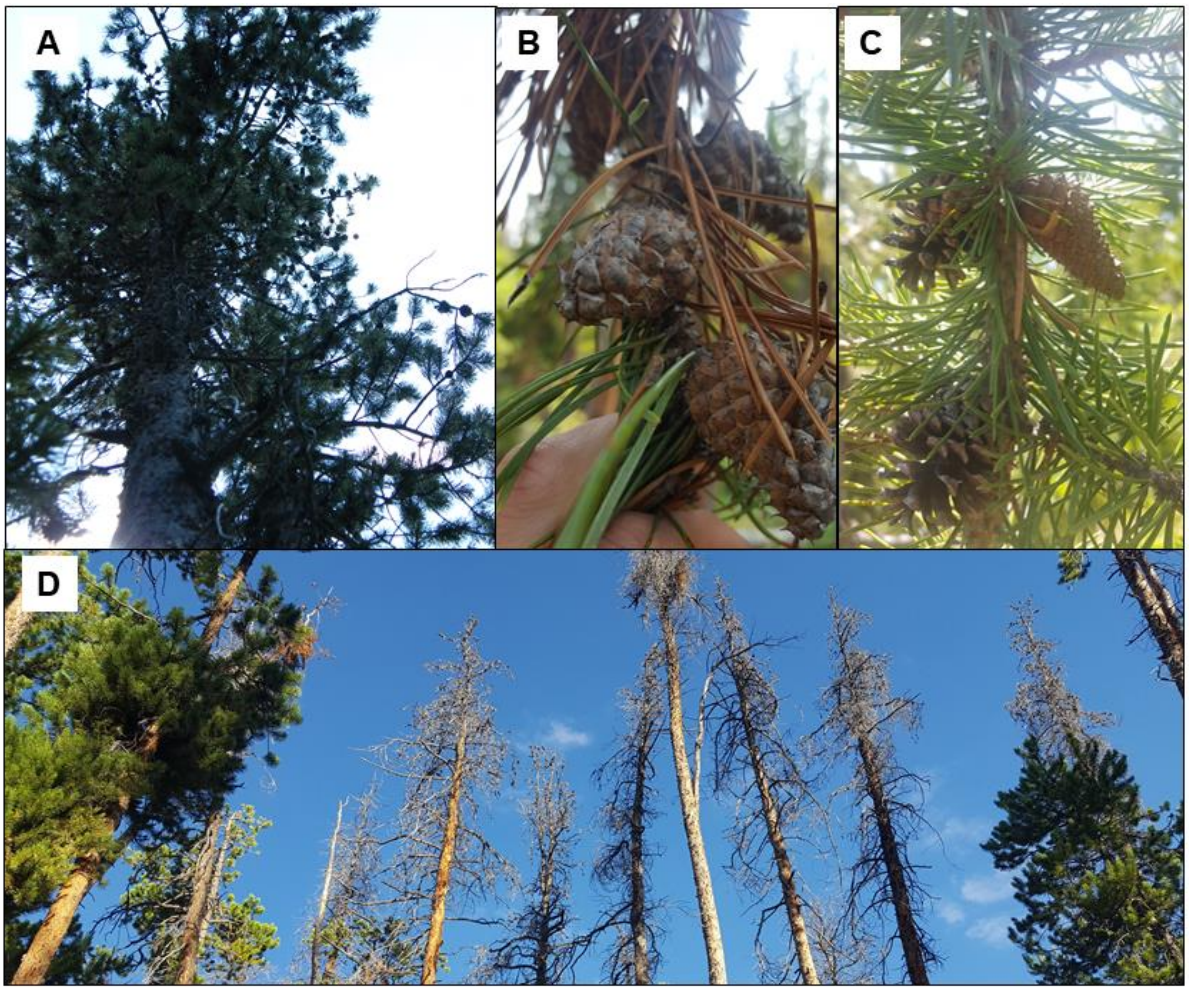

Figure 2.3. Photos of variation in serotiny and canopy seed storage in lodgepole pine A) non-serotinous *Pinus contorta* var. *murrayana*, B) complete and C) partial serotiny in *Pinus contorta* var. *latifolia*, D) mature lodgepole pine canopy following mountain pine beetle outbreak.

Additional examples of the variability of serotiny among populations within species indicate serotiny is characterized by high phenotypic plasticity (Martin-Sanz et al. 2016). Weakly serotinous species *Pinus canariensis* and *P. pinaster* have been shown to produce thick bark (a fire resister strategy) where the fire regime consists of low severity surface fires, and a

low proportion of serotinous cones (less than 40% and 60%, respectively) relative to where the fire regime consists of stand-replacing fires (Climent et al. 2004, Tapias et al. 2004). *Pinus coulteri*, another weakly serotinous species, has serotinous cones only where it intergrades with highly flammable chapparal vegetation and patches of the conifer, *Hesperocyparis sargentii*, a serotinous species subject to stand-replacing fires (Ne'eman et al. 1999), suggesting that *P. coulteri* only produces serotinous cones where conditions favor post-fire colonization (Borchert 1985). However, for *P. halepensis* stands that burned twice within a 16-year period [a decreased fire interval as compared with the historical fire return interval range of 25 to 125 years (Ne'eman et al. 2004)], production of serotinous cones and overall reproductive capacity were decreased as compared with stands that experienced a single fire within the same period (Espelta et al. 2008). This suggests that there are limits to the magnitude of change possible in serotiny as a trait in response to rapid fire regime change.

2.5.3.2 Variability within populations

In addition to variability in environmental conditions at broad spatial scales, microclimate and fine-scale topography can influence cone serotiny within populations and within stands. *Pinus coulteri* individuals on stand edges were found to have nearly 100% open cones, while trees on the interior of stands had some proportion of closed cones (Borchert 1985), suggesting that the proportion of cones opened through xeriscence varies within stands for some weakly serotinous species. Furthermore, stand dynamics have separate influences on cone production, and resource allocation is complex. At the individual tree level, total cone production (of serotinous and non-serotinous cones) increased with tree size (holding tree age constant) in *P. contorta*, while serotinous cone production was unrelated to tree size or stand density (Turner et al. 2007). However, at the stand level, cone density increased with increasing stand density.

Conversely, in *P. coulteri* and *P. halepensis*, cone production is delayed in high density stands, but decreased stand density does not result in increased serotiny (Borchert 1985, Moya et al. 2008, Agne et al. 2022). Many stand- and within-stand-level variables influence serotiny of individual plants, and characterizing populations as serotinous or non-serotinous may lead to loss of detail regarding fine-scale processes.

2.5.3.3 Variability within individual plants

The percentage of an individual tree's cones that are serotinous at a given point in time varies widely among and within species. While cone opening over time as cones age can produce a mix of open and closed cones on a single plant for most serotinous species (Midgley and Enright 2000, Lamont and Enright 2000, de Gouvenain et al. 2019), production of a combination of serotinous and non-serotinous cones on individual plants has been primarily documented in *Pinus* spp. For the most highly serotinous species, such as *Pinus attenuata* and *P. halepensis*, the proportion of an individual's total cones that are serotinous is over 95% (Vogl 1973, Keeley et al. 1999, Espelta et al. 2011), while estimates in *P. contorta* are over 90% (Lotan 1967, Muir and Lotan 1985). Variability of cone type within *Leptospermum scoparium* individuals is rare; plants have either serotinous or non-serotinous cones (Bond et al. 2004), as is the case for most serotinous angiosperms (Lamont et al. 2020). Conversely, individuals of serotinous conifer species including *Cupressus sempervirens* (Lev-Yadun 1995) and *Pinus banksiana* (Gauthier et al. 1993) typically develop a combination of serotinous and non-serotinous cones. Observations of *Pinus banksiana* and *P. contorta* from the Rocky Mountains in North America indicate that individuals with serotinous cones, non-serotinous cones (Figure 2.3C), and a combination of both are usually present within populations, and that proportions of each type of individual vary with terrain and latitude (Teich 1970). Further, variation in cone opening temperatures can vary

within individuals, with important consequences for seed release following fire of variable intensity or where ambient temperatures are high (Tapias et al. 2001, Wyse et al. 2019).

Partial opening of cones, and the retention of seed within cones with open scales, has also been noted in some serotinous species. Partially open cones represented approximately 10% of total cones in *Cupressus sempervirens* in Italy (Battisti et al. 2003) and this phenomenon is common in populations of *P. muricata* in northern California (M. Agne, personal observation Figure 2.4A). *Pinus coulteri* and *P. torreyana* often retain seed within portions of partially open cones nearest to the branch or tree bole (Keeley and Zedler 1998), which are thought to be an important seed source following stand-replacing fire (Minnich 1980). However, germination tests from partially opened *Pinus contorta* cones indicate a significant decrease in germination capacity of seed from partially opened cones as compared with closed cones (Teste et al. 2011b). This suggests that partially opened cones may influence estimates of overall canopy seed bank when calculated from estimated cone counts. Rather than classifying cones as serotinous or non-serotinous, seed retained in partially opened cones should be accounted for by quantifying the percentage of each cone that is closed when estimating canopy seed banks. Potential for warming climate to increase incidence of xeriscence resulting in whole cone or individual follicle opening for strongly serotinous species (Figure 2.4B-D) further supports the utility of this method, when possible, although studies on this phenomenon are needed.

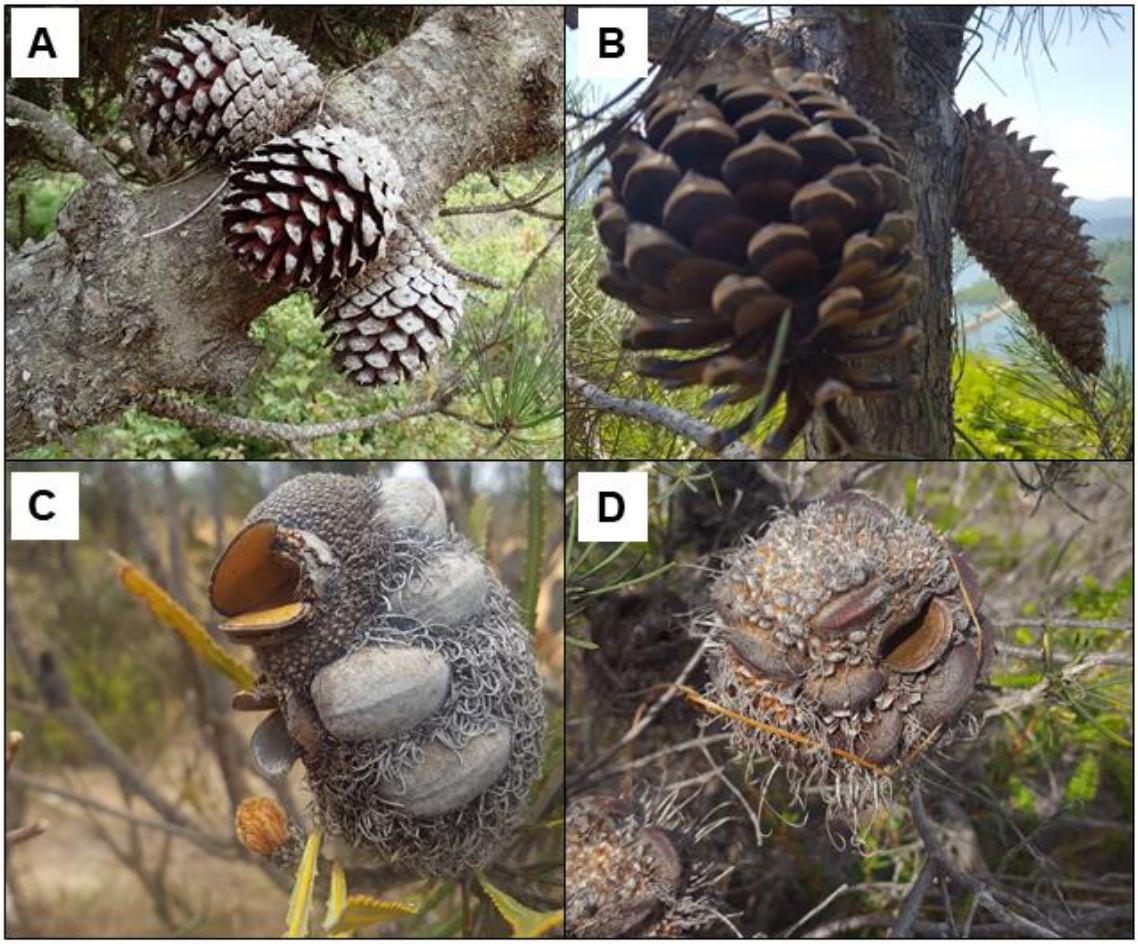

Figure 2.4. Serotinous cone opening through various mechanisms. A) Opening of a fraction of scales at the cone level, due to weak serotiny, in *Pinus muricata*, B) opening of a fraction of cones at the plant level, in *P. attenuata*, opening of a fraction of follicles at the cone level, in C) *Banksia hookeriana*, and D) *B. leptophylla*.

Note: Opening presumed to be facilitated by warming temperatures in the (historically) strongly serotinous species represented in panels B-D (Enright and Lamont, Keeley and Zedler 1998). All photos taken by M. Agne.

2.5.3.4 Serotiny variability over time

For many serotinous species, the production of serotinous cones varies over time, due to several factors. Serotinous cone production is strongly related to plant age in some species. *Pinus contorta* can produce serotinous cones by 15 years of age (Turner et al. 2007), but the highest levels of serotiny occur in stands up to 140 years of age, the mean fire return interval in the

system (Schoennagel et al. 2003). This trend indicates that within-stand serotiny increases until the mean fire return interval before decreasing, as is expected provided that serotiny is an adaptation to stand-replacing fire. Low levels of serotiny within young *P. contorta* may also represent a mechanism favoring protracted post-fire recruitment in low density stands (Lotan and Perry 1983). *P. halepensis* begins producing cones, ~95% of which are serotinous, at five years of age, and significantly declines with respect to percent serotiny by 30-50 years of age (Tapias et al. 2001), the approximate fire return interval of the species (Agee 1998). Decreased production of serotinous cones in older plants is hypothesized as an adaptation against senescence risk (the likelihood that an individual tree will die prior to the next stand-replacing fire) (Tonnabel et al. 2012), but additional research on this phenomenon is needed to understand how this mechanism operates and whether there is evidence for decreased serotiny with plant age across serotinous species.

Serotiny can also vary through time as a function of external biotic and abiotic environmental factors. *Pinus halepensis* in Spain is strongly influenced by drought, which in addition to seed release from serotinous cones, is associated with decreased overall seed and cone production and immature cone termination, leading to significant decreases in the canopy seed bank (Nathan et al. 1999, Nathan and Ne'eman 2004, Espelta et al. 2011). Stand density is also related to serotiny in *P. halepensis*. Low density stands on xeric sites are associated with lower levels of serotiny than high density stands on mesic sites (Moya et al. 2008). Thinning treatments that resulted in decreased stand density resulted in similar trends; serotinous cone opening increased as compared with unthinned, denser stands, while inducing cone production in previously non-reproductive individuals (Verkaik and Espelta 2006). Seed release from serotinous cones due to thinning is likely an adaptation to take advantage of resource availability

during inter-fire periods. However, in the youngest stands (approximately 10 years of age), serotinous cones remained closed, which is hypothesized as a safeguard against immaturity risk (Verkaik and Espelta 2006), an opposite mechanism to weak serotiny facilitating infilling post-fire for other serotinous species (Lotan and Perry 1983). Similarly, serotiny in *P. halepensis* in Israel was strongly inversely related to tree height, a relationship hypothesized to be an adaptation to compensate for the limitation to long distance seed dispersal in small stature plants (Goubitz et al. 2004).

Further complicating the question of variability of serotiny over time and space is the issue of scaling to seed counts from cone counts. Given the inherent difficulty of counting individual seeds within cones, particularly for addressing stand-level questions, cone counts are nearly always used as a surrogate for seed counts, despite being less strongly linked mechanistically to recruitment (Lamont 2021). Testing variability of seed counts within cones through time and space is therefore challenging. However, studies which have aimed to obtain seed counts from individual cones indicate that between-cone variability in seed count for a given species can vary widely with environmental conditions, such as drought during the year of cone production (Espelta et al. 2011), cone age (De Magistris 2001), parasitism by fungal pathogens (Battisti et al. 2003), and attack from insect granivores (Enright et al. 1996). The many variables that influence the seed-cone relationship within species indicate that scaling up from cone density to seed density should be done with caution. Furthermore, some serotinous species retain serotinous cones for multiple years, but seeds contained within cones decline steeply with respect to viability after two years in *Picea mariana* (Viglas et al. 2013) and after five years in *Banksia burdettii* (Lamont and Barker 1988) and B. spinulosa (Whelan and Ayre 2020). Similarly, several serotinous *Hesperocyparis* spp. have inherently low seed viability,

which can be further exacerbated with extended exposure to extreme temperatures (Milich et al. 2012). Given that other serotinous species retain a considerable amount of viable seed within closed cones for decades (e.g., Pinus attenuata, Keeley and Zedler 1998), accounting for age effects on within-cone seed viability must be considered in the context of individual species' life history traits.

2.6 SEROTINY AND GLOBAL CHANGE

The syndrome of serotiny confers potential costs and benefits upon woody plant species. Given the many drivers of canopy seed bank variability, and the multiple spatial and temporal scales at which they occur, it is difficult to predict whether serotiny will benefit individual population or species persistence. Indeed, this relationship is likely to vary among species and regional climatic conditions. While local extirpation of serotinous species is a concern in some areas (Enright et al. 2015), invasion by serotinous conifers following fire is a critical management issue in South America, where there are no native serotinous species (Franzese and Raffaele 2017), but fire has selected for increased serotiny over a relatively short period in exotic *Pinus radiata* populations (Ripa et al. 2020). Further, *P. radiata* can experience cone opening under ambient temperatures suggesting high invasion potential even where fire is infrequent (Wyse et al. 2019). This suggests, paradoxically, that serotinous species may be positioned to capitalize on warming temperatures and increased fire activity in naïve environments. However, it remains unclear whether serotinous species' origins during a fiery period has prepared them to persist in various regions under future climatic conditions and fire regimes.

There are several key knowledge gaps that must be filled to understand how serotinous species will respond to a warming climate and increased fire activity. Despite a considerable body of research on serotiny as a trait (Lamont et al. 2020), many of the mechanisms that

mediate serotinous cone production through time and space are poorly understood. Future research should be conducted to improve understanding of the relative effects of biotic and abiotic drivers of serotinous cone production (e.g., climate, tree size, stand density, tree disease, seed predation) and their influence on seed availability at spatial scales from individual plants to populations. Additional studies on controls on seed viability within cones, particularly under warming climate, are also needed. Finally, both empirical and modeling studies are needed in systems across the globe to understand how shortened fire intervals and warming climate influence propagule availability within populations over time since establishment, and how these mechanisms may influence regeneration following subsequent fire (i.e., interval squeeze, Enright et al. 2015). Further insights on these mechanisms will contribute to an increased understanding of the constraints on populations of serotinous species in a warmer climate.

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Chapter 3. FUEL PROFILES AND SEVERE REBURN POTENTIAL RECOVER RAPIDLY AFTER STAND-REPLACING FIRE IN CLOSED-CONE PINE FORESTS

3.1 ABSTRACT

Accelerating disturbance frequency under a warming climate increases the potential for multiple disturbances to overlap and produce compound effects that erode resilience — the capacity to experience disturbance without transitioning to an alternative state. A key concern is the potential for amplifying or attenuating feedbacks via interactions among successive, linked disturbance events. Following severe wildfires, fuel limitation is a negative feedback that may reduce the likelihood of subsequent fire. However, the duration of, and pre-fire vegetation effects on, fuel limitation remain key unknowns with high management relevance. To address this knowledge gap, we characterized fuel profiles over a 35-year post-fire chronosequence in California closed-cone pine forests, a system with stand dynamics comparable to stand-replacing fire regimes in other temperate and boreal conifer forests with much longer fire return intervals. We used this system to ask: 1) How do fuel profiles change with time since fire relative to quantities sufficient to support stand-replacing fire? 2) How do trajectories of fuel profiles differ between forests established from different pre-fire vegetation legacies — specifically areas that were forest vs. non-forest pre-fire? As a useful comparison, we capitalized on an opportunity to compare fuel profiles to quantities that supported stand-replacing fire during the 2018 Carr Fire, a large (> 90,000 ha) wildfire that burned through our study area shortly after data collection. Overall, downed woody and live woody fuels accumulated quickly, reaching levels capable of supporting severe fire after 10–15 years. Canopy fuels peaked at 20 years post-fire but were at

levels capable of supporting severe fire from 15 years onwards. Pre-fire vegetation legacy drove divergence in post-fire downed surface fuel trajectories, but effects on live woody and canopy fuels were minor. Fuel profiles in California closed-cone pine forests can support subsequent severe fire within 10 years, a fraction of the historical fire return interval (30-90 years), but potential for severe fire remains lower for an extended period in areas where pre-fire vegetation was non-forest. Our findings show that the negative feedback of fuel limitation disappears quickly following fire, suggesting the potential for erosion of forest resilience associated with climate-driven short-interval stand-replacing reburns.

3.2 INTRODUCTION

Climate change is altering terrestrial ecosystems globally through changes to disturbance regimes (Trumbore et al. 2015). Changing disturbance regimes linked to warming climate have been documented for forested ecosystems globally (Seidl et al. 2014, Millar and Stephenson 2015, Prichard et al. 2017), and changes in frequency, size, and/or severity of disturbances may have abrupt and substantial effects on ecosystem structure and function (Turner 2010). A key concern underpinning these effects from changing disturbance regimes is the potential for erosion of forest resilience, defined as the capacity of an ecosystem to experience disturbance without transitioning to an alternative state (Holling 1973).

Changing disturbance regimes may increase the likelihood of synergistic interactions among disturbances. Fire activity in many forested ecosystems between the early 2000s to the early 2020s (Boer et al. 2020, Higuera and Abatzoglou 2020) has been characterized by increases in fire season length (Jolly et al. 2015, Balch et al. 2017), average fire size (Dennison et al. 2014), annual area burned (Littell et al. 2009), and fire frequency (Brown and Johnstone 2012, Fairman et al. 2017, Turner et al. 2019). Of particular concern is in ecosystems characterized by

a high severity fire regime, when overlapping fires occur at substantially shorter intervals than the historical fire return interval (i.e., short-interval severe reburns; Donato et al. 2009). When they occur, short-interval severe reburns can erode material legacies (*sensu* Johnstone et al. 2016) — including surviving trees, standing snags and seed source — and may produce compound (*sensu* Paine et al. 1998) or synergistic effects on ecosystems. Such compound effects from short-interval severe reburns can manifest as decreased abundance of a formerly dominant tree species (Bowman et al. 2014, Enright et al. 2014, Turner et al. 2019), altered forest structure (Fairman et al. 2017), or conversion from forest to non-forest (Brown and Johnstone 2012).

A key constraint on the potential for compound disturbances to occur is whether disturbances are linked (*sensu* Simard et al. 2011); that is, whether one disturbance can affect the likelihood or magnitude of a subsequent disturbance. In the case of short-interval, stand-replacing reburns, the occurrence of one stand-replacing fire may reduce (i.e., be negatively linked with) the likelihood of a severe reburn through negative feedbacks on fuel availability. Fuel limitation is a negative feedback that may reduce the likelihood of subsequent fire immediately following severe fire (Fontaine et al. 2012, Parks et al. 2015, 2016, Harvey et al. 2016), but the duration of fuel-limitation varies with species composition and stand dynamics (Prichard et al. 2017). In forests where fire activity is generally not fuel-limited and fire potential is strongly controlled by the occurrence of an ignition (ignition-limited) or antecedent weather conditions (climate-limited; *sensu* Littell et al. 2009), fuels were historically of relatively low importance for understanding the conditions under which fire could occur (Romme 1982, Moritz et al. 2004). However, fire regimes previously characterized as climate- or ignition-limited are likely to more frequently experience conditions conducive to fire initiation and fire spread under a warming climate and increasing anthropogenic ignitions (Westerling et al. 2011, Balch et al.

2017). Previous studies in climate- or ignition-limited forests with high severity fire regimes suggest that fuels sufficient to carry fire are present within a fraction of the time of the mean fire return interval following wildfire (Nelson et al. 2016, 2017, McNamara et al. 2019b). However, understanding how fuel profiles develop continuously over time and when critical thresholds for fire hazard may be crossed are key knowledge gaps to building a better understanding of linked interactions among fires.

Feedback duration and magnitude from prior disturbance (e.g., fuel limitation), likely differ depending on the legacy of pre-disturbance vegetation, with important implications for forest contraction or expansion. The potential for forest contraction following short-interval stand-replacing reburns is of particular concern for management of forests dominated by serotinous obligate seeders, species with low ability to survive fire and that regenerate from an on-site canopy seed bank (Lamont et al. 1991). Where reburn frequency outpaces canopy seed bank development, serotinous populations are unlikely to persist (Enright et al. 2015). Conversion from forest to non-forest following short-interval, stand-replacing reburns has already occurred in some forests dominated by obligate seeders in both North America (Brown and Johnstone 2012, Turner et al. 2019) and Australia (Bowman et al. 2014). Alternatively, for serotinous species that reach reproductive maturity at an early age, forests have the potential to expand into non-forest ecosystems following periods characterized by high levels of fire activity (Johnstone and Chapin 2003, Buma et al. 2013, Krause and Whitlock 2017, Reilly et al. 2019). Such expansion of serotinous tree species into pre-fire grassland or shrub-dominated ecosystems has occurred after single severe fire events (Forrestel et al. 2011, Harvey et al. 2011), suggesting that non-forest to forest conversion represents a separate post-fire pathway possible in systems characterized by a forest and non-forest mosaic. Forests established from different pre-fire

vegetation legacies (e.g., forest vs. non-forest pre-fire) are likely to differ with respect to post-fire structural attributes, such as standing snag and downed woody surface fuel abundance (Figure 3.1). Differences in how pre-fire vegetation legacy affects reburn potential may have important implications for linked disturbance interactions.

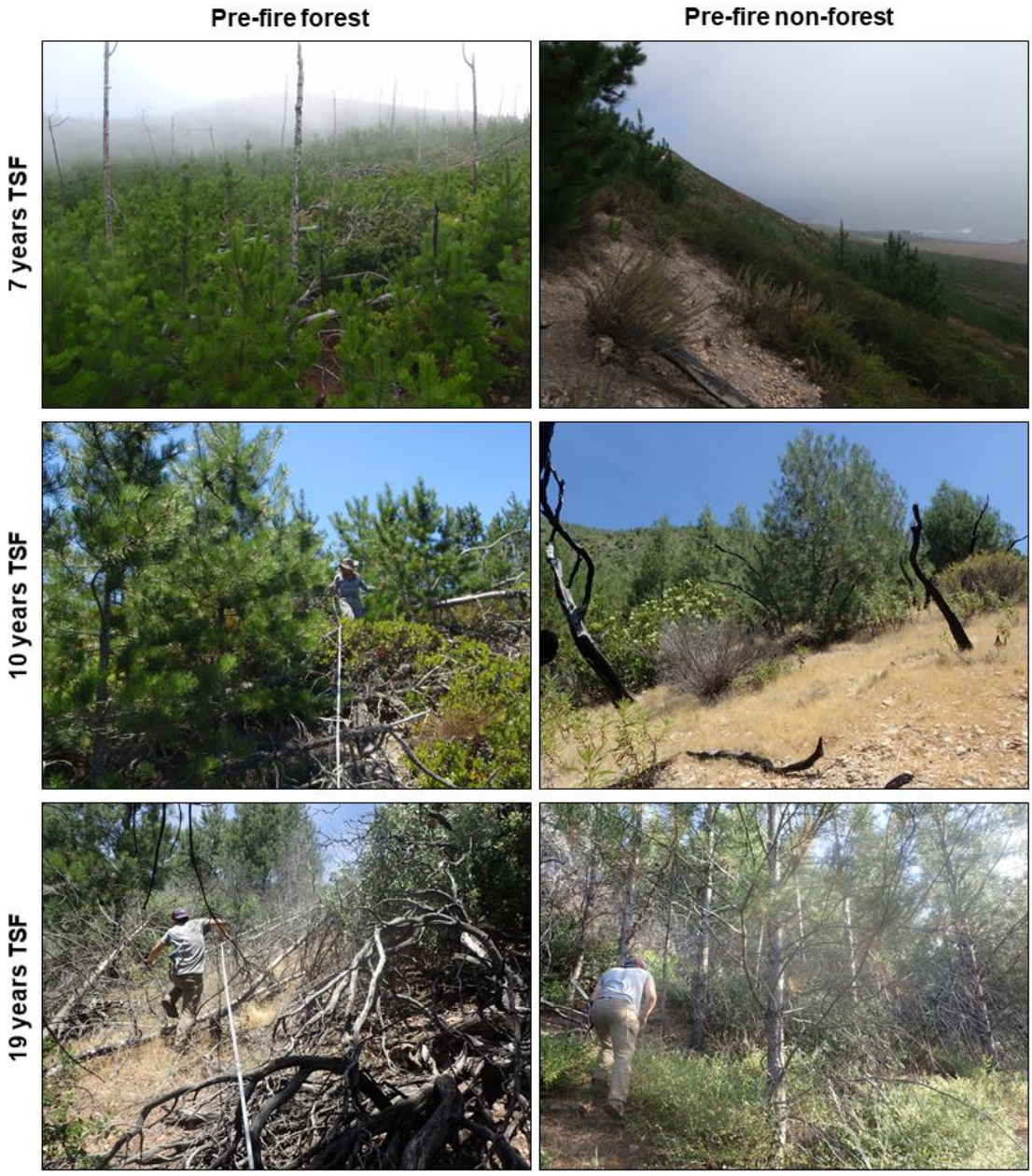

Figure 3.1. Fuel profiles at various times since fire (TSF) in closed-cone pine forests that were characterized by forest preceding the most recent fire (left column) or non-forest preceding the most recent fire (right column).

The closed-cone pine forests of California, USA, are a model system for understanding the mechanisms of serotinous forest resilience as stand-replacing fire frequency increases from climate warming. These forests are characterized by a stand-replacing fire regime like other serotinous forests in North America (e.g., lodgepole pine [*Pinus contorta*], jack pine [*P. banksiana*]), but stand development occurs more rapidly (Vogl 1973, Harvey et al. 2011). California closed-cone pines reach reproductive maturity at a younger age and proceed through the stages of stand dynamics more quickly than other serotinous forests in North America (Keeley et al. 1999, Harvey and Holzman 2014). These forests also experience stand-replacing fire relatively frequently, with mean fire return intervals varying from 30 to 90 years (Vogl 1973, Sugnet 1985, van de Water and Safford 2011). Therefore, gaining an empirical understanding of fuel profiles across the inter-fire period is more logistically feasible than in most other obligate seeding serotinous forests in North America in which fire return intervals are considerably longer (Romme 1982, Gauthier et al. 1996). Insights from California closed-cone pine forests may illuminate the mechanisms driving fire regimes and species persistence in forests in which these processes unfold on much longer temporal scales.

To build an understanding of the key mechanisms underpinning the likelihood of short-interval severe reburns in obligate seeding conifer forests, we conducted a field study to examine trends in fuel accumulation over a time since fire (TSF) gradient in California closed-cone pine forests dominated by either bishop pine (*Pinus muricata*) or knobcone pine (*P. attenuata*). We asked: 1) how do fuel profiles, including surface and canopy fuel loads, change with TSF relative to values sufficient to support stand-replacing fire, and 2) how do trajectories of fuel profiles differ between forests established from different pre-fire vegetation legacies—specifically areas that were forest vs. non-forest pre-fire? We expected trends similar to fuel profile development

in other serotinous forests (Nelson et al. 2016, McNamara et al. 2019b) but that the accelerated pace of stand development in California closed-cone pine forests would lead to more rapid fuel accumulation. Specifically, with increasing TSF, we expected dead down woody, litter, herbaceous, and live woody fuel loads to increase and plateau after the period of snagfall and canopy closure and the canopy fuel load to increase continuously. Further, because pre-fire forest successional age can affect fuel profiles (Nelson et al. 2016), we expected stands that were forest preceding the last fire to have greater peak dead down woody, litter, herbaceous, live woody and canopy fuel loads compared to stands that were previously non-forest. Finally, we capitalized on an opportunity to compare fuel profiles to values that supported stand-replacing fire in these forests during the 2018 Carr Fire, a large (> 90,000 ha) wildfire that burned through our study area shortly after data collection. Our study provides key insight for management of forested ecosystems in which short-interval severe reburn potential is high and for which fuels management could alter the period of fuel limitation (Skinner and Agee 2005).

3.3 METHODS

3.3.1 *Study area*

The study area is bounded by the coastal mountain ranges and Sierra Cascade foothills in northern and central California and spans the distributions of bishop and knobcone pine in California where stand-replacing fire has occurred since 1982 (Appendix A – Figure 3.8). The study area encompasses low elevation to lower montane zones (84–1344 m above sea level) and has a Mediterranean climate with hot, dry summers and cool, wet winters. The climate covers a wide range of average winter (January) temperatures (3.3–12.2 °C), average summer (July) temperatures (14.9–26.9 °C), and annual average precipitation (467–1996 mm; 800-m gridded 30 year climate normals from 1981–2010 [PRISM Climate Group 2019]). Bishop pine occupies

areas that receive less total precipitation (annual average precipitation of 467–1034 mm) than where knobcone pine occurs (785–1996 mm). Further, bishop pine occupies areas that experience lower variation in temperature across seasons, with averages ranging from 8.8–12.2 °C in January and 14.9–18.7 °C in July vs. 3.3–9.9 °C in January and 20.7–26.9 °C in July for knobcone pine. Both species experience strong seasonality in precipitation (with at least 94% falling between October and May [PRISM Climate Group 2019]) and a moderating effect of summer fog (Vogl et al. 1977, Torregrosa et al. 2016). The historical fire regime is characterized by stand-replacing fire for both species, with mean return intervals ranging from 30–90 years (Sugnet 1985, van de Water and Safford 2011), although there is evidence of non-stand-replacing fire occurrence in both species ranges (Finney and Martin 1989, Fry et al. 2012). Closed-cone pine plant communities are often densely forested but are also represented by low density, open stands that overtop chaparral and co-occur with diverse shrub and herbaceous communities. Common co-occurring shrub species include chamise (*Adenostoma fasciculatum*), toyon (*Heteromeles arbutifolia*), and evergreen huckleberry (*Vaccinium ovatum*) as well as a variety of *Ceanothus* spp. and *Arctostaphylos* spp. Resprouting broadleaf trees, most commonly *Quercus* spp., are also represented on the landscape, and this ecosystem is characterized by a high diversity of herbaceous vegetation, including *Acmispon glaber*, *Lupinus* spp., and *Mimulus* spp.

3.3.2 *Study design and field sampling*

To quantify fuel profile development over time, we established a chronosequence of plots representing 2–35 years TSF across the study area. To capture this range of TSF across California closed-cone pine forests, 15 fires (each representing a single TSF) were selected using Monitoring Trends in Burn Severity (MTBS) data (Eidenshink et al. 2007), species distribution

maps, and local land management information to identify past fires since 1982 that were at least 100 ha in size and overlapped our target species' ranges (Appendix A – Figure 3.8). Plot locations were at least 50 m from roads and covered the range of topographic positions and stand density within each fire perimeter. Each plot represented a unique single-aged cohort of closed-cone pine that established following high severity fire, defined as > 90% mortality of individuals from the previous pre-fire cohort. Plots were separated by a distance of at least 100 m, with shorter distances possible when plots were on opposing topographic positions (e.g., N vs. S aspect). The number of plots sampled varied between two and ten per fire due to sampling constraints (e.g., fire size, closed-cone pine forest area) with a total sample size of 79 plots, which were established in the summers of 2017 and 2018 (Table 3.1).

At each plot, we measured downed surface fuels (dead down woody fuels, litter depth, and substrate cover), live and standing dead herbaceous, shrub, and tree biomass < 2 m in height, and canopy fuels (live and standing dead tree and shrub biomass > 2 m in height). Downed woody surface fuels were measured along three transects (with the exception that 16 plots had two transects) established in randomly selected cardinal directions and using standard planar intercept methods (Brown 1974). Total transect length varied between plots; 1-hr fuels (< 0.64 cm) were counted along a total length of 4–6 m, 10-hr (0.64–2.54 cm) fuels were counted along a total length of 10–15 m, 100-hr (2.54–7.62 cm) fuels were counted along a total length of 20–30 m, and 1000-hr (> 7.62 cm) fuels were counted along a total length of 35.6–54 m (see Appendix A for detailed sampling methodology). We identified 1000-hour fuels to species when possible, categorized them using a 1–5 decay class rating system (Sollins 1982), and measured the diameter of every piece where it crossed the transect.

Table 3.1. Sample fires with mean (standard deviation), number of plots per fire (n) and plot-level post-fire California closed-cone pine stand characteristics.

Fire name	TSF[1] (years)	Fire year	Dominant species	n	Live BA[2] (m^2/ha)	Live density[3] (trees/ha)	Average tree height (m)	QMD[4] (cm)
Cuesta	2	2015	PIAT[5]	7	NA	110,556 (63,088)	0.2 (0.1)	NA
Butler	5	2013	PIAT	2	1.06 (0.13)	7,043 (1,744)	0.6 (0.2)	1.4 (0.3)
North Ranch VMP	5	2012	PIMU[6]	6	1.17 (1.00)	13,274 (10,001)	1.1 (0.4)	1.6 (1.0)
Stafford	6	2012	PIAT	2	0.53 (0.40)	1,837 (1,692)	1.8 (0.2)	2.0 (0.3)
North Ranch (North Unit)	7	2010	PIMU	5	5.62 (3.83)	45,910 (23,983)	1.1 (0.4)	1.2 (0.2)
North Ranch (South Unit)	8	2009	PIMU	4	3.91 (3.61)	6,381 (4,901)	2.2 (1.0)	3.2 (1.6)
Motion	10	2008	PIAT	8	5.3 (2.07)	3,493 (3,667)	4.2 (0.8)	5.6 (1.9)
Diablo	10	2007	PIMU	6	2.71 (1.79)	2,034 (1,319)	3.2 (1.3)	4.4 (1.9)
Bear	14	2004	PIAT	9	16.51 (6.25)	3,444 (4,898)	7.9 (1.7)	10.6 (4.2)
Whiskeytown	15	2003	PIAT	2	10.01 (3.14)	2,880 (1,804)	6.9 (0.4)	6.6 (0.7)
Sugar	19	1999	PIAT	6	19.70 (14.73)	4,689 (5,355)	7.5 (0.7)	8.7 (2.3)
Hwy 41	23	1994	PIAT	3	19.99 (12.50)	2,389 (1,641)	9.2 (2.3)	11.0 (2.5)
Vision	23	1995	PIMU	10	37.70 (17.06)	6,953 (9,156)	10.1 (2.6)	15.7 (8.4)
Las Pilitas	32	1985	PIAT	3	25.59 (3.40)	2,735 (448)	11.2 (0.5)	10.9 (1.6)
Diablo Canyon	35	1982	PIMU	6	14.33 (6.03)	710 (434)	13.3 (2.5)	16.2 (3.4)

[1]Time since fire at time of sampling, which occurred over two years, leading to fires that occurred in multiple years having the same time since fire
[2]Basal area
[3]Total live tree density, a population estimate rather than the canopy tree density estimate (trees/ha over two m) presented as a canopy fuel metric
[4]Quadratic mean diameter
[5]Knobcone pine (*Pinus attenuata*)
[6]Bishop pine (*Pinus muricata*)

Substrate cover, litter depth, and herbaceous and live woody fuels from shrubs and trees were measured along two 18 m transects at each plot. We estimated substrate percent cover of litter, wood, bare soil, rock, and moss and measured litter depth within a 10 by 10 cm square at 1-m increments along each transect (n = 36). We measured herbaceous and live woody fuels using a point-intercept method (Fontaine et al. 2012) in which we tallied vegetation intercepting the transect into three height bins (≤ 0.5 m, 0.5–1.0 m, 1.0–2.0 m). Individuals intercepting the transect were also classified as live or dead and assigned to species for trees and shrubs or life form for forbs and graminoids (hereafter, combined as herbaceous). For all shrubs that were intercepted, crown volume measurements (shrub total height and two perpendicular crown widths) were taken.

We measured canopy fuels and post-fire stand structure within a central subplot at each plot. Central subplot size radii varied with post-fire stand density and ranged from 2 m to 18 m. If the central subplot radius was < 8 m, we estimated stand density within four additional 1 m radius microplots located in the cardinal directions from subplot center (total sampling area range: 25.1—1017.9 m2). All trees were categorized as live or dead, assessed for structural damage (e.g., dead or broken top), and measured for diameter at breast height (DBH; 1.37 m above ground) and total height. We reconstructed stand structure conditions preceding the last stand-replacing fire by measuring the DBH of all standing and fallen snags. However, reconstruction was not possible at plots nine years TSF and older at which most snags had fallen (n = 56).

Ten of our 79 plots reburned in the 2018 Carr Fire; eight at 10 years TSF and two at 15 years TSF. The wildfire occurred approximately one month following initial fuels measurement, so that our fuels estimates approximate available fuel at the time of fire. We revisited these plots

in May 2019, approximately 10 months following wildfire, to assess burn severity as determined by percent canopy tree mortality. We compared minimum and median fuel load values from plots where high severity fire (> 90% canopy tree mortality) occurred (n = 6) to understand how values for fuel loads across the chronosequence correspond to values capable of supporting high severity fire (Table 3.2).

Table 3.2. Minimum, maximum, and median pre-fire fuel profile values from plots that burned with high severity fire (> 90% canopy mortality, n = 6) in the 2018 Carr Fire.

Fuel variable	Minimum	Maximum	Median
1-hr fuel load (Mg/ha)	0.09	0.55	0.22
10-hr fuel load (Mg/ha)	0.93	3.08	1.69
100-hr fuel load (Mg/ha)	1.16	8.60	5.74
1000-hr sound fuel load (Mg/ha)	0.00	22.60	1.27
1000-hr rotten fuel load (Mg/ha)	0.63	46.89	3.27
Litter depth (cm)	1.8	3.0	2.6
Herbaceous fuel load (Mg/ha)	0.12	1.40	0.77
Woody shrub fuel load (Mg/ha)	2.90	17.77	8.63
Standing tree surface fuel load (Mg/ha)	0.38	4.75	3.26
Proportion litter cover	0.43	0.70	0.59
Proportion wood cover	0.02	0.23	0.05
CV of proportion litter cover	44	87	59
CV of proportion wood cover	137	332	261
Proportion herbaceous cover	0.03	0.33	0.18
Proportion tree cover	0.03	0.44	0.29
Proportion shrub cover	0.33	0.69	0.51
Proportion vegetation cover	0.58	0.83	0.81
Available canopy fuel load (Mg/ha)	2.73	8.18	4.12
Canopy bulk density (kg/m^3)	0.042	0.086	0.057
Canopy base height (m)	2.1	4.9	2.9
Stand height (m)	5.5	9.5	6.5
Live stand density (trees/ha)	906	10567	2323
Snag density (trees/ha)	0	127	0
Live basal area (m^2/ha)	3.68	12.09	6.77
Dead basal area (m^2/ha)	0.00	0.17	0.00

3.3.3 *Fuel calculations*

3.3.3.1 Surface fuel load

We calculated downed woody surface fuel load (Mg/ha) for each fuel size class (1-, 10-, 100-, 1000-hour) individually, using standard planar intercept methods (Brown 1974). We separated 1000-hour fuels further into sound (decay class 1–3; bole of downed log intact) and rotten (decay class 4–5; bole of downed log breaking apart). We averaged litter depth measurements for all transects within each plot (n = 36) to obtain plot-level litter depth estimates. Herbaceous and live woody fuels were calculated from point intercept data for each plot. The herbaceous fuel load (Mg/ha) was estimated by summing graminoid and forb biomass, which were each calculated from percent cover (estimated as the proportion of sample points at which a graminoid or forb was intercepted) using general graminoid and *Lupinus* spp. equations (Means et al. 1994). We estimated the live woody shrub fuel load (Mg/ha) using published equations employed by the Fuel Characteristic Classification System (Prichard et al. 2013) to estimate individual shrub crown biomass from shrub dimensions measured, summing across each plot and scaling to the hectare. The live woody tree fuel load (Mg/ha) was estimated by assigning each interception as foliage or branch and multiplying published values of specific leaf mass or oven dry weight (Wilson et al. 1986, Abrams and Kubiske 1990), respectively, by the sampling area (defined as the intercept pole width * transect length), summing across each plot and scaling to the hectare (see Appendix A – Table 3.3 for herbaceous and live woody fuel load equations).

We quantified composition by allocating herbaceous, live woody tree, and live woody shrub fuel loads to three vertical strata (≤ 0.5, 0.5 – 1.0, 1.0 – 2.0 m), proportionally to the number of live and dead interceptions measured in the field. For shrubs that extended into the canopy layer, biomass was allocated to the surface and canopy layer in proportion to total height

(see Appendix A for additional detail on herbaceous and live woody fuel calculations).We also calculated the proportion of sample points (n = 36) within all transects at each plot at which a live herb, shrub, tree, and vegetation of all life forms was intercepted. Substrate cover was assessed by averaging within-plot estimates of litter cover and wood cover to obtain plot-level cover estimates. To assess within-stand heterogeneity of substrate cover, we calculated the coefficient of variation (CV) for litter cover and wood cover (Fraterrigo and Rusak 2008). This approach is useful for understanding within-plot fuel connectivity where within-stand heterogeneity is high (Donato et al. 2013).

3.3.3.2 Canopy fuel load

Canopy fuels were estimated using field measurements and/or model equations. Stand height reflects the maximum height of a live tree sampled at each plot, as measured in the field. For all stands with stand height > 2 m, canopy bulk density (kg/m^3) and canopy base height (m) were calculated from field measurements using equations developed for lodgepole pine (Cruz et al. 2003), as equations for knobcone pine and bishop pine are not available in the scientific literature. We calculated available canopy fuel load as total foliage biomass of all standing trees > 2 m plus 50% of live and dead branch biomass (Mg/ha) (Reinhardt et al. 2006a). Foliage, live branch, and dead branch biomass were estimated using published equations for Pinus spp., or closely related species (Means et al. 1994, Jenkins et al. 2003, Prichard et al. 2013), summing across each plot and scaling to the hectare (see Appendix A for additional canopy fuel calculation detail). For stands with stand height < 2 m, we assumed canopy fuels were zero and that all trees were part of the live woody tree layer (described in surface fuel load calculations). We calculated the density of live trees in the canopy layer by summing the number of live trees > 2 m and scaling to the hectare (hereafter, live stand density [trees/ha]). Snag density (trees/ha)

was calculated similarly and included all standing dead trees killed by the previous fire and standing dead trees > 2 m that had established post-fire and subsequently died. We calculated live and dead basal area (m^2/ha) using the same subset of live and dead trees.

3.3.4 *Vegetation structure preceding the most recent fire*

We classified the pre-fire vegetation legacy of each plot (pre-fire forest or non-forest ecosystem) using field-based measurements of pre-fire structure and aerial imagery taken in the years 1994 – 2015 from the National Agriculture Imagery Program (NAIP) or National Aerial Photography Program (NAPP) (United States Department of Agriculture 2020, United States Geological Survey 2020). Where elements of the pre-fire stand (standing snags and dead shrubs killed by the last fire) were apparent, we used field measures. In plots > 9 years TSF, most snags had fallen, and we relied on aerial imagery to reconstruct pre-fire vegetation legacy. We considered plots to be forested pre-fire if there were at least ten trees within 18 m of plot center prior to fire (~100 trees/ha). Plots classified as non-forested prior to the most recent fire generally had zero trees within 18 m of plot center prior to fire and were presumed forested via post-fire expansion from an adjacent forest ecosystem. Plots > 23 years TSF (n = 9) were not classified due to data availability limitations for sampled plots that burned prior to 1994.

3.3.5 *Statistical analysis*

To address question 1 (fuel load development following fire), we used generalized additive models (GAMs) to assess the effect of TSF on all surface and canopy fuel variables. GAMs are highly flexible and are ideal for understanding nonlinear relationships (Wood 2006, Simpson 2018) and have been used in previous chronosequence studies of trends over TSF (Valentine et al. 2014, Jenkins et al. 2020). To assess the temporal trajectory of the surface fuel

load, we fit models for six downed surface fuel response variables (1-hr, 10-hr, 100-hr, 1000-hr sound, and 1000-hr rotten fuels, litter depth), herbaceous, live woody shrub, and live woody tree fuel loads. Further, we used a descriptive approach to understand the composition of live surface fuels by plotting mean values within a single TSF for herbaceous, woody shrub, and woody tree biomass within three vertical strata (≤ 0.5, 0.5 – 1.0, 1.0 – 2.0 m) by live versus dead biomass. We fit models for proportion of each of the following vegetation and ground cover types in the surface layer: herbaceous, shrub, tree, total vegetation, litter, and wood. We also fit models for CV of proportion litter cover and CV of proportion wood cover. To assess canopy fuel loads, we fit models for eight canopy fuel response variables (canopy bulk density, available canopy fuel load, canopy base height, stand height, live stand density, snag density, live basal area, and dead basal area).

Each model fit to address question 1 included TSF as the predictor variable of interest and three biologically meaningful environmental covariates likely to affect stand growth: mean annual standardized precipitation evapotranspiration index (SPEI), elevation, and heat load index (HLI). Mean annual SPEI and elevation represent proxies for growing conditions expected to primarily vary between dominant species and regionally (i.e., among fire perimeters). Mean annual SPEI was represented using 800m resolution gridded 30 year 1981–2010 normals obtained from the Westwide Drought Tracker (Abatzoglou et al. 2017; https://wrcc.dri.edu/). Elevation for each plot was obtained using a Garmin GPS unit. Topoclimatic differences within fire perimeters were represented by HLI, a measure that incorporates latitude, slope, and aspect into a single metric that corresponds to plot-level differences in microclimate (McCune and Keon 2002). Bishop pine and knobcone pine occupied distinct ranges of values for mean annual SPEI and elevation but are interspersed across HLI (Appendix A – Figures 3.9 – 3.17),

suggesting these covariates capture distinctions between dominant species as well as variation within forests dominated by each species. Covariates were inspected for collinearity and concurvity prior to model implementation. To understand whether these covariates were useful additions to our models, we used a likelihood ratio test to compare the goodness of fit of the model including environmental covariates (full model) to a univariate model of TSF and each response variable (nested model). The full model form had a significantly improved fit over the nested model for 22 of 25 variables (Appendix A – Tables 3.4 – 3.6). For consistency we chose to implement a GAM with the full model form for each fuel response variable.

To address question 2 (effect of pre-fire vegetation legacy on fuel profile trajectories), we fit additional GAMs for each fuel response variable assessed in question 1. Each model included the predictor variables of TSF, a categorical effect of pre-fire legacy (i.e., forest preceding the last fire vs. non-forest preceding the last fire), and a TSF-pre-fire legacy interaction term. The analysis included the subset of plots burned since 1994 (n = 70) for which there were pre-fire legacy classification data from either aerial imagery or field data.

For all models, we used restricted maximum likelihood estimation (REML) to choose smoothing parameters and the number of basis functions for each predictor variable (Wood 2011). In general, this approach avoids overfitting, but we also visually inspected model fit for evidence of overfitting. When REML resulted in knots (i.e., changes in the basis function) where there were no data for a given covariate, we refit the model with successively fewer basis functions for that covariate until no knots occurred where data were lacking for any covariate in the model. After assessing model assumptions, proportion cover response variables were modeled with a beta distribution and all remaining surface and canopy fuel variables were modeled using a scaled t distribution for heavy tailed data. We performed all analyses in R

version 3.6.0 (R Development Core Team 2019). Modeled effect plots were produced with the packages “ggplot2” (Wickham 2016), “ggpubr” (Kassambara 2020), “viridis” (Garnier et al. 2018), and “voxel” (Garza et al. 2018). Likelihood ratio tests comparing candidate models were conducted with the package “lmtest” (Zeileis and Hothorn 2002). Statistical analyses of continuous TSF effects on fuel loads using GAMs were conducted with the package “mgcv” (Wood 2011, Wood et al. 2016). Given the variability inherent in fuels (Keane 2016), we interpreted $P \leq 0.01$ as strong evidence of an effect, $P \leq 0.05$ as moderate evidence of an effect and $P \leq 0.10$ as suggestive evidence of an effect.

3.4 RESULTS

3.4.1 *Post-fire stand characteristics*

All sampled stands were dominated by a single post-fire cohort of closed-cone pines, but stand structure differed greatly with TSF (Table 3.1). Mean density of the post-fire cohort (including trees in the canopy layer as well as trees included in the live woody tree fuel load) ranged from 110,600 (sd = 63,100) trees/ha at two years TSF to 710 (sd = 434) trees/ha at 35 years TSF. Mean live basal area in stands with trees above breast height ranged from 0.5 m^2/ha at five years TSF to 37.7 m^2/ha in stands at 23 years TSF. Quadratic mean diameter ranged from 1.1 cm at five years TSF to 16.1 cm at 35 years TSF, while mean tree height ranged from 0.2 m at two years TSF to 13.2 m at 35 years TSF. Stand characteristics were similar between the two species at comparable TSF (Table 3.1), supporting our approach of combining the species as a single forest type.

3.4.2 *Surface fuel load*

Surface fuels increased with TSF, and the magnitude and direction of change differed among specific fuel components. There was strong evidence of linear increases in 1-hr and 10-hr fuel loads over TSF (Figure 3.2a, b), reaching 0.6 Mg/ha and 4.0 Mg/ha, respectively, at 35 years TSF (Appendix A – Table 3.7). There was suggestive evidence of an increase in the 100-hr fuel load until 15 years TSF, thereafter plateauing at approximately 7.0 Mg/ha (Figure 3.2c). The

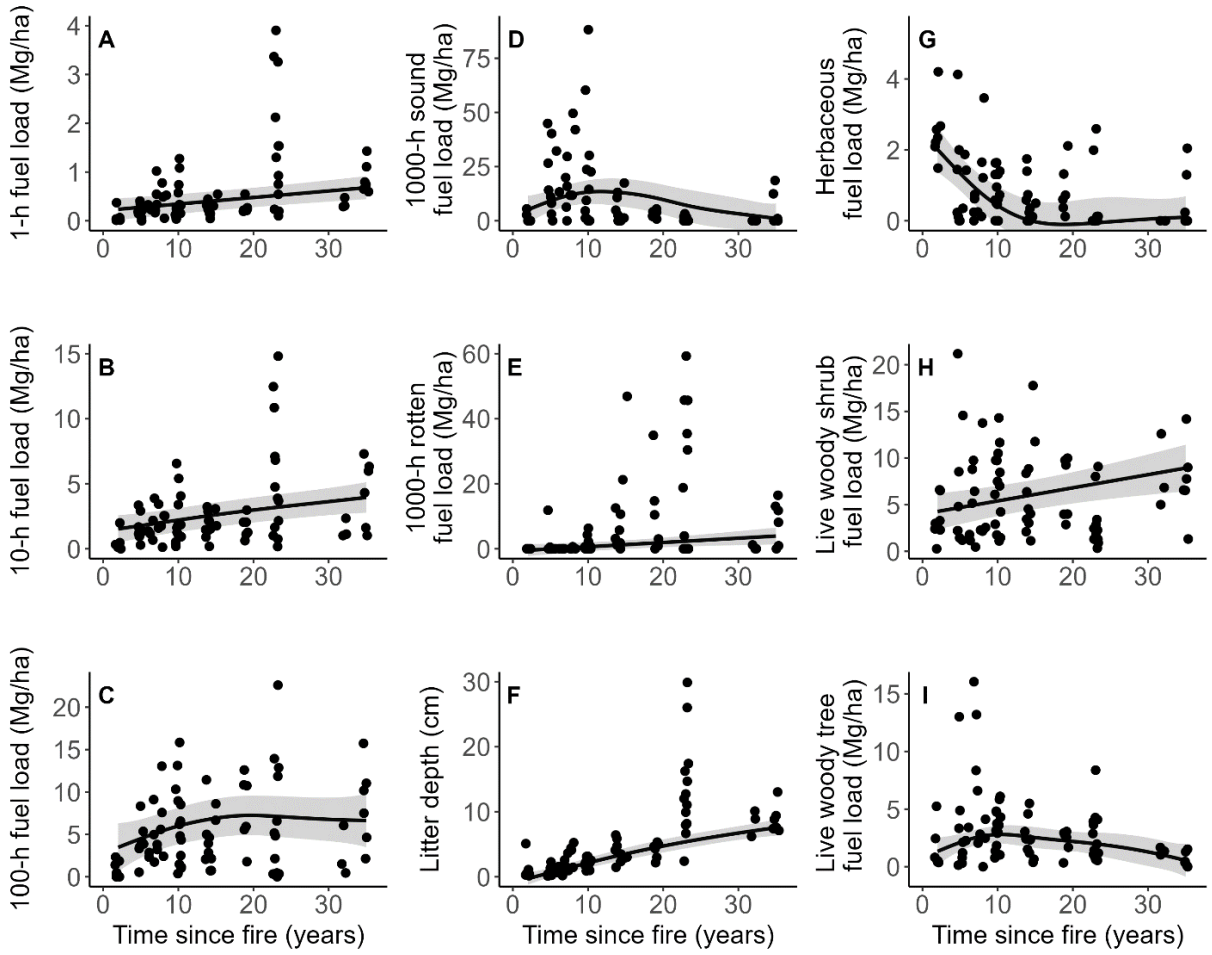

Figure 3.2. Partial effects of time since fire (TSF) on surface fuel load variables.

Note: Here, and in Figures 3.4, 3.5, generalized additive models take the form ~ TSF + annual standardized evapotranspiration index (SPEI) + elevation + heat load index (HLI). Lines represent estimated partial effect, shading represents 95% confidence intervals, and each dot is a plot (n = 79).

1000-h sound fuel load peaked at 13.7 Mg/ha at 11 years TSF, before declining to approximately zero by three decades post-fire (Figure 3.2d). The 1000-h rotten fuel load increased linearly with TSF, but there was considerable variation around this relationship from 15 to 23 years TSF that was poorly captured by the model (relative deviance = 5.15, Figure 3.2e). Litter depth increased with TSF, reaching 7.6 cm at 35 years TSF (Figure 3.2f). In general, within 10 years TSF, downed surface fuel loads reached levels that supported high severity fire in the 2018 Carr Fire (Table 3.2). Five of six downed surface fuel components were related to annual SPEI and elevation, generally declining with increasing SPEI (i.e., more mesic conditions), and non-monotonic with elevation, with minima generally between 600 and 900 m (Appendix A – Table 3.7, Figures 3.9 – 3.10). The 10-hr fuel load and litter depth were related to HLI, but strength of this relationship was weak compared with effects of other predictors in each model (Appendix A – Table 3.7, Figure 3.11).

The live surface fuel layer was characterized by a rapid increase in biomass over the first 10 years TSF (Figure 3.3a), although individual fuel components varied in their development (Figure 3.2g, i, Appendix A – Table 3.7). Within the first 10 years TSF, total live surface fuel biomass met or exceeded levels observed several decades post-fire (Figure 3.3a). During this period, live surface fuels were composed mainly of live biomass from tree and shrub crowns, and to a lesser degree, herbaceous vegetation, mostly occurring below 1 m in height (Figure 3.3b). As time progressed, dead biomass made up an increasing proportion of this fuel layer (Figure 3.3a), and the proportion of biomass > 1 m in height increased over TSF (Figure 3.3b). The herbaceous fuel load decreased over time, declining from 2.0 Mg/ha at two years TSF to approximately zero by 15 years TSF (Figure 3.2g). Conversely, the live woody shrub fuel load increased linearly over TSF, reaching 8.9 Mg/ha on average at 35 years TSF (Figure 3.2h). After

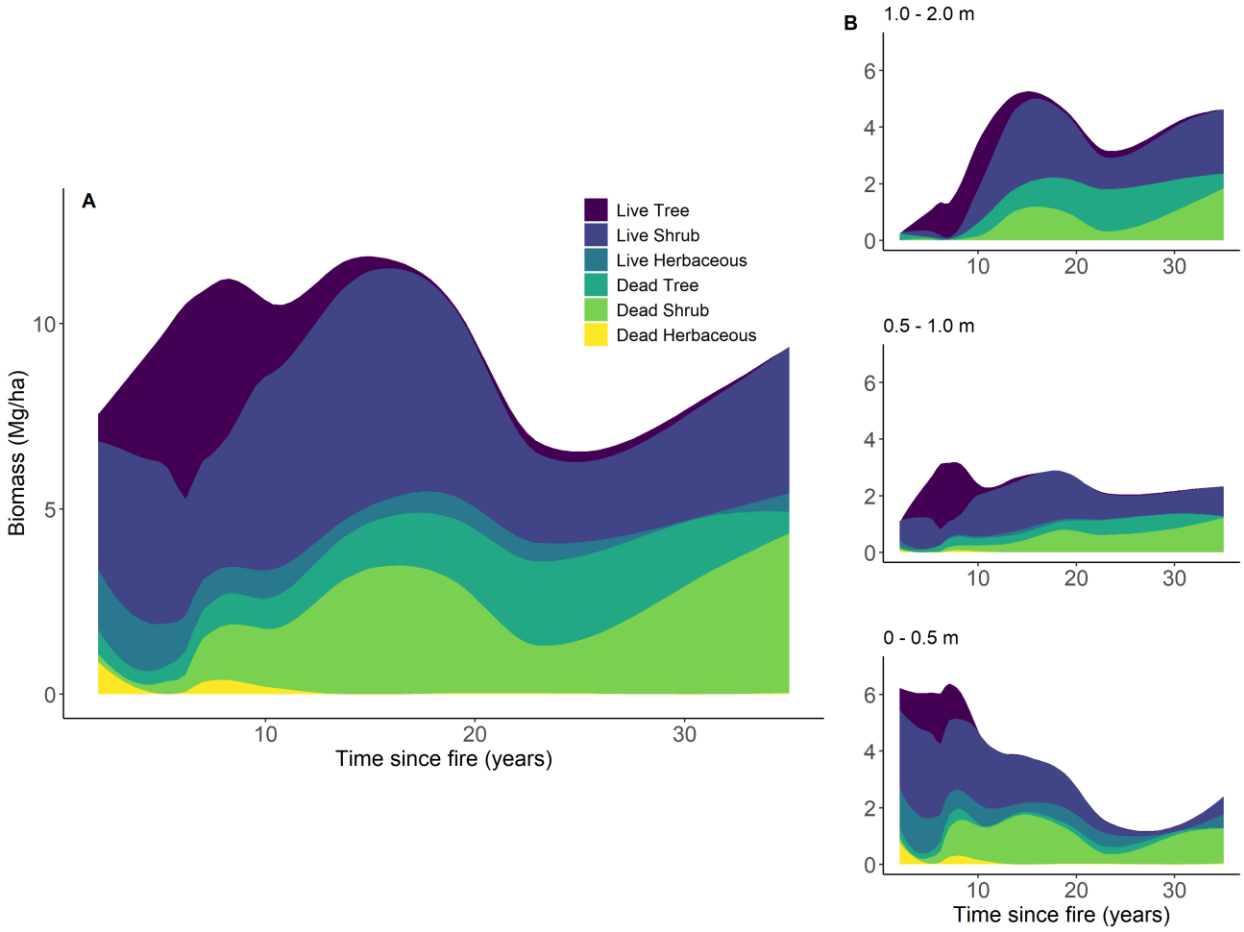

Figure 3.3. a: Cumulative standing biomass in the surface layer (within 0–2 m of the ground) b: Cumulative standing biomass in the surface layer by vertical stratum (1.0–2.0, 0.5–1.0, and 0–0.5 m of the ground).

Note: Colors represent averages of plot-level estimates of each biomass category for each measured time since fire (TSF) interpolated across the chronosequence using a loess smoother (span = 0.5).

10 years TSF, live and dead shrub biomass made up the greatest proportion of the live surface fuel layer (Figure 3.3a). There was suggestive evidence that the live woody tree surface fuel load increased, peaking at 2.8 Mg/ha at 10 years TSF before declining to 0.5 Mg/ha at 35 years TSF (Figure 3.2i). However, this model has relatively low explanatory power (relative deviance = 13.2, Appendix A – Table 3.7) and does not capture the rapid increase and decline in the live woody tree surface fuel load between six and eight years TSF characterized by values

two to five times the peak mean value (Figure 3.3a). Live surface fuel values that supported high severity fire in the Carr Fire varied widely and included values modeled at two years TSF through values exceeding the modeled range (Table 3.2). Covariate effects on the live surface fuel load were weak compared with TSF effects (Appendix A – Table 3.7). However, the herbaceous fuel load reached a minimum between 200 and 300 m elevation and at moderate annual SPEI, while the live woody shrub fuel load increased with both annual SPEI and HLI (Appendix A – Figures 3.9 – 3.11).

Overall, vegetation cover decreased while downed fuel substrate cover increased over TSF (Figure 3.4a–d). Herbaceous cover decreased over time, from an estimated 40% at two years TSF to 5% at 15 years TSF, remaining stable for the remainder of the chronosequence (Figure 3.4a). Tree cover within the surface layer peaked at 21% at seven years TSF, then declined to 5% by 15 years TSF, remaining stable for the remainder of the chronosequence as trees ascended to the canopy layer (Figure 3.4c). Total vegetation cover decreased monotonically over TSF, from an estimated 55% at two years TSF to 36% at 35 years TSF (Figure 3.4d). Shrub cover did not change with TSF and remained consistent at approximately 31% (Figure 3.4b). Litter cover proportion increased from an estimated 43% at two years TSF to 88% at 16 years TSF, before declining and stabilizing between 75 and 80% at 23 years TSF (Figure 3.4e). The CV of litter cover proportion followed an inverse trend to that of litter cover proportion, indicating the greatest heterogeneity of within-plot litter cover measurements occurred at five years TSF and the greatest homogeneity occurred at 15 years TSF (Figure 3.4f). Wood cover proportion increased with TSF, although this change was modest in magnitude as compared with the change in litter cover over time (Figure 3.4g), reaching its peak and plateauing at an estimated 13% at 17 years TSF. The CV of wood cover proportion decreased with TSF,

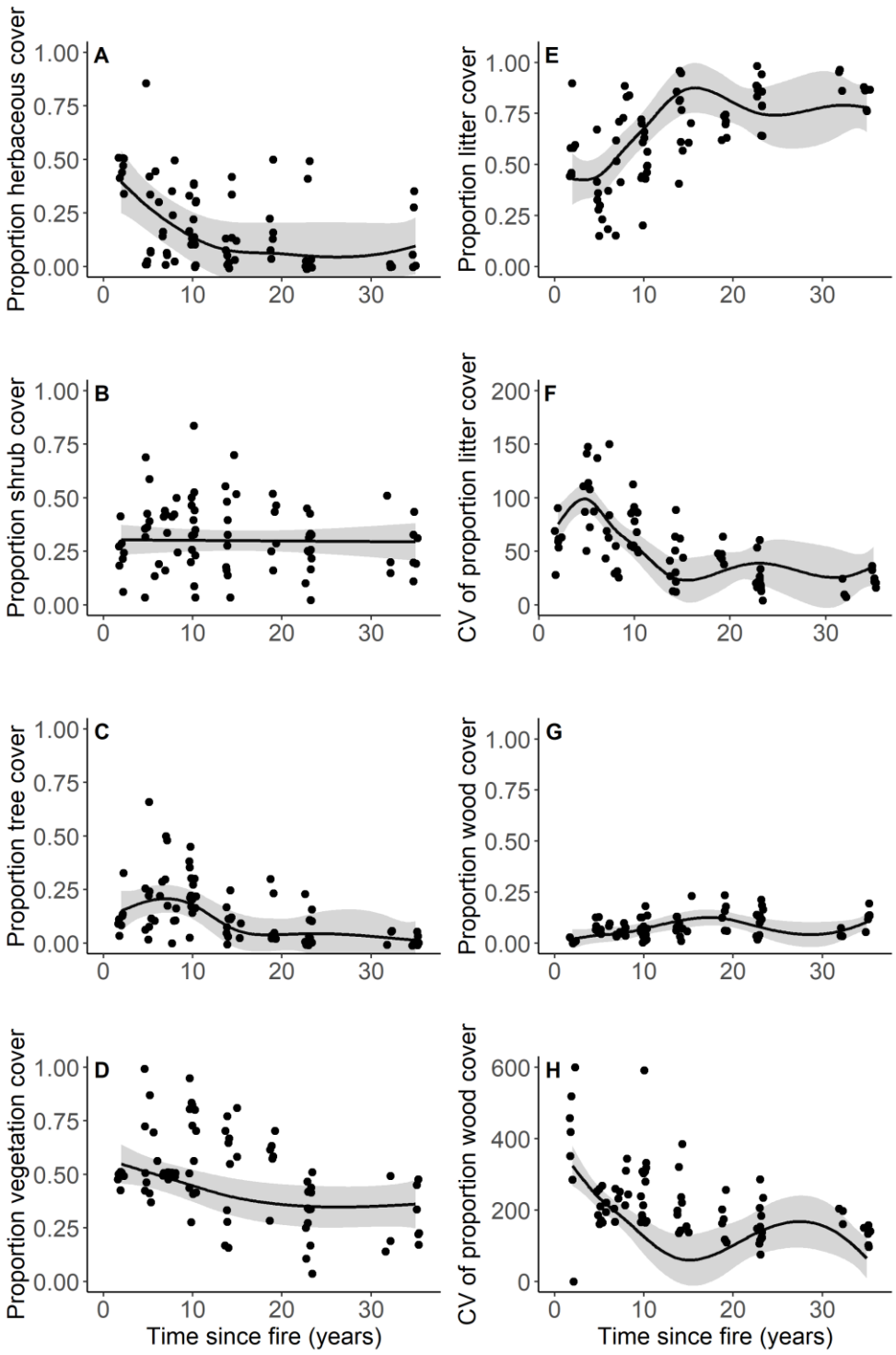

Figure 3.4. Partial effects of time since fire (TSF) on vegetation and substrate cover variables.

Note: Model form and symbols described in Figure 3.2 caption.

indicating that within-plot estimates of wood cover increased in homogeneity in older stands (Figure 3.4h). Although TSF was the most consistently significant predictor of vegetation and substrate cover, annual SPEI, elevation, and HLI had suggestive to strong effects on seven, six, and four variables, respectively (Appendix A – Table 3.8). In general, substrate cover decreased and vegetation cover increased with increasing annual SPEI and HLI, while the effects of elevation varied by fuel component (Appendix A – Figures 3.12 – 3.14).

3.4.3 *Canopy fuel load*

Canopy fuels generally increased over time since fire (Figure 3.5; Appendix A – Table 3.9). Available canopy fuel load increased up to a plateau of 13.5 Mg/ha by 23 years TSF (Figure 3.5a). Canopy bulk density increased until its peak of 0.11 kg/m^3 at 23 years TSF, decreasing to 0.05 kg/m^3 after three decades post-fire (Figure 3.5b). Canopy base height and stand height both increased over TSF (Figure 3.5c, d). Live stand density of canopy trees peaked at 2,500 trees/ha at 19 years TSF, but individual plot densities varied by several orders of magnitude between eight and 23 years TSF (Figure 3.5e). Live basal area increased with TSF, plateauing after 20 years TSF at approximately 19 m^2/ha (Figure 3.5g). Snag density did not vary with TSF, but dead basal area decreased from its peak at two years TSF to approximately zero by 10 years TSF before increasing again after 20 years TSF (Figure 3.5h). Canopy fuels reached levels that supported high severity fire in the Carr Fire between 9 and 15 years TSF (Table 3.2). The effect of TSF was consistently the strongest predictor for the canopy fuel models (Appendix A – Table 3.9). However, six canopy fuel variables declined with increasing annual SPEI and seven canopy fuel variables were non-monotonic with elevation, generally peaking between 600 and 900 m (Appendix A – Figures 3.15 – 3.17).

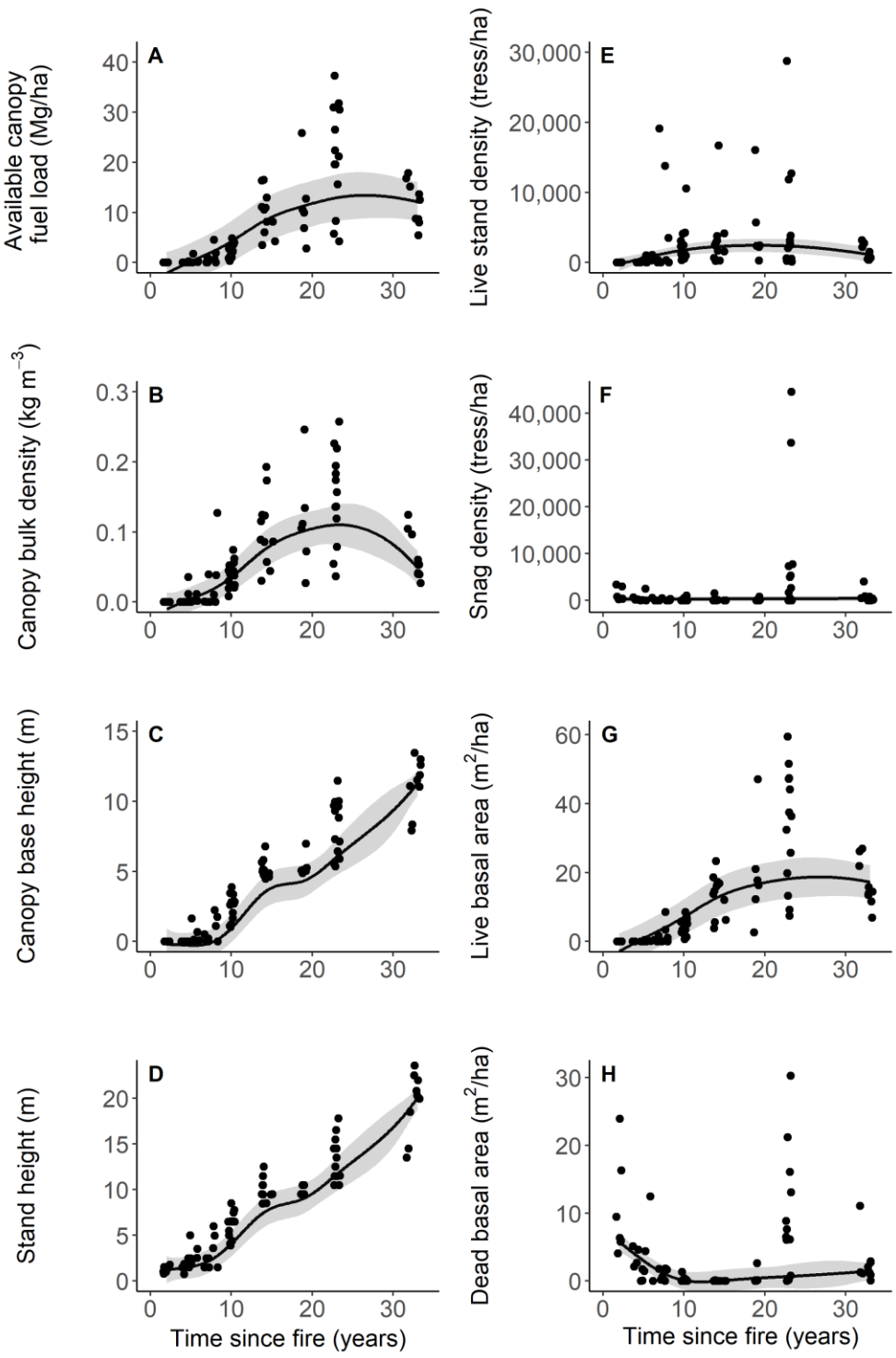

Figure 3.5. Partial effects of time since fire (TSF) on canopy fuel load variables. Note: Model form and symbols described in Figure 3.2 caption.

3.4.4 *Pre-fire legacy effects on surface and canopy fuel loads*

Pre-fire vegetation legacy had a strong effect on the trajectory of the downed woody surface fuel load and influenced live woody surface fuels to a lesser degree (Figure 3.6). Downed woody surface fuels of all size classes increased with TSF at pre-fire forested plots but remained stable at low levels at pre-fire non-forested plots (Figure 3.6a-e). Peak mean values for 1-hr, 10-

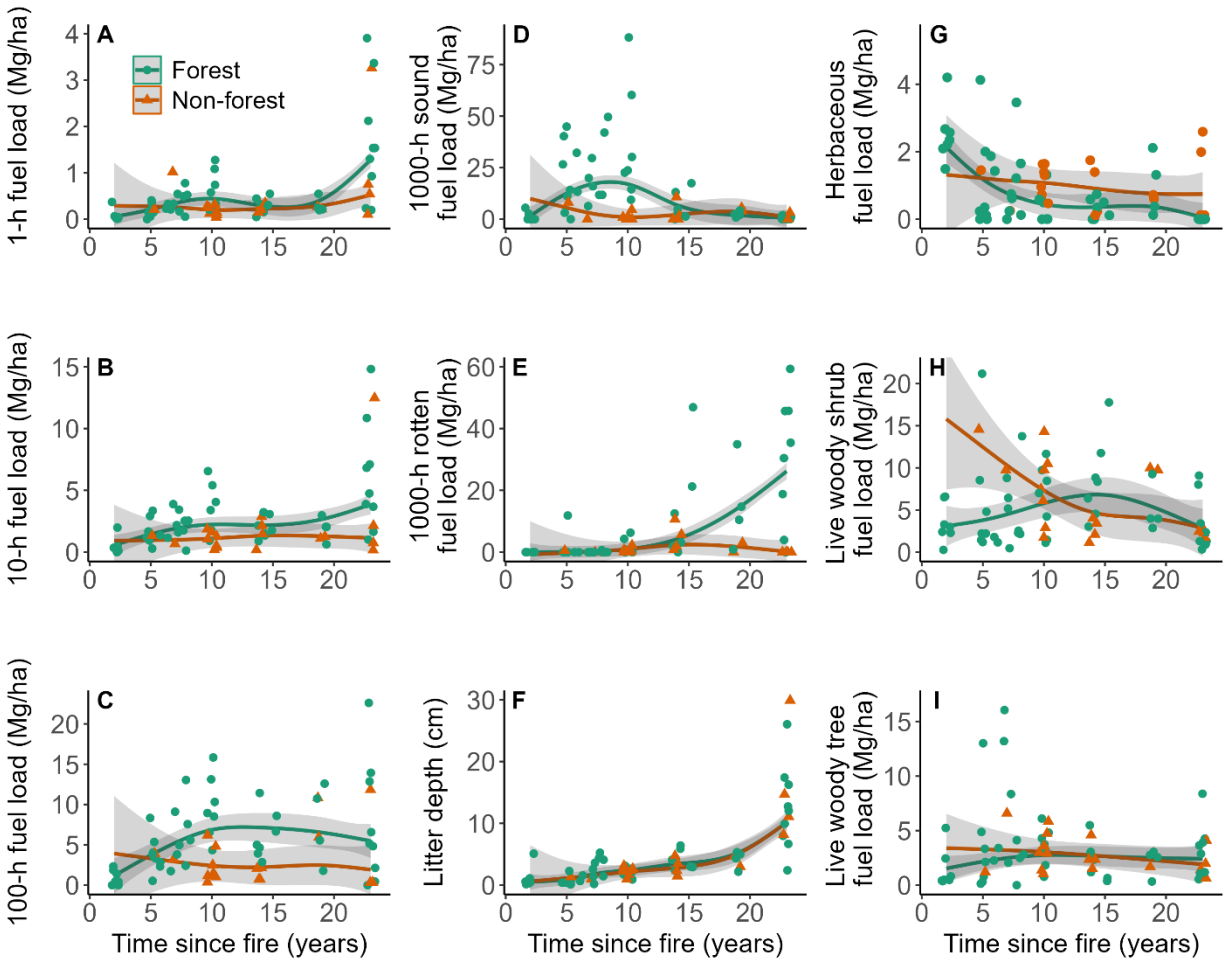

Figure 3.6. Effects of time since fire (TSF) and pre-fire vegetation legacy on surface fuel load variables.

Note: Here, and for Figure 3.7, generalized additive models take the form ~ TSF + pre-fire vegetation legacy + TSF * pre-fire vegetation legacy, for 2–23 years TSF. Lines represent the estimated effect of TSF for each pre-fire vegetation legacy, shaded areas represent 95% confidence intervals, and each dot represents a plot (n = 70).

hr, and 100-hr fuels were 2.6-, 2.8-, and 1.9-fold greater, respectively, at pre-fire forested versus pre-fire non-forested plots (Appendix A – Table 3.10). At pre-fire forested plots, 1000-hr sound fuels increased to 18.0 Mg/ha at 9 years TSF before declining to approximately zero by 19 years TSF, while 1000-hr rotten fuels increased to 26.2 Mg/ha by 23 years TSF (Figure 3.6d–e). Conversely, at pre-fire non-forested plots, there was no change in 1000-hr sound or 1000-hr rotten fuels, which remained under 5 Mg/ha from five years TSF onwards (Figure 3.6d–e). The live woody shrub fuel load also followed separate early post-fire trajectories by pre-fire vegetation legacy, although trajectories converged by 10 years TSF (Figure 3.6h). Litter depth, the herbaceous fuel load, and the live woody tree surface fuel load did not differ between plots that were forested versus non-forested pre-fire (Figure 3.6f, g, i).

Canopy fuels varied minimally by pre-fire legacy; canopy bulk density, canopy base height, stand height, live stand density, and snag density did not differ between plots that were forested versus non-forested pre-fire (Figure 3.7b–f). However, at approximately 19 years TSF fuel profile trajectories diverged by pre-fire legacy with respect to available canopy fuel load and live basal area (Figure 3.7a, g). The available canopy fuel load and live basal area at pre-fire non-forest plots were approximately 60% and 50%, respectively, of values for pre-fire forested plots at 23 years TSF (Appendix A – Table 3.11). Further, dead basal area followed a U-shaped trend at pre-fire forested plots, reaching a minimum at 16 years TSF, but remained stable at a low level in pre-fire non-forested plots (Figure 3.7h).

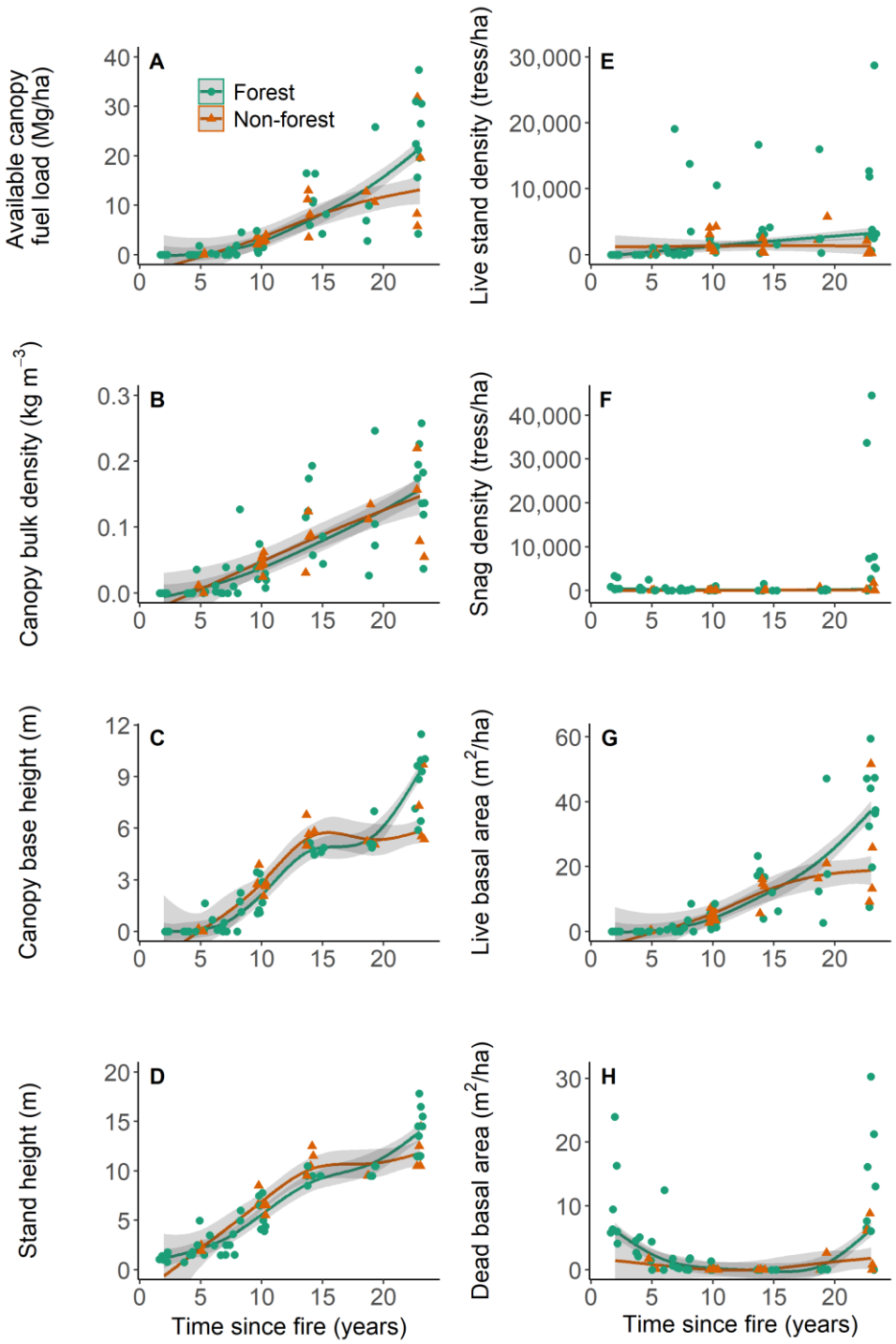

Figure 3.7. Effects of time since fire (TSF) and pre-fire vegetation legacy on canopy fuel load variables.

Note: Model form and symbols described in Figure 3.6 caption.

3.5 DISCUSSION

Understanding when and where changing disturbance regimes may result in linked disturbances that erode forest resilience is critical for managing forests under increasingly fire-prone climate conditions. Our findings demonstrate that fuel accumulation in California closed-cone pine forests occurs rapidly following stand-replacing fire, and these findings provide insights to mechanisms of linked disturbances in fire-prone forests. The period of fuel limitation is brief compared with the historical fire return interval, suggesting high potential for short-interval severe reburn occurrence to increase with climate warming and continued anthropogenic ignitions. Pre-fire vegetation legacy was a strong driver of fuel profile trajectories; stands that were non-forest pre-fire (comprising approximately a quarter of sampled plots) were characterized by an extended period of comparatively low downed woody fuel loads and therefore lower capacity to carry severe fire as compared to areas that were forested pre-fire. Timing of fuel development and pre-fire vegetation legacy can have substantial effects on subsequent disturbance activity and forest resilience with important implications for timing and effectiveness of management interventions (Prichard et al. 2017).

3.5.1 *Rapid accumulation of fuels sufficient to carry fire*

Our finding that fuels met or exceeded values capable of supporting a severe reburn by approximately 10 years post-fire provides insight into the key mechanism behind reburn patterns observed in coniferous forests in the western US (Parks et al. 2015, Harvey et al. 2016, Buma et al. 2020). Downed woody surface fuels followed a similar pattern to those described in previous studies of post-fire fuel dynamics, with low amounts immediately post-fire and a subsequent peak or plateau coinciding with the processes of snag fragmentation and snagfall (Harmon et al. 1986, Hall et al. 2006, Dunn and Bailey 2015). However, the rapid trajectories of surface fuel

load accumulation in our study have important implications for fire occurrence and severity — two important dimensions of linked disturbances.

Fine woody surface fuels are important for probability of ignition, rate of spread, and fireline intensity (Rothermel 1972) and within 5–10 years TSF quantities were sufficient to support stand-replacing fire. This rapid accumulation and homogenization of fine woody surface fuels continued for decades following fire and peaked at values approximately 2–3 times greater than in mixed-conifer forests (Fahnestock 1976, Schmidt et al. 2008, Pierce et al. 2012, Lydersen et al. 2015), Rocky Mountain lodgepole pine forests (Klutsch et al. 2009, Battaglia et al. 2010, Simard et al. 2011), and Baker cypress (*Hesperocyparis bakeri*) forests (McNamara et al. 2019b). Fine woody surface fuels observed within 10–24 years TSF in mixed conifer and ponderosa pine forests are comparable to those observed at similar TSF in this study (Hall et al. 2006, Dunn and Bailey 2015, Stevens-Rumann et al. 2020). However, in other forest systems fine woody surface fuels peak within 25 years TSF (Hall et al. 2006, Dunn and Bailey 2015), whereas in California closed-cone pine forests, accumulation continues for at least 35 years TSF. Inputs are predominantly driven by fragmentation of snags and fire-killed shrubs prior to post-fire snagfall, while inputs after snagfall can be attributed to density-dependent mortality of overstory trees (Keyser et al. 2009). Dense post-fire tree establishment immediately following fire in serotinous forests leads to earlier canopy closure than documented in non-serotinous forests (Harvey et al. 2011), while associated early crown recession provides a consistent input of fine fuels following snagfall that is absent from non-serotinous forests that establish and develop over a longer period following fire (Stevens-Rumann et al. 2020). Collectively, these patterns of woody fuel accumulation suggest that fine fuels sufficient to support severe reburns

are present well in advance of canopy closure and for several decades following the previous fire.

The rapid accumulation and decay of coarse woody surface fuels following fire carries implications for substantial changes in high severity reburn potential over the first decade post-fire. The peak we observed in the 1000-hr sound fuel load at 11 years TSF was earlier than in other coniferous forests in which coarse wood accumulates for at least 20 years following fire (Hall et al. 2006, Dunn and Bailey 2015, Stevens-Rumann et al. 2020). Although many coniferous forests have high snag fall rates in the first decade post-fire, snag retention for decades is common (Everett et al. 1999, Grayson et al. 2019), compared with our findings of near zero standing dead basal area by 10 years TSF (Figure 3.5h). The rapid snag fall rate in California closed-cone pine forests is related to relatively small tree size (Grayson et al. 2019) and strong winds driving early snagfall along the coast (S. Bisbing, personal observation). The peak 1000-hr sound fuel load (13.7 Mg/ha) was low in magnitude compared to other forests within several decades of high severity fire, reaching 10 to 30% of values observed in mixed conifer and lodgepole pine forests (Fahnestock 1976, Dunn and Bailey 2015, Nelson et al. 2016, Stevens-Rumann et al. 2020). Low coarse woody surface fuels are related to small tree size and low stand basal area of mature California closed-cone pine stands compared with other forests (Vogl et al. 1977). Conversely, jack pine and Baker cypress forests, which are similar in structure to California closed-cone pine forests, have coarse woody surface fuels comparable to quantities observed in this study at similar TSF (Stocks 1987, McNamara et al. 2019b). Sound coarse woody surface fuels increase surface fire intensity (Rothermel 1972), suggesting that potential surface fire intensity may peak around 10 years TSF. However, plots that burned severely in the Carr Fire had coarse woody surface fuel loads at the time of fire (median < 5

Mg/ha; Table 3.2) that were well below this peak, showing that in young forests, stand-replacing fire can occur at relatively low fireline intensities and in the absence of substantial downed coarse wood.

Post-fire shrub growth drove rapid and sustained live surface fuel accumulation. Early post-fire development of live surface fuels can drive short-interval severe reburn potential in forests characterized by stand-replacing fire (Agee and Huff 1987, Harvey et al. 2016). Post-fire shrub growth is especially rapid where adaptations such as resprouting or soil stored seed banks are common (Fontaine et al. 2012, Dunn and Bailey 2015), as they are in California closed-cone pine forests. Peak woody shrub biomass reached 60% of the peak values reported for post-fire Cascades mixed conifer forests (Dunn and Bailey 2015) and 20–50% of values for chaparral at similar TSF (Bohlman et al. 2018) but was comparable to values reported for mature Baker cypress forests (McNamara et al. 2019b). Lower shrub biomass in serotinous forests is likely due to early interspecific competition with trees as compared with non-serotinous forests (Harvey and Holzman 2014). Post-fire forest fuel succession studies from other coniferous forests show an asymptote in shrub biomass development within 25 years TSF (Dunn and Bailey 2015) and subsequent senescence of the shrub layer, accompanied by decreased potential for severe surface fire (Agee and Huff 1987, Odion et al. 2010). Conversely, our results show linearly increasing shrub biomass and approximately constant shrub cover (~31%) across the chronosequence (Figures 3.2h, 3.4b), suggesting that shrub biomass and associated surface fire potential continue to increase with little senescence for an extended period compared with other coniferous forests. Considerable variation at individual TSF was apparent, suggesting that factors other than fuel age are important determinants of woody shrub biomass (Regelbrugge and Conard 2002). Although we accounted for covariates, factorial interspersion of covariates is a limitation of

many observational and chronosequence studies (Walker et al. 2010), and future work could explicitly test the influence of topographic and climatic gradients on fuel profiles.

In addition to increases in total biomass with TSF, changes in the composition of the live surface layer have implications for surface fire potential. This fuel layer was dominated by live and dead shrub biomass by 10 years TSF (Figure 3.3), following the senescence of the herbaceous layer and ascension of the closed-cone pine cohort to the canopy (Figure 3.2g, i). Herbaceous biomass peaked within several years post-fire before declining to near zero (Figure 3.2g; Figure 3.3a), similar to findings in post-fire chaparral and Baker cypress forests, in which herbaceous biomass is a minor component of the fuels complex (Guo 2001, McNamara et al. 2019b). Shifts in composition from flashy herbaceous fuels to woody shrub biomass capable of supporting higher intensity fires (Weatherspoon and Skinner 1995) suggest greater flame lengths and difficulty of suppression over time. Further, the live surface layer increased with respect to proportion dead from 10–20 years TSF (Figure 3.3a), similar to trends in mixed chaparral (Bohlman et al. 2018). Dead material accumulates under live shrub crowns due to competition and shading (Regelbrugge and Conard 2002) and is associated with increased surface heating and fire duration (Fontaine et al. 2012). Live and dead shrub material also became evenly distributed across the vertical profile of the standing surface layer by 20 years TSF (Figure 3.3b), increasing the potential for crown fire initiation, especially where canopy base heights are low (Figure 3.5c, Van Wagner 1977).

Sufficient canopy fuels to support a crown fire were present well before the mean fire return interval, suggesting high potential for short-interval crown fire occurrence. Canopy fuels increased through the canopy closure phase (Figure 3.5a, b, e), before stabilizing at a level above that required to support high severity fire, similar to trends in other forests characterized by

stand-replacing fire regimes (Agee and Huff 1987, Nelson et al. 2017). The available canopy fuel load stabilized by 20 years TSF at 13.5 Mg/ha (Figure 3.5a), comparable to values observed at similar TSF in serotinous jack pine and Aleppo pine (*P. halepensis*) forests, and approximately 50% greater than those in young lodgepole pine forests (Stocks 1987, Mitsopoulos and Dimitrakopoulos 2007, Nelson et al. 2016). Conversely, peak canopy bulk density (0.11 kg/m3) was low, between 50–75% of values from other young serotinous forests (Mitsopoulos and Dimitrakopoulos 2007, Nelson et al. 2016). Canopy bulk density in the oldest stands (0.05 kg/m^3) was 18–50% of that in lodgepole pine forests, ponderosa pine forests (Cruz et al. 2003, Roccaforte et al. 2008, Battaglia et al. 2010, Simard et al. 2011), and mixed conifer forests (Reinhardt et al. 2006b, Schmidt et al. 2008, Pierce et al. 2012). Canopy bulk density values exceeding 0.1 kg/m^3 are more likely to support active crown fire under a range of weather conditions (Agee 1993), suggesting that active crown fire potential in California closed-cone pine forests is highest between 19 and 25 years TSF (Figure 3.5b). However, by 15 years TSF, available canopy fuel load and canopy bulk density exceeded values capable of carrying crown fire in mature Spanish pine forests under moderate burning conditions (Fernández-Alonso et al. 2013), and between nine and 15 years TSF reached values that supported high severity fire in the Carr Fire (Table 3.2). Furthermore, as extreme fire conditions become more common with continued climate warming (Williams et al. 2019), fuel thresholds for active crown fire are likely to further decrease.

3.5.2 *Fuel profile trajectories differ by pre-fire vegetation legacy*

The contrast between fuel profile trajectories in forests with differing pre-fire vegetation legacies has important implications for the likelihood of subsequent high severity fire. Nearly 25% of sampled plots were non-forest prior to the most recent fire, showing that post-fire

establishment of a closed-cone pine forest can occur through nearby seed dispersal (Forrestel et al. 2011, Harvey et al. 2011), or an *in situ* seed source, as is more common for many serotinous species (He et al. 2004, McNamara et al. 2019a). At plots that were non-forest prior to the most recent fire, downed woody surface fuel quantities remained low for over two decades for all fuel sizes, reflecting values comparable to those in oak woodlands with a low-intensity surface fire regime (Tietje et al. 2002). These values are a fraction of that in forest-dominated ecosystems at similar TSF (Dunn and Bailey 2015, Nelson et al. 2016, Stevens-Rumann et al. 2020). Conversely, minor differences in standing surface and canopy fuels by pre-fire vegetation legacy indicate similar reproductive capacity of shrub or tree species within dispersal distance (Turner et al. 2019), although this trend may differ following short-interval high severity fire due to decreased seed dispersal from young forests (Gill et al. 2021). Divergence in the canopy fuel profile between 19 and 23 years TSF suggests that differences in post-fire forest structure may become more apparent following the canopy closure phase (Figure 3.7a, g), but plots established from both pre-fire vegetation legacies have canopy fuel profiles comparable those sufficient to carry crown fire in many forests (Mitsopoulos and Dimitrakopoulos 2007, Roccaforte et al. 2008, Fernández-Alonso et al. 2013). Therefore, susceptibility to severe surface fire may be delayed in pre-fire non-forest compared with pre-fire forested plots due to low downed woody fuels (Rothermel 1972). However, fuel limitation attributed to pre-fire vegetation legacy is likely to decline after 15 years TSF due to similar canopy fuel profiles that can support severe fire. Additional pre-fire structural characteristics not investigated here, such as stand age, size class distribution, stand density, and canopy seed bank size can contribute to differences in fuel profiles (Nelson et al. 2016) and could be investigated in future studies of fuel dynamics over time.

Pre-fire vegetation legacy of non-forest may serve as a useful analog to understand how fuel profiles could influence subsequent fire activity following future short-interval severe reburns. Compared to longer intervals, short-interval reburns can drastically reduce downed woody surface fuels (Donato et al. 2016, Stevens-Rumann et al. 2020), similar to the difference we observed between pre-fire non-forest and pre-fire forest stands. Delayed development of downed woody surface fuels combined with comparable stand development suggests that stands resulting from forest expansion following fire or repeat severe fires could serve as unburned or low severity patches in subsequent short-interval severe reburns. Such areas could provide a seed source for regeneration of adjacent stands that would otherwise experience immaturity risk (Gill et al. 2021) and/or type conversion to non-forest. However, whether stands with similar canopy fuel development also have similar reproductive capacity development in the form of a canopy seed bank represents a key uncertainty in understanding the effect of forest expansion patches on forest resilience to future disturbance.

3.5.3 *Management implications*

Rapid fuel recovery in California closed-cone pine forests suggests that managers can expect high fire potentials in young forests well before the historical mean fire return interval. The short (< 10 years) period of fuel limitation following a stand-replacing fire is a key mechanism supporting observational patterns of reburn potential across coniferous forests in the western US (Parks et al. 2015, Harvey et al. 2016, Buma et al. 2020). In the historical fire regime, fuels were typically not limiting to fire activity in closed-cone pine forests. However, warming climate and increased anthropogenic ignitions (Westerling et al. 2011, Balch et al. 2017), coupled with our findings, suggest that these forests could experience high severity fire 3–9 times more frequently than historical mean fire return interval estimates of 30–90 years (Vogl

1973, Sugnet 1985, Van de Water and Safford 2011). Such an increase in fire activity could result in compound effects on the demography and structure of serotinous forests, leading to localized population loss of serotinous species (Keeley et al. 1999) or broad-scale forest to non-forest conversion (Brown and Johnstone 2012) if fire occurs prior to reproductive maturity. Where conserving serotinous populations is a priority, suppressing fire within young stands with sufficient fuels but low cone abundance may be warranted. However, the timing of sufficient canopy seed bank development for stand replacement and how this might differ across broad environmental gradients and with site characteristics such as microclimate and stand structure remains poorly understood.

Our findings show that downed woody surface fuel loads are low for decades after fire in areas of post-fire forest expansion into non-forest. Areas of post-fire serotinous forest expansion are often localized, existing in a mosaic of forest and non-forest patches (Forrestel et al. 2011). The resultant heterogeneity following a single fire event could create patches with lower resistance to control or greater tree survival in a subsequent fire (Sikkink and Keane 2012), than would be observed without patches where recent forest expansion into non-forest occurred. Managers could identify these areas within a post-fire landscape to understand where areas may serve as a natural fire break or where surface fire intensity may be lower, particularly within ~15 years TSF prior to substantial canopy fuel load development. Understanding where recent post-fire expansion has occurred is also important for conserving serotinous species with increased fire activity, as these areas may contain surviving trees to provide a seed source to adjacent stands should a short-interval severe fire occur prior to reproductive maturity.

Fuel reduction treatments are often considered in fire-prone forests as a tool to protect values at risk, and in the wildland-urban interface. However, such treatments are costly, and

optimizing treatments to attain maximum fire hazard reduction is often desired. Our findings suggest that fuel reduction treatments would need to be carried out on a < 10-year interval to meaningfully reduce fire hazard. Feasibility of such frequent treatments may be limited to small spatial extents (Agee and Skinner 2005), suggesting that treatments should be prioritized to protect areas of high ecological or cultural value. Further, trade-offs of fuel reduction treatments with competing objectives such as plant population conservation are poorly understood. Data on how trajectories of fire potentials align with those of reproductive capacity and ability of a plant population to self-replace following fire (Enright et al. 2014) are needed to understand how frequent fuel reduction treatments may impact California closed-cone pine populations.

3.6 CONCLUSION

Rapid post-fire accumulation of fuels suggests that closed-cone pine forests may be vulnerable to short-interval severe reburns at frequencies far exceeding the historical mean fire return interval as the climate continues to warm. Pre-fire vegetation legacy strongly influences fuel profiles and a mosaic of pre-fire vegetation may promote resilience to short-interval severe reburns at broad spatial scales. Understanding how trajectories of fuel accumulation align with development of the canopy seed bank is important for understanding the potential for serotinous forest resilience to increasing frequency of short-interval severe reburns.

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3.8 APPENDIX A

3.8.1 *Study area*

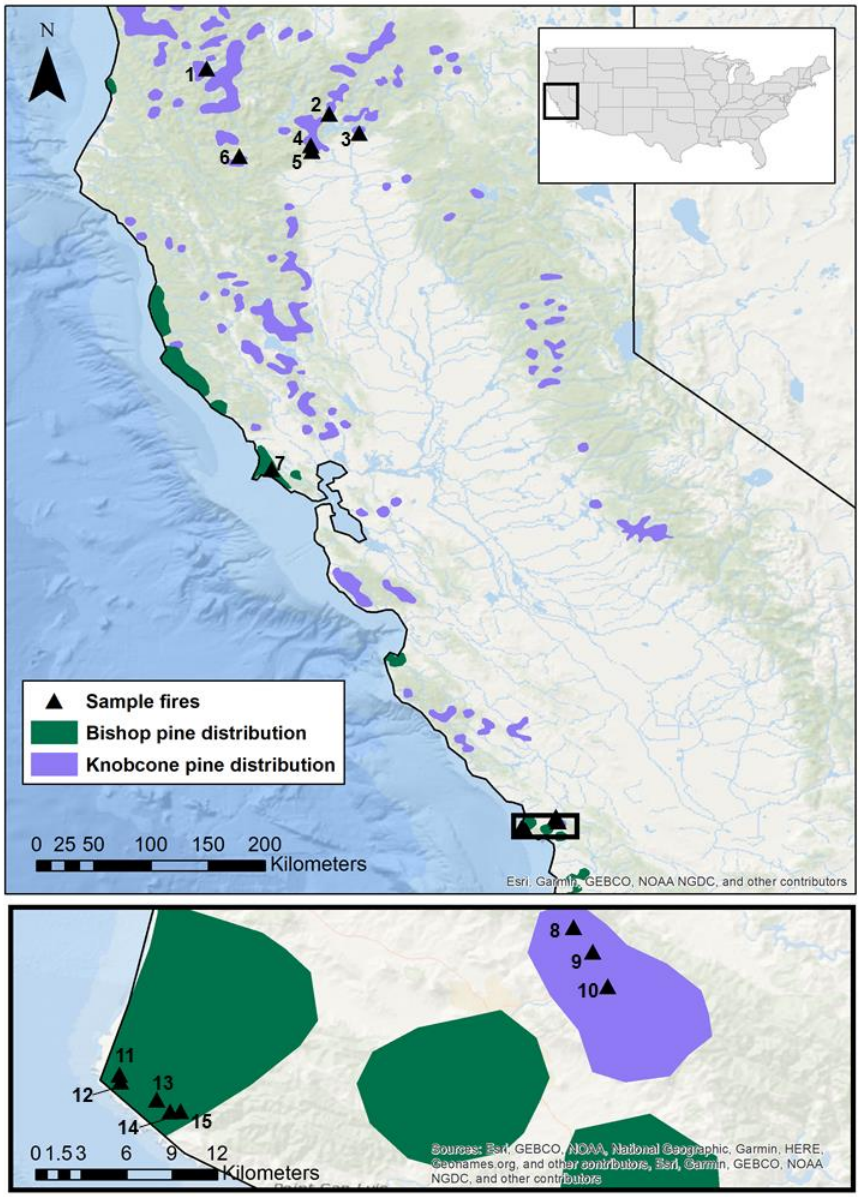

Figure 3.8. Study area map numbered with the 15 sample fires and bishop pine and knobcone pine species distributions.

Notes: Upper inset shows the study area within the continental United States, lower inset shows the southern portion of the study area.
Sample fires (year): 1: Butler (2013), 2: Sugar (1999), 3: Bear (2004), 4: Motion (2008), 5: Whiskeytown Rx Burn (2003), 6: Stafford (2012), 7:Vision (1995), 8: Cuesta (2015), 9: Hwy 41 (1994), 10: Las Pilitas (1985), 11: North Ranch North Unit Rx Burn (2010), 12: North Ranch VMP Rx Burn (2012), 13: Diablo (2007), 14: North Ranch South Unit Rx Burn (2009), 15: Diablo Canyon (1982).

3.8.2 *Extended fuel measurement and calculation methodology*

3.8.2.1 Fuel measurements

At each plot, we measured dead down woody fuel, live biomass, and ground cover data to characterize the fuels. Downed woody fuels were measured using standard planar intercept methods (Brown 1974). Total transect length varied with collection year and dominant species. Two 17.8 m transects were established in all bishop pine plots, except for those measured within the Vision Fire perimeter (23 years TSF), for which three 18 m transects were established. Two 17.8 m transects and one 9 m were established in knobcone pine measured with the Cuesta, Hwy 41, and Las Pilitas Fires (2, 23, and 32 years TSF, respectively) and three 18 m transects were established in all other knobcone pine plots. All transects were established in arbitrarily selected cardinal directions. For 17.8 and 18 m transects, we counted 1-hour fuels within the first two meters of each transect, 10-hour fuels within the first five meters of each transect, 100-hour fuels within the first ten meters of each transect, and 1000-hour fuels (i.e., coarse woody debris) along the entire transect. We identified 1000-hour fuels to species, categorized them using a 1-5 decay class rating system (Sollins 1982), and measured the diameter of each piece. Fuels were counted along 9 m transects using the same methods except 1- and 10-hour fuels were counted within the first 1.5 meters, 100-hour fuels were counted within the first 3 meters.

3.8.2.2 Herbaceous, live woody shrub, and live woody tree surface fuel load calculations

Herbaceous, live woody shrub, and live woody tree surface fuel loads were calculated from point intercept data for each site. We used general graminoid and a *Lupinus* spp. equation (Table 3.3) to estimate graminoid and forb biomass, respectively. Percent cover was estimated as the number of points along a transect at which a graminoid or forb was intercepted divided by

the total points measured (n = 36). Graminoid and forb biomass were combined to represent herbaceous biomass and scaled to the sampling area (transect length * intercept pole diameter) to obtain an estimate of plot-level herbaceous fuel load (Mg ha^{-1}). We estimated individual shrub biomass (Mg ha^{-1}) using equations employed by the Fuel Characteristic Classification System (FCCS; Prichard et al. 2013), using species-specific equations when available and the general deciduous or evergreen shrub equation for all other species (Table 3.3). Percent cover was estimated for use in these calculations as the average crown width of an individual shrub divided by the total transect length. The equations partition shrub biomass into stem biomass and crown biomass. The live woody shrub fuel load represents foliage and twigs under two meters in height and is considered available biomass with respect to fire potential (Prichard et al. 2013). Plot-level live woody shrub fuel load (Mg ha^{-1}) was estimated by summing individual crown biomass over all shrubs within a plot. To obtain the live woody tree surface fuel load, we first assigned each interception as foliage or branch. For each foliage interception, we multiplied specific leaf mass of a related species, (0.1965 mg mm^{-1}, an average value for *P. resinosa*; Abrams and Kubiske 1990), by the pole diameter, representing the sampling plane, to obtain an estimate of the biomass of the portion of the needle falling within the sampling plane. For each branch interception, we multiplied species-specific oven-dry weight on green volume basis (*P. attenuata* = 390 kg m^{-3}, *P. muricata* = 450 kg m^{-3}; (Wilson et al. 1986) by branch area * intercept pole diameter for calculation. Foliage and branch biomass were summed across the plot, then scaled to the plot area (intercept pole area * 36 measurement points) to obtain the standing tree surface fuel load (Mg ha^{-1}).

Table 3.3. Biomass equations for conversion of point intercept measurements of herbaceous, shrub, and tree species to available biomass used for calculation of the herbaceous fuel load, woody shrub fuel load, and standing tree surface fuel load.

Source species	Species (measured)	Available biomass (Mg/ha)	Citation
Herbaceous			
Graminoid spp.	all graminoids	[(1.9204 * Percent Cover)/ sampling area (m^2)] * 0.01	Means et al. 1994
Lupinus spp.	all forbs	[(2.044 * Percent Cover)/ sampling area (m^2)] * 0.01	Means et al. 1994
Shrub			
Broadleaf deciduous shrubs	*Acmispon glaber*	2.2417 * 0.4 * 2000 * Percent Cover * 0.01 * Height (ft) * 0.0005	Prichard et al. 2013
	Corylus cornuta		
	Pteridium aquilinum		
	Quercus douglasii		
	Quercus kelloggi		
	Rubus ursinus		
	Styrax redivivus		
Broadleaf evergreen shrubs	*Arbutus menziesii*	2.2417 * 0.5 * 3000 * Percent Cover * 0.01 * Height (ft) * 0.0005	Prichard et al. 2013
	Chrysolepis chrysophylla var. minor		
	Dendromecon rigida		
	Eriodictyon californicum		
	Frangula californica		
	Notholithocarpus densiflorus		
	Pickeringia montana		
	Quercus agrifolia		
	Quercus chrysolepis		
	Ribes marshallii		
	Ribes sanguineum		
	Ribes speciosum		
	Umbellularia californica		
	Unknown evergreen shrub		
Adenostoma fasciculatum	*Adenostoma fasciculatum*	2.2417 * 0.4 * 0.17 * Percent Cover	Prichard et al. 2013
Arctostaphylos patula	*Arctostaphlos canescens*	2.2417 * 0.5 * 0.141 * Percent Cover	Prichard et al. 2013
	Arctostaphylos obispoensis		
	Arctostaphylos patula		
	Arctostaphylos pechoensis		
	Arctostaphylos tomentosa		
	Arctostaphylos virgata		
	Arctostaphylos viscida		

Source species (cont)	Species (measured) (cont)	Available biomass (Mg/ha) (cont)	Citation (cont)
Artemesia tridentata	*Baccharis pilularis*	2.2417 * 0.35 * 230.586 * Percent Cover * 0.0005	Prichard et al. 2013
Ceanothus chaparral	*Ceanothus sp.*	2.2417 * 0.5 * 0.372 * Percent Cover	Prichard et al. 2013
	Ceanothus foliosus var. medius		
	Ceanothus papillosus		
	Ceanothus thyrsiflorus		
	Ceanothus thyrsiflorus var. griseus		
	Heteromales arbutifolia		
Ceanothus velutinus	*Ceanothus cuneatus*	2.2417 * 0.5 * 0.108 * Percent Cover	Prichard et al. 2013
Lonicera canadensis	*Toxicodendron diversilobum*	2.2417 * 0.35 * (0.9266 + 0.2727) * Percent Cover * 0.0248	Prichard et al. 2013
Vaccinium alaskense	*Vaccinium ovatum*	2.2417 * 0.35 * (-7.22 + 17.307) * Percent Cover * 0.0045	Prichard et al. 2013
Tree			
Pinus resinosa (foliage)	*Pinus attenuata* *Pinus muricata*	Sample length * 0.1965 mg mm^{-1} / sample area	Abrams and Kubiske 1990
Pinus attenuata (branch)	*Pinus attenuata*	0.5 * (Sample volume * 0.39 Mg m^3)/ sample area	Wilson et al. 1986
Pinus muricata (branch)	*Pinus muricata*	0.5 * (Sample volume * 0.45 Mg m^3)/ sample area	Wilson et al. 1986

3.8.2.3 Canopy fuel load calculations

Available canopy fuel load (ACFL) was calculated as total foliage biomass of all standing trees > 2 m plus 50% of live and dead branch biomass (Mg ha^{-1}) (Reinhardt et al. 2006). Foliage, live branch, and dead branch biomass were estimated for individual trees with DBH ≥ 2.5 cm within the fixed area plots using published equations for *Pinus* spp. (Jenkins et al. 2003, Prichard et al. 2013). We estimated foliage and stem biomass for all trees < 2.5 cm DBH using a *Pseudotsuga menziesii* sapling equation as species-specific equations were unavailable (Means et al. 1994). For trees < 2.5 cm DBH, we assumed foliage alone contributes to ACFL. For shrubs > 2 m in height, we included the proportion of shrub crown biomass > 2 m in the calculation of

ACFL. Adjustments to biomass calculations were made for dead (100% reduction in foliage biomass, 33% reduction in branch biomass), diseased (10% reduction in foliage biomass), and damaged trees (20% reduction in foliage biomass, 10 or 20% fine branch biomass for trees with broken and dead tops, respectively) as compared to a live tree of the same DBH (Smith et al. 2003). Plot-level foliage, live branch, and dead branch biomass were summed over all individuals within a plot and scaling to the hectare to obtain ACFL.

3.8.3 *Extended results*

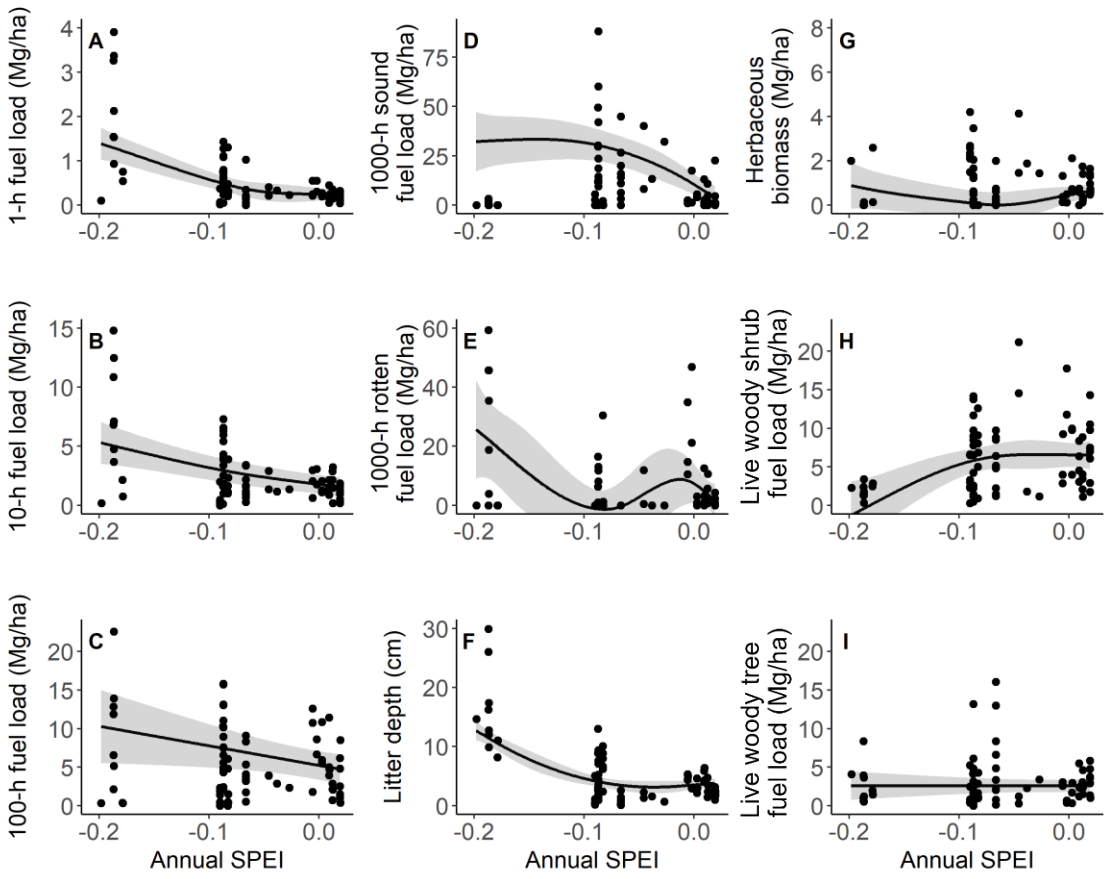

Figure 3.9. Partial effects of annual standardized evapotranspiration index (SPEI) on surface fuel load variables.

Note: Here, and in subsequent figures, generalized additive models represented take the form ~ time since fire (TSF) + annual SPEI + elevation + heat load index (HLI), lines represent estimated partial effect, shading represents 95% confidence intervals, each dot is a plot (n = 79).

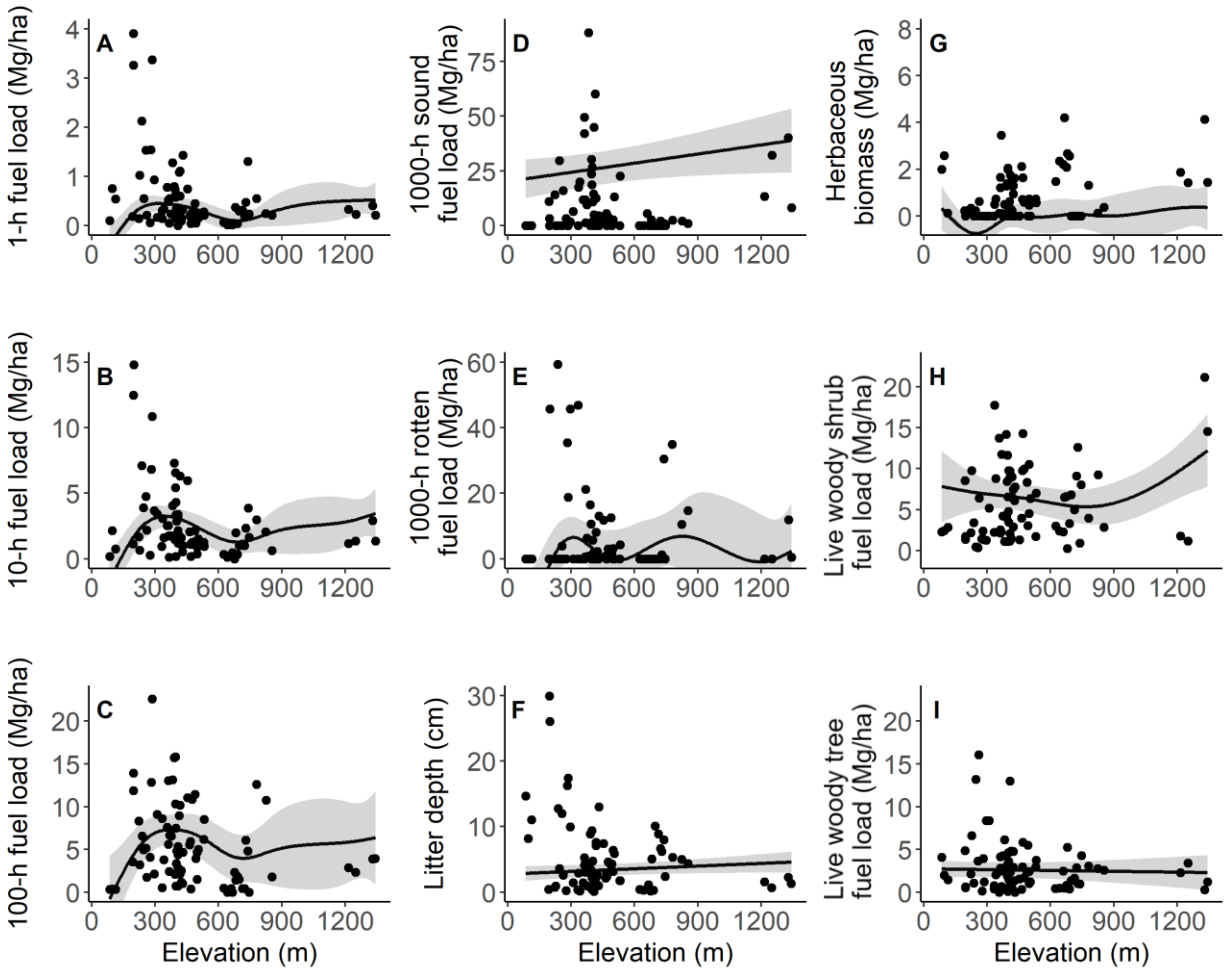

Figure 3.10. Partial effects of elevation on surface fuel load variables.

Note: Model form and symbols described in Figure 3.9 caption.

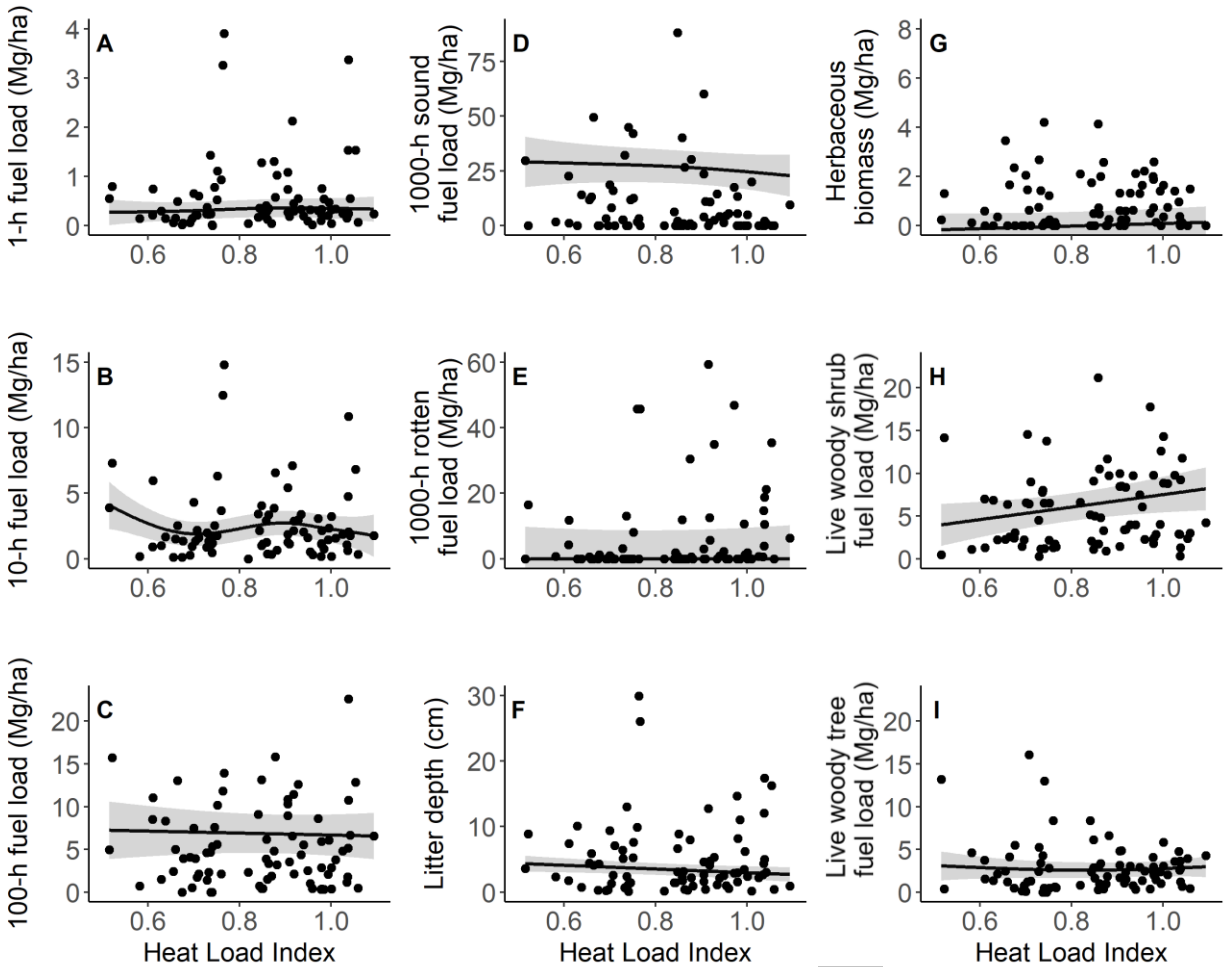

Figure 3.11. Partial effects of heat load index (HLI) on surface fuel load variables.

Note: Model form and symbols described in Figure 3.9 caption.

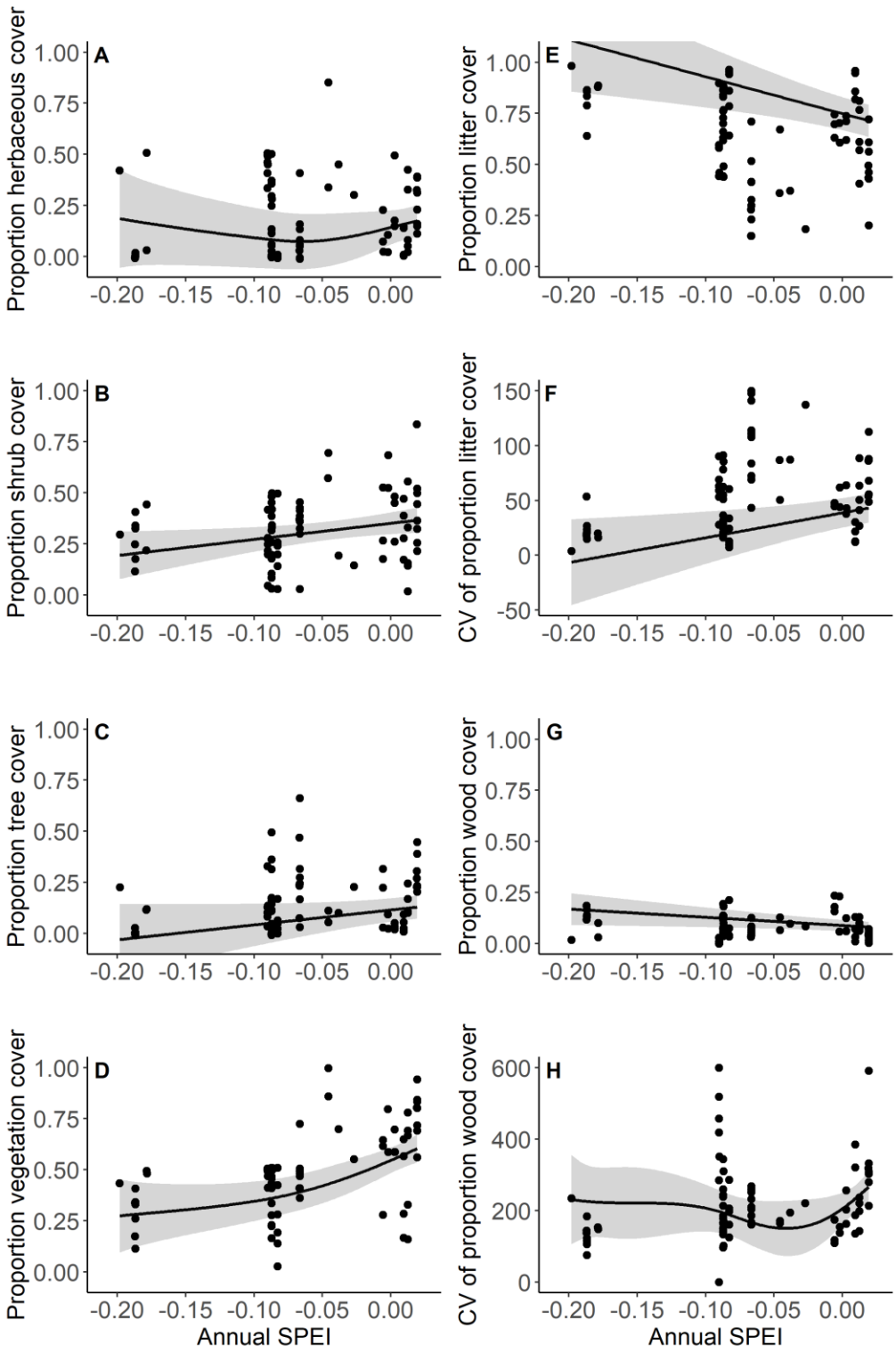

Figure 3.12. Partial effects of annual standardized evapotranspiration index (SPEI) on substrate and vegetation cover variables.

Note: Model form and symbols described in Figure 3.9 caption.

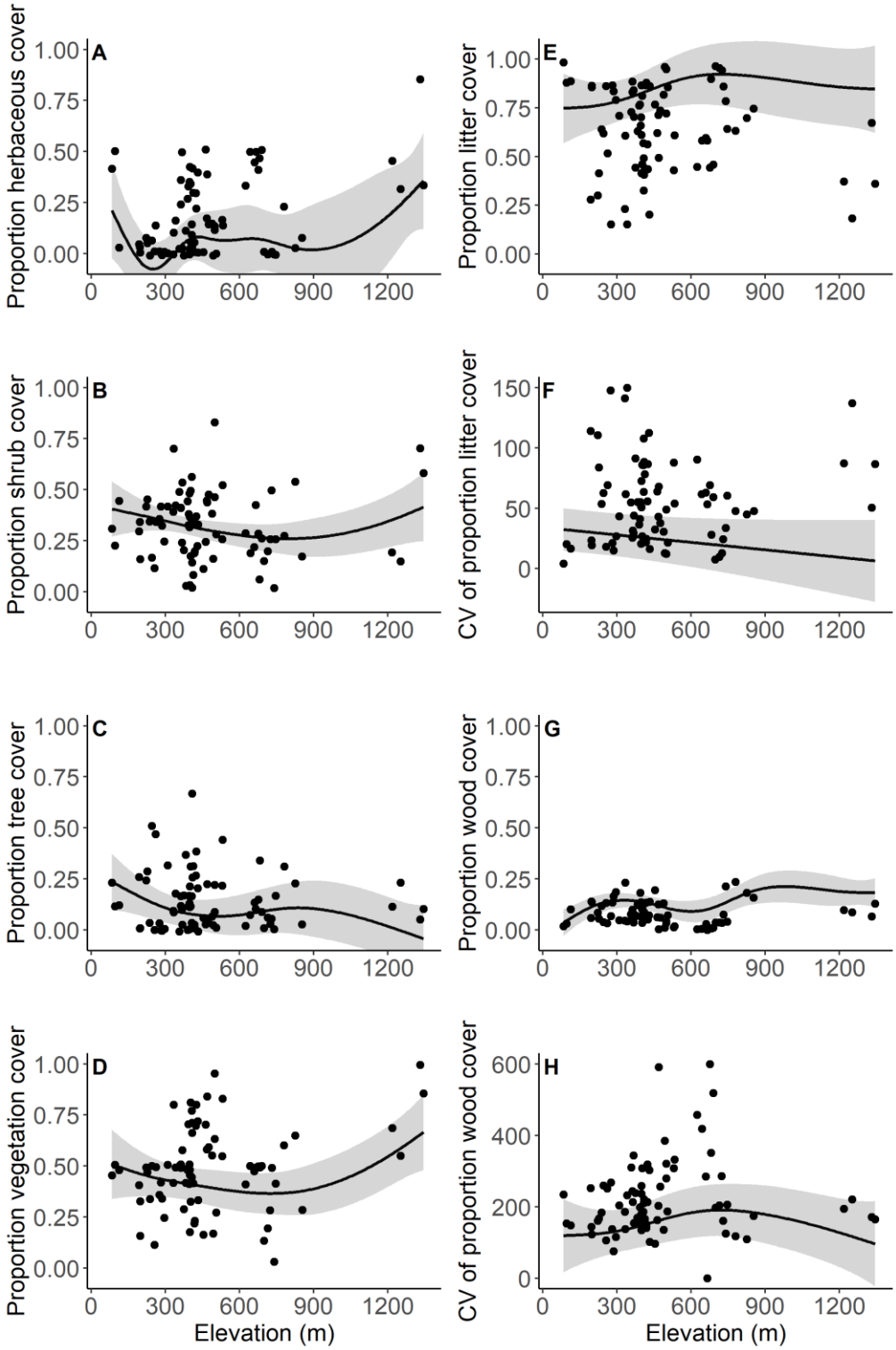

Figure 3.13. Partial effects of elevation on substrate and vegetation cover variables.

Note: Model form and symbols described in Figure 3.9 caption.

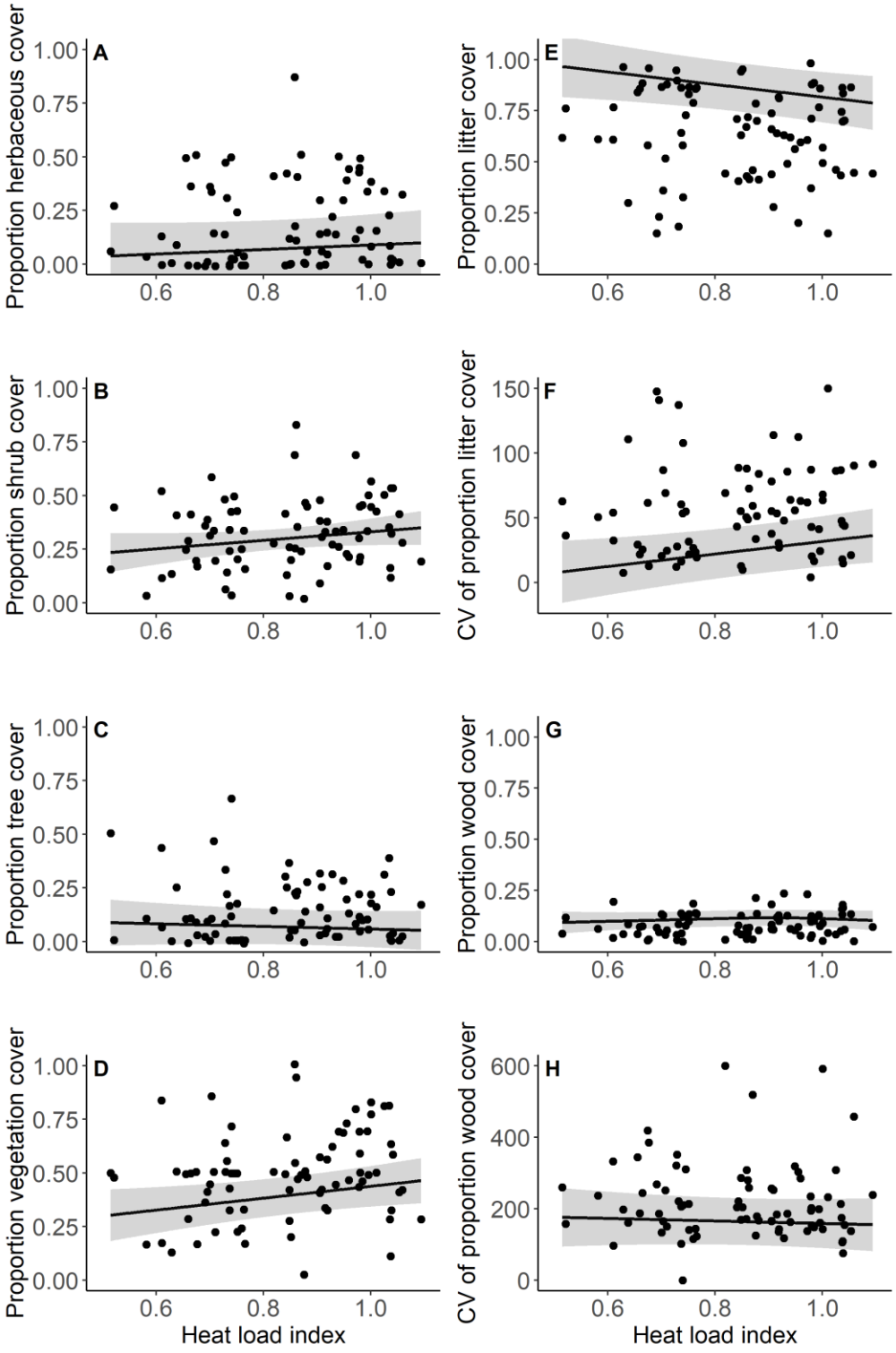

Figure 3.14. Partial effects of heat load index (HLI) on substrate and vegetation cover variables. Note: Model form and symbols described in Figure 3.9 caption.

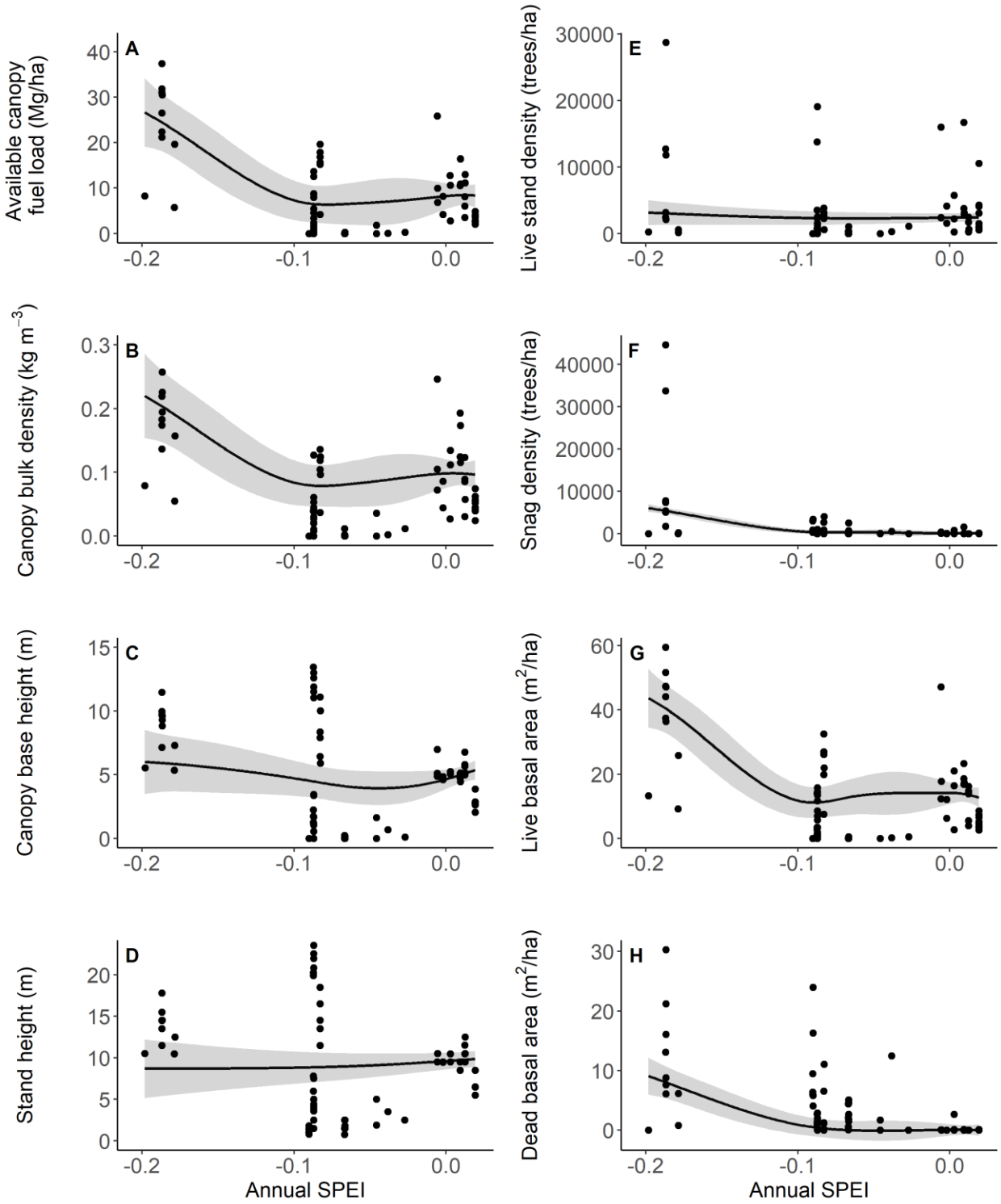

Figure 3.15. Partial effects of annual standardized evapotranspiration index (SPEI) on canopy fuel load variables.

Note: Model form and symbols described in Figure 3.9 caption.

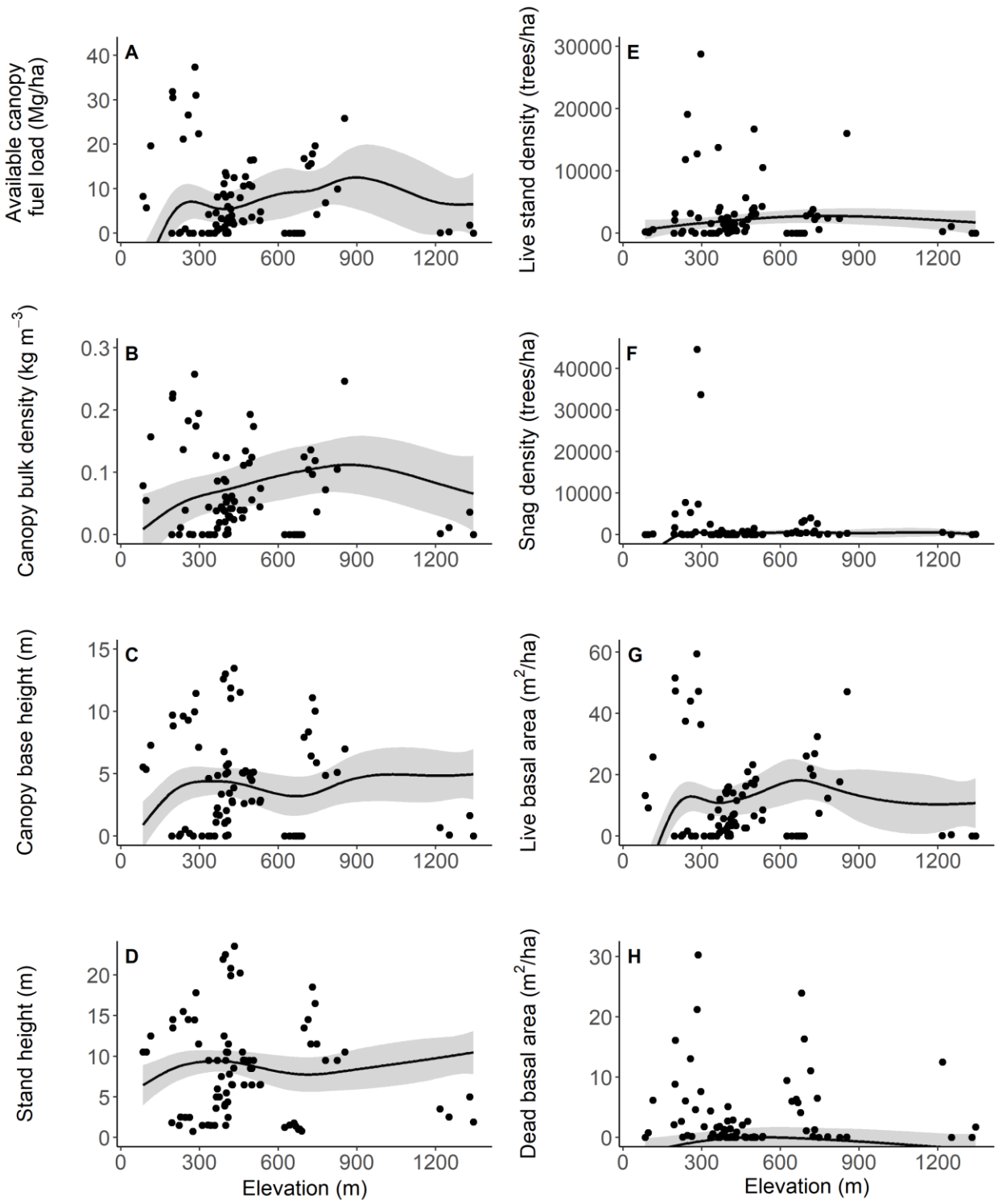

Figure 3.16. Partial effects of elevation on canopy fuel load variables.

Note: Model form and symbols described in Figure 3.9 caption.

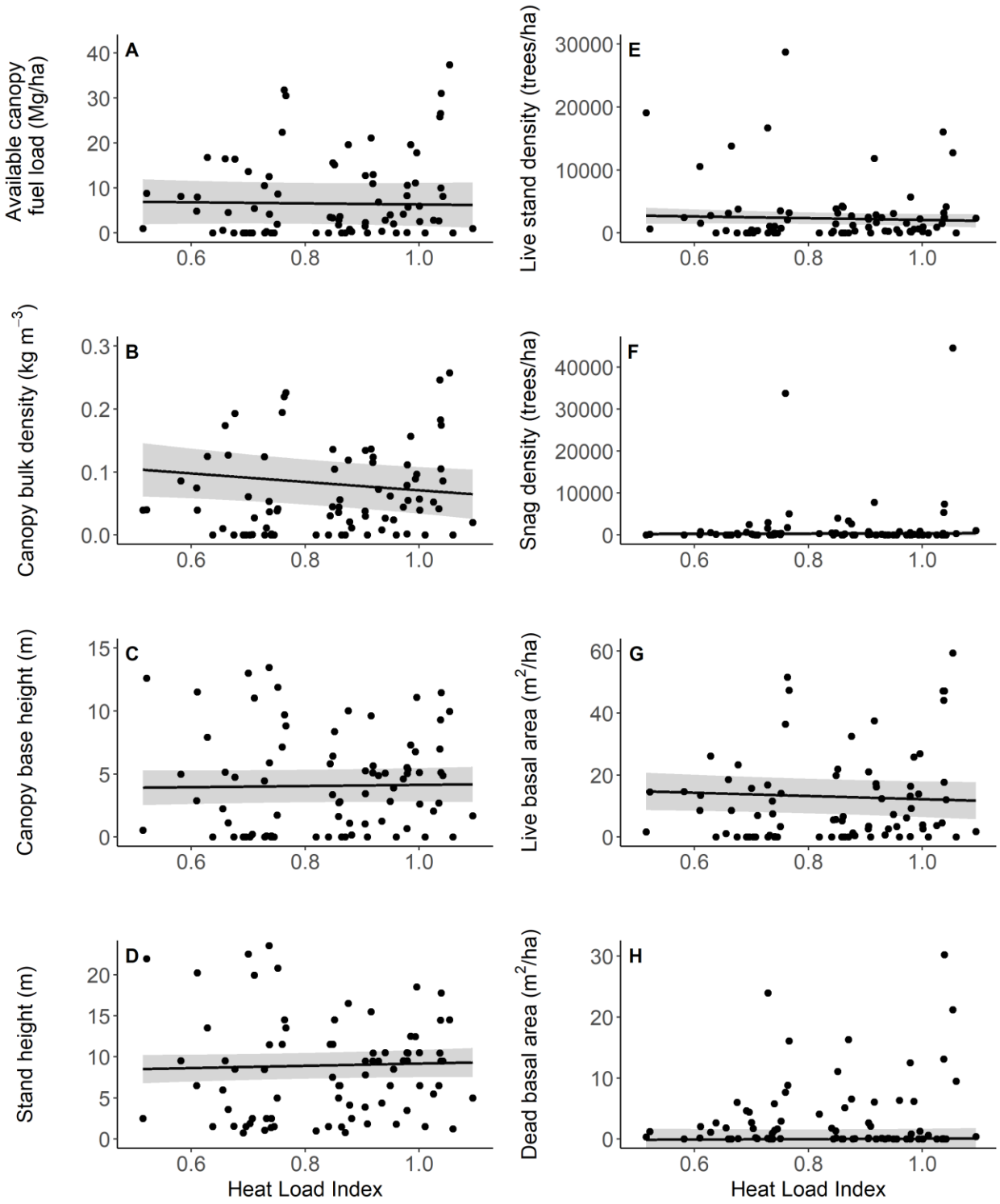

Figure 3.17. Partial effects of heat load index (HLI) on canopy fuel load variables.

Note: Model form and symbols described in Figure 3.9 caption.

Table 3.4. Likelihood ratio test results for comparisons of full and reduced model forms for each surface fuel load response variable.

	Degrees of freedom	Log likelihood	Chi square	P
1-hr fuel load				
~ s(TSF[1])[2]	4.00	-45.05		
~ s(TSF) + s(HLI[3]) + s(Annual SPEI[4]) + s(Elevation)[5]	15.23	-19.53	51.04	<0.001
10-hr fuel load				
~ s(TSF)	4.00	-166.93		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	16.94	-141.22	51.42	<0.001
100-hr fuel load				
~ s(TSF)	5.22	-228.37		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	12.48	-218.66	19.41	0.007
1000-hr sound fuel load				
~ s(TSF)	8.69	-294.35		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	13.82	-286.07	16.56	0.005
1000-hr rotten fuel load				
~ s(TSF)	4.00	-270.39		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	8.31	-268.43	3.92	0.416
Litter depth				
~ s(TSF)	10.44	-173.86		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	10.72	-158.49	30.75	<0.001
Herbaceous fuel load				
~ s(TSF)	5.81	-97.56		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	15.95	-78.46	38.20	<0.001
Live woody shrub fuel load				
~ s(TSF)	6.83	-224.16		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	10.83	-215.53	17.26	0.002
Live woody tree surface fuel load				
~ s(TSF)	6.68	-171.81		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	10.33	-170.93	1.757	0.780

Notes: Where $P < 0.05$, the full model has a significant improvement in fit as compared with the reduced model.
[1]TSF = time since fire
[2]Reduced model form
[3]HLI = heat load index
[4]SPEI = standardized precipitation evapotranspiration index
[5]Full model form

Table 3.5. Likelihood ratio test results for comparisons of full and reduced model forms for each substrate and vegetation cover response variable.

	Degrees of freedom	Log likelihood	Chi square	P
Proportion herbaceous cover				
~ s(TSF[1])[2]	3.63	134.75		
~ s(TSF) + s(HLI[3]) + s(Annual SPEI[4]) + s(Elevation)[5]	16.86	158.28	47.07	<0.001
Proportion shrub cover				
~ s(TSF)	3.00	32.93		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	7.78	38.75	11.64	0.040
Proportion tree cover				
~ s(TSF)	5.54	124.42		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	10.78	132.54	16.26	0.006
Proportion vegetation cover				
~ s(TSF)	3.00	16.92		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	11.86	45.68	57.52	<0.001
Proportion litter cover				
~ s(TSF)	4.40	36.73		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	14.15	55.51	37.55	<0.001
CV of proportion litter cover				
~ s(TSF)	6.73	-366.86		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	13.35	-352.52	28.68	<0.001
Proportion wood cover				
~ s(TSF)	8.76	143.78		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	17.07	166.98	46.38	<0.001
CV of proportion wood cover				
~ s(TSF)	10.26	-449.56		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	15.32	-433.72	31.68	<0.001

Notes: Where $P < 0.05$, the full model has a significant improvement in fit as compared with the reduced model.
[1]TSF = time since fire
[2]Reduced model form
[3]HLI = heat load index
[4]SPEI = standardized precipitation evapotranspiration index
[5]Full model form

Table 3.6. Likelihood ratio test results for comparisons of full and reduced model forms for each canopy fuel load response variable.

	Degrees of freedom	Log likelihood	Chi square	P
Available canopy fuel load				
~ s(TSF[1])[2]	10.74	-218.28		
~ s(TSF) + s(HLI[3]) + s(Annual SPEI[4]) + s(Elevation)[5]	18.90	-206.87	22.83	0.004
Canopy bulk density				
~ s(TSF)	9.31	150.26		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	13.56	158.51	16.49	0.002
Canopy base height				
~ s(TSF)	4.00	-130.41		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	20.59	-92.02	76.78	<0.001
Stand height				
~ s(TSF)	9.95	-146.51		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	18.10	-132.61	27.79	<0.001
Live stand density				
~ s(TSF)	6.05	-730.86		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	11.76	-724.91	11.91	0.064
Dead stand density				
~ s(TSF)	6.19	-665.43		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	18.26	-641.62	47.61	<0.001
Live basal area				
~ s(TSF)	10.90	-254.18		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	17.88	-236.70	34.96	<0.001
Dead basal area				
~ s(TSF)	10.25	-191.27		
~ s(TSF) + s(HLI) + s(Annual SPEI) + s(Elevation)	15.17	-180.29	21.96	<0.001

Notes: Where $P < 0.05$, the full model has a significant improvement in fit as compared with the reduced model.
[1]TSF = time since fire
[2]Reduced model form
[3]HLI = heat load index
[4]SPEI = standardized precipitation evapotranspiration index
[5]Full model form

Table 3.7. Effects of time since fire (TSF), heat load index (HLI), elevation, and annual standardized precipitation evapotranspiration index (SPEI) on surface fuel load response variables from generalized additive models (GAMs).

Fuel variable	Peak year	Peak mean value	Parameter	k	edf[1]	Chi square	P		Deviance explained
1-hr fuel load	35	0.6	TSF	10	1.00	14.65	<0.001	***	36.4
			HLI	10	1.63	1.01	0.646		
			Elevation	10	5.40	37.22	<0.001	***	
			SPEI	10	2.31	48.75	<0.001	***	
10-hr fuel load	35	4.0	TSF	10	1.27	14.68	<0.001	***	35.4
			HLI	10	3.48	10.10	0.050	*	
			Elevation	10	5.23	40.16	<0.001	***	
			SPEI	10	1.63	17.64	<0.001	**	
100-hr fuel load	19	7.3	TSF	8	1.97	4.81	0.086	.	26.3
			HLI	10	1.00	0.11	0.742		
			Elevation	10	4.16	12.72	0.029	*	
			SPEI	10	1.00	4.83	0.028	*	
1000-hr sound fuel load	11	13.7	TSF	10	2.74	10.88	0.023	*	26.4
			HLI	10	1.06	0.37	0.570		
			Elevation	10	3.16	15.13	0.004	**	
			SPEI	10	2.22	11.45	0.004	**	
1000-hr rotten fuel load	35	4.0	TSF	10	1.00	6.21	0.012	*	5.15
			HLI	10	1.83	2.17	0.431		
			Elevation	10	1.00	0.23	0.629		
			SPEI	10	1.00	0.88	0.348		
Litter depth	35	7.6	TSF	10	1.78	142.93	<0.001	***	61.6
			HLI	10	1.00	4.84	0.028	*	
			Elevation	10	1.00	2.77	0.096	.	
			SPEI	10	2.94	134.80	<0.001	***	
Herbaceous fuel load	2	2.0	TSF	4	2.54	30.80	<0.001	***	40.6
			HLI	10	1.00	0.90	0.344		
			Elevation	10	5.40	14.69	0.018	*	
			SPEI	10	2.28	5.49	0.072	.	
Live woody shrub fuel load	35	8.9	TSF	10	1.00	9.07	0.002	**	23.7
			HLI	10	1.00	6.61	0.010	*	
			Elevation	10	2.88	4.08	0.275		
			SPEI	10	2.01	14.09	0.001	**	
Live woody tree surface fuel load	10	2.8	TSF	10	2.82	8.62	0.073	.	13.2
			HLI	10	1.50	0.72	0.667		
			Elevation	10	1.00	0.12	0.726		
			SPEI	10	1.00	0.002	0.967		

[1]edf represents effective degrees of freedom, where values near 1 indicate a linear relationship and increasing values represent an increasingly complex relationship

Table 3.8. Effects of time since fire (TSF), heat load index (HLI), elevation, and annual standardized precipitation evapotranspiration index (SPEI) on substrate and vegetation cover response variables from generalized additive models (GAMs).

Fuel Variable	Model distribution	Peak year	Peak mean value	Parameter[1]	edf[2]	Chi square	P		Deviance explained
Proportion herbaceous cover	Beta	2	0.4	TSF	3.11	40.37	<0.001	***	68.8
				HLI	2.53	5.33	0.152		
				Elevation	2.80	8.79	0.051	.	
				SPEI	3.97	19.04	0.002	**	
Proportion shrub cover	Beta	2	0.31	TSF	1.00	0.001	0.970		15.6
				HLI	1.00	3.45	0.063	.	
				Elevation	2.25	3.86	0.192		
				SPEI	1.00	4.06	0.044	*	
Proportion tree cover	Beta	7	0.21	TSF	2.26	33.08	<0.001	***	60.8
				HLI	1.00	1.22	0.270		
				Elevation	3.31	9.37	0.053	.	
				SPEI	1.00	11.32	<0.001	***	
Proportion vegetation cover	Beta	2	0.55	TSF	2.04	10.17	0.008	**	64.6
				HLI	1.00	4.50	0.034	*	
				Elevation	3.52	20.10	<0.001	***	
				SPEI	1.84	16.62	<0.001	***	
Proportion litter cover	Beta	16	0.88	TSF	4.26	60.94	<0.001	***	66.5
				HLI	1.00	6.84	0.009	**	
				Elevation	4.05	10.88	0.050	*	
				SPEI	1.00	11.89	<0.001	***	
CV of proportion litter cover	scaled t	5	99	TSF	6.30	87.75	<0.001	***	56.3
				HLI	1.03	5.18	0.023	*	
				Elevation	1.00	2.67	0.102		
				SPEI	1.00	6.22	0.013	*	
Proportion wood cover	Beta	17	0.13	TSF	2.31	21.65	<0.001	***	72.8
				HLI	2.82	4.82	0.204		
				Elevation	6.63	57.74	<0.001	***	
				SPEI	1.10	1.76	0.267		
CV of proportion wood cover	scaled t	2	324	TSF	4.61	106.13	<0.001	***	45.2
				HLI	1.00	0.63	0.429		
				Elevation	1.00	0.57	0.452		
				SPEI	4.17	38.24	<0.001	***	

[1]All parameters in each model were fit with k =10

[2]edf represents effective degrees of freedom, where values near 1 indicate a linear relationship and increasing values represent an increasingly complex relationship

Table 3.9. Effects of time since fire (TSF), heat load index (HLI), elevation, and annual standardized precipitation evapotranspiration index (SPEI) on canopy fuel load response variables from generalized additive models (GAMs).

Fuel variable	Peak year	Peak mean value	Parameter	k	edf[1]	Chi square	P		Deviance explained
Available canopy fuel load	26	13.5	TSF	10	1.90	74.13	<0.001	***	68.3
			HLI	10	1.00	0.16	0.635		
			Elevation	10	4.62	19.19	0.002	**	
			SPEI	9	6.39	89.04	<0.001	***	
Canopy bulk density	23	0.11	TSF	10	3.81	76.95	<0.001	***	57.2
			HLI	10	1.00	2.75	0.097	.	
			Elevation	10	1.78	2.63	0.286		
			SPEI	10	2.51	20.38	<0.001	***	
Canopy base height	33	11.3	TSF	10	5.20	1137.21	<0.001	***	84.0
			HLI	10	1.00	0.02	0.899		
			Elevation	10	6.01	45.98	<0.001	***	
			SPEI	10	3.02	27.88	<0.001	***	
Stand height	33	20.0	TSF	10	4.82	1267.30	<0.001	***	82.6
			HLI	10	1.00	0.04	0.847		
			Elevation	10	4.31	16.07	0.010	*	
			SPEI	10	2.75	13.61	0.003	**	
Live stand density	19	2500	TSF	10	2.64	16.04	0.001	**	19.9
			HLI	10	1.00	1.17	0.279		
			Elevation	10	2.27	6.09	0.081	.	
			SPEI	10	1.57	0.79	0.544		
Snag density	33	410	TSF	10	1.01	0.39	0.546		39.4
			HLI	10	1.00	0.47	0.495		
			Elevation	10	7.99	274.06	<0.001	***	
			SPEI	10	3.82	298.94	<0.001	***	
Live basal area	27	19.0	TSF	10	2.80	96.81	<0.001	***	68.5
			HLI	10	1.02	1.87	0.179		
			Elevation	10	6.91	91.38	<0.001	***	
			SPEI	10	3.54	78.73	<0.001	***	
Dead basal area	2	5.8	TSF	10	3.85	64.85	<0.001	***	36.8
			HLI	10	1.00	0.07	0.789		
			Elevation	10	2.83	6.83	0.134		
			SPEI	10	2.70	50.03	<0.001	***	

[1]edf represents effective degrees of freedom, where values near 1 indicate a linear relationship and increasing values represent an increasingly complex relationship

Table 3.10. Effect of time since fire (TSF) by pre-fire legacy (forest or non-forest) on surface fuel load response variables from generalized additive models (GAMs) with the form: response ~ TSF + pre-fire legacy + TSF : pre-fire legacy.

Response and predictor variables	β	SE	Z	Peak TSF	Peak mean value	edf	Chi square	P	Deviance explained
1-hr fuel load (Mg/ha)									
Forest pre-fire (intercept)	0.49	0.04	12.50					<0.001	22.6
Non-forest pre-fire (intercept)	-0.20	0.10	-1.91					0.056	
TSF : forest pre-fire				23	1.3	3.98	109.17	<0.001	
TSF : non-forest pre-fire				23	0.5	2.8	4.02	0.32	
10-hr fuel load (Mg/ha)									
Forest pre-fire (intercept)	2.26	0.19	12.18					<0.001	20.3
Non-forest pre-fire (intercept)	-1.15	0.43	-2.68					0.007	
TSF : forest pre-fire				23	3.9	2.72	32.08	<0.001	
TSF : non-forest pre-fire				15	1.4	1.87	0.11	0.957	
100-hr fuel load (Mg/ha)									
Forest pre-fire (intercept)	5.46	0.49	11.21					<0.001	23.9
Non-forest pre-fire (intercept)	-2.83	1.10	-2.57					0.01	
TSF : forest pre-fire				13	7.3	2.55	17.53	<0.001	
TSF : non-forest pre-fire				2	3.9	1.75	0.23	0.929	
1000-hr sound fuel load (Mg/ha)									
Forest pre-fire (intercept)	8.94	0.91	9.82					<0.001	34.4
Non-forest pre-fire (intercept)	-5.82	2.36	-2.47					0.014	
TSF : forest pre-fire				9	18.0	3.98	64.81	<0.001	
TSF : non-forest pre-fire				2	10.0	2.8	1.32	0.817	
1000-hr rotten fuel load (Mg/ha)									
Forest pre-fire (intercept)	7.03	0.61	11.56					<0.001	26.7
Non-forest pre-fire (intercept)	-6.36	1.45	-4.38					<0.001	
TSF : forest pre-fire				23	26.2	3.07	273.87	<0.001	
TSF : non-forest pre-fire				15	2.6	2.13	0.63	0.775	
Litter depth (cm)									
Forest pre-fire (intercept)	3.80	0.26	14.84					<0.001	43.5
Non-forest pre-fire (intercept)	-0.17	0.66	-0.25					0.801	
TSF : forest pre-fire				23	10.1	3.89	173.29	<0.001	
TSF : non-forest pre-fire				23	10.1	2.73	63.11	<0.001	
Herbaceous fuel load (Mg/ha)									
Forest pre-fire (intercept)	0.65	0.10	6.41					<0.001	31.9
Non-forest pre-fire (intercept)	0.36	0.24	1.49					0.137	
TSF : forest pre-fire				2	2.1	3.03	44.47	<0.001	
TSF : non-forest pre-fire				2	1.3	2.1	1.1	0.763	
Live woody shrub fuel load (Mg/ha)									
Forest pre-fire (intercept)	4.68	0.53	8.85					<0.001	21.1
Non-forest pre-fire (intercept)	2.99	1.22	2.44					0.015	
TSF : forest pre-fire				14	6.9	2.76	7.94	0.057	
TSF : non-forest pre-fire				2	15.8	1.9	9.88	0.011	
Live woody tree surface fuel load (Mg/ha)									
Forest pre-fire (intercept)	2.43	0.28	8.56					<0.001	5.0
Non-forest pre-fire (intercept)	0.37	0.60	0.62					0.534	
TSF : forest pre-fire				11	2.8	1.93	3.4	0.363	
TSF : non-forest pre-fire				2	3.4	1.33	1.29	0.507	

Notes: β, SE, and Z values are presented for intercept estimates while edf (effective degrees of freedom) and chi square values are presented for TSF-pre-fire legacy estimates. β represents the intercept estimate at TSF = 0 and z statistic and p values represent evidence of difference from zero for forest pre-fire (intercept). For non-forest pre-fire (intercept) values, β represents the additive effect on the fuel response variable for non-forest pre-fire legacy as compared with forest pre-fire legacy, and z statistic and p values represent evidence of difference between forest and non-forest pre-fire legacies. Peak mean value and peak TSF represent the maximum estimated value for the response variable and the associated TSF by pre-fire legacy. Edf represents the linearity of each relationship, chi square and associated p values represent the strength of evidence of a relationship between TSF and the response variable by pre-fire legacy. Deviance explained represents the total explanatory power of the model.

Table 3.11. Effect of time since fire (TSF) by pre-fire legacy (forest or non-forest) on canopy fuel load response variables from generalized additive models (GAMs) with the form: response ~ TSF + pre-fire legacy + TSF : pre-fire legacy.

Response and predictor variables	β	SE	Z	Peak TSF	Peak mean value	edf	Chi square	P	Deviance explained
Available canopy fuel load (Mg/ha)									
Forest pre-fire (intercept)	7.00	0.46	15.09					<0.001	54.0
Non-forest pre-fire (intercept)	-1.89	1.04	-1.82					0.068	
TSF : forest pre-fire				23	21.5	2.75	308.67	<0.001	
TSF : non-forest pre-fire				23	13.1	1.96	37.87	<0.001	
Canopy bulk density (kg/m^3)									
Forest pre-fire (intercept)	0.061	0.01	13.24					<0.001	51.0
Non-forest pre-fire (intercept)	0.001	0.01	0.09					0.931	
TSF : forest pre-fire				23	0.16	2.02	161.89	<0.001	
TSF : non-forest pre-fire				23	0.15	1.44	40.63	<0.001	
Canopy base height (m)									
Forest pre-fire (intercept)	3.46	0.11	31.80					<0.001	79.7
Non-forest pre-fire (intercept)	-0.48	0.30	-1.63					0.104	
TSF : forest pre-fire				23	9.3	5.28	1020.4	<0.001	
TSF : non-forest pre-fire				23	5.8	3.5	119.1	<0.001	
Stand height (m)									
Forest pre-fire (intercept)	6.86	0.20	33.98					<0.001	90.5
Non-forest pre-fire (intercept)	-0.01	0.49	-0.02					0.986	
TSF : forest pre-fire				23	13.9	4.12	533.55	<0.001	
TSF : non-forest pre-fire				23	11.8	2.89	83.38	<0.001	
Live stand density (trees/ha)									
Forest pre-fire (intercept)	1559	227	6.88					<0.001	15.4
Non-forest pre-fire (intercept)	-271	455	-0.59					0.552	
TSF : forest pre-fire				23	3250	1.21	24.24	<0.001	
TSF : non-forest pre-fire				15	1350	1.06	0.03	0.96	
Snag density (trees/ha)									
Forest pre-fire (intercept)	211	56	3.74					<0.001	4.2
Non-forest pre-fire (intercept)	-163	118	-1.39					0.166	
TSF : forest pre-fire				2	400	1.91	4.325	0.157	
TSF : non-forest pre-fire				23	150	1.37	0.538	0.77	
Live basal area (m^2/ha)									
Forest pre-fire (intercept)	11.60	0.70	16.68					<0.001	57.2
Non-forest pre-fire (intercept)	-3.77	1.60	-2.36					0.018	
TSF : forest pre-fire				23	37.2	3.18	410.47	<0.001	
TSF : non-forest pre-fire				23	18.9	2.27	37.47	<0.001	
Dead basal area (m^2/ha)									
Forest pre-fire (intercept)	2.39	0.26	9.09					<0.001	31.9
Non-forest pre-fire (intercept)	-1.63	0.64	-2.56					0.011	
TSF : forest pre-fire				23	6.4	4.05	107.38	<0.001	
TSF : non-forest pre-fire				23	1.8	2.85	2.97	0.453	

Notes: β, SE, and Z values are presented for intercept estimates while edf (effective degrees of freedom) and chi square values are presented for TSF-pre-fire legacy estimates. β represents the intercept estimate at TSF = 0 and z statistic and p values represent evidence of difference from zero for forest pre-fire (intercept). For non-forest pre-fire (intercept) values, β represents the additive effect on the fuel response variable for non-forest pre-fire legacy as compared with forest pre-fire legacy, and z statistic and p values represent evidence of difference between forest and

non-forest pre-fire legacies. Peak mean value and peak TSF represent the maximum estimated value for the response variable and the associated TSF by pre-fire legacy. Edf represents the linearity of each relationship, chi square and associated p values represent the strength of evidence of a relationship between TSF and the response variable by pre-fire legacy. Deviance explained represents the total explanatory power of the model.

Chapter 4. DEMOGRAPHIC PROCESSES UNDERPINNING POST-FIRE RESILIENCE IN CALIFORNIA CLOSED-CONE PINE FORESTS: THE IMPORTANCE OF FIRE INTERVAL, STAND STRUCTURE, AND CLIMATE[1]

4.1 ABSTRACT

The resilience of serotinous obligate-seeding plants to fire may be compromised if increasing fire frequency curtails time available for canopy seed bank accumulation (i.e., immaturity risk), but how various drivers affect seed availability at the time of fire is poorly understood. Using field data from California closed-cone pine (*Pinus attenuata* and *P. muricata*) stands, we assess two critical demographic processes during the inter-fire period—reproductive capacity and mortality. At tree- and stand-levels, we test how these processes are affected by stand age and are mediated by biotic and abiotic factors. We found that stand age was the key driver of reproductive capacity; older stands had a greater proportion of reproductively mature individuals and greater closed cone density. Stand density mediated the effect of age; greater stand density resulted in greater closed cone density and a lower proportion of reproductively mature individuals, but reproductive capacity in low- and high-density stands converged over time. Increased moisture

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stress reduced the stand-level proportion reproductively mature trees but had no effect on closed cone density. Mortality was strongly associated with density-dependent thinning and increased in stands with high moisture stress. Reproductive capacity began to increase sharply 10 years post-fire and by 20 years immaturity risk was low. However, prior to 20 years, low-density stands with high moisture stress may be more susceptible to immaturity risk. Understanding these relationships is critical to predicting serotinous population persistence under changing climate and disturbance conditions.

4.2 INTRODUCTION

Widespread changes to climate and disturbance regimes are altering plant populations in terrestrial ecosystems globally (Johnstone et al. 2016). Changes in size, frequency, seasonality, or severity of a disturbance regime can have strong effects on ecosystem structure and function (Turner 2010). Such changes can combine with direct effects of climate warming to erode resilience – the capacity of an ecosystem to absorb disturbance and reorganize without transitioning to an alternative state (Walker et al. 2004). Fire activity has increased in many temperate forest and woodland ecosystems during the period from 2000 to the early 2020s (Parks and Abatzoglou 2020, Boer et al. 2020), challenging resilience mechanisms that promote post-fire recovery and driving ecosystem type conversion (e.g., conversion from forest to non-forest; Coop et al. 2020). Such transitions are most likely where plant adaptations to fire are misaligned with fire characteristics (Pausas and Keeley 2014, Johnstone et al. 2016).

Serotinous obligate seeders – non-sprouting species that accumulate and store canopy seed banks over multiple years – depend upon predictable fire return intervals that exceed the time needed to develop a canopy seed bank sufficient for self-replacement (Lamont and Enright 2000). Although typically adapted to stand-replacing fires, serotinous plant populations may be

threatened through three important mechanisms that collectively make up the interval squeeze framework of Enright et al. (2015). First, shortened fire-free intervals can lead to immaturity risk if populations burn before accumulating a sufficient canopy seed bank (Keeley et al. 1999). Second, stressful climate conditions during the first year post-fire—a crucial window for serotinous populations in which most recruitment occurs following *en masse* seed release (Turner et al. 1999, Harvey and Holzman 2014) – can result in recruitment failure even if sufficient seed is available (Enright et al. 2014, Hansen and Turner 2019). Third, warming and drying climate can directly affect demographic processes by delaying or decreasing reproductive capacity and increasing plant mortality (Enright et al. 2015). Shifts in demographic processes can combine with changing disturbance regimes to produce compound disturbance effects (*sensu* Paine et al. 1998), where multiple drivers create a synergistic effect on resilience. Shortened fire intervals and post-fire recruitment failure have been increasingly documented in recent years (Fairman et al. 2017, Stevens-Rumann et al. 2018, Davis et al. 2019, Turner et al. 2019). However, the effects of warming climate on demographic processes and the implications for seed availability at the time of fire are poorly understood, representing a key gap in understanding serotinous plant population persistence under future climate (Davis et al. 2018).

Demographic processes in plants are controlled by many drivers occurring at multiple levels of organization. The probability of producing seeds (i.e., reproductive maturity) strongly increases with plant age in perennial, obligate seeder species (Harper 1977, Viglas et al. 2013), as does individual seed production (Andrus et al. 2020). Seed production similarly increases with plant size (Davi et al. 2016), as greater access to resources generally results in greater seed production (Greene et al. 2002). However, trade-offs between vegetative growth and seed production can occur during early successional stages and when intraspecific competition is high

(Climent et al. 2008). High initial population density can drive high intraspecific competition and delay age to reproductive maturity by years to decades (Borchert 1985), resulting in low individual seed production as compared with individuals in low-density stands (Esler and Cowling 1990, Alfaro-Sánchez et al. 2015). However, despite lower tree-level production, high-density stands may have greater stand-level seed production when compared with low-density stands (Moya et al. 2007, Turner et al. 2007). Moisture stress also affects plants via delayed maturity and chronic or acute reductions in seed production (Redmond et al. 2012) and by increasing mature tree mortality, thereby decreasing the population of reproductive individuals (Williams et al. 2013), especially where competition for resources is strong (Andrus et al. 2021). Warm and dry conditions can also trigger cone opening for some serotinous species, further depleting the canopy seed bank available at time of next fire (Borchert 1985, Verkaik and Espelta 2006). Compounding these climatic stressors, damage caused by biotic agents (e.g., insect pests, diseases) may further decrease seed production and seed availability for some tree species (Schaffer et al. 1983, Singh and Carew 1990). Understanding how these factors interact to influence demographic processes is critical to predicting how serotinous plant populations may respond following increasing fire frequency under a warming climate.

The closed-cone pine forests of California, USA, are a model system for understanding demographic mechanisms of serotinous forest resilience with climate warming and concomitant altered disturbance regimes. Typically, these forests are dominated by a single cohort of closed-cone pines established following stand-replacing fire—similar to other serotinous forests in North America [e.g., lodgepole pine (*Pinus contorta*), jack pine (*P. banksiana*)]—but stand development occurs more rapidly (Vogl 1973, Harvey et al. 2011). California closed-cone pines reach reproductive maturity at a young age and proceed through the stages of stand dynamics

quickly compared with other serotinous forests in North America (Keeley et al. 1999, Harvey and Holzman 2014). Stands are also short-lived with relatively short inter-fire periods (Sugnet 1985, van de Water and Safford 2011). Because of the rapid pace of stand development, empirical measurement of demographic processes across the inter-fire period is more logistically feasible than in other obligate seeding serotinous forests in North America with much longer fire return intervals (Romme 1982, Gauthier et al. 1996). Insights from California closed-cone pine forests may illuminate demographic mechanisms that control species persistence in forests in which these processes unfold across longer temporal scales.

In this study, we used field data collected in California closed-cone pine stands dominated by either knobcone pine (*P. attenuata*) or bishop pine (*P. muricata*) across the early stages of the inter-fire period to address these knowledge gaps about the demographic mechanisms underpinning post-fire resilience. Specifically, to assess the relative effects of multiple drivers on reproductive capacity and tree mortality—two demographic processes that are important for post-fire resilience—we asked: 1) How does reproductive capacity develop over time since stand-replacing fire? 2) How do biotic and abiotic factors drive variability in reproductive capacity at individual tree- and stand-levels? 3) How does stand-level density-dependent tree mortality vary across abiotic and biotic drivers, and what are the implications for the canopy seed bank? We expected that: 1) Time to a high proportion of individuals within a stand reaching reproductive maturity is short and canopy seed bank production increases rapidly over time. 2) Tree size and stand age have the strongest effects on both measures of reproductive capacity at tree- and stand-levels, respectively. Increased stand density has negative effects on tree-level reproductive capacity and stand-level reproductive maturity, and positive effects on canopy seed bank production. Conversely, warmer, drier climate, disease incidence, shrub cover and less

fertile soil have negative effects on both measures of reproductive capacity at both levels of organization. 3) Stand-level density-dependent mortality increases with warmer, drier climate, greater disease incidence, greater shrub cover and stand density, resulting in decreased reproductive capacity. Understanding the relative magnitudes of multiple drivers of demographic processes is key to anticipating serotinous population persistence with implications for conifer-dominated forests across North America.

4.3 METHODS

4.3.1 *Study area and site selection*

This study was conducted in closed-cone pine stands in California, USA within the Klamath Mountains and Northern and Southern Coast Ranges in areas that have experienced stand-replacing fires since 1985 (Appendix B – Figure 4.7). The region has a Mediterranean climate and covers a wide range of average winter (January) temperatures (3.3–12.2 °C), average summer (July) temperatures (14.9–26.9 °C), and annual average precipitation [467–1996 mm; 800-m gridded 30 year climate normals from 1981–2010 (PRISM Climate Group 2019)]. There is a strong seasonality in precipitation, with >90% falling between October and May, and summer fog produces a moderating effect across the study area (Vogl et al. 1977, Torregrosa et al. 2016). Bishop pine occupies areas that receive less annual precipitation (467–1034 mm), and lower seasonal variation (due in part to coastal proximity) in average temperature (8.8–12.2 °C in January and 14.9–18.7 °C in July) than knobcone pine (average annual precipitation of 785–1996 mm, mean temperatures of 3.3–9.9 °C in January and 20.7–26.9 °C in July).

The study area encompasses low elevation to lower montane zones [84–1344 m above sea level (asl)], with bishop pine occupying a narrower elevational zone (84–413 m asl) than knobcone pine (334–1344 asl). Stands are often characterized by steep slopes and soils are

typically shallow and rocky, with serpentine substrate common for knobcone pine (Vogl et al. 1977). Closed-cone pine communities often occur as dense forest stands for several decades following establishment but can also be characterized by low-density stands interspersed with chaparral. Common co-occurring shrub species include *Adenostoma fasciculatum, Arctostaphylos* spp., *Ceanothus* spp., *Heteromeles arbutifolia, Vaccinium ovatum. Quercus* spp. are also common, existing both in shrub and tree form. Herbaceous vegetation, where it is present, commonly includes *Acmispon glaber, Lupinus* spp., and *Mimulus* spp.

To establish a chronosequence of stand age in bishop pine and knobcone pine forests, we selected 15 fires that overlapped the target species' ranges using Monitoring Trends in Burn Severity data (Eidenshink et al. 2007), species distribution maps, and local land management information. The sample fires occurred between 1985 and 2013 and contained patches of high-severity, stand-replacing fire. Plots were established in monodominant, even-aged stands of the target species that established following the previous fire, with stand ages ranging from 4–32 years, and we assumed that all trees had established within the first post-fire growing season. Although there is evidence of seedling establishment 2–3 years post-fire (Vogl et al. 1977), the vast majority (>95%) of establishment following stand-replacing fire occurs in the first post-fire growing season for both bishop pine (Holzman and Folger 2005) and knobcone pine (M.C. Agne, unpublished data). The historical fire regime is characterized by mean return intervals between 30–90 years (Sugnet 1985, van de Water and Safford 2011), suggesting that the chronosequence covers the period during which immaturity risk is greatest (i.e., the first several decades post-fire). Plots were established at least 50 m from roads and had no evidence of management following the most recent fire. Plots covered the range of topographic features and stand densities within each fire perimeter and were separated by at least 100 m, except when on

opposing aspects. During the summers of 2016–2020, we established 31 and 38 plots in bishop pine and knobcone pine stands, respectively. Two to ten plots were sampled in each past fire (each fire represented a single stand age), varying by area that met our sampling criteria.

4.3.2 *Field data collection*

We measured live, standing dead, and fallen trees from the most recent post-fire cohort within a central subplot at each plot. Central subplot radii were chosen to capture ~50 trees and thus varied with stand density, ranging from 2–18 m (total sampling area range: 12.6–1017.9 m^2). All trees were assessed for disease presence (western gall rust, pitch canker) and measured for diameter at breast height (DBH; 1.37 m above ground). All mature cones were tallied by status: closed (majority of cone scales sealed), open (majority of cone scales open), or damaged (evidence of seed predation or mechanical damage). Full visibility of tree crowns allowed counting of all cones on each tree. Field work occurred in warm and dry weather, so scale contraction (and mischaracterization of cones) due to high relative humidity (Vogl 1973) was unlikely. We did not directly assess seed density within cones, but estimates of seed density within closed cones range from 61–95 and 62–78 mean seeds $cone^{-1}$ for knobcone pine (Fry and Stephens 2013) and bishop pine, respectively (S. Bisbing, unpublished data), with seed viability >60% upon reproductive maturity for both species. Tallies of trees and cones by status were scaled to the plot to obtain per hectare (trees ha^{-1} and cones ha^{-1}) estimates. We measured understory and shrub cover along two 18-m transects at each plot using a point-intercept method (Fontaine et al. 2012). We tallied shrubs intercepting the transect at 1-m intervals (n = 36) and divided shrub interceptions by the number of points measured to obtain an estimate of shrub cover.

4.3.3 *Climate and site condition variables*

We obtained climate data at a monthly resolution for our sites from ClimateNA, a software package that locally downscales historical climate data to scale-free point estimates (Wang et al. 2016). Given that our analysis seeks to understand climate effects on aggregate measures of demographic trends over the inter-fire period (e.g., canopy seed bank accumulation over multiple growing seasons), we aggregated annual climate variables as a mean value for the entire growing period (one year following the most recent fire to the year of measurement) for each plot. We considered growing season (March to October) mean annual precipitation and cumulative moisture deficit (CMD) as candidate predictors given the importance of water availability to reproductive capacity and demographic performance in seasonally dry forests (Redmond et al. 2012). The two predictors were collinear, so we assessed parallel model forms with each climate variable included during model evaluation (detailed under *Statistical analysis*).

In addition to regional climate, we characterized site-level topo-climate using three topographic predictors: heat load index (HLI), topographic position index (TPI), and topographic wetness index (TWI). HLI represents the amount of direct incident radiation to a site (McCune and Keon 2002), TPI represents its relative topographic position (i.e., ridge or valley) (Weiss 2001, De Reu et al. 2013), and TWI reflects a site's potential moisture balance (Gessler et al. 1995). We calculated these indices from 30-m digital elevation models (U.S. Geological Survey 1999) using the Geomorphometry and Gradient Metric Toolbox (Evans et al. 2014) in ArcMap version 10.6.1 (ESRI 2018). Only HLI was retained as a candidate predictor for model fitting due to collinearity among topographic variables and poor interspersion of TPI and TWI across stand age.

We also obtained spatial data that reflected soil characteristics from the Probabilistic Remapping of SSURGO (POLARIS) database, a spatially contiguous soils dataset that provides a suite of ecologically relevant soils variables (Chaney et al. 2016). We extracted depth to bedrock and percent soil clay as two candidate predictors as they represent a proxy for soil fertility and can influence forest productivity (Romanyà and Vallejo 2004, Wall and Westman 2006). However, depth to bedrock was strongly collinear with mean growing season CMD, so only percent soil clay was retained as a candidate predictor for model fitting.

4.3.4 *Statistical analysis*

To address questions 1 and 2, we fit generalized linear mixed models for each of the following response variables: tree-level probability of reproductive maturity (cone presence/absence on individual live trees), tree-level cone production [total cones (of all classes) individual^{-1} on live trees with ≥1 cone], stand-level proportion reproductively mature individuals (proportion of standing live and dead trees within a stand with ≥1 cone; hereafter, stand-level proportion mature trees), and stand-level closed cone density (closed cones on standing live and dead trees ha^{-1}). To address question 3, we fit a generalized linear mixed model for the response variable stand-level tree mortality of the post-fire cohort (standing and fallen dead trees ha^{-1}). Tree-level probability of reproductive maturity was fit with a binomial error structure while tree-level cone production was fit with a negative binomial error structure. Stand-level proportion mature trees was fit with a zero-inflated beta error structure as appropriate for proportion data (Zuur et al. 2009). Stand-level closed cone density and tree mortality were fit with zero-inflated negative binomial error structures and an offset term [log(plot area)] to account for variable sampling area (Zuur et al. 2009). All models fit with a negative binomial error structure were also fit with a Poisson error structure, but Poisson-distributed models were removed from

consideration due to overdispersion. Stand-level models included a random effect of fire, and candidate models included the following suite of potential fixed predictor variables: stand age (years since last stand-replacing fire), species, stand density [density of the post-fire cohort, including live and dead individuals (log transformed trees ha^{-1})], shrub percent cover, HLI, percent soil clay, mean growing period precipitation or CMD, and stand age – stand density interaction. Tree-level models included nested random effects of plot within sample fire, and candidate models included the stand-level fixed predictor variables included for the stand-level models and the following tree-level predictor variables: DBH, disease incidence, DBH – stand age, DBH – species, and DBH – stand density interactions. Predictor variables were assessed for collinearity prior to model fitting.

Models were fit using standardized predictors (mean-centered per two standard deviations) to discern relative effects of each predictor. Models with all terms included were fit for each response variable, and model diagnostic tests were conducted. When the full model did not meet assumptions, a suite of new models was fit, each with a single predictor term (all except stand age) removed. This process was repeated until a model was fitted that met assumptions. If two models with the same number of predictors met assumptions, the model with the lowest AICc was selected for inference. We interpreted $P \leq 0.01$ as strong, $P \leq 0.05$ as moderate, and $P \leq 0.10$ as suggestive evidence of an effect (Ramsey and Schafer 2012). Models were fit with the *glmmTMB* package (Brooks et al. 2017), diagnostics were conducted using *DHARMa* (Hartig 2021), and effects were visualized using *broom* (Robinson et al. 2021), *ggeffects* (Lüdecke 2018), *ggplot* (Wickham 2016), *ggpubr* (Kassambara 2020), and *jtools* (Long 2020). Analyses were conducted in R version 4.0.5 (R Core Team 2021).

4.4 RESULTS

We counted 68,400 cones on 4,573 trees (2,121 knobcone pine and 2,452 bishop pine), 3,855 of which were live when sampled (1,960 knobcone pine and 1,895 bishop pine). Stand structure varied widely both within and across stand age (Table 4.1). Stand density ranged from 147–82,800 live trees ha^{-1}. Live basal area and quadratic mean diameter were highly correlated with stand age, with median values of 0.5 m^2 ha^{-1} and 2.0 cm at 6 years and 26.2 m^2 ha^{-1} and 10.4 cm at 32 years (Table 4.1).

Table 4.1. Summary statistics for stand structure attributes by stand age.

Stand age	Plots (n)	Species	Trees (n)	Mean cones per tree	Quadratic mean diameter (cm)		Stand density (live trees ha^{-1})		Live basal area (m^2 ha^{-1})	
					med[1]	range	med[1]	range	med[1]	range
4	4	PIMU	276	0	NA	NA	3932	1840–6068	0.41	0.06–0.93
5	2	PIAT	114	0	NA	NA	7582	6013–9151	1.06	0.97–1.15
5	3	PIMU	122	0.01	NA	NA	5659	3830–9549	0.75	0.44–2.31
6	2	PIAT	95	0.10	2.0	1.8–2.2	1837	640–3034	0.53	0.25–0.81
7	4	PIMU	585	0.14	1.2	1.0–1.5	54643	13440–82761	4.50	2.38–11.12
8	3	PIAT	150	0.53	3.0	1.0–3.7	7112	1890–29412	1.98	0.17–3.90
8	4	PIMU	225	1.01	2.8	1.5–5.4	6797	643–16977	2.62	1.31–9.09
10	8	PIAT	464	1.89	5.6	3.1–9.0	2763	671–11332	4.90	2.62–8.64
10	6	PIMU	475	9.85	3.6	2.7–7.0	1723	553–3631	2.45	0.69–5.71
14	9	PIAT	456	13.33	8.8	3.5–16.6	4106	943–18104	17.71	5.70–24.98
15	2	PIAT	110	2.08	6.6	6.1–7.0	3417	2236–4598	10.01	7.78–12.23
19	6	PIAT	341	17.23	8.9	6.0–11.1	2412	1297–16043	17.13	3.46–47.11
23	3	PIAT	189	62.74	12.2	8.1–12.6	2735	603–3979	20.02	7.48–32.48
23	10	PIMU	769	75.39	13.8	4.0–29.2	2910	147–28736	40.80	9.18–59.43
32	3	PIAT	202	47.06	10.4	10.3–12.6	2785	2288–3183	26.15	21.95–28.67

[1] med = Median

4.4.1 *Reproductive capacity over time since fire*

Cones were first present in stands by five years post-fire for bishop pine and six years post-fire for knobcone pine (Table 4.1; Figure 4.1), but time to reproductive maturity varied, with some stands lacking cones until eight years post-fire for both species. Average cone density remained under 10,000 cones ha^{-1} for at least 10 years post-fire, after which there was a steep

and continuous linear increase in cone production (Figure 4.1). Incidence of cones on dead trees and damaged cones increased with time but closed cones represented the greatest proportion at all ages (Figure 4.1A) and increased most steeply with age (Figure 4.1B).

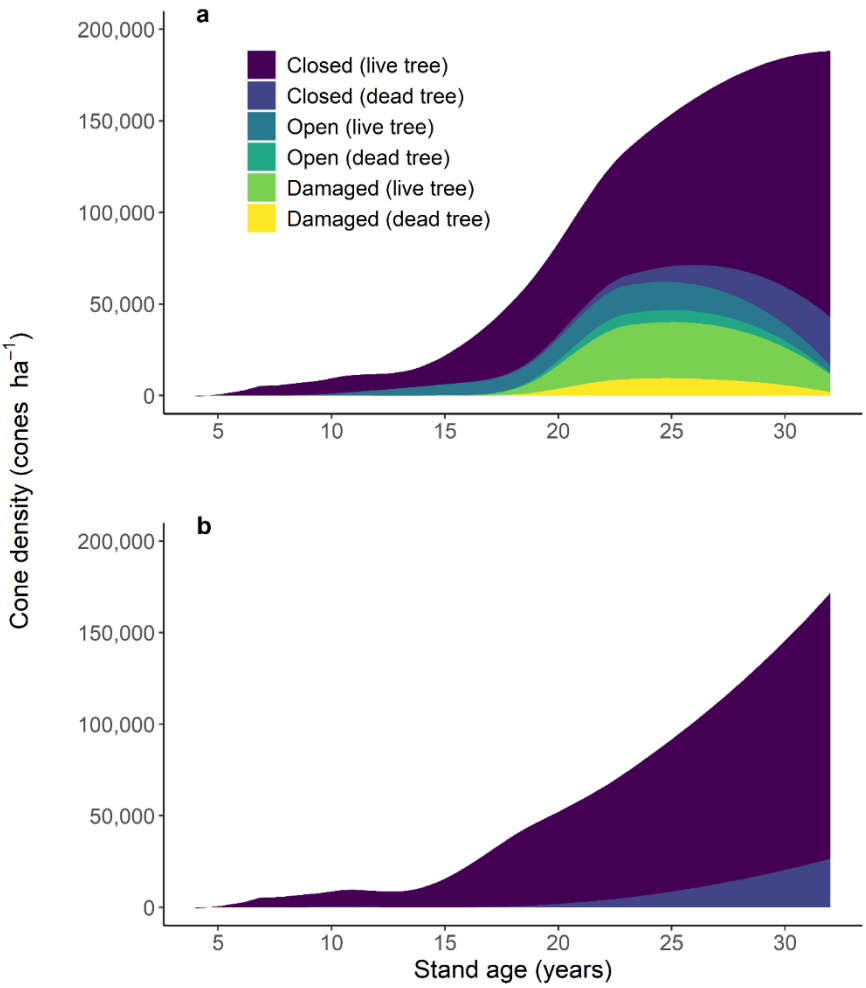

Figure 4.1. Stand-level cone density by stand age for (A) all cone class (closed, open, damaged) by tree status (live, dead) combinations, (B) closed cones (cones presumed to contribute to the canopy seed bank) by tree status.

Note: Colors represent average plot-level estimates by category for each stand age interpolated across the chronosequence using a loess smoother (span = 0.5).

4.4.2 *Tree-level reproductive capacity*

Tree-level reproductive capacity was strongly associated with tree DBH, with an effect size more than two times greater than other predictors (Figures 4.2, 4.3; Appendix B – Table 4.2). Tree-level probability of reproductive maturity increased from near zero for trees <2 cm

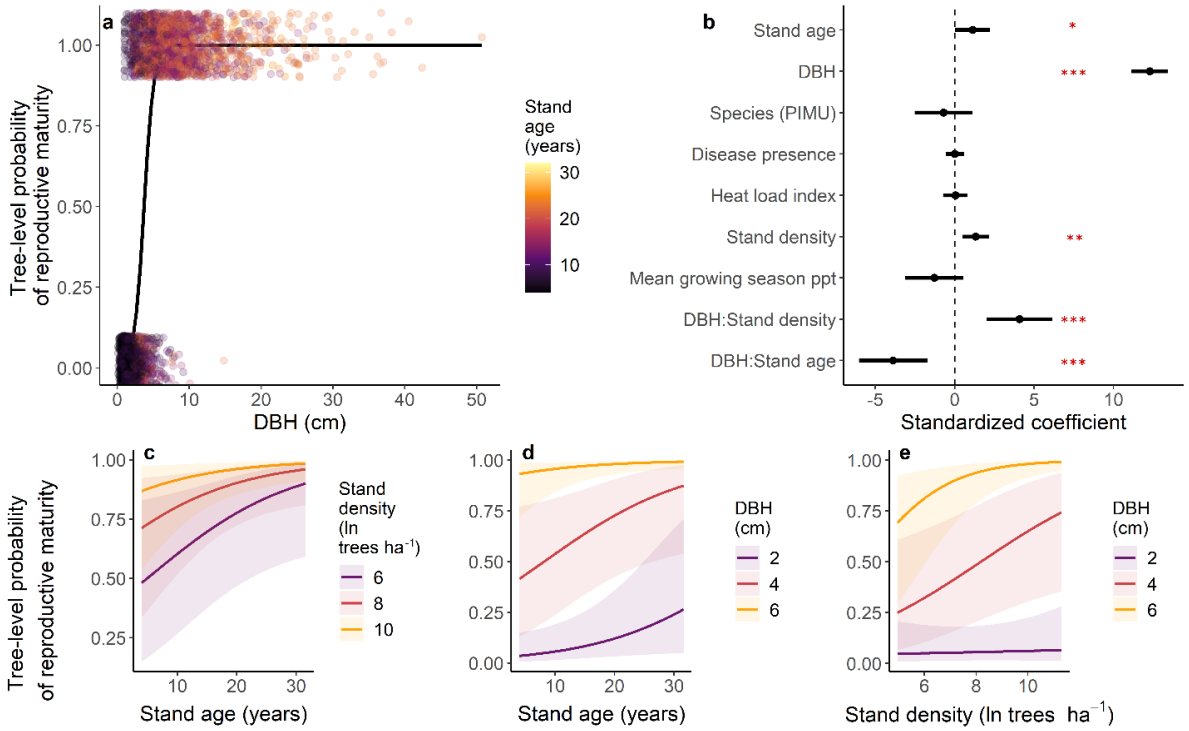

Figure 4.2. Effects of covariates from the tree-level probability of reproductive maturity model. (A) Partial effect of DBH. Here, and for subsequent figures, the solid line represents the median estimate with remaining covariates held at their means. Each point, shaded by stand age, represents a tree (n = 3,855). (B) Effects of covariates on tree-level probability of reproductive maturity. Here, and for subsequent figures, dots represent medians and horizontal lines represent 95% CI. Effects for each continuous predictor are per two standard deviations. Strength of evidence for effect sizes are indicated by: *** (P < 0.001), ** (P < 0.01), * (P < 0.05), + (P < 0.10). (C-E) Change in stand age or stand density and probability of reproductive maturity across gradients of significant covariates. Here, and for subsequent figures, solid lines represent median estimates and shaded areas represent 95% CI. Predictions consider the effect of each covariate combination individually, holding remaining covariates at their means.

DBH to nearly 100% for trees >9 cm DBH, irrespective of all other drivers (Figure 4.2A). There was a similarly strong effect of DBH on tree-level cone production, where cone production increased slowly for trees <10 cm DBH but increased exponentially for trees >15 cm DBH (Figure 4.3A, B). Trees of a similar DBH had a greater probability of reproductive maturity and greater cone production in older stands than trees with the same DBH in younger stands (Figures 4.2D, 4.3D). For example, probability of reproductive maturity for a tree of 4 cm DBH increased by >40% (Figure 4.2D) and cone production for a tree of 10 cm DBH increased by a factor of four (Figure 4.3D) between stand ages of 10 and 30 years. The effect of DBH lessened with stand age (Figures 4.2B, 4.3B); differences in both measures of reproductive capacity associated with DBH decreased in older stands (Figures 4.2D, 4.3D).

Contrary to our expectation, stand density had a positive effect on tree-level probability of reproductive maturity (Figure 4.2B). Trees in high-density stands were associated with a ~40% greater probability of reproductive maturity than trees in low-density stands at an age of 10 years, but this difference decreased to ~10% by 30 years (Figure 4.2C). The positive effect of stand density was greatest for trees of larger DBH and there was no effect for trees <2 cm DBH (Figure 4.2E). As expected, trees in low-density stands had greater cone production, although this effect decreased in older stands (Figure 4.3B, G). However, for trees with relatively large DBH, the effect of stand density on cone production was less than for smaller trees, with wide variation around the estimated effect (Figure 4.3E). Holding other covariates constant, bishop pine individuals had double the cone production of knobcone pine, but there was no difference in probability of reproductive maturity between species (Figures 4.2B, 4.3B, C). Cone production of trees in stands with high soil clay was double that of trees in stands with low soil clay (Figure

4.3B, F). Disease incidence, HLI, mean growing season CMD or precipitation, and shrub cover had no effect on tree-level reproductive capacity (Appendix B – Figures 4.8, 4.9).

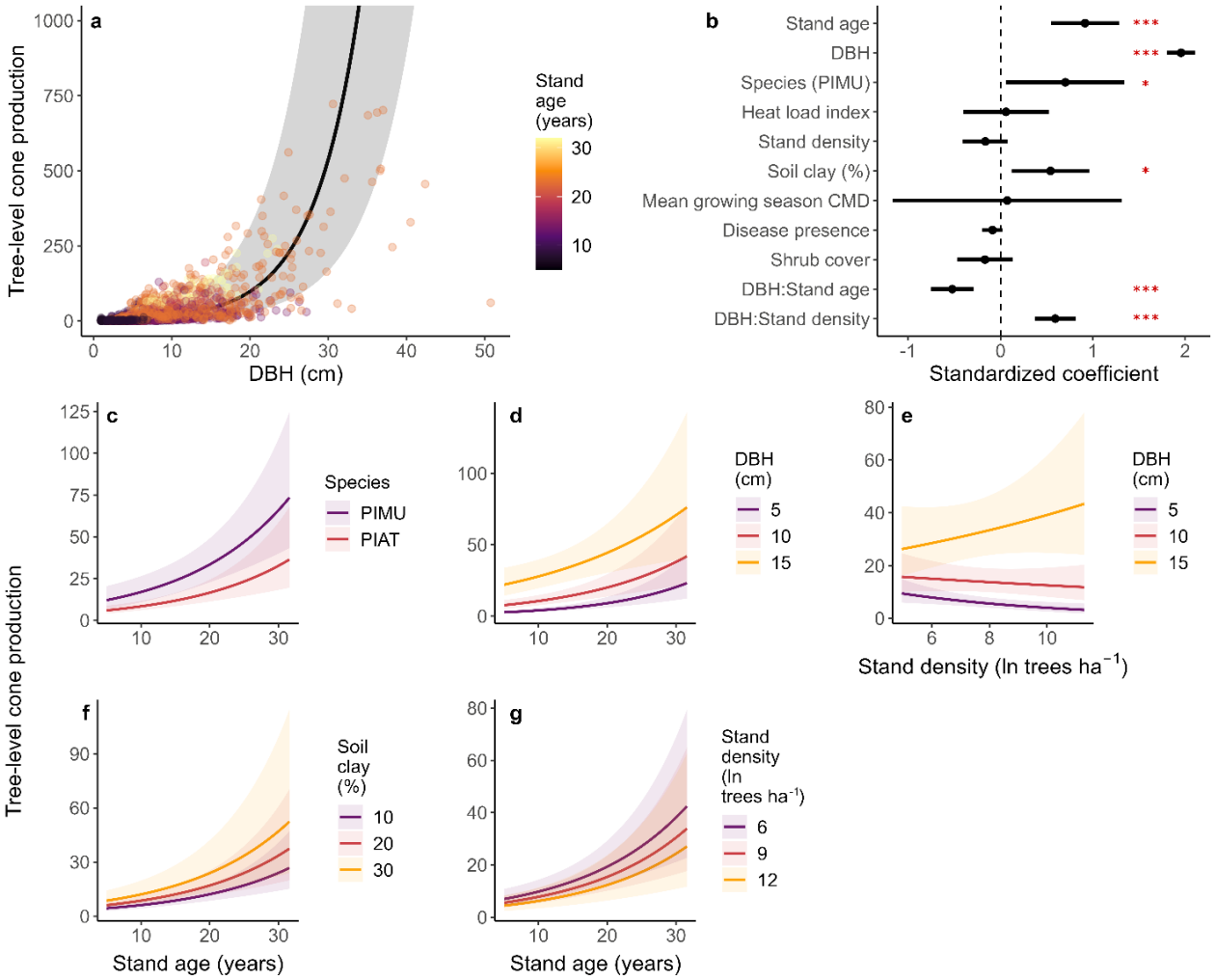

Figure 4.3. Effects of covariates from the tree-level cone production model. (A) Partial effect of DBH. Each point, shaded by stand age, represents a tree (n = 1,806). (B) Effects of covariates on tree-level cone production. (C-H) Change in stand age and cone production across gradients of significant covariates. Symbols are described in Figure 4.2.

4.4.3 *Stand-level reproductive capacity*

Stand-level reproductive capacity increased strongly with stand age. Stand-level proportion mature trees ranged from 0 to nearly 100%, with all observations of 0% occurring in

stands <10 years and all observations >90% occurring in stands ≥14 years (Figure 4.4A). Estimated closed cone density increased by approximately two orders of magnitude between the initial years of reproductive maturity (5-6 years) and 30 years (Figure 4.5A). The effect of stand age was mediated by stand density, with contrasting effects on each measure of stand-level reproductive capacity (Figures 4.4B, 4.5B; Appendix B – Table 4.3). There were strong negative effects of stand density and its interaction with stand age on proportion mature trees (Figure 4.4B). For 10-year-old stands, proportion mature trees was estimated at >50% for low-density

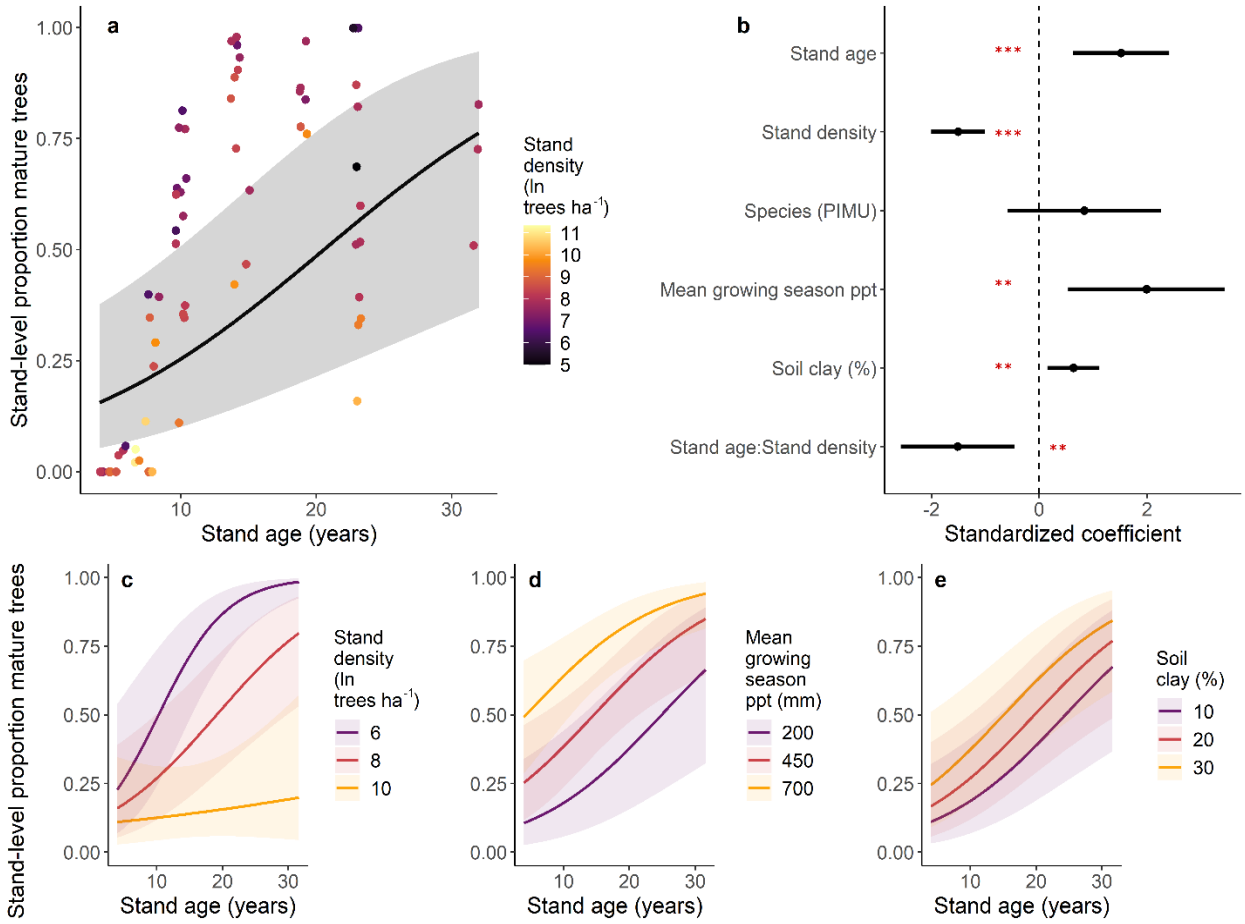

Figure 4.4. Effects of covariates from the stand-level proportion mature trees model. (A) Partial effect of stand age. Each point, shaded by stand density (log-transformed), represents a plot (n = 69). (B) Effects of covariates on stand-level proportion mature trees. (C-E) Change in stand age and proportion mature trees across gradients of significant covariates. Symbols are described in Figure 4.2.

stands, compared with <25% for moderate to high-density stands, and the difference increased over time (Figure 4.4C). Conversely, there was a strong positive effect of stand density on closed cone density, which declined with stand age (Figure 4.5B). For young stands, estimated closed cone density was more than an order of magnitude greater in high-density stands than in low-density stands, but after ~20 years, closed cone densities were similar across stands of all densities (Figure 4.5C). Effects of regional climate also varied by response variable. Mean growing season precipitation had a strong positive effect on proportion mature trees (Figure

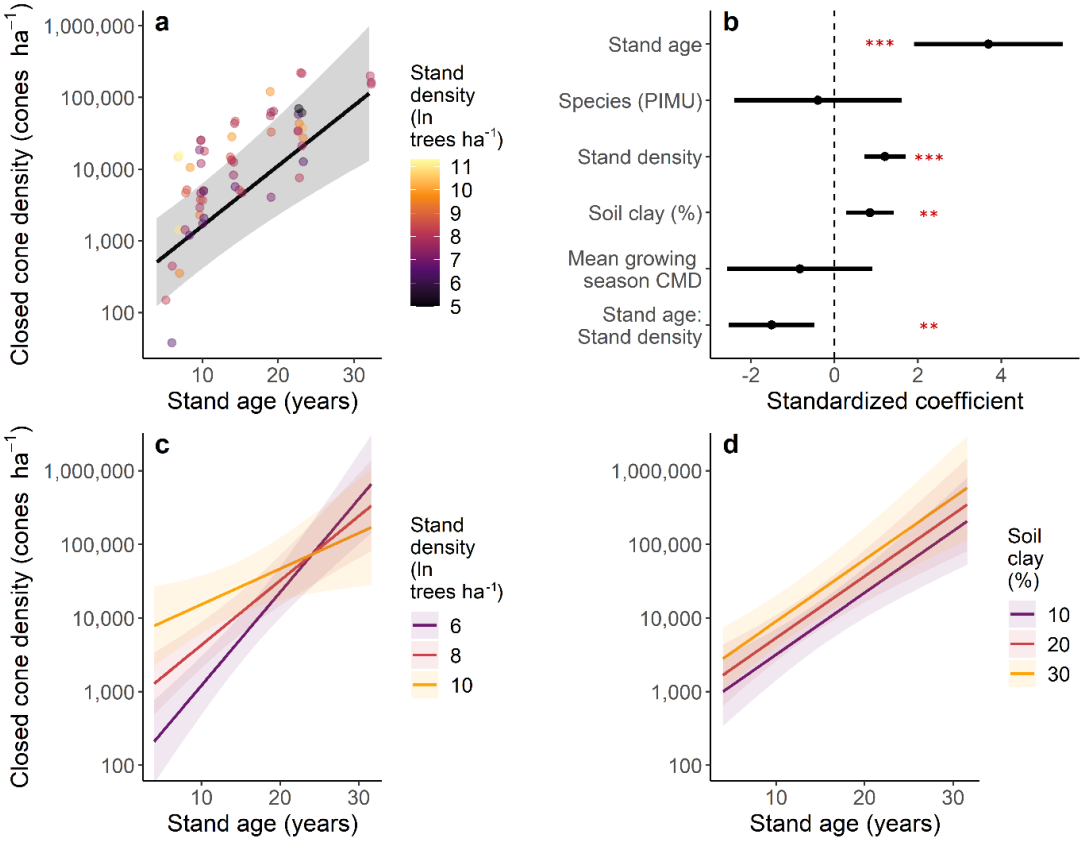

Figure 4.5. Effects of covariates from the stand-level closed cone density model. (A) Partial effect of stand age. Each point is shaded by stand density (log-transformed) and represents a plot (n = 69). (B) Effects of covariates on stand-level closed cone density. (C-D) Change in stand age and closed cone density across gradients of significant covariates. Symbols are described in Figure 4.2.

4.4B), while mean growing season CMD had no effect on closed cone density (Figure 4.5B). Greater soil clay had positive effects on both measures (Figures 4.4E, 4.5D), although this effect was lower magnitude than other significant covariates in each model (Figures 4.4B, 4.5B). Stand-level reproductive capacity did not differ between species (Figures 4.4B, 4.5B; Appendix B – Figures 4.10, 4.11).

4.4.4 *Stand-level tree mortality*

For stands ten years and older (n = 47), observed stand-level tree mortality in the post-fire cohort ranged from 0–85,100 dead trees ha^{-1}, and was strongly positively correlated with stand-level proportion dead trees (Appendix B – Figure 4.12). Stand density and stand age drove tree mortality (Figure 4.6B; Appendix B – Table 4.3); tree mortality in high-density stands was two orders of magnitude greater than that of low-density stands of the same age (Figure 4.6D). Similarly, tree mortality increased by nearly two orders of magnitude between 10- and 30-year-old stands of the same density (Figure 4.6A, D). Moisture stress further exacerbated tree mortality (Figure 4.6B); high mean growing season CMD was associated with approximately season CMD (Figure 4.6E). Bishop pine also had significantly greater tree mortality than knobcone pine stands of a similar age and stand density (Figure 4.6C), while HLI had no effect (Figure 4.6B; Appendix B – Figure 4.13).

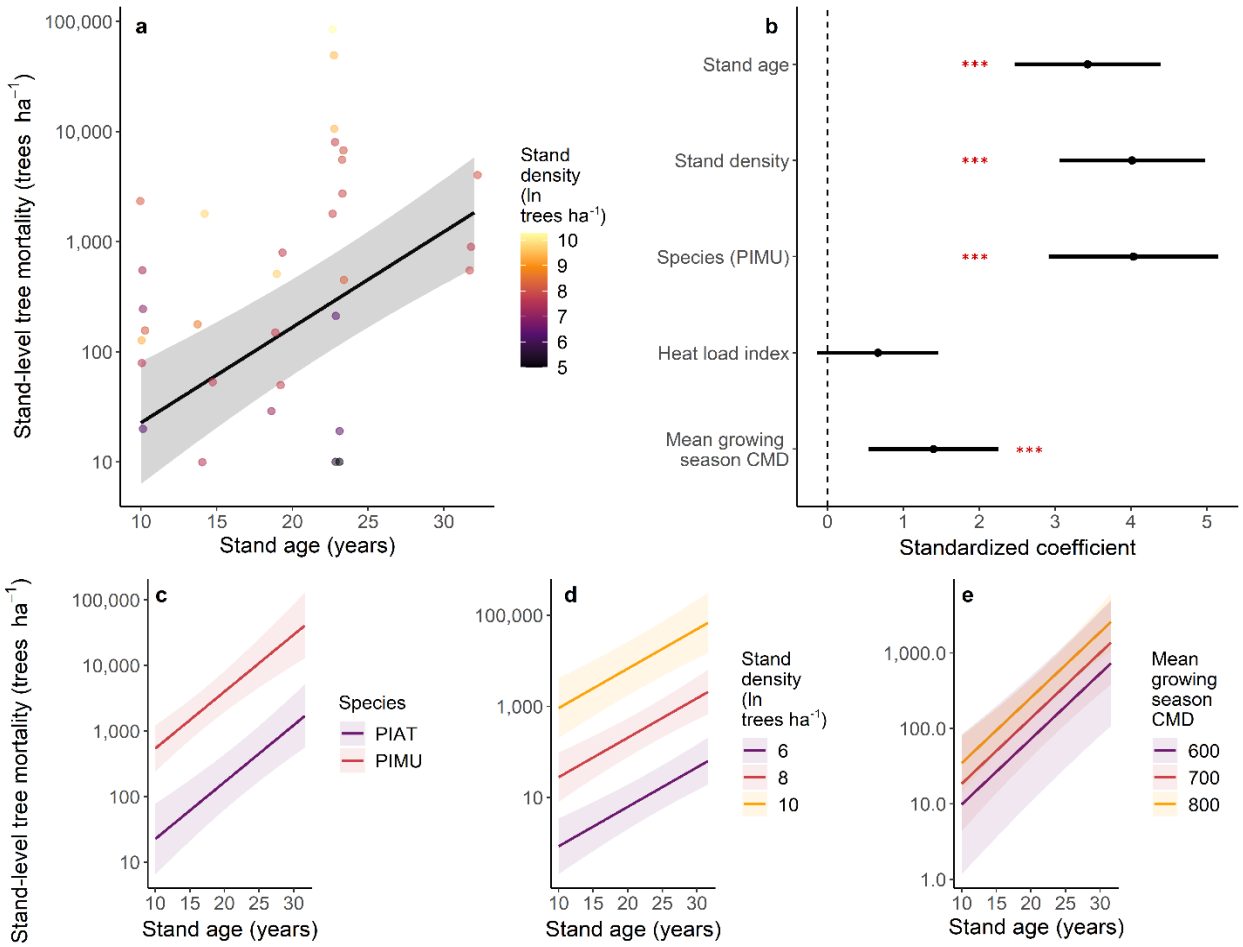

Figure 4.6. Effects of covariates from the stand-level tree mortality model. (A) Partial effect of stand age. Each point, shaded by stand density (log-transformed), represents a plot (n = 47). Note: Two points at 49,400 and 85,100 trees ha-1 were omitted for interpretability. (B) Effects of covariates on stand-level tree mortality. (C-E) Change in stand age and tree mortality across gradients of significant covariates. Symbols are described in Figure 4.2. one order of magnitude greater tree mortality compared with stands with low mean growing

4.5 Discussion

Our study identifies three critically important drivers of demographic processes in serotinous forests as they develop following stand-replacing fires. First, stand age is the key driver of reproductive capacity—older stands have greater reproductive capacity regardless of all other

drivers. Second, intraspecific competition associated with stand density mediated tree- and stand-level reproductive capacity at a given stand age, while interspecific competition from shrubs had no detectable effect. Third, there were modest decreases in reproductive capacity and increases in tree mortality associated with warm and dry regional climate, although topo-climate had little effect. Collectively, these findings have important implications for serotinous forest resilience in a changing climate. Overriding other factors is the minimum fire-free period necessary for serotinous population persistence—change in other drivers cannot compensate for the importance of the fire interval. However, once stands exceed the minimum fire-free period, differences in stand structure produce divergent outcomes in reproductive maturity for stands of the same age. Our results are also consistent with the demographic shift described by Enright et al. (2015) suggesting that warming and drying conditions constrain the reproductive output of serotinous populations during the fire-free period. Although the demographic mechanisms underpinning resilience are aligned to current conditions, continued climate warming and increased fire activity may have profound effects on serotinous forest persistence.

Rapid post-fire canopy seed bank accumulation suggests that the window for immaturity risk is brief for California closed cone pine species. Closed cone development first occurred at five and six years for bishop pine and knobcone pine, respectively, suggesting that complete loss of these species from a site would occur if fire return intervals were shorter than this period – currently a rare occurrence. Early onset of cone production is common in strongly serotinous species adapted to frequent stand-replacing fire (Enright et al. 1996, Turner et al. 2007, Climent et al. 2008), serving as an important mechanism of resilience to population loss to short-interval fire (Tapias et al. 2001). Population self-replacement, however, requires a considerably longer fire-free interval (Burrows 2008, Gosper et al. 2013). Estimates for knobcone pine suggest the

mean cone to seedling conversion ratio is 1:1 (M.C. Agne, unpublished data), or ~60–100 seeds for one established seedling (Fry and Stephens 2013). Therefore, mean canopy seed bank accumulation to regenerate at 1,500 seedlings ha^{-1} [low seedling density for closed-cone pine (Keeley et al. 1999)] and at 15,000 seedlings ha^{-1} [moderate seedling density for closed-cone pine (Holzman and Folger 2005)] does not occur until 10 and 20 years, respectively. Although self-replacement is dependent on a variety of factors, we expect that the seedling density associated with self-replacement is toward the high end of this range. Canopy seed bank accumulation may begin to slow near the end of our chronosequence (~30 years; Figure 1a), suggesting that sufficient seed is stored and available to regenerate the stand before three decades post-fire (Lamont et al. 1991). Thus, seed limitation is likely prior to 10 years and is unlikely after 20 years post-fire. Additional factors can alter seed availability for stands of any age, but their effects are most important between 10 and 20 years post-fire. Further, although our study focused on factors in the post-fire environment that control demographic processes, differences between pre-fire stand structure, fire intensity or fire season may have important effects on the post-fire cohort and could be considered in future studies.

Although stand age is the key driver of reproductive capacity in California closed-cone pines, strong effects of intraspecific competition suggest buffering against immaturity risk differs with stand structure. Negative effects of intraspecific competition on tree-level cone production are common for serotinous species (Esler and Cowling 1990, Moya et al. 2008). However, we found that this applied most strongly to trees with the smallest DBH. Tree-level reproductive capacity was greatest for relatively large trees, regardless of other factors, suggesting a synergy rather than trade-off between vegetative and reproductive growth (Alfaro-Sánchez et al. 2015). These tree-level effects scaled up to delay the peak in stand-level reproductive maturity, similar to

findings for *P. coulteri* and *P. halepensis* (Borchert 1985, Moya et al. 2008). Despite negative effects on tree-level cone production, high stand densities during the first two decades of stand development increased the canopy seed bank, with the increase in cone-bearing trees outweighing the decrease in cones per tree, similar to other serotinous species (Esler and Cowling 1990, Moya et al. 2007, Turner et al. 2007). Despite strong intraspecific competition, high post-fire stand densities provide a buffer against immaturity risk should a subsequent fire occur prior to the mean fire return interval, as well as a post-fire environment with low interspecific competition (Harvey and Holzman 2014). Short-interval fire activity is common within the study area (Reilly et al. 2019) and fire intervals <20 years may increase with continued climate warming. By ~20 years, closed cone density converges across levels of stand density, indicating that the range of stand structural development pathways that occur for serotinous species (Harvey and Holzman 2014, Turner et al. 2016) can lead to sufficient canopy seed bank development, given adequate time.

Tree mortality associated with regional moisture stress suggests a demographic shift is expected with climate warming in California closed-cone pine forests. Stand-level tree mortality was primarily associated with stand age and density, suggesting the dominant process controlling mortality was density-dependent thinning, consistent with expected stand dynamics (Harvey et al. 2011). However, an additional effect of high growing season cumulative moisture deficit suggests that warming climate may exacerbate background mortality, similar to findings in subalpine forests (Andrus et al. 2021). Increased tree mortality could decrease the reproductive capacity of stands if live trees cannot compensate for the loss of reproductively mature trees through increased cone production. Our assessment of tree mortality necessarily underestimates mortality rates due to disappearing evidence of mortality of small trees over time; future studies

that track stands over time may provide more precise estimates. Stand-level reproductive maturity was also delayed where growing season precipitation was low, signaling some evidence of direct climate effects on reproductive capacity. However, there was no evidence of depressed canopy seed bank availability due to regional or local climate. Climate can also influence seed density within cones and seed viability (Moya et al. 2007), which were not evaluated in this study. Further research on annual cone and seed production responses to annual variation in climate is needed to predict future demographic trends.

Our findings have broad implications for demographic mechanisms underpinning serotinous forest persistence across North America. We expect that while rates of cone production vary among species, the period prior to reproductive maturity is brief relative to the historical mean fire return interval (Tapias et al. 2001, Turner et al. 2007). However, time to canopy seed bank accumulation sufficient for self-replacement is considerably longer and varies with stand density (Moya et al. 2007). Rapid development of a large canopy seed bank in high-density stands suggests that high establishment densities exhibited by serotinous conifers (Verkaik and Espelta 2006, Harvey and Holzman 2014) represent a resilience mechanism to short-interval fires. While serotinous populations may be able to persist at lower densities following a single short-interval severe fire (Keeley et al. 1999, Turner et al. 2019), they are unlikely to withstand recurrent short-interval fire activity (Espelta et al. 2008, Bassett et al. 2015). Demographic rates must be assessed in the context of the expected shortening of the fire-free interval to understand when erosion of serotinous forest resilience to fire may occur. While not investigated here, demographic trends for longer fire intervals are also needed to determine how the potential for senescence risk affects long-term persistence of serotinous conifers.

4.6 CONCLUSION

Reproductive capacity recovered rapidly following high-severity fire in California closed-cone pine forests, suggesting that the window for immaturity risk is brief. Differences in the canopy seed bank among stand trajectories suggest that high-density stands are more buffered against immaturity risk than are low-density stands during the critical early post-fire window. Evidence of decreased reproductive capacity and increased tree mortality associated with moisture stress suggest that a demographic shift may further dampen seed availability. Although the demographic mechanisms we investigate here are aligned to relatively frequent high-severity fires, continued climate warming and increased fire activity may overwhelm these mechanisms. Understanding how fuels and associated fire hazard develop in tandem with reproductive capacity is critical for predicting serotinous forest persistence under future conditions.

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4.8 APPENDIX B

4.8.1 *Study area*

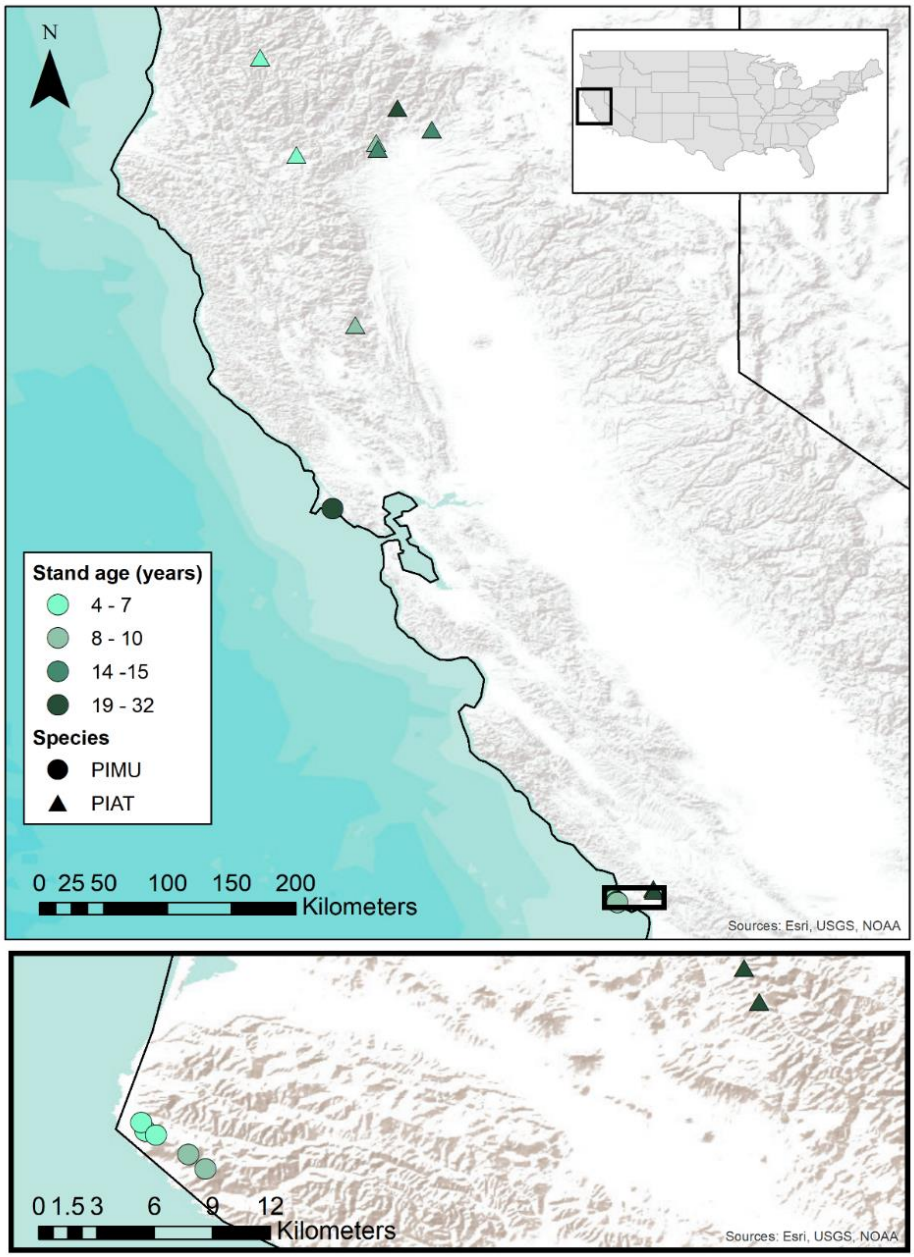

Figure 4.7. Study area map. Points are shaded by stand age (years since fire) and symbols represent the dominant species, *Pinus attenuata* (PIAT) or *Pinus muricata* (PIMU).

Notes: Each point represents a single stand age by species combination and represents 2 – 10 plots. Bottom inset shows the southernmost part of the study area at a finer resolution. Top right inset shows the study area in the context of the continental United States.

4.8.2 *Extended results*

Table 4.2. Results of mixed effects models for tree-level probability of reproductive maturity and tree-level cone production as a function of tree- and stand-level covariates.

Tree-level probability of reproductive maturity				
		95% CI		
Predictor	β[1]	lower	upper	p
Intercept	1.641	0.611	2.671	0.002
Stand age	1.130	0.028	2.232	0.044
DBH[2]	12.296	11.139	13.452	<0.001
Species (PIMU[3])	-0.699	-2.515	1.117	0.451
Disease presence	0.005	-0.577	0.586	0.987
Heat load index	0.044	-0.730	0.818	0.911
Stand density[4]	1.316	0.485	2.148	0.002
Mean growing season precipitation	-1.279	-3.105	0.547	0.170
DBH:Stand density[4]	4.078	1.991	6.165	<0.001
DBH:Stand age	-3.877	-6.033	-1.720	<0.001

Tree-level cone production				
		95% CI		
Predictor	β[1]	lower	upper	p
Intercept	2.535	2.239	2.831	<0.001
Stand age	0.915	0.545	1.286	<0.001
DBH[2]	1.955	1.801	2.110	<0.001
Species (PIMU[3])	0.702	0.060	1.343	0.032
Heat load index	0.060	-0.405	0.524	0.802
Stand density[4]	-0.164	-0.409	0.080	0.188
Soil clay	0.541	0.119	0.963	0.012
Mean growing season CMD	0.073	-1.167	1.314	0.908
Disease presence	-0.087	-0.197	0.023	0.122
Shrub cover	-0.168	-0.471	0.135	0.277
DBH:Stand age	-0.523	-0.756	-0.289	<0.001
DBH:Stand density[4]	0.592	0.372	0.813	<0.001

[1]Effect sizes are for standardized coefficients (mean-centered per two standard deviations), [2] Diameter at breast height, [3] *Pinus muricata* (bishop pine), [4]Stand density was log-transformed prior to standardizing coefficients

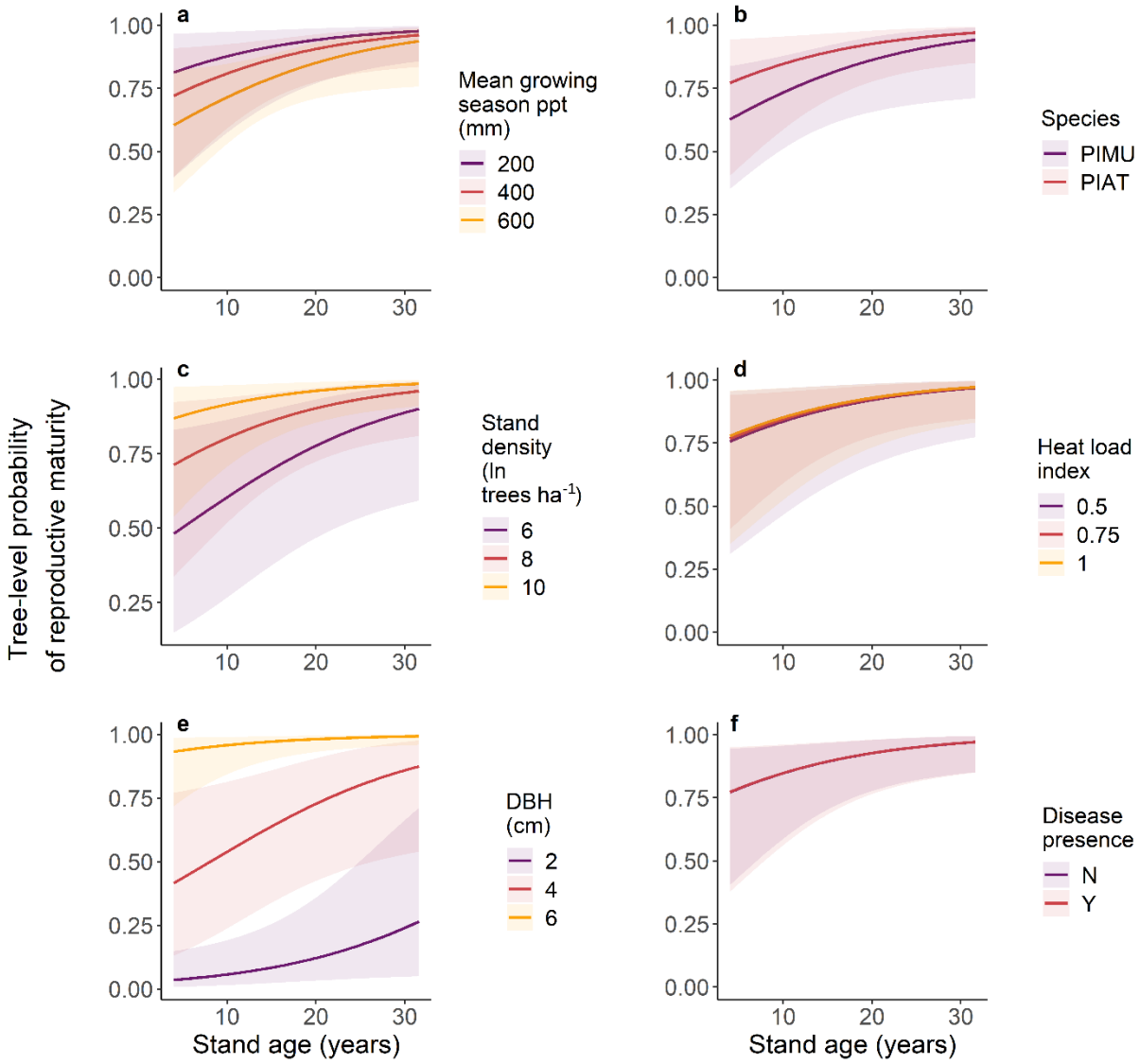

Figure 4.8. Change in stand age and tree-level probability of reproductive maturity across gradients of all tree-level and stand-level covariates included in the model.

Notes: Solid lines represent median estimates and shaded areas represent 95% confidence intervals. Predictions consider the effect of diameter and each covariate individually, holding all other covariates at their means.

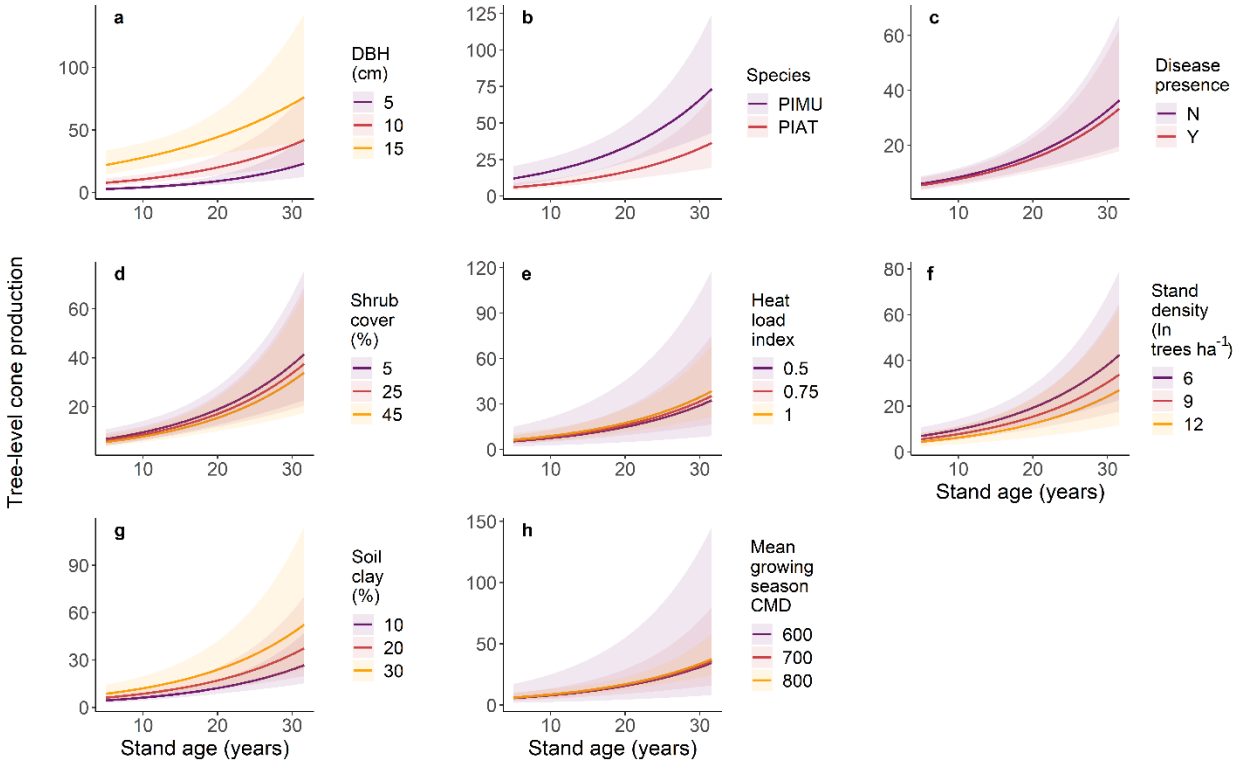

Figure 4.9. Change in stand age and tree-level cone production across gradients of all tree-level and stand-level covariates considered in the model.

Notes: Solid lines represent median estimates and shaded areas represent 95% confidence intervals. Predictions consider the effect of diameter and each covariate individually, holding all other covariates at their means.

Table 4.3. Results of mixed effects models for stand-level proportion mature trees, closed cone density, and tree mortality as a function of stand-scale covariates.

Stand-level proportion mature trees				
		95% CI		
Predictor	β[1]	lower	upper	p
Intercept	-0.275	-0.973	0.423	0.440
Stand age	1.519	0.623	2.416	<0.001
Species (PIMU[2])	0.837	-0.584	2.259	0.248
Stand density[3]	-1.507	-2.007	-1.008	<0.001
Mean growing season precipitation	1.995	0.537	3.452	0.007
Soil clay	0.634	0.150	1.119	0.010
Stand age:Stand density[3]	-1.513	-2.573	-0.454	0.005

Stand-level closed cone density (cones ha^{-1})				
		95% CI		
Predictor	β[1]	lower	upper	p
Intercept	8.830	7.662	9.998	<0.001
Stand age	3.692	1.908	5.475	<0.001
Species (PIMU[2])	-0.397	-2.409	1.615	0.699
Stand density[3]	1.209	0.708	1.709	<0.001
Soil clay	0.848	0.280	1.417	0.003
Mean growing season CMD[4]	-0.834	-2.570	0.902	0.346
Stand age:Stand density[3]	-1.511	-2.541	-0.481	0.004

Stand-level tree mortality (standing dead trees ha^{-1})				
		95% CI		
Predictor	β[1]	lower	upper	p
Intercept	3.502	2.796	4.208	<0.001
Stand age	3.428	2.467	4.389	<0.001
Species (PIMU[2])	4.032	2.915	5.149	<0.001
Stand density[3]	4.013	3.054	4.972	<0.001
Heat load index	0.664	-0.136	1.465	0.104
Mean growing season CMD[4]	1.397	0.538	2.257	0.001

[1]Effect sizes are for standardized coefficients (mean-centered per two standard deviations), [2]*Pinus muricata* (bishop pine), [3]Stand density was log-transformed prior to standardizing coefficients,[4]Cumulative moisture deficit

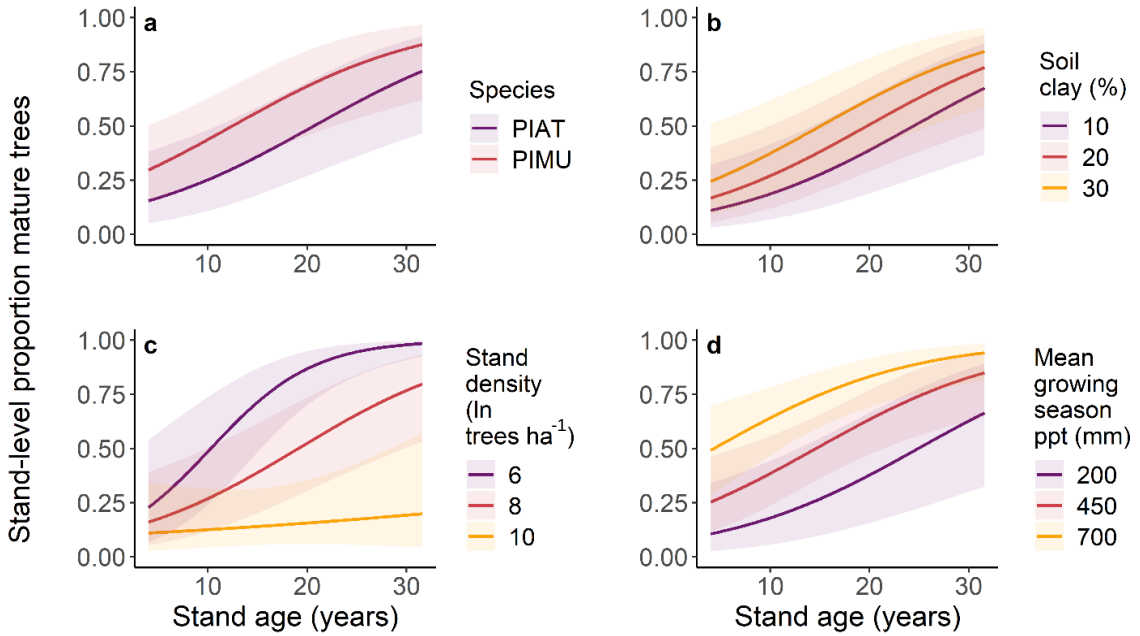

Figure 4.10. Change in stand age and stand-level proportion mature trees across gradients of all stand-level covariates considered in the model.

Notes: Solid lines represent median estimates and shaded areas represent 95% confidence intervals. Predictions consider the effect of stand age and each covariate individually, holding all other covariates at their means.

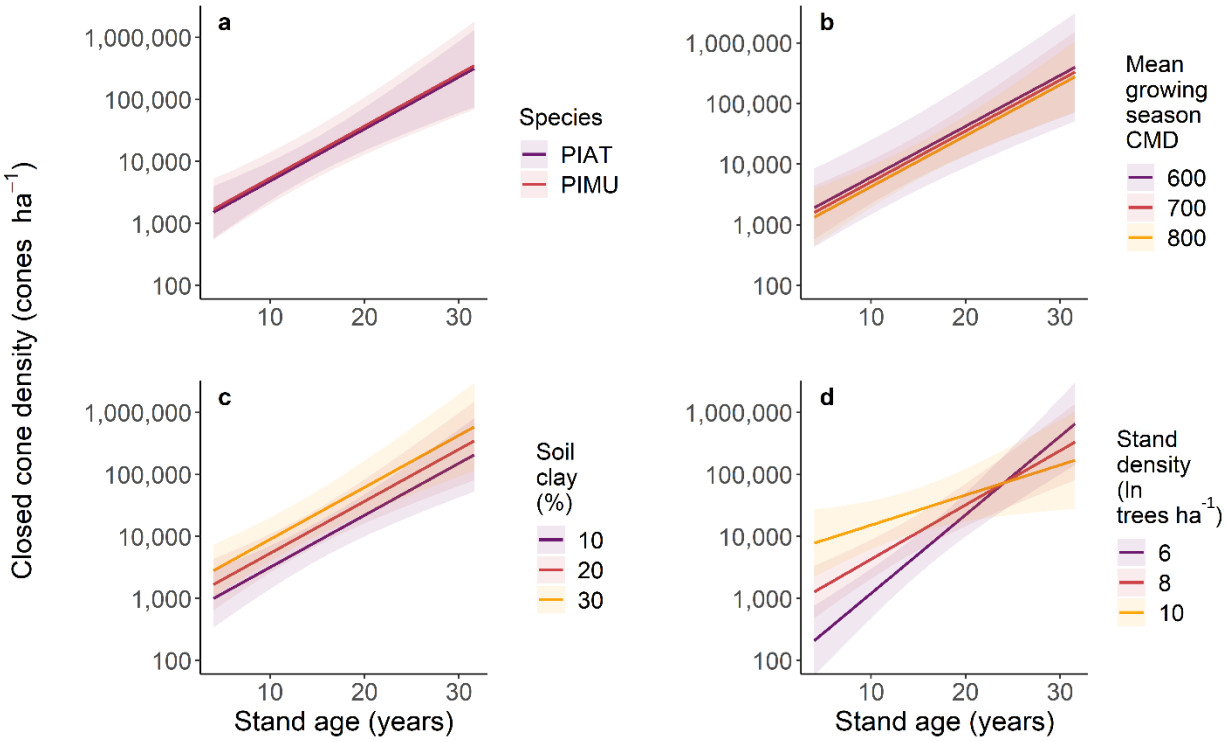

Figure 4.11. Change in stand age and stand-level closed cone density across gradients of all stand-level covariates considered in the model.

Notes: Solid lines represent median estimates and shaded areas represent 95% confidence intervals. Predictions consider the effect of stand age and each covariate individually, holding all other covariates at their means.

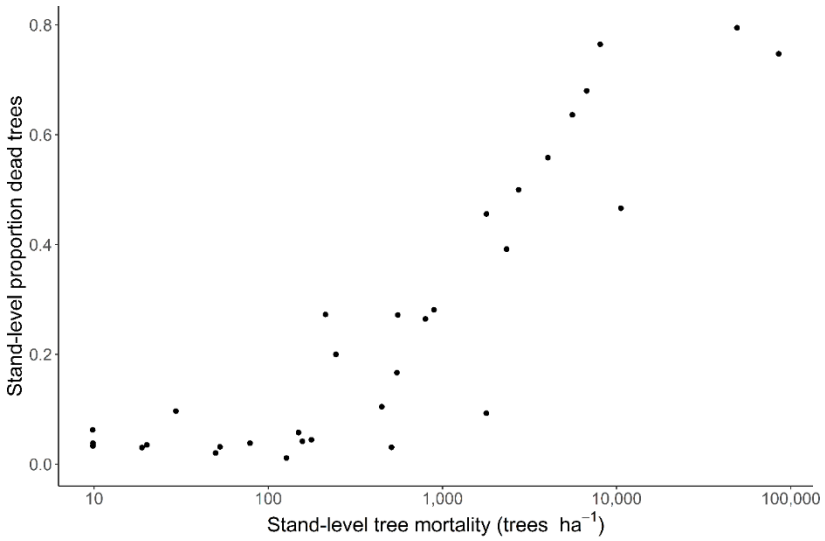

Figure 4.12. Stand-level tree mortality by density versus stand-level proportion dead trees for stand ages ≥10 (n = 47). Spearman's rank correlation ρ = 0.956.

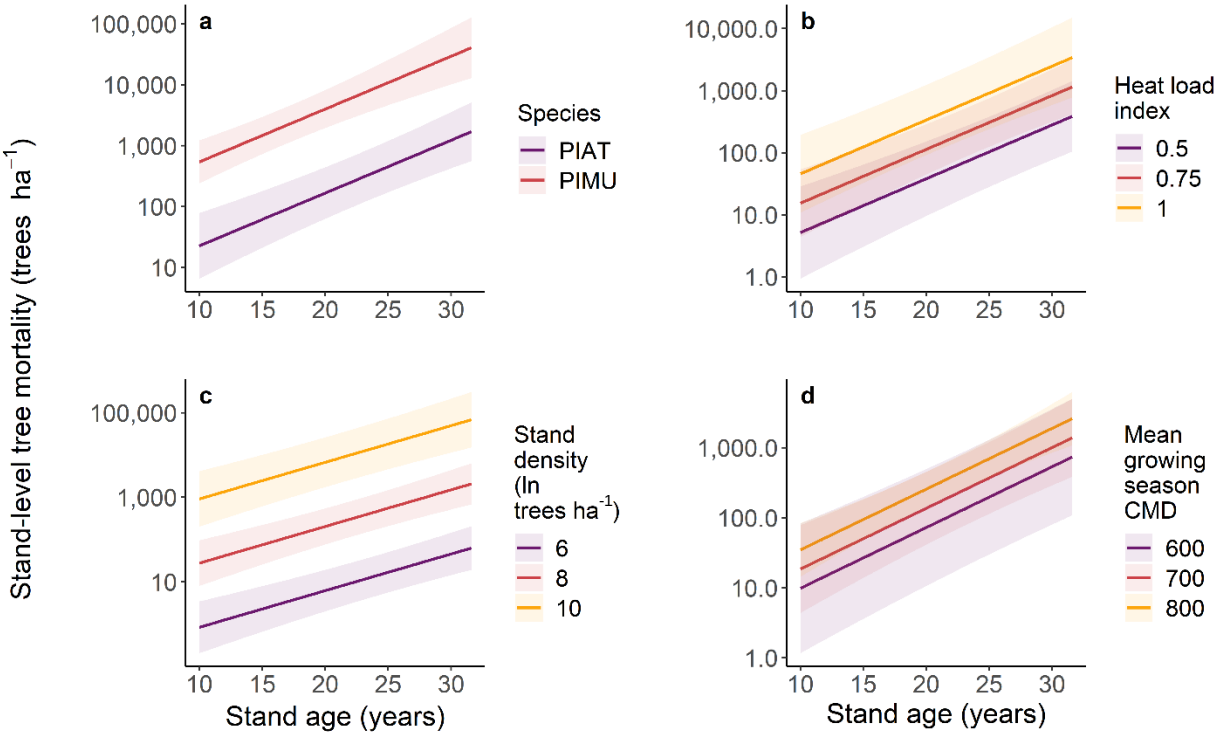

Figure 4.13. Change in stand age and stand-level tree mortality across gradients of all stand-level covariates considered in the model.

Notes: Solid lines represent median estimates and shaded areas represent 95% confidence intervals. Predictions consider the effect of stand age and each covariate individually, holding all other covariates at their means.

Chapter 5. SEROTINOUS FOREST RESILIENCE IS ERODED BY SHORT-INTERVAL FIRES AND POST-FIRE CLIMATE CONDITIONS

5.1 ABSTRACT

Climate change is eroding forest resilience to disturbance directly and indirectly through warming climate and increasing disturbance activity. Forests characterized by stand-replacing fire regimes and serotinous species may be particularly at risk as they require a sufficient inter-fire period for canopy seed bank development and suitable climate conditions for recruitment in the post-fire growing season. Although both resilience mechanisms are critical to serotinous forest persistence, the relative importance of these controls on post-fire regeneration in serotinous forests remains poorly understood. We used data from plots established in severely burned knobcone pine (*Pinus attenuata*) forests across a range of past fire intervals to assess the effects of seed supply and post-fire climate on post-fire regeneration. We evaluated effects of fire interval and pre-fire canopy seed bank (proxies for seed supply), post-fire climate, and microsite characteristics on three metrics of post-fire tree regeneration (seedling density, probability of self-replacement, percent population recovery). Seed supply consistently had the strongest effect on post-fire regeneration. Post-fire seedling density and percent population recovery increased by two orders of magnitude between 6- and 31-year fire intervals (historical fire return interval estimated at 30-90 years), while probability of self-replacement increased from ~0% to ~100%. Similarly, increasing the canopy seed bank by two orders of magnitude increased seedling density and percent population recovery by two orders and one order of magnitude, respectively and increased the probability of self-replacement by >50%. Increased post-fire cumulative moisture deficit exacerbated the effect of seed supply; high moisture stress conditions required

an additional 4-6 years to reach similar regeneration to low moisture stress conditions. The overriding effect of seed supply – strongly driven by pre-fire stand age – on post-fire regeneration suggests that indirect effects of climate change through altered disturbance regimes are likely to have a profound impact on serotinous forests. Although direct effects of warming are lower in magnitude, they may have significant implications for forest recovery where seed supply nears a threshold. These findings reveal how fire interval, climate, and microsite combine to determine vulnerability to forest loss in the future, informing management and vulnerability mapping.

5.2 INTRODUCTION

Evidence from ecosystems worldwide indicates that climate change is eroding forest resilience to disturbance (Trumbore et al. 2015) – defined as an ecosystem's capacity to experience disturbance without transitioning to an alternative state (Gunderson 2000). Direct effects of warming climate, including increasing moisture stress as well as drought and heatwave events are leading to increases in tree mortality and forest die-offs (Williams et al. 2013, Allen et al. 2015, Matusick et al. 2018). Indirect effects of climate change in the form of altered disturbance regimes are also influencing forest resilience through decreased capacity to recover post-disturbance (Seidl et al. 2017). Increasing fire activity attributed to climate change is already apparent (Abatzoglou and Williams 2016), with evidence of an extended fire season (Jolly et al. 2015), increased total area burned (Boer et al. 2020, Abatzoglou et al. 2021, Collins et al. 2022), and proportion area burned with high severity (Parks and Abatzoglou 2020, Collins et al. 2021) in forests around the globe. Understanding how direct and indirect effects of climate change combine to affect forest resilience is critical to understanding when and where forests may be vulnerable to non-forest conversion (Coop et al. 2020, Falk et al. 2022).

Post-fire tree regeneration is a key indicator of resilience in fire-prone forests as it sets the template for the post-disturbance forest trajectory. Declines in post-fire regeneration have been observed in many forest ecosystems since the early 2000s (Stevens-Rumann et al. 2018) and have been mechanistically linked to both changes in the historical fire regime and changes in post-fire climate conditions. For species that depend on surviving trees to provide a seed source for post-fire regeneration, increasing fire severity and fire size can result in decreases in post-fire regeneration due to high mortality of seed trees within a fire perimeter and increased distance to an unburned edge (Gill et al. 2021). Such changes in the fire regime have led to decreases in post-fire regeneration in montane and subalpine forests in the western US (Crotteau et al. 2013, Collins and Roller 2013, Kemp et al. 2016, Chambers et al. 2016, Busby et al. 2020, Boag et al. 2020). High moisture stress during the growing season also leads to poor post-fire regeneration outcomes (Harvey et al. 2016, Hansen and Turner 2019, Davis et al. 2019). Where uncharacteristically high fire severity is followed by extreme drought conditions, complete conifer regeneration failure and non-forest conversion has been observed and is likely to continue with warming climate (Guiterman et al. 2018).

Forests characterized by stand-replacing fire regimes and dominated by serotinous species (trees that release seeds from cones when heated by fire) may be particularly at risk in a warmer and more fire-prone world (Enright et al. 2015). Although these species are well-adapted to large stand-replacing fires as they do not depend on a live seed source for post-fire recruitment, a sufficient interval between fires to develop the canopy seed bank is critical for post-fire resilience of serotinous species (Enright et al. 2014). Short-interval fires prior to the accumulation of a sufficient on-site seed source can lead to significant decreases in post-fire recruitment (Keeley et al. 1999, Brown and Johnstone 2012, Turner et al. 2019). Further,

serotinous species are also an important "harbinger" of changes to resilience across other types of forest ecosystems. In many North American conifer forests, serotinous conifers are foundation species, in that they are the first trees to establish following a fire, and thus set the template for long-term forest recovery following severe fire (Turner et al. 1999). Yet because they depend on abundant seed availability at the time of fire as well as a relatively brief window of time with suitable post-fire climatic conditions for seedling establishment and germination, they could be affected by changes to fire activity and post-fire climate. Such forests dominate several key regions of western North America including montane and coastal forests in Southern Oregon and California, and subalpine forests of the Cascades and Northern US Rockies, but are relatively understudied compared to other forests in the region.

One key mechanism of resilience following fire in forests dominated by serotinous species is a sufficient seed bank stored in the canopy of mature trees, producing the ability to recruit *en masse* from seed released within the first post-fire year. Serotinous coniferous forests often regenerate at densities exceeding 100,000 seedlings per hectare following stand-replacing fire in North America (Harvey and Holzman 2014; Turner et al. 2016), but realization of this regeneration potential requires a sufficient canopy seed bank for self-replacement at the time of fire. Indirect climate change effects in the form of an altered fire regime may erode this resilience mechanism if fire activity increases in young stands during the early years of reproductive maturity (Agne et al. 2022). If a short-interval stand-replacing fire (i.e., severe reburn) occurs prior to the accumulation of a sufficient canopy seed bank, compound effects (*sensu* Paine et al. 1998) from two successive fires may convert forests to non-forest, or substantially shift tree species composition (Brown and Johnstone 2012).

A second mechanism of resilience following fire for serotinous species is climate conditions suitable for tree recruitment in the first post-fire year. Low post-fire tree regeneration densities (i.e., an order of magnitude or more below pre-fire stand densities) and even complete recruitment failure, are more likely with increasing annual moisture deficit (i.e., direct effect of climate change; Stevens-Rumann et al. 2018), indicating that fire followed by drought can produce compound effects. These trends appear to be most pronounced in dry forests (Harvey et al. 2016, Davis et al. 2019, Rodman et al. 2019) and projections for increasingly warm and dry conditions suggest further declines in post-fire seedling recruitment through the 21st century (Rodman et al. 2020). Inter-annual variability in regional climate within a decade post-fire can lead to opportunities for protracted recruitment (Littlefield 2019), while topographic complexity, variation in soils and competition with shrub species can lead to widely variable recruitment outcomes across microsite conditions (Harvey et al. 2016, Busby et al. 2020, Hoecker et al. 2020). However, the risk of recruitment failure is exacerbated in serotinous conifers, as seed dispersal primarily occurs in a pulse following fire (Johnson and Fryer 1989; Keeley and Zedler 1998). Most serotinous conifer recruitment occurs in the first year post-fire, with relatively little recruitment in subsequent years (Turner et al. 1999, Donato et al. 2009, Harvey and Holzman 2014). When harsh climate conditions (e.g., drought, heatwaves) co-occur with this brief recruitment window, recruitment failure could lead to non-forest conversion, even if seed is available following fire (Enright et al. 2014).

Although climate warming is likely to affect post-fire climate conditions and on-site seed availability, the relative importance of these factors in successful post-fire serotinous conifer recruitment has not been investigated within a single framework. Serotinous forests offer a powerful opportunity to ask such questions because seeds are contained on site and issues of

distance to seed source are much less important. To understand the effect of short-interval severe reburns on serotinous forests, we asked: How are three indicators of forest resilience to severe fire (seedling density, probability of self-replacement, and percent population recovery) affected by seed supply at the time of fire and post-fire conditions? We expected that increasing seed supply as functions of stand age and density – (estimated using fire interval and pre-fire canopy seed bank size) would have strong positive effects on post-fire regeneration due to increased time to accumulate seed and protection of seeds within cones at taller stand statures (Figure 5.1). We

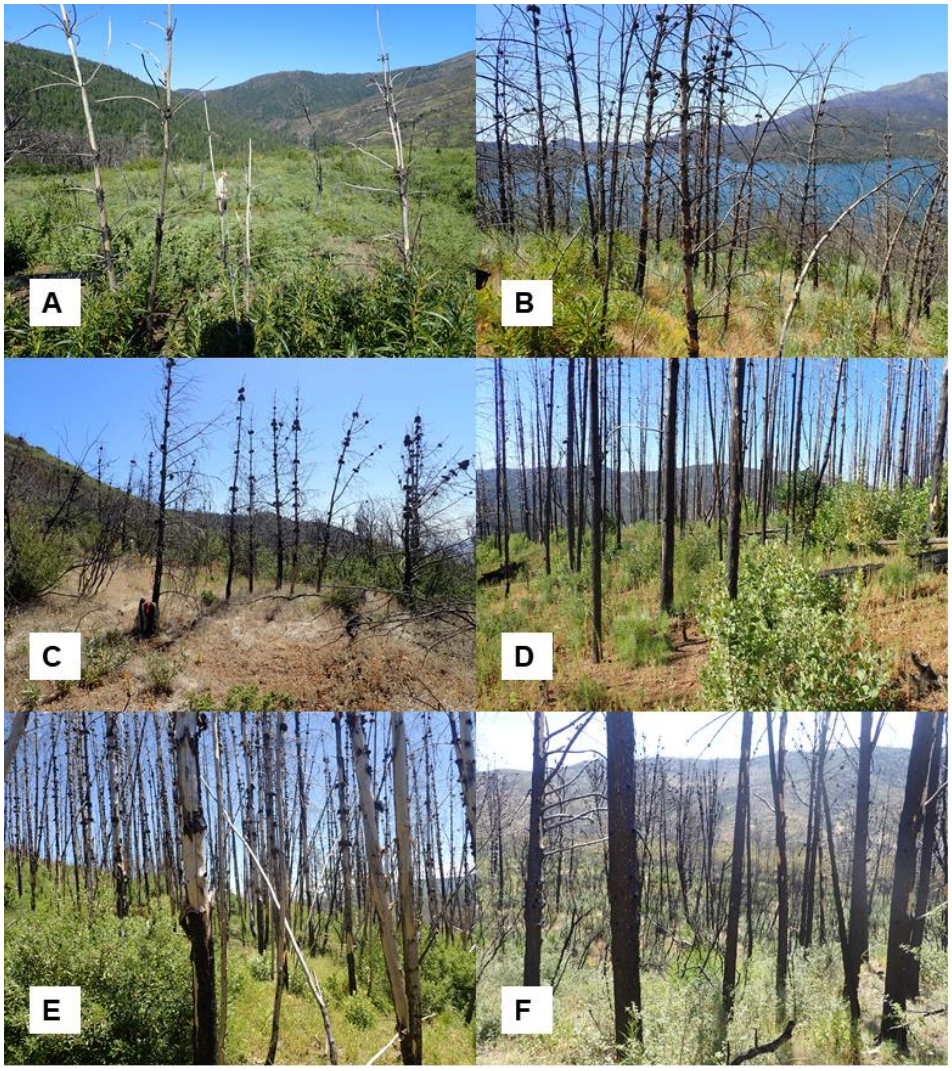

Figure 5.1. Post-fire forest structure in knobcone pine (*Pinus attenuata*) forests following fire intervals of A) 6 years, B) 10 years, C) 17 years, D) 22 years, E) 31 years, and F) long unburned (>34 year fire interval).

also expected that for a given seed supply, post-fire regeneration would decrease with warm and dry post-fire climate. We also accounted for microsite-level effects in our models, and we expected decreased post-fire regeneration on xeric microsites (warm and dry topoclimate), where soils are relatively shallow and poor, and with high shrub competition. Understanding how direct (post-fire climate) and indirect (on-site seed availability) effects of climate change influence post-fire recruitment individually and how they interact is critical for predicting how forests will respond to fire in the future.

5.3 METHODS

5.3.1 *Study area*

This study was conducted in knobcone pine (*Pinus attenuata*) stands in Oregon and California, USA within the Klamath Mountains and Northern Coast Range which experienced stand-replacing fire in 2018 (Figure 5.2). We selected three large fires that burned through knobcone pine forests (U.S. Geological Survey 1999a) during the summer of 2018 in which to establish field plots: the Carr Fire, Klondike Fire, and Mendocino Complex. The study area is characterized by a Mediterranean climate including a strong seasonality in precipitation, with >90% falling between October and May (PRISM Climate Group 2019). Climate varies strongly among study fires, with the Klondike fire in the northern Klamath Mountains representing the coolest and wettest area (average annual precipitation = 1897 mm and average January and July temperatures are 5.1 and 19.8 °C, respectively). The Carr fire in the southern Klamath Mountains represents the warmest site (average January and July temperatures are 6.8 and 25.9 °C, respectively) with a moderate amount of precipitation (average annual precipitation = 1572 mm). The Mendocino Complex in the Northern Coast Range has a moderate temperature (average

January and July temperatures are 5.8 and 23.2 °C, respectively) and represents the driest site (average annual precipitation = 1126 mm).

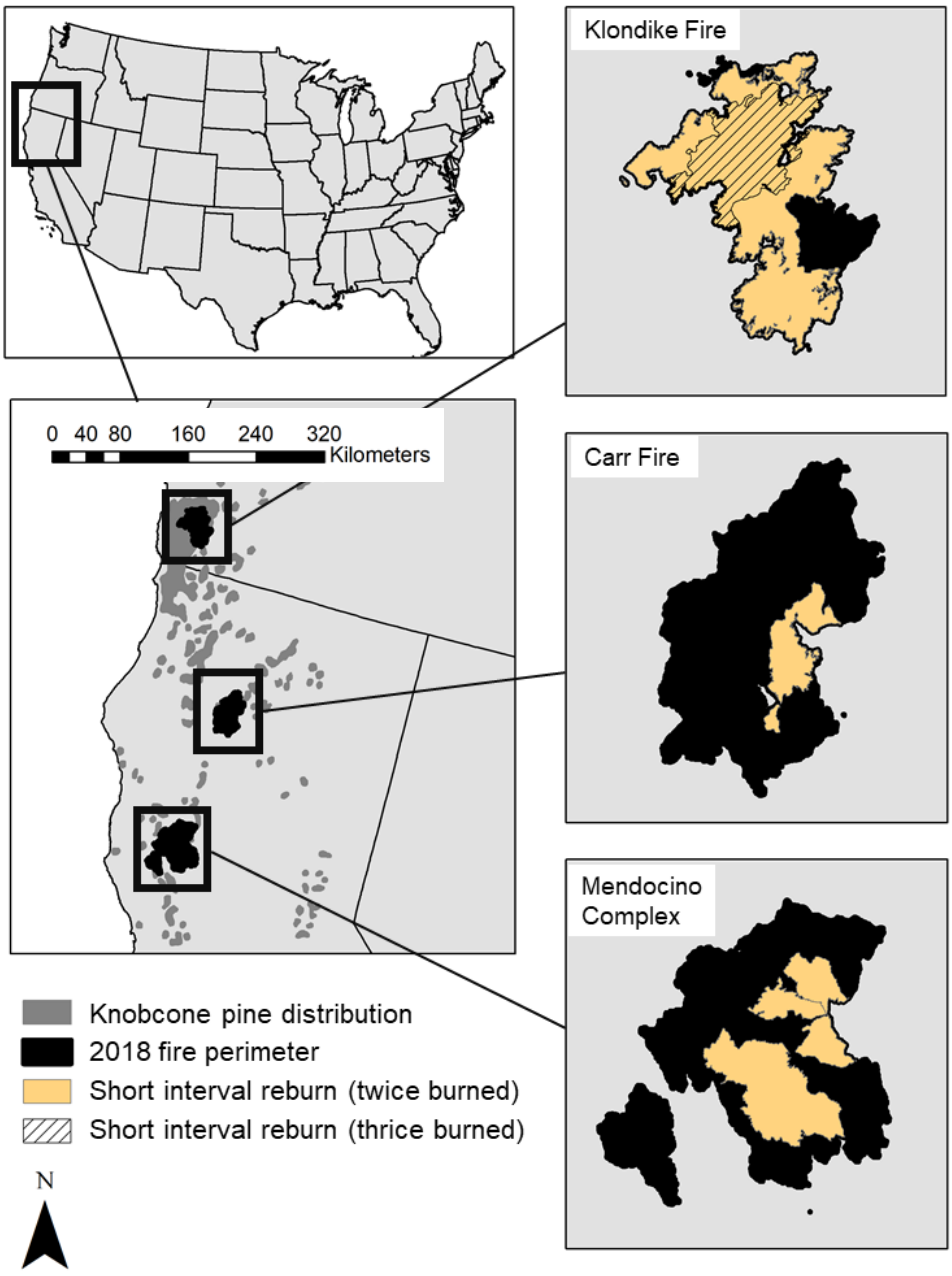

Figure 5.2. Post-fire regeneration study area map.

Top left: Continental United States with box around study region. Bottom left: Knobcone pine distribution in study region with the three 2018 sample fire perimeters. Right: 2018 sample fire perimeters with area reburned shaded by twice and thrice burned between 1984 and 2018.

The study area encompasses low elevation to lower montane zones (320 - 1243 m above sea level [asl]). Stands are often characterized by steep slopes and soils are typically shallow and rocky, with serpentine substrate common for knobcone pine (Vogl et al. 1977). Serpentine soils are acidic with low nutrient concentrations, leading to low productivity and a limited plant community (Vogl 1973). Knobcone pine-dominated plant communities often occur as mono-dominant, dense forest stands for several decades following establishment but can also co-occur with Douglas-fir (*Pseudotsuga menziesii*) or exist at a low density interspersed with chaparral. Understory plant communities vary across the study area with a high diversity of shrub and herbaceous species represented. Common co-occurring shrub species include *Adenostoma fasciculatum, Arctostaphylos* spp., *Ceanothus* spp., *Heteromeles arbutifolia*, and *Toxicodendron diversilobum*. *Arbutus menziesii*, *Chrysolepis chrysophylla*, *Notholithocarpus densiflorus*, and *Quercus* spp. are also common, existing both in shrub and tree form. Herbaceous vegetation commonly includes *Acmispon glaber*, *Lupinus* spp., and *Mimulus* spp.

5.3.2 *Site selection*

To select sites, we used Monitoring Trends in Burn Severity data (MTBS; Eidenshink et al. 2007), to identify fire history after 1984 and prior to each 2018 fire to determine the fire intervals present within the range of knobcone pine for each of the sample fires. Collectively, seven known fire intervals, ranging from 6 to 31 years, overlapped knobcone pine within the three 2018 fires. The historical fire regime is characterized by mean return intervals between 30 – 90 years (van de Water and Safford 2011), suggesting that the longest known fire interval approximates the historical mean. Within the Klondike Fire, there were areas that have burned three times in the MTBS record (in 1987, 2002, and 2018), i.e., at successive intervals of 15 and 16 years. Given the similarity of fire intervals and that distributions of pre-fire structure and post-

fire regeneration characteristics overlapped with those of areas only burned twice (in 2002 and 2018, Appendix C – Figure 5.8), we did not differentiate between twice and thrice burned plots and combined them by their most recent fire interval (16 years). Additionally, knobcone pine forest with unknown prior fire history was present in each of the three 2018 sample fires (i.e., fire interval > 34 years). In each 2018 fire, we stratified our field sampling to establish at least 5 plots within each known fire interval, and at least 5 plots in areas unburned since 1984 (and no recorded fire history in the CAL FIRE FRAP database [https://frap.fire.ca.gov/mapping/gis-data/]), hereafter, long interval plots. Criteria for inclusion in our sample included: pre-fire dominance or codominance of knobcone pine, burned with high severity (100% overstory tree mortality) in 2018, and burned with high severity in prior fire (as determined by stand structure—the presence of a single cohort of knobcone pine prior to 2018 fire). Plots with no available prior fire history were not required to meet the criteria of having burned with high severity in the prior fire as we lacked information on prior burn severity. Potential sample locations were selected in ArcGIS (Environmental Systems Research Institute [ESRI] 2018) using aerial imagery, species distribution maps, and burn severity maps prior to the field season. When pre-identified plot locations did not meet the criteria for sampling, we moved the plot location to the nearest area that met the criteria and arbitrarily established a plot center within an appropriate patch. Plot replicates within fire intervals were established to cover the range of topography and pre-fire stand structure present. Plots were placed at least 100 m apart and were placed at least 50 m from roads and trails.

5.3.3 *Field methods*

During the summer of 2020, we established 71 field plots in which we collected pre-fire stand structure, tree regeneration, and understory vegetation data, using a plot design modified

from established protocols (Harvey et al. 2016). To assess pre-fire stand structure, we measured diameter at breast height (DBH, measured 1.37 m from the ground), recorded the species of each standing and fallen tree and counted open and closed cones on each knobcone pine killed by the most recent fire. Trees from the pre-fire stand that did not reach DBH were tallied by their cone count. Data were collected within a variable radius plot aimed at capturing approximately 50 pre-fire trees and with a maximum plot radius of 18 m. Tree regeneration was measured within a default of four 2 x 16 m belt transects oriented to the clockwise side of the cardinal directions from plot center. The sampling area was decreased to four 1 x 16 m belt transects when seedling counts would have exceeded 400 using the default plot size. The sampling area was increased to encompass the entire pre-fire stand plot when seedling counts would have been under 40 using the default plot size. Within the regeneration sampling area, we counted all tree seedlings by species, assigned them as live or dead. For knobcone pine only, we assigned seedlings as second year (established within the growing season following fire) if bud scars were present and first year (established within the second growing season following fire) if bud scars were absent and cotyledons were present. Understory vegetation cover was measured within eight 1 x 1 m subplots placed along each belt transect at the edge of the plot and half the distance between plot center and the edge of the plot. Within each subplot, we estimated (to the nearest 5%) understory vegetation cover by life form (shrub, graminoid, forb, tree). We collected a GPS point, elevation, slope, and aspect from each plot center.

5.3.4 *Climate and microsite condition variables*

We obtained climate data for our plots from ClimateNA, a software package that locally downscales climate data to scale-free point estimates (Wang et al. 2016). We obtained 30-year normals (from 1981-2010) as well as data at a monthly resolution for the post-fire water year

(October 2018 to September 2019) to assess the effect of post-fire climate on regeneration success. We considered two possible measures: absolute post-fire water year cumulative moisture deficit (CMD) and the z-score of the post-fire water year CMD as compared with the 30-year normal (Table 5.1). Both measures can be used to reflect moisture stress as experienced by a plant, but a z-score rather than an absolute value is often used to understand ecological effects of post-fire climate as deviation from the long-term average climate in a location may be more important than absolute climate (e.g., Harvey et al. 2016, Stevens-Rumann et al. 2018). However, following data exploration, we opted to use absolute post-fire water year CMD (hereafter, post-fire CMD) in our models. Exploratory analyses indicated that the 2018-2019 water year was relatively cool and wet across the study region, resulting in negative z-scores across all study sites (Appendix C – Figure 5.9), reducing the utility of such a variable to reflect moisture stress.

Table 5.1. Summary of predictor variables included in statistical models of post-fire regeneration.

Variable	Mean	Median	Range
Fire interval (years)	16	16	6 - 31
Pre-fire canopy seed bank (ln[cones ha^{-1}])	9.08	9.37	5.01 - 11.75
Soil clay (%)	17	16	9 - 26
Depth to bedrock (cm)	91	88	69 - 123
Post-fire CMD	538	556	350 - 822
Shrub cover (%)	29	29	1 - 71
Topographic wetness index	6.9	6.9	4.4 - 10.8
Topographic position index	0.18	0.22	-0.78 – 1.78
Heat load index	0.79	0.80	0.63 - 0.94
Post-fire CMD z-score*	-0.93	-0.99	-1.48 - -0.02

*Not used in final models — included here for illustrative purposes. CMD z-score range includes negative values only indicating that the post-fire year was wetter than the 30-year normal period (1981-2010).

We further characterized the post-fire environment using three topographic predictors to infer plot-level topo-climate: heat load index (HLI), topographic position index (TPI), and

topographic wetness index (TWI; Table 5.1). HLI represents the direct incident radiation at a site (McCune and Keon 2002), TPI represents a site's relative topographic position relative to neighboring cells (Weiss 2001, De Reu et al. 2013), and TWI reflects the potential moisture balance at a site (Gessler et al. 1995). We used the Geomorphometry and Gradient Metric Toolbox (Evans et al. 2014) in ArcMap version 10.6.1 (ESRI 2018) to calculate each topographic predictor from 30-m digital elevation models (U.S. Geological Survey 1999b). Soil characteristics were characterized using data from the Probabilistic Remapping of SSURGO (POLARIS) database, a spatially contiguous soils dataset of ecologically relevant soils variables (Chaney et al. 2016). For each of our plots, we extracted depth to bedrock and percent soil clay (Table 5.1) as two candidate predictors that can influence forest productivity and affect soil fertility (Romanyà and Vallejo 2004, Wall and Westman 2006).

5.3.5 *Statistical analyses*

To test the effects of seed supply, post-fire climate and microsite characteristics on post-fire regeneration in knobcone pine forests, we fit generalized linear mixed models for three complementary response variables: total post-fire seedling density (seedlings ha^{-1}), probability of self-replacement (i.e., post-fire seedling density ≥ pre-fire stand density), and percent population recovery (i.e., knobcone pine post-fire seedling density as a percent of pre-fire knobcone pine density). For each response variable, we fit two models with separate focal predictor variables: fire interval (years between stand-replacing fires) and pre-fire canopy seed bank density, defined as open cones on standing and fallen trees killed by the most recent fire (ln [cones ha^{-1}]). We assessed these predictors separately as they are strongly correlated (Appendix C – Figure 5.10), but each may be mechanistically linked to regeneration success. Each of the six models included a random effect of sample fire and the following covariates: post-fire CMD, HLI, TPI, TWI,

shrub cover and percent soil clay or depth to bedrock (Table 5.1). Total post-fire seedling density models were fit to post-fire seedling counts using a negative binomial error structure and an offset term (log[plot areas]) to account for variable plot sizes (Zuur et al. 2009). Probability of self-replacement models were fit using a binomial error structure. Percent population recovery models were fit to post-fire seedling counts using a negative binomial error structure and an offset term (log[pre-fire tree count]). All models fit using a negative binomial error structure were also fit with a Poisson error structure, but Poisson-distributed models were removed from further consideration due to overdispersion.

Each generalized linear mixed model was fit using standardized predictor variables (mean-centered per two standard deviations) to understand relative effects of each predictor. A full model with all candidate predictors included was fit for each response variable, and model diagnostic tests were conducted. When the full model did not meet model assumptions, we fit a suite of new models using single term deletions (models were fit with each term dropped except fire interval or pre-fire canopy seed bank). Model diagnostics were conducted on each reduced model. If all reduced models failed to meet model assumptions, this process was repeated with additional single term deletions until a model was fitted that met assumptions. When two models with an equal number of predictors met assumptions, the model with the lowest AICc was selected for inference. We interpreted $P \leq 0.01$, $P \leq 0.05$, and $P \leq 0.10$ as strong, moderate, and suggestive evidence of an effect, respectively (Ramsey and Schafer 2012). All analyses were conducted in R version 4.0.5 (R Core Team 2021). Models were fit with the *glmmTMB* package (Brooks et al. 2017) and model diagnostics were conducted with *DHARMa* (Hartig 2021). Visualizations of model effects were created with the packages *broom* (Robinson et al. 2021),

ggeffects (Lüdecke 2018), *ggplot* (Wickham 2016), *ggpubr* (Kassambara 2020), and *jtools* (Long 2020).

5.4 RESULTS

We counted a total of 15,111 seedlings, 99% of which were knobcone pine. At most plots, 100% of the conifer regeneration was knobcone pine though plot-level values ranged from 51 to 100% knobcone pine (Table 5.2), with most of the remaining conifer regeneration composed of Douglas-fir. Where the pre-fire stand was composed of knobcone pine and Douglas-fir, knobcone pine generally became more dominant post-fire (Table 5.2; Appendix C – Figure 5.11). Ninety-six percent of knobcone pine seedlings established within the first growing season post-fire and were therefore 2 years old at the time of sampling (Table 5.2). We counted 51,187 cones on 4,336 dead knobcone pine trees to characterize the pre-fire canopy seed bank and pre-fire stand structure varied widely among and within fire intervals (Table 5.2; Appendix C – Figure 5.12).

5.4.1 *Post-fire seedling density*

Post-fire seedling density ranged from 138 to 250,200 seedlings ha^{-1} across the study area; all plots had at least some knobcone pine regeneration (Table 5.2). For plots with previous fire intervals of known length (fire intervals up to 31 years), the selected model showed a strong positive effect of fire interval on post-fire seedling density (Table 5.3; Figure 5.3a). Between fire intervals of 6 and 31 years, there was an estimated increase of two orders of magnitude, from ~1,000 to ~100,000 seedlings ha^{-1}, respectively (Figure 5.4a). Data from long unburned plots (with unknown fire history) suggest that the relationship between fire interval and post-fire seedling density is non-linear, declining at some point after ~31 years (the longest known fire

Table 5.2. Summary statistics of plot-level pre-fire and post-fire stand structure by fire interval (fire int) in years (yrs). Values represent median (minimum – maximum) values for each variable at each fire interval.

		Pre-fire					Post-fire		
Fire int (yrs)	n	Basal area* (m^2 ha^{-1})	Stand density* (trees ha^{-1})	Canopy seed bank† (cones ha^{-1})	Avg cones $tree^{-1}$	Proportion knobcone pine (by density)	Seedling density* (trees ha^{-1})	Proportion knobcone pine (by density)	Proportion second year seedlings
6	5	1.3 (0.4-2.4)	7,261 (4,576-24,918)	348 (149-846)	0.1 (0.03-0.2)	1 (1.00-1.00)	249 (149-1,442)	1 (1.00-1.00)	1 (1.00-1.00)
10	8	4.9 (1.1-8.8)	2,338 (162-7,894)	5,391 (1,415-10,544)	1.7 (0.7-4.3)	1 (1.00-1.00)	1,183 (469-6,875)	1 (1.00-1.00)	0.89 (0.71-1.00)
15	6	7.5 (3.8-25.3)	3,366 (1,210-4,426)	3,222 (668-6,631)	1.3 (0.3-2.4)	1 (1.00-1.00)	1,317 (943-2,734)	1 (1.00-1.00)	0.98 (0.92-1.00)
16	14	8.4 (0.5-30.7)	1,840 (334-10,823)	10,494 (501-47,619)	6.0 (1.6-16.3)	0.99 (0.16-1.00)	12,644 (138-116,374)	1 (0.51-1.00)	0.96 (0.71-1.00)
17	7	7 (2.1-11.7)	2,288 (842-6,543)	25,083 (4,577-34,660)	5.8 (4.4-12.8)	1 (1.00-1.00)	1,890 (289-13,174)	1 (1.00-1.00)	0.97 (0.85-1.00)
22	6	20.2 (6.2-21.3)	2,143 (305-4,742)	13,959 (157-29,692)	7.7 (0.5-11.3)	1 (1.00-1.00)	10,469 (1,172-18,203)	1 (1.00-1.00)	1.00 (0.98-1.00)
31	6	26.7 (11.6-38.1)	3,547 (522-6,543)	85,360 (48,095-126,674)	32.1 (12.1-92.1)	1 (0.97-1.00)	118,516 (39,219-250,156)	1 (1.00-1.00)	0.99 (0.98-1.00)
long	19	16.5 (4.5-48.8)	865 (79-3,531)	17,350 (6,543-33,472)	80.6 (2.0 – 214.1)	0.91 (0.09-1.00)	13,766 (599-134,062)	1 (0.95-1.00)	0.93 (0.86-1.00)

*Values represent total basal area, stand density and post-fire seedling density for conifer tree species only

†Canopy seed bank represents open cones on knobcone pine only

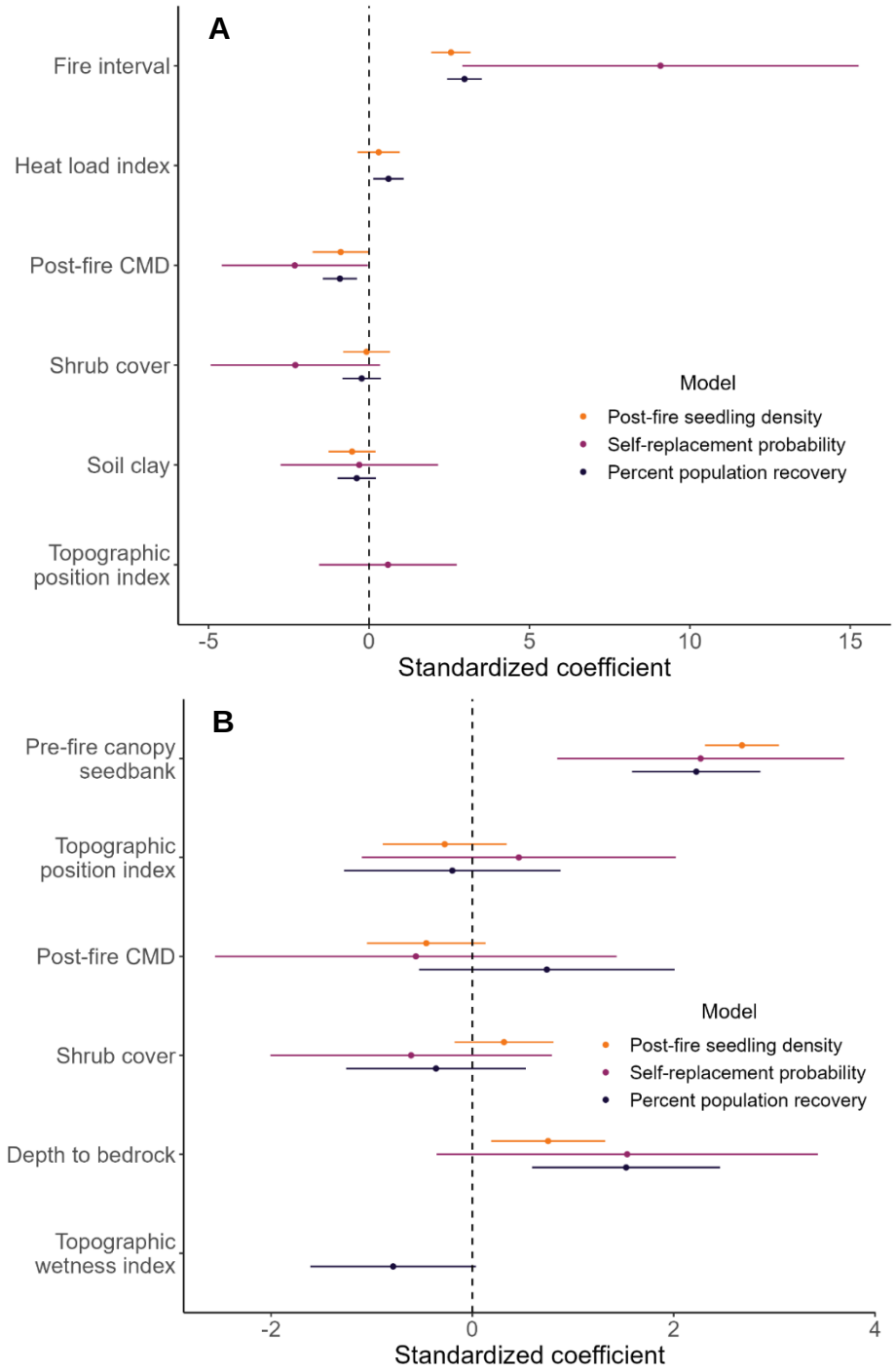

Figure 5.3. Effects of predictor variables in A) fire interval and B) canopy seed bank models on post-fire seedling density, probability of self-replacement, and percent population recovery. Notes: Dots represent medians, horizontal lines represent 95% confidence intervals, and both are shaded by model (response variable). The effects for each predictor are per two standard deviations.

interval, Figure 5.4a). Further, there was a modest negative effect of increasing post-fire CMD on post-fire seedling density (Figure 5.3a). Holding all other predictors constant, post-fire seedling density decreased by nearly an order of magnitude from areas of lowest to highest post-fire moisture stress (low vs. high CMD; Figure 5.5a). There was no evidence of an effect of heat load index, shrub cover, or soil clay content (Figure 5.3a, Figure 5.5b-d).

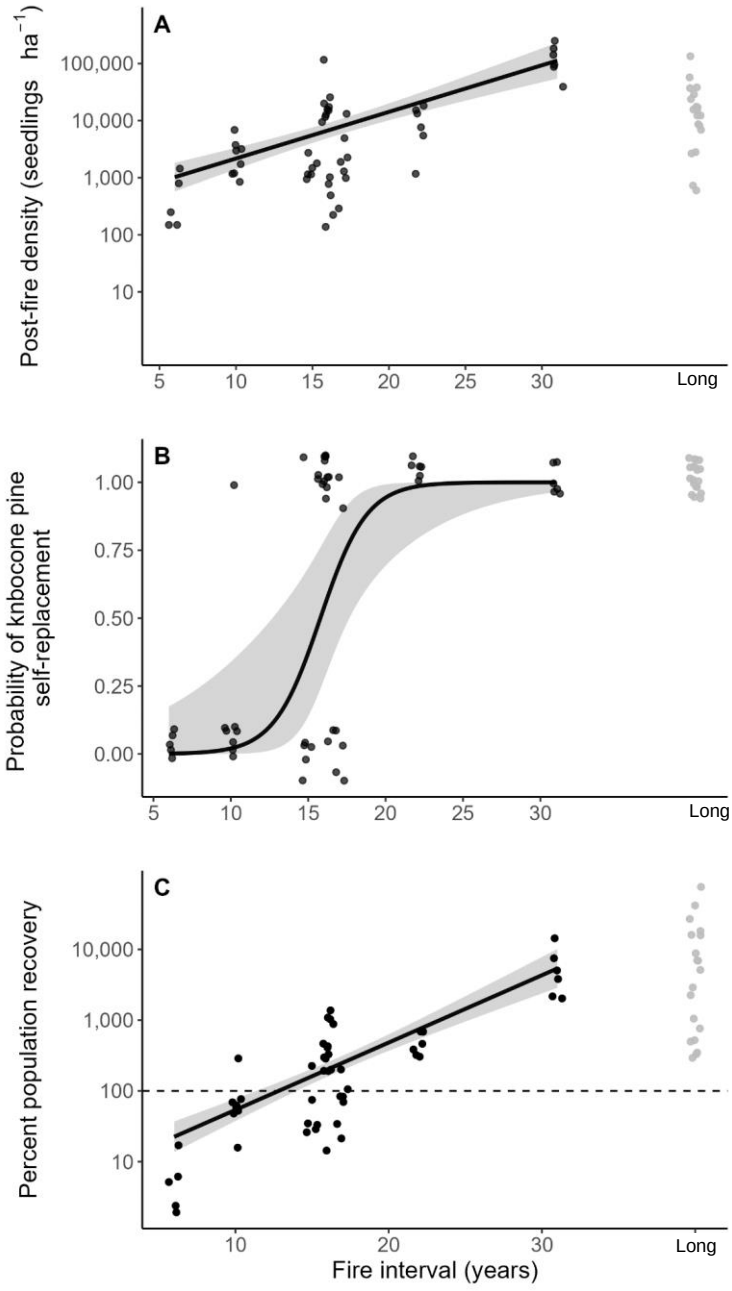

Figure 5.4. Partial effect plots of fire interval (years) on A) post-fire density (seedlings ha^{-1}), B) probability of knobcone pine self-replacement (post-fire seedling density > pre-fire stand density), and C) percent population recovery. Notes: The solid line represents the median estimate with all other covariates held at their means and the shaded region represents the 95% confidence interval. The dashed line represents the line of self-replacement in panel C. Each point represents a plot; black points represent plots with known fire intervals used to fit the model (n = 52), gray points represent plots with unknown "long" fire intervals and were not used to fit the model but are presented for reference (n = 19).

In the model that used canopy seed bank rather than fire interval, there was strong evidence of a positive effect of pre-fire canopy seed bank on post-fire seedling density (Table 5.3, Figure 5.3b). Holding all covariates at their means, pre-fire canopy seed banks of 665, 10,900, and 73,000 cones ha^{-1} resulted in an estimated 1,000, 10,000, and 50,000 knobcone pine seedlings ha^{-1}, respectively (Figure 5.6a). There was strong evidence of a positive effect of depth to bedrock (Figure 5.3b) with an estimated four-fold increase in post-fire seedling density at plots with the deepest (~120 cm) versus shallowest (~70 cm) depth to bedrock in the study area (Figure 5.7b). There was no evidence of an effect of post-fire CMD, TPI, or shrub cover (Figure 5.3b, Figure 5.7a, c, d).

5.4.2 *Probability of self-replacement*

Knobcone pine self-replacement (where seedling density two years post-fire reached or exceeded pre-fire density) occurred at 68% of plots. There was evidence of a strong positive effect of fire interval on probability of self-replacement for fire intervals up to 31 years (Table 5.3, Figure 5.3a). Holding all covariates at their means, probability of self-replacement was estimated at 5% for an 11-year interval, 50% for a 16-year interval, and 95% for a 20-year interval (Figure 5.4b). Data from long unburned plots suggest that this trend continues beyond the 31-year chronosequence (Figure 5.4b). Post-fire CMD had a moderate negative effect on probability of self-replacement, with an additional four years needed to reach a given probability of self-replacement for areas of high compared to low post-fire moisture stress (Figure 5.5e). Mean shrub cover had a suggestive negative effect on probability of self-replacement, but with considerable uncertainty around this relationship (Figure 5.3a, Figure 5.5f). There was no effect of TPI or soil clay content on probability of self-replacement (Figure 5.3a, 5.5g-h). In the model that used canopy seed bank rather than fire interval, there was evidence of a strong positive

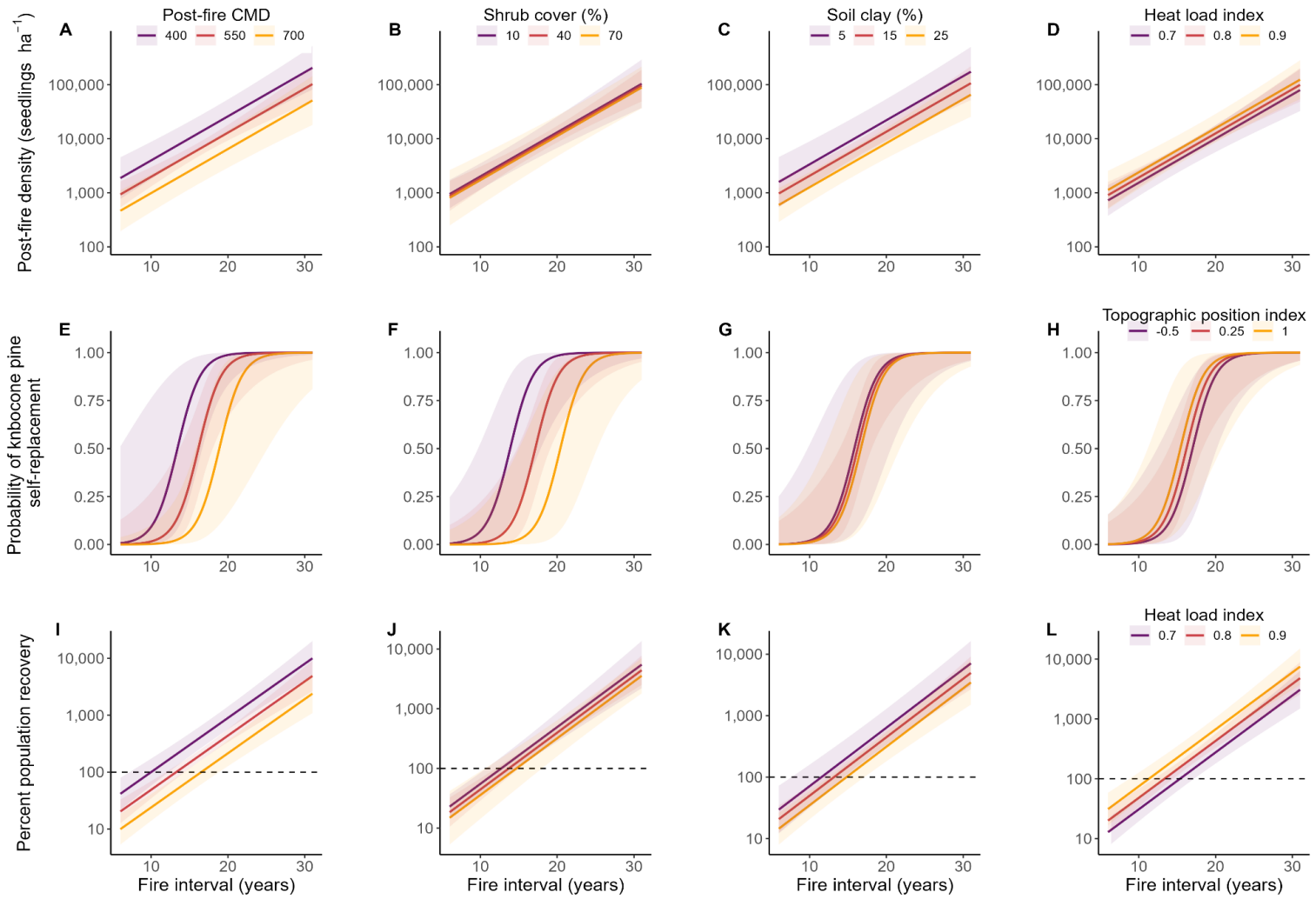

Figure 5.5. Change in fire interval and (A-D) post-fire density (seedlings ha^{-1}), (E-H) probability of knobcone pine self-replacement, (I-L) percent population recovery across gradients of covariates in each model.

Notes: Solid lines represent median estimates, shaded areas are 95% CI. Predictions consider the effect of each covariate individually with other covariates held at the means. Each column has a single legend except for the right column, where panels have their own legends. Dashed lines are the line of self-replacement for I-L.

effect of pre-fire canopy seed bank on probability of self-replacement (Table 5.3, Figure 5.3b), estimated at 50% and 95% for pre-fire canopy seed banks of 1,400 and 80,800 cones ha^{-1}, respectively, holding all covariates at their means (Figure 5.6b). There was no evidence of an effect of any covariates considered in this model (Figure 5.3b, Figure 5.7e-h).

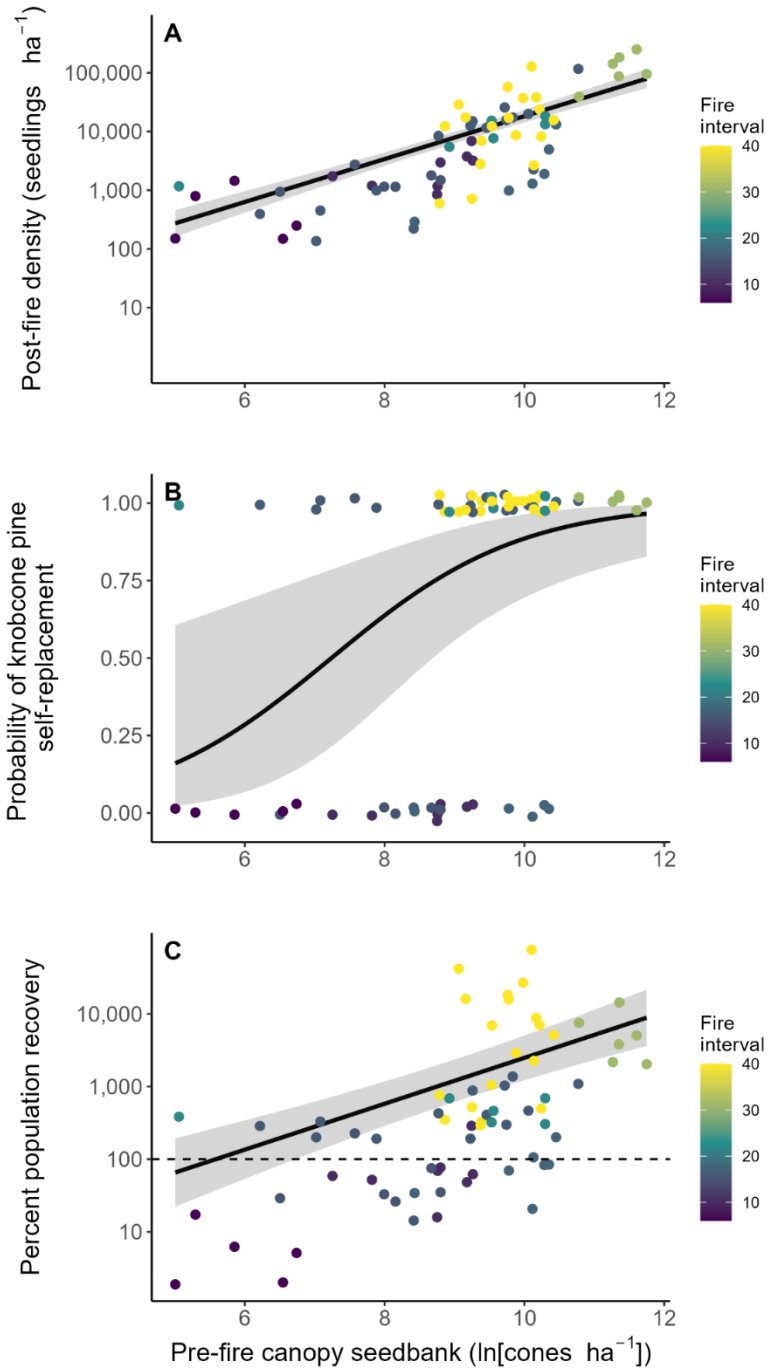

Figure 5.6. Partial effect plots of pre-fire canopy seed bank (ln[cones ha^{-1}]) on A) post-fire density (seedlings ha^{-1}), B) probability of knobcone pine self-replacement (post-fire seedling density > pre-fire stand density), and C) percent population recovery

Notes: The solid line represents the median estimate with all other covariates held at their means and the shaded region represents the 95% CI. The dashed line represents the line of self-replacement in panel C. Points are shaded by fire interval and each point represents a plot (n = 71).

5.4.3 *Percent population recovery*

For fire intervals up to 31 years, the fitted model showed strong evidence of a positive effect of fire interval on post-fire knobcone pine density percent of pre-fire knobcone pine density (hereafter, percent population recovery; Table 5.3, Figure 5.3a). Percent population recovery was estimated at 50% following a 10-year fire interval and from 13-year to 31-year fire intervals, increased from 100% to 2000% (i.e., a 20-fold increase in population density post-fire; Figure 5.4c). Long interval plots encompassed a broad range of values, representing three-fold to 764-fold increases (median = 51-fold increase) from pre-fire to post-fire, suggesting that this metric of regeneration success may continue to increase over time beyond the bounds of the known fire intervals (Figure 5.4c). Post-fire CMD had a strong negative effect on percent population recovery (Figure 5.3a). Compared with areas of low post-fire CMD, an estimated additional six years were needed to reach the same percent population recovery for areas with high post-fire CMD (Figure 5.5i). Conversely, HLI had a moderate positive effect (Figure 5.3a); areas with low HLI required an additional four years to reach a given value of percent population recovery compared with areas with high HLI (Figure 5.5l). There was no effect of shrub cover or soil clay content on percent population recovery (Figure 5.3a, Figure 5.5j-k).

For the model that considered pre-fire canopy seed bank rather than fire interval, there was strong evidence of a positive effect of pre-fire canopy seed bank on percent population recovery (Table 5.3, Figure 5.3b). Percent population recovery was estimated at 100% and 1000% for pre-fire canopy seed banks of 300 and 6,000 cones ha^{-1}, respectively (Figure 5.6c). There was strong evidence of a positive effect of depth to bedrock (Figure 5.3b); for sites with similar pre-fire canopy seed banks, there was an estimated four-fold increase in percent population recovery at plots with the deepest versus shallowest depth to bedrock in the study

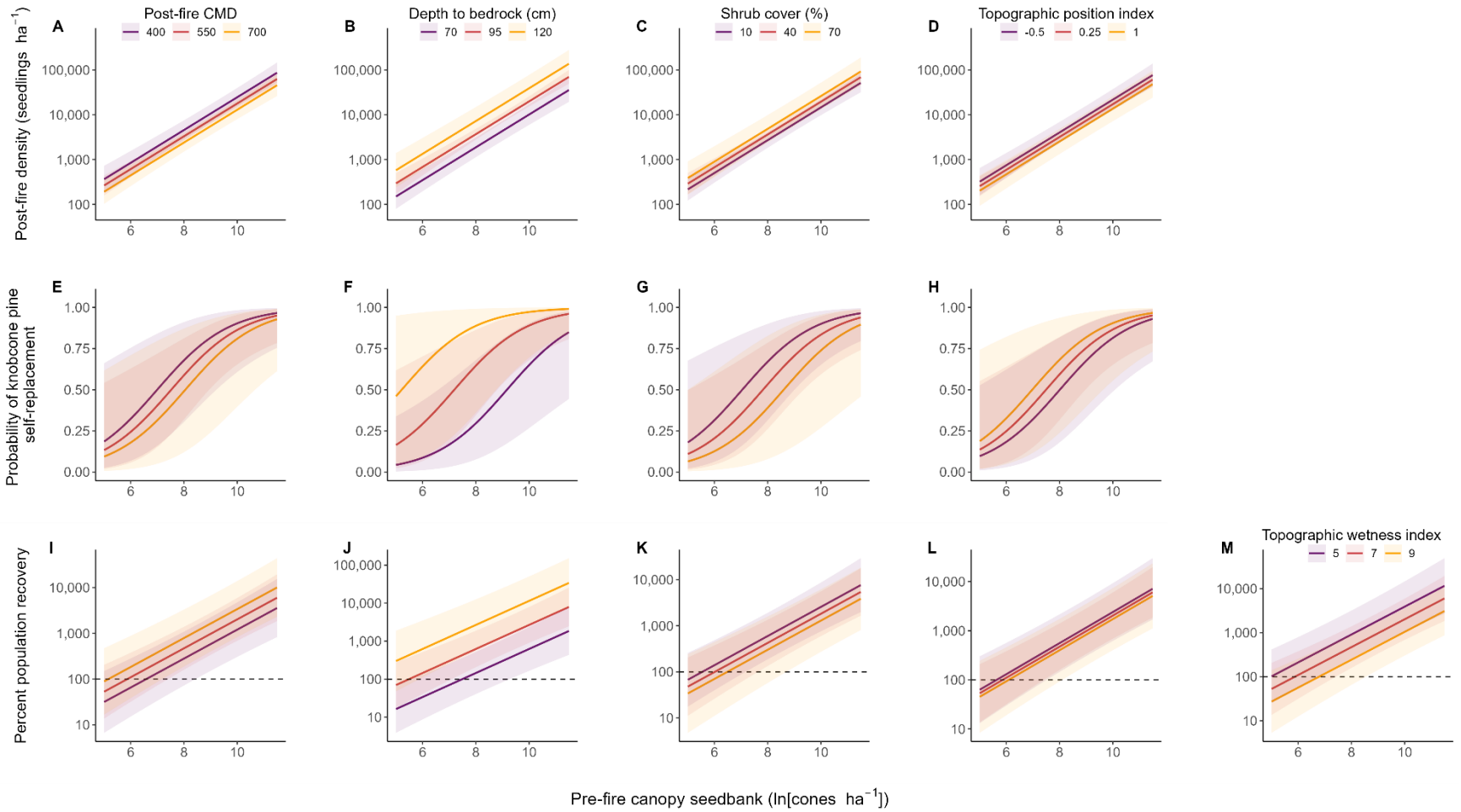

Figure 5.7. Change in pre-fire canopy seed bank and (A-D) post-fire density (seedlings ha^{-1}), (E-H) probability of knobcone pine self-replacement, (I-M) percent population recovery across gradients of covariates in each model.

Notes: Solid lines represent median estimates, shaded areas represent 95% CI. Predictions consider the effect of each covariate individually, holding other covariates at their means. Legends apply to all panels in each column. Dashed lines are the line of self-replacement for I-M.

area (Figure 5.7j). Further, there was suggestive evidence of a negative effect of TWI (Figure 5.8m) but overlap of the 95% confidence interval suggests uncertainty regarding the directionality of this effect (Figure 5.3b). There was no evidence of an effect of post-fire CMD, shrub cover, or TPI (Figure 5.3b, Figure 5.7i, k, l).

Table 5.3. Model output from generalized linear mixed models of fire interval and pre-fire canopy seedbank [ln(cone density)] – on three measures of post-fire regeneration.

Post-fire seedling density

~ Fire interval + Post-fire CMD + Shrub cover + Soil clay + HLI | Sample fire

		95% CI		
Effect	Beta	lower	upper	p
Intercept	8.912	8.624	9.201	<0.001
Fire interval	2.555	1.945	3.165	<0.001
Post-fire CMD	-0.882	-1.758	-0.005	0.049
Shrub cover	-0.077	-0.804	0.650	0.836
Soil clay	-0.529	-1.262	0.205	0.158
HLI	0.301	-0.359	0.962	0.372

~ ln(cone density) + Post-fire CMD + Shrub cover + Depth to bedrock + TPI | Sample fire

		95% CI		
Effect	Beta	lower	upper	p
Intercept	9.001	8.783	9.218	<0.001
ln(Cone density)	2.678	2.311	3.046	<0.001
TPI	-0.275	-0.891	0.342	0.383
Post-fire CMD	-0.458	-1.046	0.131	0.127
Shrub cover	0.315	-0.176	0.806	0.209
Depth to bedrock	0.753	0.187	1.320	0.009

Probability of knobcone pine self-replacement

~ Fire interval + Post-fire CMD + Shrub cover + Soil clay + TPI | Sample fire

		95% CI		
Effect	Beta	lower	upper	p
Intercept	0.516	-0.564	1.597	0.349
Fire interval	9.085	2.908	15.263	0.004
Post-fire CMD	-2.313	-4.591	-0.036	0.046
Shrub cover	-2.296	-4.936	0.345	0.088
Soil clay	-0.303	-2.759	2.152	0.809
TPI	0.590	-1.552	2.732	0.589

Notes: CMD = cumulative moisture deficit, HLI = heat load index, TPI = topographic position index, TWI = topographic wetness index

Table 5.3 (continued)

~ ln(cone density) + Post-fire CMD + Shrub cover + Depth to bedrock + TPI | Sample fire

		95% CI		
Effect	Beta	lower	upper	p
Intercept	1.183	0.131	2.236	0.028
ln(Cone density)	2.267	0.842	3.693	0.002
TPI	0.462	-1.098	2.021	0.562
Post-fire CMD	-0.561	-2.555	1.433	0.581
Shrub cover	-0.608	-2.007	0.790	0.394
Depth to bedrock	1.538	-0.356	3.432	0.111

Percent population recovery

~ Fire interval + Post-fire CMD + Shrub cover + Soil clay + HLI | Sample fire

		95% CI		
Effect	Beta	lower	upper	p
Intercept	5.425	5.204	5.645	<0.001
Fire interval	2.976	2.435	3.518	<0.001
Post-fire CMD	-0.906	-1.440	-0.372	<0.001
Shrub cover	-0.227	-0.828	0.373	0.458
Soil clay	-0.383	-0.981	0.215	0.210
HLI	0.608	0.133	1.083	0.012

~ln(cone density) + TWI + TPI + Post-fire CMD+ Shrub cover+ Depth to bedrock| Sample fire

		95% CI		
Effect	Beta	lower	upper	p
Intercept	6.899	5.843	7.954	<0.001
ln(Cone density)	2.225	1.587	2.862	<0.001
TWI	-0.787	-1.608	0.035	0.061
TPI	-0.199	-1.275	0.877	0.717
Post-fire CMD	0.740	-0.530	2.009	0.253
Shrub cover	-0.361	-1.252	0.531	0.428
Depth to bedrock	1.528	0.594	2.461	0.001

5.5 DISCUSSION

By simultaneously testing the effects of seed supply and post-fire growing conditions on serotinous forest resilience to fire, our study highlights several key insights with implications for fire-prone ecosystems. First, seed supply at the time of fire was by far the most important factor driving each measure of post-fire forest recovery, suggesting that the indirect effects of climate

change via altered fire regimes currently outweigh the direct effects of warming climate. This was true for direct measures of seed supply or indirect proxies of seed supply based on the interval between severe fires, suggesting that multiple sources of data with varying levels of detail can be valuable for anticipating outcomes of forest resilience to fire. Second, the direct effects of post-fire climate conditions on post-fire forest recovery, while minor compared to the effects of seed source, can combine with seed supply to cause compounding effects near thresholds of seed availability when fire intervals are short (e.g., < 15 years). While there is little to no evidence that fire intervals and post-fire climate have combined to lead to complete post-fire tree regeneration failure thus far, trends in both fire frequency and warming climate suggest that outcomes may differ in the near future. Finally, our findings are relevant for fire and vegetation management in serotinous forests and can help inform management goals of expanding or reducing the extent of serotinous forests.

Our finding that seed supply was by far the most important driver of post-fire regeneration suggests that the indirect effects of climate change via altered disturbance regimes may override the direct effects of climate change on tree survival. A strong effect of fire interval – a key control on seed availability at the time of fire – on post-fire regeneration has been noted in many systems dominated by obligate seeding trees, particularly where serotinous species are prevalent (Brown and Johnstone 2012, Enright et al. 2014, Turner et al. 2019, Whitman et al. 2019). Post-fire seedling density following long interval fires can exceed that following short-interval fires by 2x to several orders of magnitude (Espelta et al. 2008, Donato et al. 2009, Hoecker and Turner 2022) as we found here. However, whereas short-interval severe reburns can lead to complete recruitment failure or conversion to non-forest where the historical fire regime was characterized by low severity fires or longer fire intervals (Coppoletta et al. 2016, Stevens-

Rumann and Morgan 2016), we saw no evidence of complete recruitment failure, suggesting high resilience of serotinous species to increases in short-interval fire relative to non-serotinous species (Hansen et al. 2018). Minimum time to self-replacement was approximately 50% of the historical mean fire return interval, which is comparable to findings from serotinous plant-dominated systems in the Mediterranean Basin and Australia (Enright et al. 1996, 2014, Espelta et al. 2008). Although fire interval is a key driver of post-fire regeneration success, the minimum fire-free period for stand self-replacement should be assessed in the context of population dynamics in an individual stand, given the wide variation in outcomes following a given fire interval (Brennan and Keeley 2019). Although several studies have shown the importance of topography for seedling establishment and survival (Hansen and Turner 2019, Littlefield 2019), which may compound with a shortened fire interval to create a harsh microclimate for seedlings (Hoecker et al. 2020), we found a relatively negligible effect of topographic variables in our study area. This is likely due to the topoedaphic restriction of knobcone pine, potentially masking effects of topography (Vogl 1973). Overall, the dominant effect of seed supply indicates that the effects of climate warming in serotinous forests are likely to occur primarily through indirect effects of changing disturbance regimes .

Our finding of a peak in post-fire seedling density at moderate fire intervals suggests a concurrent peak in seed availability linked to changes in stand structure over time since fire. Declines in post-fire seedling density following long unburned intervals as compared with a 31-year interval are likely linked to a trade-off between individual cone production and stand-level canopy seed bank size across varying stand density. While individual trees in low density stands produce more cones than individual trees in high density stands, high density stands generally have greater canopy seed banks than low density stands after controlling for stand age (Agne et

al. 2022). Stands that burned on a 31-year interval were four times denser than long unburned stands prior to fire, supporting this mechanism. Further, long unburned stands may represent areas where stands are approaching senescence risk, the loss of stand-level reproductive capacity as trees age and die in the absence of fire (Enright et al. 2015), eroding the canopy seed bank available at the time of fire. Previous work suggests that this may occur in stands ranging from 60 – 80 years of age (Vogl 1973, Fry et al. 2012). Although we did not directly quantify this phenomenon within this study, previous work at a regional scale suggests that fire exclusion may be leading to senescence risk and loss of knobcone pine in parts of its range (Reilly et al. 2019). However, the demographic processes underpinning this range contraction are poorly understood. Additional work is needed to quantify declines in tree-level and stand-level reproductive capacity in senescing knobcone pine forests, to understand how fire exclusion may cause loss of knobcone pine at various spatial scales.

Canopy seed bank size can vary widely with stand structure and microsite characteristics for a given stand age (Agne et al. 2022), underscoring that fire interval is not an exact proxy for seed supply at the time of fire, though it can provide a range of potential values when directly estimating the canopy seed bank is not feasible. Models that incorporated pre-fire canopy seed bank showed a strong effect of seed supply and a relative lack of significance in any additional covariates. This suggests that pre-fire canopy seed bank may integrate the effects of seed supply with climate and microsite conditions important for post-fire regeneration, compared with fire interval which requires climate and microsite covariates to be controlled for. Thus, when used as a sole predictor variable, pre-fire canopy seed bank is a more useful for predicting post-fire regeneration outcomes than is fire interval. Although some previous work has quantified cone development and potential seed supply across a range of stand structures (Enright and Lamont

1989, Andrus et al. 2020, Gill et al. 2021, Agne et al. 2022), the distance to the nearest live tree or unburned edge is often considered a proxy for post-fire seed availability, regardless of tree size, age, or species life history. As short-interval fires inevitably increase with increasing fire activity due to climate change, further work is needed to understand how reproductive capacity of conifer species develops in fire-prone forests.

Post-fire climate had a strong mediating effect on post-fire regeneration near thresholds of seed supply, suggesting that it may play an increasingly important role in the future as warm post-fire years occur more frequently. Although fire interval was consistently the strongest predictor of post-fire regeneration outcomes, increases in post-fire CMD had a significant negative effect across post-fire regeneration response variables. This finding is consistent with findings across North American coniferous forests indicating that moisture stress within the first several years post-fire is an important filter on regeneration success (Harvey et al. 2016, Kemp et al. 2019, Davis et al. 2019, Rodman et al. 2019). Further, the high proportion of second year seedlings measured suggests that the post-fire recruitment window is very brief for knobcone pine, similar to previous findings for this region (Donato et al. 2009, Tepley et al. 2017). This supports the importance of suitable climate conditions in the first post-fire growing season, rather than over an extended period, for knobcone pine regeneration. However, the lack of complete recruitment failure at any site suggests knobcone pine forests may be more resilient to harsh post-fire conditions than many forests which have seen increased incidence of zero conifer regeneration post-fire in recent decades (Stevens-Rumann et al. 2018). The relative magnitude of the effect of post-fire climate suggests that this factor is likely to be most important for stands near the self-replacement threshold with respect to seed supply – stands that burn on ~13-18-year fire intervals. For shorter fire intervals, the seed supply is limiting, and favorable post-fire

climate conditions cannot overcome the lack of seed source. For longer fire intervals, the seed supply is large, and while unfavorable post-fire climate may decrease total seedling density, it is unlikely to push a stand below the self-replacement threshold. Post-fire climate conditions may increasingly constrain regeneration as short-interval fires continue to occur, and possibly increase, in stands with seed supply near the self-replacement threshold. Future work could be undertaken to integrate seed supply and projected climate in vulnerability mapping to anticipate where post-fire regeneration may decline or fail.

Although our study identifies apparent thresholds of fire frequency and post-fire climate that could lead to loss of knobcone pine resilience, our results suggest that it may be well-suited to current and near-future climate and fire regimes. Although fire intervals capable of decreasing knobcone pine density are possible, intervals within this range (<16 years) represented only 9% of the total area that burned knobcone pine forest in 2018 (M.C. Agne, unpublished data). Despite clear potential for knobcone pine forests to burn on relatively short intervals, the likelihood of occurrence on a scale that would threaten resilience on a broad spatial scale is currently low. Conversely, the potential for local knobcone pine densification following short-interval severe reburns is high, especially when co-occurring with non-serotinous conifers – although robust regeneration may occur following a single short-interval fire if high severity patch sizes are relatively small (Donato et al. 2009). Increases in the proportion of post-fire regeneration that was knobcone pine versus Douglas-fir, particularly in stands that have experienced three severe fires in a 31-year span (Appendix C – Figure 5.11), suggests that knobcone pine could increase in dominance where severe fire frequency increases (Buma et al. 2013). Future fire conditions may facilitate range expansion or changes in forest composition, especially where knobcone pine is currently a poor competitor. However, we note our study area

experienced a relatively cool and wet post-fire growing season relative to site-specific 30-year normals (Table 5.1); additional work is needed to capture the potential effects of a post-fire drought year on tree regeneration. Further, there is considerable uncertainty inherent in extrapolating the outcome of a cohort of second-year seedlings to a mature forest, especially given changing climate (Kueppers et al. 2017). Seedling attrition rates are likely to vary widely among species and with annual variation in climate, local topography, and soil conditions (Hansen and Turner 2019, Hoecker et al. 2020, Carroll et al. 2021). Following post-fire regeneration over time would provide important insights into population dynamics following tree establishment and prior to maturation.

Our study has implications for the management of knobcone pine, and serotinous forests more broadly, as fire regimes change. Where fostering resilience (self-replacement) of knobcone pine forests is the goal, wildfire fire should be excluded from stands for a minimum of 50% of the historical MFRI (estimated at 30 - 90 years; van de Water and Safford 2011), or several years longer where post-fire moisture stress is high or increased post-fire density relative to the pre-fire stand is desired. Where density reduction of knobcone pine is the objective, high intensity fire on an interval <50% of the historical MFRI (10 – 15 years post-fire) may achieve this aim (Keeley et al. 1999), although there are likely to be challenges with implementation of prescribed burning in this forest type (Fry et al. 2012). Eradication of knobcone pine is unlikely following one fire unless a severe reburn occurs within 4 – 5 years of a previous high severity fire – prior to cone development and maturation (Keeley et al. 1999, Agne et al. 2022). However, fuel limitation following severe fire lasting at least five years has been observed in lower montane forests in Oregon and California (Donato et al. 2013, Coppoletta et al. 2016), suggesting that reburns are unlikely to recur on an interval estimated to represent 5 – 15% of the length of the historical

MFRI. Recurrent short-interval severe reburns may eventually remove knobcone pine from a site (Keeley et al. 1999), but it is unclear how such an increase in fire activity would affect fuel loads and subsequent reburn potential in the long term (Hurteau et al. 2019, Abatzoglou et al. 2021). Further, populations of resprouting species could be favored over obligate seeding species, as has been noted in other ecosystems (Enright et al. 2014, Barton and Poulos 2018, but see Keeley et al. 2016), possibly facilitating a transition to hardwood-dominated woodlands or chaparral. While populations of desired species such as California black oak (*Quercus kelloggii*) are sustained following relatively short fire intervals (Hammett et al. 2017), recurrent high severity short-interval fire favors populations composed of a high density of small stature stems rather than oak woodland structure (Nemens et al. 2018). Further, the potential for increases in non-native species may increase with increased fire activity (Smith et al. 2019), and transition to non-forest is likely if fire is sufficiently frequent to eradicate knobcone pine from a forest stand.

This work has implications for serotinous forest resilience to increasing fire frequency in forests across North America. Seed supply is likely the primary constraint on post-fire regeneration in other forests historically dominated by very high densities of serotinous species following severe fire. We expect that seed supply begins to accumulate soon after fire for many serotinous conifer species (Tapias et al. 2001, Turner et al. 2007), suggesting that instances of single short-interval fires that lead to complete recruitment failure may be rare in such forests. However, similar to our findings, short-interval fires leading to regeneration below self-replacement levels have been noted in other forests dominated by serotinous conifers (Brown and Johnstone 2012, Turner et al. 2019). Although climate change effects on serotinous forests are likely to primarily occur through indirect effects of altered fire regimes, warming climate may have a direct effect on seed supply (Redmond et al. 2012, Enright et al. 2015, Agne et al.

2022), suggesting that understanding drivers of demographic rates for individual species is key to anticipating effects of shortening fire intervals.

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5.7 APPENDIX C

5.7.1 *Extended results*

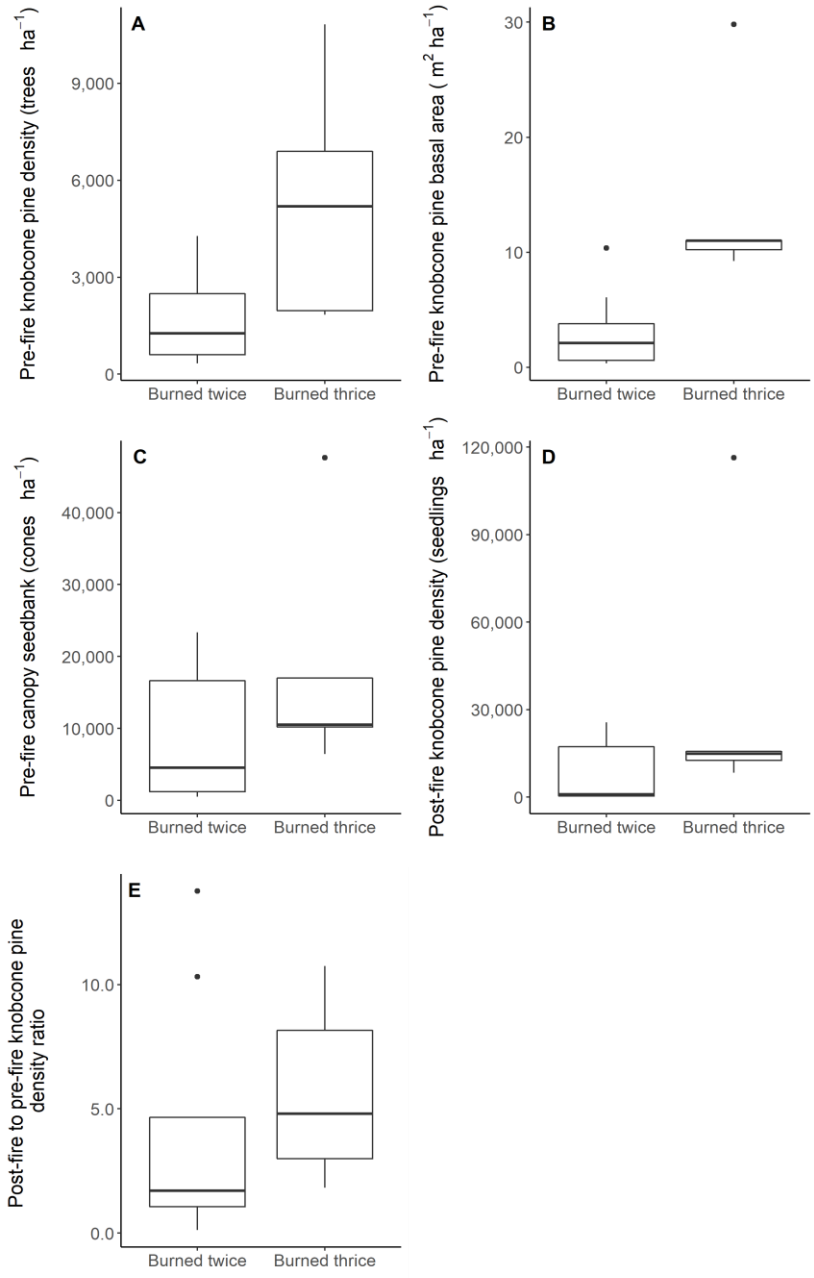

Figure 5.8. Comparison of pre-fire structure and post-fire regeneration at 2x and 3x burned plots of the same recent fire interval.

Notes: All plots reburned on a 16-year fire interval. N = 9 with no previous recorded fire history (burned in 2002 and 2018; Burned twice) and n = 5 that experienced stand-replacing fire 15 years prior (burned in 1987, 2002, and 2018; Burned thrice).

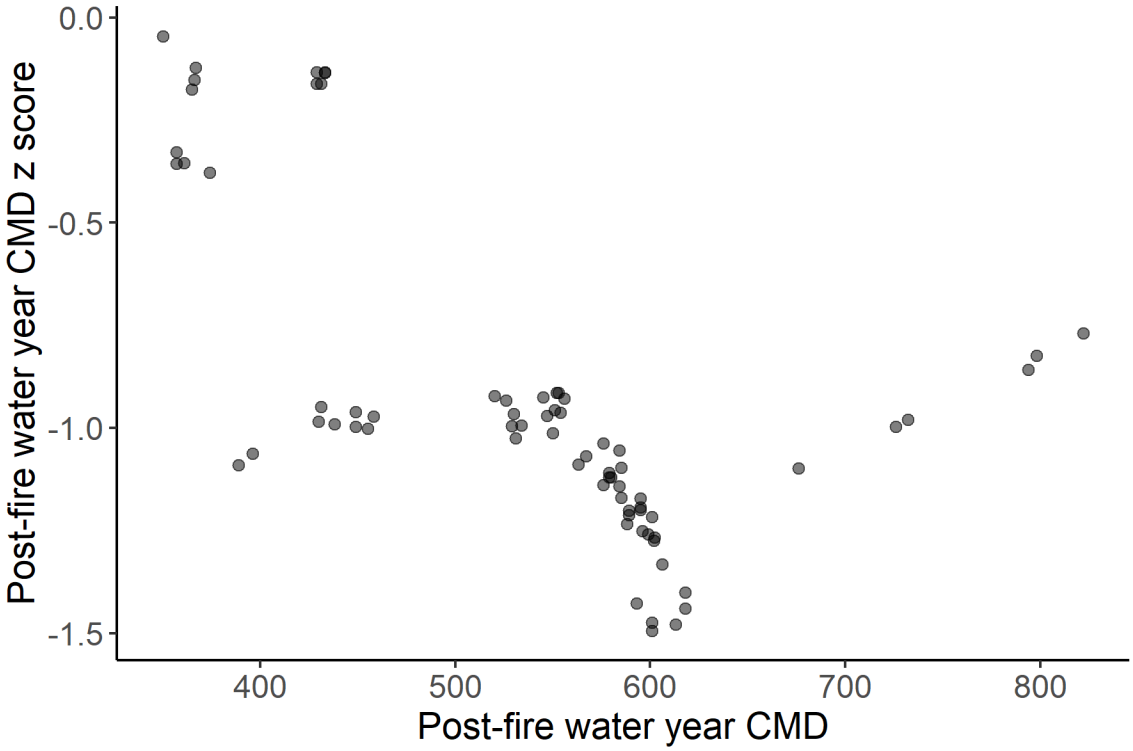

Figure 5.9. Post-fire water year cumulative moisture deficit (CMD) versus post-fire water year CMD z score of the mean CMD of the 1981-2010 normal.

Note: While all plots experienced a lower moisture deficit (cooler and wetter post-fire water year – October 2018 – September 2019) than the 30-year normal, the plots with the lowest post-fire water year CMD had CMD z scores with the lowest deviation from the 30-year normal. That is, the sites with the coolest and wettest post-fire year also experienced the least increase in moisture/decrease in moisture deficit as compared to the long-term average for the site.

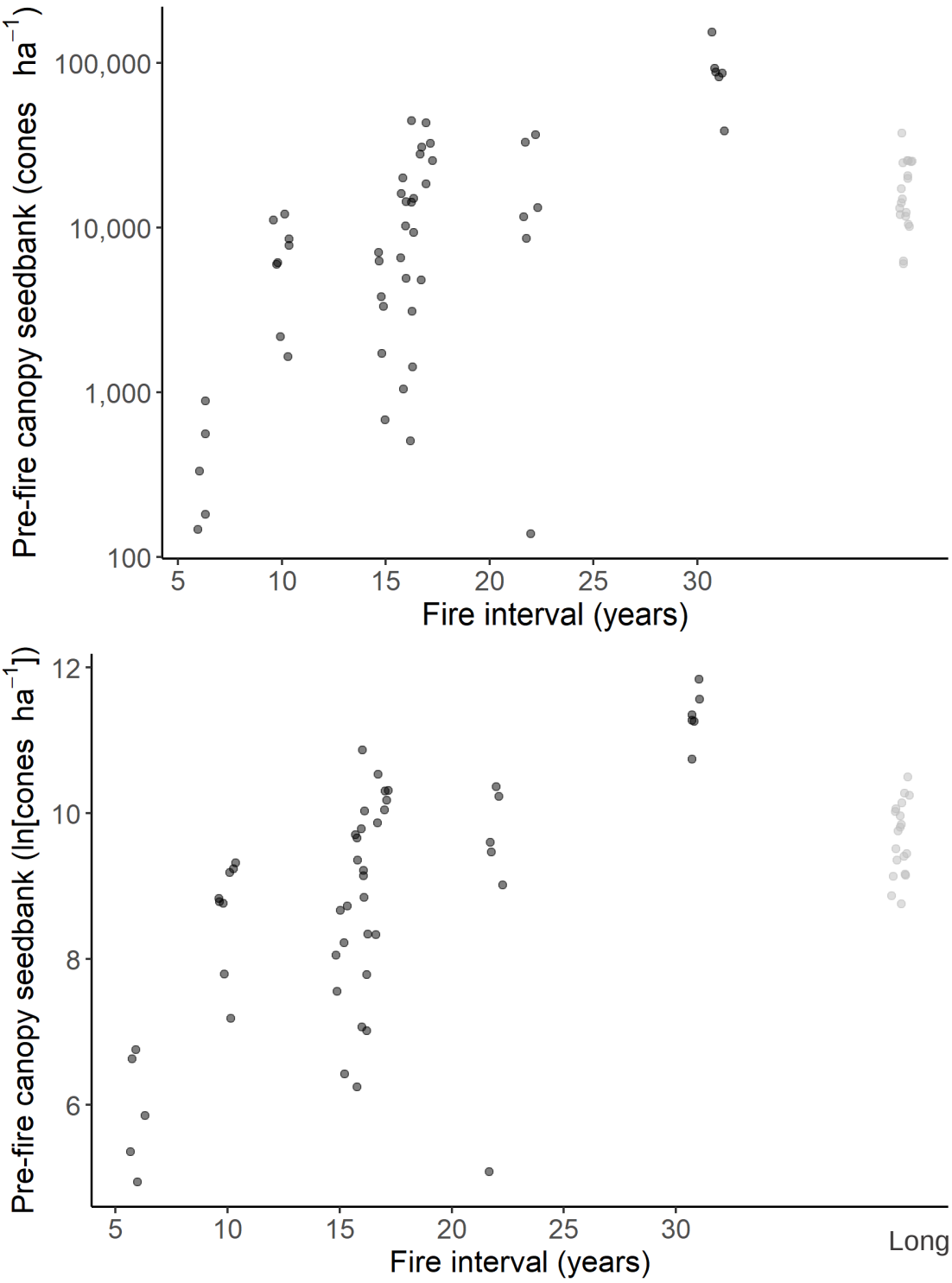

Figure 5.10. Fire interval versus pre-fire canopy seedbank.

Notes: Top panel in cones ha^{-1} and bottom panel in ln(cones ha^{-1}). Pearson correlation coefficient = 0.67. Points from long interval plots included for reference.

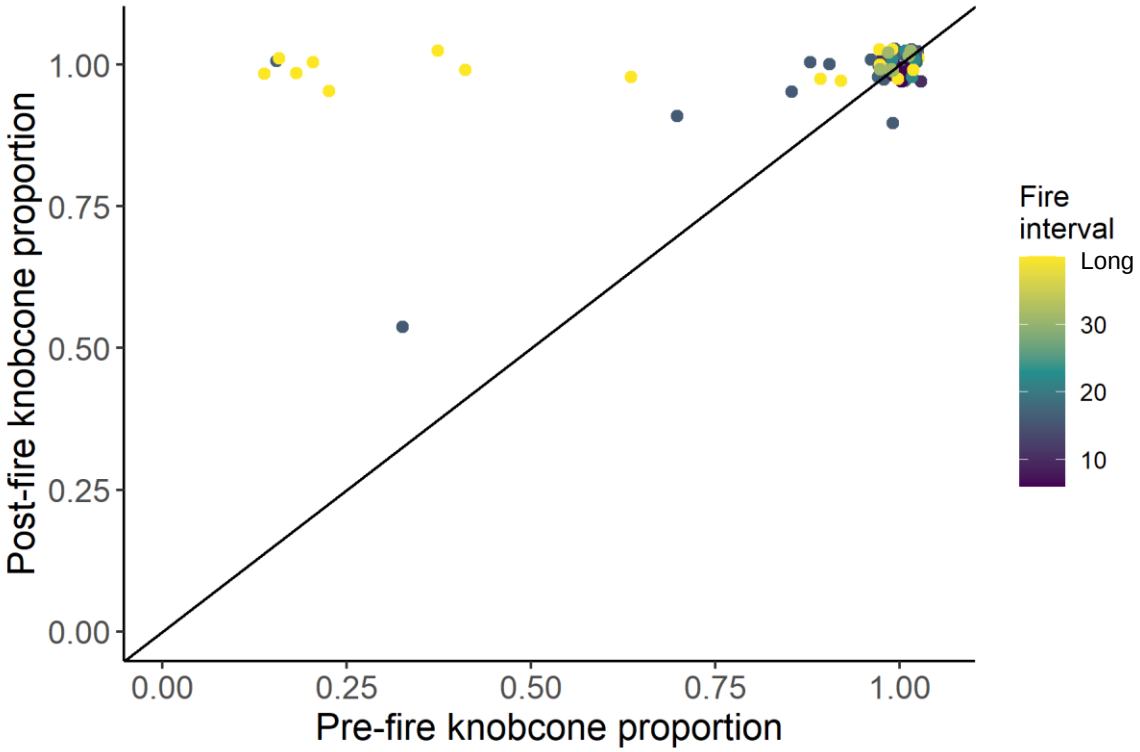

Figure 5.11. Pre-fire knobcone pine proportion of pre-fire conifer stems versus post-fire knobcone pine proportion of post-fire conifer seedlings colored by fire interval.

Note: Points above the diagonal line increased with respect to knobcone pine proportion while points below the diagonal line decreased with respect to knobcone pine proportion. In most plots, post-fire knobcone pine proportion neared 100%. Many long interval plots increased substantially with respect to knobcone pine proportion.

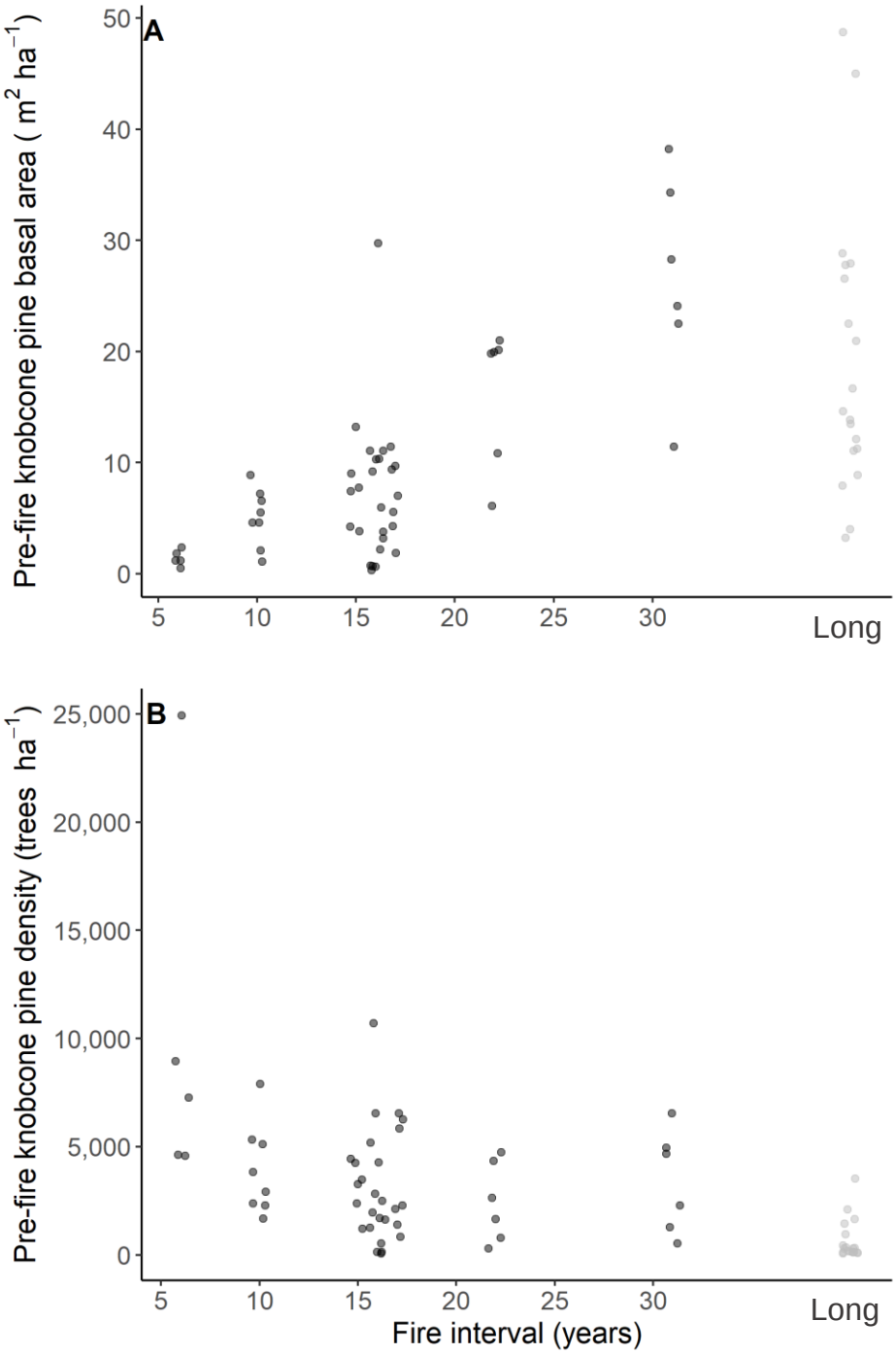

Figure 5.12. Scatterplot of pre-fire knobcone pine by A) basal area and B) density versus fire interval.

Note: Pre-fire basal area increases with fire interval (Pearson correlation coefficient = 0.75) while stand density decreases with increasing fire interval (Pearson correlation coefficient = -0.31). although variation within fire interval appears to meet or exceed the variation among fire intervals for both metrics.

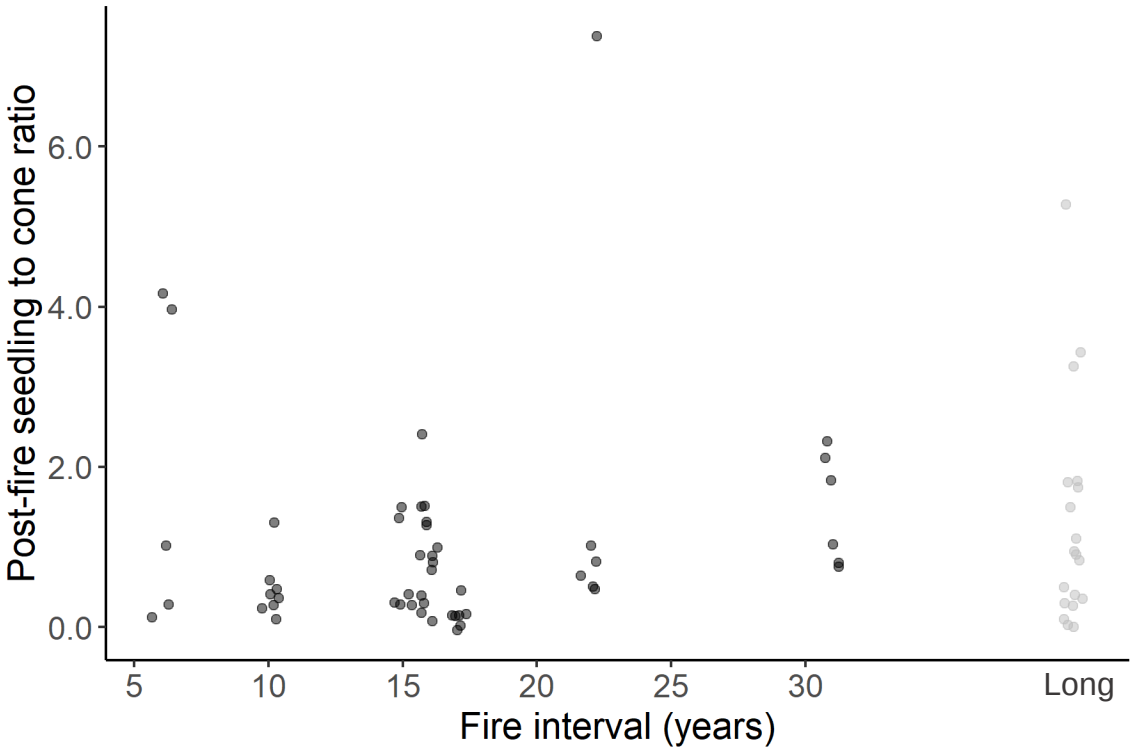

Figure 5.13. Scatterplot of post-fire seedling to pre-fire cone ratio by fire interval.

Note: Values range from 0.05 – 7.5 post-fire seedlings per pre-fire cone (median = 0.7, mean = 1.1). Most plots (95%) fell between 0.05 – 3.3 post-fire seedlings per pre-fire cone, suggesting that values above 4.0 may represent areas with an adjacent seed source not represented by the plot measurement.

Chapter 6. CONCLUSIONS

This research provides important insight regarding resilience mechanisms to increased fire activity and warming climate in North American coniferous forests dominated by serotinous tree species. Building on the interval squeeze hypothesis (Enright et al. 2015), this work provides a framework for understanding direct and indirect climate change effects on serotinous populations, while considering important feedbacks. Using the model system of California closed-cone pine forests, this framework guides understanding of when and where resilience of serotinous populations may erode, with significant implications for forest and fire management as the climate continues to warm.

Collectively, the findings of this dissertation indicate that climate change effects on California closed-cone pine forest resilience are likely to occur primarily through indirect effects from changing disturbance regimes. Rapid recovery of fuels following stand-replacing fire suggests high potential for increasing fire frequency, with fuels capable of supporting severe reburns at 3 – 9 times the frequency (Chapter 3) of the historical fire regime (van de Water and Safford 2011). Canopy seed bank storage (seed availability) is also strongly driven by stand age (Chapter 4), and both are key drivers of post-fire regeneration success (Chapter 5), indicating that shortening fire intervals are likely to be associated erosion of post-fire resilience. While the greatest magnitude of ecological change in closed-cone pine forests is likely to be borne through increased fire activity, direct effects of warming on reproductive capacity (Chapter 4) and post-fire regeneration (Chapter 5) are also apparent. Although these effects are of smaller magnitude, they may be particularly important around thresholds of seed availability (Chapter 5), with the potential to strengthen and compound with effects of increasing fire activity as climate warming continues.

Despite potential for increased fire activity with climate warming, important feedbacks may prevent losses of serotinous conifers over broad spatial and temporal scales. Decreasing tree populations from pre- to post-fire following a single short-interval reburn (Chapter 5) may signal declining resilience (Stevens-Rumann et al. 2018). However, the reproductive capacity of individual trees in such post-fire stands eventually compensates for the low density of the serotinous population (Chapter 4), representing an important compensatory mechanism fostering resilience over multiple fire cycles. Such stands may also remain fuel-limited for an extended period, as trees make up a significant component of the fuel load (Chapter 3), representing a negative feedback that constrains potential for recurrent short-interval severe reburns. Post-fire invasion of serotinous conifers into pre-fire non-forested patches can also occur, often producing a similar stand structure with a low serotinous population density and an extended period of fuel limitation (Chapter 3). These mechanisms suggest that oscillations in stand density between generations may represent a typical mode of serotinous population persistence across multiple fire cycles.

Anticipating vulnerability to resilience loss of serotinous populations following increased fire activity requires understanding temporal development of both reburn potential and regeneration potential. Within such a framework, three stages exist across early post-fire stand development following stand-replacing fire (Figure 6.1). The first post-fire stage is "fuel-limited/seed-limited" – where recent fire has consumed combustible fuel and the regenerating stand is reproductively immature. The second stage is "fuel sufficient/seed-limited" – where fuels have accumulated due to vegetative regrowth and snagfall, while the reproductive capacity of the regenerating stand remains low to absent. The third stage is "fuel sufficient/seed sufficient" – where fuels have accumulated and stand reproductive capacity is high. The first and

third stages represent periods in which vulnerability to serotinous population resilience loss is low – due to low probability of reburn associated with fuel limitation during the first stage, and

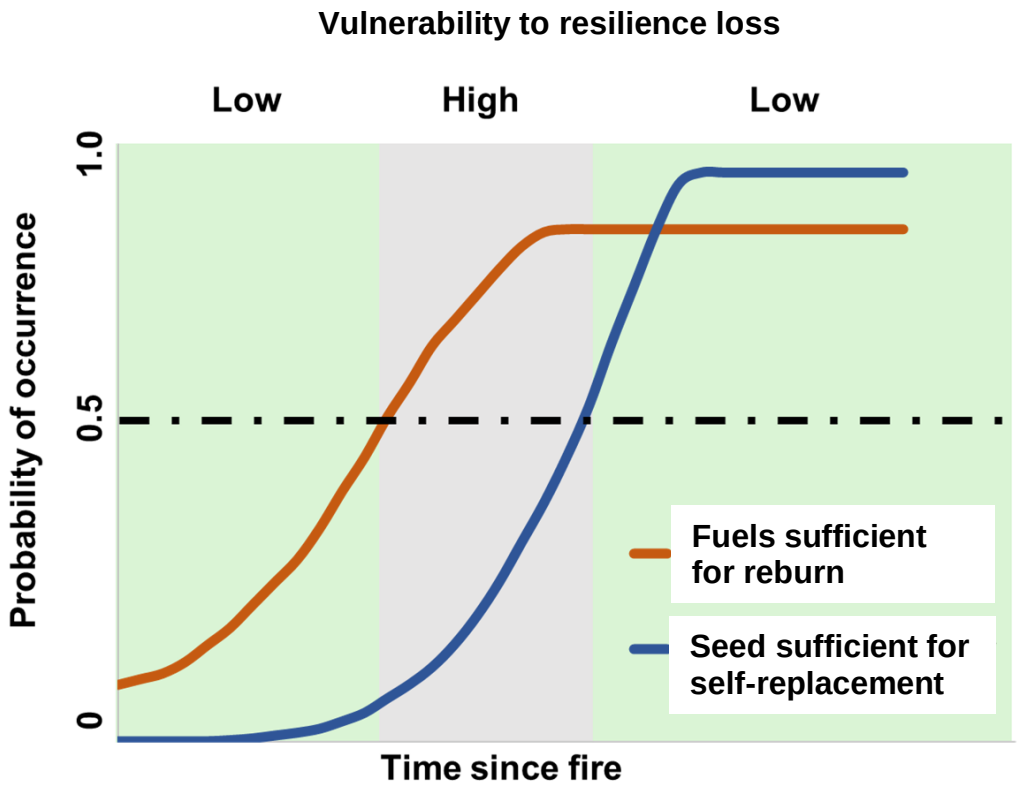

Figure 6.1. Conceptual diagram of vulnerability framework for serotinous populations, with green regions representing "fuel-limited/seed-limited" and "fuel sufficient/seed sufficient" stages and the gray region representing the "fuel sufficient/seed-limited" stage.

due to high probability of regeneration facilitating population self-replacement should a reburn occur during the third stage. The second stage represents a period of high vulnerability to serotinous population resilience due to ample fuel accumulation to support a reburn but lack of seed supply for regeneration should a reburn occur. California closed-cone pine forests pass through the first stage of this framework within a decade post-fire, although the period of fuel-limitation can vary by pre-fire vegetation legacy (Chapter 3). By 15 years post-fire on average, these forests enter the third stage of this framework (Chapter 5), suggesting that the period of high vulnerability to resilience loss (i.e., the second stage of the framework) is brief. However,

high moisture stress during the inter-fire period (Chapter 4) and/or immediately post-fire (Chapter 5) can extend this window by several years, and continued climate warming may further exacerbate this relationship. While the findings here are specific to California closed-cone pine forests, this framework, which integrates seed supply and fuel availability, could be applied more broadly to evaluate potential resilience to reburns and climate warming in other serotinous forests using forest type-specific demographic and fuel development data.

Findings from this work indicate the critical importance of the timing and extent of seed availability to post-fire regeneration following short-interval reburns (Chapter 4, Chapter 5). Although some previous work has quantified seed availability and cone development following fire (Gil et al. 2021), the distance to the nearest live tree or unburned edge is often considered a proxy for post-fire seed availability, regardless of tree size, age, or species life history. As short-interval fires inevitably increase with increasing fire activity due to climate change, further work is needed to understand how reproductive capacity of conifer species develops in fire-prone forests. While this work focused on understanding early post-fire outcomes (within two years following fire), long-term dynamics can have substantial impacts on forest recovery following disturbance. The post-fire plot network and findings from Chapter 5 provide an excellent opportunity to build longitudinal studies and track demographic trends in these stands over time. Further, additional work is needed to understand the demographic importance of senescence risk, the loss of reproductive maturity as trees age and die in the absence of fire (Enright et al. 2015). Although there is broad evidence that senescence risk is occurring due to fire exclusion in knobcone pine forests specifically (Reilly et al. 2019), how it constrains seed supply at the time of fire, thereby resulting in a second period in which fuel is sufficient and seed limiting, is poorly understood.

While California closed-cone pine forests appear to be resilient to direct and indirect climate change effects that have occurred thus far, continued warming and increases in fire activity may erode resilience. However, post-fire forest expansion into pre-fire non-forest and fuel limitation associated with localized serotinous population reduction following multiple short-interval fires could provide important negative feedbacks on potential increases in fire activity, facilitating species persistence at a broader spatial scale. Anticipation of post-fire forest resilience in serotinous forests requires integration of temporal trends in fuel accumulation and demographic rates, suggesting a need for increased understanding of species-specific demographic rates. This work provides a framework for understanding how coniferous forests dominated by serotinous species may respond to climate change effects in ecosystems across North America, with implications for guiding post-fire management.

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