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*Utah State University*

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HIDDEN MECHANISMS OF CLIMATE IMPACTS IN WESTERN FORESTS:  
INTEGRATING THEORY AND OBSERVATION

FOR CLIMATE ADAPTATION

by

Sara J. Germain

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

of

DOCTOR OF PHILOSOPHY

in

Ecology

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Logan, Utah  
2022

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## ABSTRACT

Hidden Mechanisms of Climate Impacts in Western Forests:  
Integrating Theory and Observation for Climate Adaptation

by

Sara J. Germain, Doctor of Philosophy

Utah State University, 2022

Major Professor: Dr. James A. Lutz  
Department: Wildland Resources

Fire, insects, and disease are necessary components of forest ecosystems. Yet, climate change is intensifying these tree stressors and creating novel dynamics that threaten forest survival. This dissertation synthesized field observations with disturbance forecasts in western forests to identify 1) how conventional modeling methods underestimate forest loss with climate change, and 2) how facilitative relationships might be harnessed by managers to prevent forest loss.

In Chapter II, I tested whether increasingly extreme weather with climate change increases Pacific yew extinction risk. I found that conventional modeling methods underestimated local extinction risk because trees were adapted to a range in average conditions, but had limited tolerance of extreme drought.

In Chapter III, I predicted the future strength of a Pacific Northwest foundational forest community. I found that heterospecific competition is more sensitive to drought than conspecific competition on dry microsites, increasing the risk of competitive

exclusion and thereby weakening mechanisms of community stability.

In Chapter IV, I examined observational evidence of the growth-differentiation balance hypothesis obtained through tree rings to measure tree resilience to over three centuries of fire exclusion, climate change, and compound drought-fire-insect disturbance. I identified legacy effects of fire suppression through decreased resistance and resilience of large *Pinus* in white fir-dominant areas. Woody species diversity, however, was able to counteract these effects.

In Chapter V, I disentangled aboveground and belowground processes promoting tree resistance to natural enemies across regional differences in climatic and environmental conditions. I found that woody species diversity increased survival of large trees comprising 17 common western species, but only if the diversity of woody neighbors shared the same mycorrhizal network.

I identified how biodiversity can increase forest resistance and resilience to disturbances, but also found climate change to be weakening the processes responsible for maintaining biodiversity. Managers must more actively preserve biodiversity to ensure forests are able to continue provisioning essential services, such as carbon storage, in the future. These four long-term studies of spatially explicit, cause-specific tree mortality provided mechanistic insights into forest assembly and change that will improve vegetation model accuracy and inform management of mature forests in western North America.

(343 pages)

## PUBLIC ABSTRACT

Hidden Mechanisms of Climate Impacts in Western Forests:  
Integrating Theory and Observation for Climate Adaptation

Sara J. Germain

Fire, insects, and disease are necessary components of forest ecosystems. Yet, climate change is intensifying these tree stressors and creating new interactions that threaten forest survival. This dissertation combined field observations with statistical predictions of changing disturbances in western forests to identify 1) how conventional models may underestimate future forest loss, and 2) how positive relationships between trees may be exploited by managers to prevent forest loss.

In Chapter II, I tested whether increasingly extreme weather with climate change increases Pacific yew extinction risk. I found that conventional modeling methods underestimated local extinction risk because trees were adapted to a range in average conditions, but had limited tolerance of extreme drought.

In Chapter III, I predicted whether future climate change will alter the strength of competition between species (heterospecifics) versus within species (conspecifics). I found that heterospecific competition is more sensitive to drought than conspecific competition, leading to higher tree mortality during drought than is currently expected.

In Chapter IV, I looked at sugar pine tree rings to measure how pines respond to three centuries of fire exclusion, drought, fire, and a bark beetle outbreak. I found that fire suppression led to higher competitive stress, which decreased pines' resilience to fire, and consequently, decreased pines' survival during a subsequent bark beetle outbreak.

Woody species diversity, however, was able to increase pine survival following fire and bark beetles by allowing higher pine growth and defenses.

In Chapter V, I tested whether beneficial relationships between trees and mutualistic fungi could help trees survive across regional differences in climate, environmental conditions, and disturbances. I found that woody species diversity increased large-diameter tree resistance to insects and disease, but only if those species shared a mycorrhizal network. Large trees comprising 17 common western species across three canonical forest types showed this pattern — despite residing in different topographic positions and climatological contexts.

I identified how biodiversity can increase forest resistance and resilience to disturbances, but also found climate change to be weakening the processes responsible for maintaining biodiversity. Managers must take a more active approach to cultivating and preserving forest tree biodiversity to ensure forests are able to continue provisioning essential services, such as carbon storage, in the future. These four long-term studies of spatially explicit, cause-specific tree mortality provided useful insights into tree survival and forest change that will improve vegetation model accuracy and inform management of mature forests in western North America.

*I*

*dedicate*

*this dissertation to*

*my dearest grandmother:*

*you loved me unconditionally and*

*taught me to fill my lungs with mountain air;*

*to raise my eyes to the tree silhouettes atop ridgelines*

*and recognize them as my ancestors, gazing down upon me*

*and offering their protection.*

*Now,*

*in like*

*kind,*

*you*

*gaze*

*upon me*

*so I may still*

*feel your love in the trees*



## ACKNOWLEDGMENTS

I am especially grateful for the endless love and support of my family, Dave, Twinkle, and Bebe: our early adventures in the desert of southern Utah cultivated my love and appreciation for the natural world, without which I would not be where I am today. I also must thank Aunt Gloria's cookies for fueling the first full draft of this dissertation. I am thankful for the many friends who have kept me happy and sane during these years, including countless nights of banter over card games that helped me recover from hours of analysis. Finally, I am forever grateful to the magic in the air at Yosemite that led me to my husband Tucker, who has been an invaluable sounding board for ideas, data visualization wizard, and source of support throughout my graduate program.

I am fondly grateful to my advisor, Jim Lutz, for his candid mentorship, spontaneous poetry, and practical advice. Jim, you once said that I may grow to hate you, as you would always push me [hard] to achieve my best; all I can do now is thank you sincerely and say that, once again, you were wrong about that first part. I thank my committee member, Justin DeRose for connecting me with the dendroecological community, providing the tools for me to take my studies in a new direction, and being patient with my many questions. I thank my other committee members Andrew Kultmatiski, Margaret Metz, and Bonnie Waring for their valuable comments on my dissertation and their advice throughout my graduate program; and I also thank Julia Burton and Mike Kuhns for their guidance as members of my initial doctoral committee. I am grateful for the participants of the Forestry Discussion group, including Karen Mock, Jim Long, Barbara Bentz, Justin DeRose, Larissa Yocom, Sasha Broadstone, Alex Howe, and David Soderberg, whose vibrant minds and probing conversations contributed

meaningfully to this dissertation.

This dissertation honors Jerry Franklin for being an early advocate of sustainable forest management and permanent plot research. I am deeply grateful to Jim Lutz, Mark Swanson, and Andrew Larson for carrying on this vision, and for their friendship and mentorship in the field. I thank all those who have worked with me in the plots over the past decade, bringing laughter, music, and ongoing friendship: Kendall Becker, Erika Blomdahl, Tucker Furniss, Sean Jeronimo, Caroline Kittle, and Soren Struckman. I also wish to thank the countless field technicians, survey experts, and volunteers who contributed their time to the establishment and maintenance of the plots, without whom this work would not be possible. Thank you for entertaining my rants about plants and for giving me kind, supportive feedback: it has helped me build confidence and become a better mentor and teacher.

This research would not have been possible without financial support provided by the National Science Foundation, Quinney College of Natural Resources, USU Ecology Center, and the Utah Agricultural Extension Station. I would like to thank the many advocates for science and conservation that have contributed ideologically, politically, and financially to the continuation of these institutions: keep fighting for science.

Sara J. Germain

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# CHAPTER I

## INTRODUCTION

### **Climate Change and Carbon Storage**

Building forest resistance and resilience to climate impacts is a global priority (Holling 1973, Anderegg et al. 2020), not only to maintain ecosystem services for human use (Thom and Seidl 2016) but also to provide a key counterbalance to increasing atmospheric carbon and climate change (Adams et al. 2010, Grassi et al. 2017). Climate warming is instigating biomass declines (Breshears et al. 2005, Allen et al. 2010), migrations (Harsch et al. 2009, Lenoir and Svenning 2015), and compositional change (Gonzalez et al. 2010, Duque et al. 2015) in forest ecosystems across the planet. Many of these changes are projected to proceed with increased severity as global warming progresses (Easterling et al. 2000, Allen et al. 2015, Millar and Stephenson 2015), foreboding an incredible loss of carbon storage that is only likely to make climate change more severe (Cox et al. 2000, Adams et al. 2010, Pan et al. 2013). Unfortunately, models of forest-climate feedbacks greatly oversimplify forest dynamics – emphasizing growth rather than mortality, focusing on direct climate effects, and characterizing forests by coarse-grain functional type – and thereby tend to overestimate future carbon storage capacity (Purves and Pacala 2008, Allen et al. 2015, Fisher et al. 2018, Anderegg et al. 2020). Investigating the direct and indirect pathways by which climate change is altering all aspects of forest demography can clarify the magnitude of climate impacts, benefitting earth science and ecology alike.

Climate change can have positive or negative impacts in forests due to the contrasting responses of tree phenology and disturbance regimes. Warmer temperatures

can increase photosynthetic rates (Ford et al. 2016) and tree recruitment (Peterson and Peterson 2001), particularly in high-elevation or -latitude systems that are currently limited by cold temperatures. While increasing the period available to photosynthesize may portend greater productivity, there is an upper limit: temperatures too high can reduce tree growth and fecundity (Clark et al. 2021, Larysch et al. 2022). Perhaps more importantly, hotter drought and its indirect effects through interactions with fire, stand densities, and insects increases tree mortality, precluding growth and continued recruitment all together (McDowell et al. 2008, Anderegg et al. 2015). Moreover, compensatory tree recruitment is highly uncertain in a climate-change context (HilleRisLambers et al. 2015, Davis et al. 2019), often unable to keep pace with rapid declines (Millar and Stephenson 2015, Coop et al. 2020). Yet, large-scale vegetation models rarely consider the nonlinear responses of multiple demographic rates to changing climate (Fisher et al. 2018). In consideration of this area for further refinement, this dissertation examines growth, recruitment, mortality, and their net balance in western temperate forests.

Temperate mixed-conifer forests of western North America (wNA) are a hotspot for carbon storage and forest-climate feedbacks. Though boreal forests store more soil carbon (Dixon et al. 1994), the highest aboveground biomass on earth is found in coastal temperate forests (Anderson-Teixeira et al. 2021). Mature forests of wNA have among the highest carbon stocks (Keith et al. 2009, Stephenson et al. 2014, Pioniot et al. 2022) and longest carbon residency times in the world (Lutz et al. 2021a, Birch et al. 2021). As such, wNA forest declines can have broadly reaching effects (Garcia et al. 2016, Swann et al. 2018) and pose a substantial threat to continued carbon storage, wildlife habitat, and

timber production alike. Unprecedented fire severity (Westerling et al. 2006, Coop et al. 2020), bark beetle outbreaks (Raffa et al. 2008, Weed et al. 2013), and drought-induced tree mortality (Van Mantgem and Stephenson 2007, Williams et al. 2013) have even rendered some forests a larger and more sustained net carbon source than expected after historical disturbances (Kurz et al. 2008, Hicke et al. 2012). Conservation of these important carbon stores hinges not just upon an accurate understanding of the rapidly changing processes underlying their decline, but also identification of mechanisms responsible for building resistance to change and resilience (i.e., recovery) following disturbance (Holling 1973, Peterson et al. 1998).

Mixed conifer forests of wNA may be particularly vulnerable to climate change due to their relatively low species richness and therefore a reduced insurance effect of biodiversity (Yachi and Loreau 1999, Jactel and Brockerhoff 2007). Compared with tropical forests, for instance, temperate coniferous forests contain tenfold fewer woody species (Lamanna et al. 2014). Individual species responses to changing climate are therefore more likely to represent a larger portion of the community and are unlikely to be tempered by redundant species (Loreau and de Mazancourt 2013). Moreover, individual species can have important controls on community-level forest dynamics (Dayton 1972, Uriarte et al. 2004), meaning their selective loss due to climate change can feedback to further reduce community diversity and stability (Ellison et al. 2005, 2019, Angelini et al. 2011). Yet, vegetation models tend to regard forests in terms of their functional type (e.g., coniferous vs. broadleaf) rather than using finer-grained characterizations of forest composition (Purves and Pacala 2008), preventing assessment of the unique vulnerability that may arise from low biodiversity in western forests. This

dissertation takes the opportunity to assess the extent to which western forest biodiversity – even in its limited state – may be able to protect forests from increasing threats of insects, disease, and competition during hotter droughts; and to identify how climate responses scale from individual species to the population and community levels.

A substantial proportion of carbon fluxes and storage in western temperate forests can be attributed to large-diameter trees (Lutz et al. 2012, 2018, 2021b). Large trees tend to have lower ratios of leaf area to stem mass, so in contrast with smaller trees, carbon storage as biomass is prioritized over high rates of carbon fixation (i.e., low relative productivity *sensu* Pioniot et al. 2022). This observation is sometimes misinterpreted to mean that large trees do not sequester as much carbon as young trees; however, large trees dominate woody productivity and show higher absolute growth rates per individual tree than smaller counterparts (Stephenson et al. 2014, Pioniot et al. 2022). Large trees' deep roots and creation of coarse woody debris, together with slow decomposition rates in temperate forests, promotes long-term storage in these pools and as recalcitrant soil carbon (Harmon and Hua 1991, Lal 2005, Zhou et al. 2006). Thus, preservation of large trees and allowing the transition of medium trees into the large-diameter cohort is central to maintaining carbon storage in living biomass, deadwood, and soil carbon pools, in addition to protecting the numerous ecosystem services provided by large trees (Lutz et al. 2018).

Despite containing large-diameter trees, it is often observed that mature forests (>100 yrs) sequester less carbon than younger forests (see Harmon 2001 for full discussion). Mature forests often fix carbon at similar rates to younger forests (equivalent net primary production), but carbon losses due to decomposition of woody debris reduce

ecosystem-level sequestration rates (Anderson-Teixeira et al. 2021). While the rate of carbon accumulation may decelerate as stands age, it still remains positive and is sometimes comparably high as younger forests (Besnard et al. 2018, Anderson-Teixeira et al. 2021); this allows mature forests to remain a valuable carbon sink (Luyssaert et al. 2008). More importantly, mature forest carbon stocks absolutely dwarf those of younger forests, especially in the temperate zone: the live and deadwood contributions of large diameter trees, uneven-aged stand structure, and long-lived soil organic carbon make mature forests the dominant source of carbon storage globally (Smithwick et al. 2002, Zhou et al. 2006, Anderson-Teixeira et al. 2021).

Unfortunately, primary forests were largely eradicated from the North American landscape by the rapacious harvest practices of early European colonizers (Birdsey et al. 2006, Pan et al. 2013). Younger forests, being more widely distributed and showing high carbon sequestration rates, have therefore become the focus of overly optimistic carbon offset programs (Canham 2021, Badgley et al. 2022). Yet, a large net carbon release is associated with converting old forests to young (either through anthropogenic or natural disturbance), making the creation of young forests for the sake of carbon sequestration a misguided choice (Harmon et al. 1990, Luyssaert et al. 2008). Moreover, high tree densities predispose young forests to more severe wildfire and outbreaks of insects or disease (Raffa et al. 2008, Rautiainen et al. 2011); this is particularly the case for fire-suppressed forests (Hessburg et al. 2022), where the sustained future of second-growth carbon stores is highly uncertain (Anderegg et al. 2020, Coop et al. 2020). In contrast, mature forests are expected to maintain biomass accumulation and carbon storage for centuries (Luyssaert et al. 2008) if they can be protected from harvest and climate change



impacts (Lutz et al. 2009, Lindenmayer et al. 2012, Bennett et al. 2015). In acknowledgement of these points, this dissertation identifies pathways to conserve mature forests and large-diameter trees in an effort to inform climate change mitigation in forest management (Swanson and Franklin 1992, Kauppi et al. 2015).

### **Forest Management: A Circular Evolution**

For millennia prior to European colonization, indigenous peoples of North America practiced sophisticated land management that prioritized prescribed fire to maintain forest health; and the cultural and practical appreciation for large trees precluded widespread fatal harvest of mature forests (Vale 2013). When European colonizers instigated the mass genocide and relocation of indigenous peoples, they indirectly eliminated anthropogenic fire ignitions and reduced fire on the landscape as well. In contrast with indigenous land use, large trees became prime targets for harvest, and intensive clear-cutting converted much of the North American landscape to secondary forest (Pan et al. 2013). Due to the solitary focus on extraction, a healthy forest became defined as one with trees growing at their maximum capacity, protected from insects, disease, and wildfire in order to preserve later yields (Odum 1969, Kolb et al. 1994). This perspective gave way to the ideology that old forests cease to accumulate carbon, a convenient justification to continue harvesting large trees.

In recent decades, the consequences of this history of clearcutting followed by overstocking in fire-suppressed secondary forests (Rautiainen et al. 2011) have come to fruition: wildfires are more severe and burn with more homogeneous effects over larger contiguous areas than ever before (Hessburg et al. 2005, North et al. 2015, Abatzoglou et al. 2021). Waking from the dream that was the colonial paradigm, managers now

acknowledge that natural disturbances – including fire, insects, and disease – are essential elements of a healthy and resilient forest (Kolb et al. 1994, Raffa et al. 2009). This has given rise to the conventional paradigm of natural disturbance-based management (Drever et al. 2006), which is accompanied by a reemergence of traditional ecological knowledge (Turner and Spalding 2013) promoting fire use (van Wagtendonk 2007) and preservation of mature forests (Swanson and Franklin 1992). Unfortunately, the legacy effects of colonialization (namely, fire suppression) make the task of restoring forests more difficult (North et al. 2022). Moreover, the lingering misconception that a healthy forest is a young, dense, and rapidly growing one that must be protected from all disturbance processes is still persistent at even the highest levels of policy making (Luyssaert et al. 2008).

As the effects of climate change compound with the extended consequences of historical forest mismanagement, managers are increasingly required to balance the conflicting objectives of preserving habitat and biodiversity, maximizing carbon storage to mitigate climate change, and continuing harvest to keep pace with the demands of a rapidly growing populous; all while reintroducing fire to the delicate tinderbox that is wNA. Extensive efforts are being made to increase forest resistance and resilience in the face of these compound stressors (Halpern 1988, Churchill et al. 2013, DeRose and Long 2014, Hood et al. 2016, Bryant et al. 2019). However, a contradiction has arisen that requires further refinement of the new healthy forest paradigm as we enter the era of climate change: fire, insects, and disease are natural and necessary components of forest ecosystems that cannot be indefinitely suppressed; yet, climate change is intensifying these stressors, creating novel dynamics that threaten forest survival (Raffa et al. 2008,

Jactel et al. 2012, Weed et al. 2013, Lancaster et al. 2017). Given that eradication of these disturbances is not advisable nor tenable, the natural next step in forest resilience research is to identify equal and opposite mechanisms of facilitation that might be harnessed by managers to reduce the magnitude of forest loss (Simard and Austin 2010, Gorzelak et al. 2015). In the absence of this more holistic perspective, even the best-intentioned silvicultural treatments may exacerbate climate change impacts (Suttle et al. 2007, Jactel et al. 2009, Clark et al. 2016).

### **Data Summary**

This dissertation draws upon the Smithsonian Forest Global Earth Observatory (ForestGEO) network of permanent forest monitoring sites (Anderson-Teixeira et al. 2015, Davies et al. 2021), which provides a holistic view of forest functioning by censusing all woody stems  $\geq 1$  cm in diameter, tracking demography over time, surveying physical and chemical soil properties, and investigating biotic drivers of tree mortality. The opportunity to investigate interactive and indirect climate effects in mature forests of wNA was provided by the long-term, spatially explicit sample of both fine-scale environmental heterogeneity within each site and regional-scale differences in edaphic factors and forest type between sites (Fig. 1.1). The large continuous spatial scale ( $>10$  ha each), large tree sample size ( $\sim 100,000$  individuals), and annual sampling interval allowed investigation of interactions between the distantly located large-diameter trees and assessment of their endemic (i.e., low rate) mortality processes over time (Lutz 2015).

The Wind River Forest Dynamics Plot (WFDP) represents low-elevation mixed-conifer forests of the Pacific Northwest, USA that have **among the highest carbon**

**stocks in the world** (Smithwick et al. 2002, Lutz et al. 2014). Recent work has shown these to contain 2 to 3 times more total carbon than other northern temperate forests and even more aboveground biomass than most tropical forests (Keith et al. 2009, Anderson-Teixeira et al. 2021). The mild coastal climate allows trees to continue fixing carbon throughout the year (Emmingham and Waring 1977, Emmingham 1982), and infrequent fire return intervals (Shaw et al. 2004) allow trees to attain very large statures and old age (Waring and Franklin 1979). Despite the theoretical potential of these old forests to continue accumulating carbon, biomass is decreasing in the WFDP: the majority of biomass is stored in large trees, and these are recently experiencing higher mortality rates than expected (Lindenmayer et al. 2012, Pioniot et al. 2022).

The Yosemite Forest Dynamics Plot (YFDP) represents mid-elevation mixed-conifer forests of the Sierra Nevada, USA (Lutz et al. 2013). Fire is the **greatest source of outward carbon flux** in forests: the YFDP burned midway through the study, allowing the investigation of interacting climate-fire drivers of carbon sequestration and storage. Though historically exposed to frequent fire, fire suppression since 1900 dramatically increased forest densities (Barth et al. 2015), and together with unprecedented global change-type drought (Adams et al. 2009, Millar and Stephenson 2015, Belmecheri et al. 2016), resulting in higher severity fire than was historically observed (Scholl and Taylor 2010, Kane et al. 2015). Thus, while fire reintroduction began the important work of restoring the forest to pre-fire suppression densities, the unexpectedly high mortality rates of large-diameter trees in the five years post-fire compounded carbon losses and revealed unforeseen legacy effects of fire suppression (Stenzel et al. 2019).

The Utah Forest Dynamics Plot (UFDP) represents high-elevation forests of the interior west and Rocky Mountain regions, comprising microcosms of multiple forest types: aspen, spruce/fir, and five-needle pines in treeline ecotones (summarized by Furniss et al. 2017). The UFDP contains individuals belonging to the longest-lived gymnosperm species (*Pinus longaeva*) and angiosperm species (*Cercocarpus ledifolius*) on earth. The life history traits of these species, extremely slow decomposition rates due to cold temperatures, and infrequent fire return intervals (DeRose and Long 2012b, Halofsky et al. 2018) allow **millennial-scale carbon storage** in living biomass and deadwood pools (Lutz et al. 2021a, Birch et al. 2021). Being a temperature-limited forest, this provides the opportunity to examine possible positive climate impacts on growth and recruitment (Peterson and Peterson 2001) alongside possible negative climate impacts via increased prevalence of insects and disease (DeRose and Long 2012a).

The research contained in this dissertation builds upon theoretical ecology (Hermes and Mattson 1992, Chesson 2000, Barbosa et al. 2009, Das et al. 2013) and field observations at these three monitoring sites to 1) test the continued relevance of past paradigms in a climate-changed future, 2) elucidate previously unseen mechanisms of forest responses to changing climate, and 3) lay the foundation for a holistic future paradigm guiding forest management and climate change mitigation in forests. This work is organized by two overarching themes: Chapters II and III quantify and forecast the direct and indirect effects of climate change on tree mortality in mature western forests at the individual, population, and community levels of organization; and Chapters IV and V identify manageable pathways of facilitation among trees and their mutualists to increase forest resistance and resilience to climate-altered disturbances across centennial temporal

periods and regional spatial scales.

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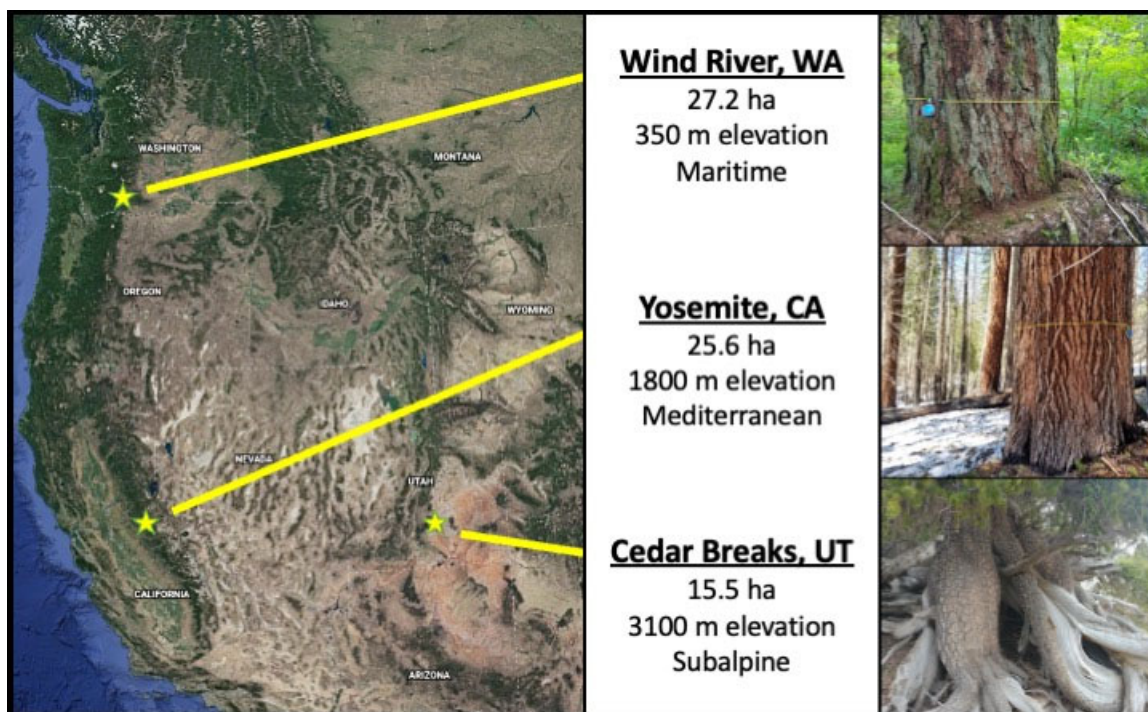
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## Figures



**Figure 1.1.** Locations in North America of the three Smithsonian Forest Global Earth Observatory field sites that were the focus of this dissertation: Wind River Forest Dynamics Plot (WFDP), Yosemite Forest Dynamics Plot (YFDP), and Utah Forest Dynamics Plot (UFDP). Plot sizes, average elevation above sea level, and climatic zoning described. Tree photos corresponding to each plot depict *Pseudotsuga menziesii* (WFDP), *Pinus lambertiana* (YFDP), and *Pinus longaeva* (UFDP).

## CHAPTER II

CLIMATE EXTREMES MAY BE MORE IMPORTANT THAN CLIMATE MEANS  
WHEN PREDICTING SPECIES RANGE SHIFTS<sup>1</sup>**Abstract**

It is well known that temperatures across the globe are rising, but climatic conditions are becoming more variable as well. Forecasts of species range shifts, however, often focus on average climate changes while ignoring increasing climatic variability. In particular, many species distribution models use space-for-time substitution, which focuses exclusively on the effect of average climate conditions on the target species across a geographic range and is blind to the possibility of range-wide population collapse with increasing drought frequency, drought severity, or climate effects on other co-occurring species. Relegated to assessments of broad demographic patterns that ignore underlying biological responses to increasing climatic variability, this prevalent method of distribution forecasting may systematically underpredict climate change impacts. We compare six models of survival and abundance of a subcanopy tree species, *Taxus brevifolia*, over 40 years of past climate change to disentangle multiple sources of uncertainty: model formulation, scale of climate effect, and level of biological organization. We show that drought extremes increased *Taxus* individual- and population-scale mortality across a wide geographic climate gradient, precluding detection of a monotonic relationship with average climate. Individual-scale climatic variability models derived from longitudinal data had the highest predictive accuracy

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<sup>1</sup> This chapter was published in *Climatic Change* on October 1, 2020, and should be cited as: Germain, S. J., and J. A. Lutz. 2020. Climate extremes may be more important than climate means when predicting species range shifts. *Climatic Change*, 163: 579-598. <http://dx.doi.org/10.1007/s10584-020-02868-2>

(82%), whereas mean climate models had the lowest accuracy (<65%). Our results highlight that conclusions drawn from forecasts of average warming alone likely underpredict climate change impacts by ignoring indicators of range-wide population declines for species sensitive to increasing climatic variability.

## **Introduction**

Predicting species range shifts is a central aim of climate impacts research (Parmesan and Yohe 2003), both to identify conservation priorities (VanDerWal et al. 2013, Urban 2015) and to inform coupled global climate models (Stark et al. 2016, Fisher et al. 2018). Changing forest distributions are a particularly large source of uncertainty when predicting future climate (Purves and Pacala 2008) due to the prominent role of forest biomes in regulating global carbon and hydrological cycles (Snyder et al. 2004, Adams et al. 2010), in tandem with the complex biotic and abiotic processes that govern forest dynamics (Franklin et al. 1987, 2002). Distribution forecasts in forests must therefore consider the suite of changes associated with global warming: gradually increasing average temperatures can allow species adaptation (Davis and Shaw 2001), for example, while extreme climate events (e.g., drought) can lead to rapid die-offs due to strains on traits that developed under historic ranges of variability (Breshears et al. 2005, McDowell et al. 2008, Allen et al. 2010, Chevin et al. 2013). Though climatic extremes are projected to grow in severity and frequency with continued climate change (Easterling et al. 2000, Field et al. 2012, Dai 2013), many species distribution models remain focused on average climate changes (e.g., Sitch et al. 2008).

The confounding roles of non-climatic factors, including trophic interactions (Bentz et al. 2010, Wisz et al. 2013), tree neighborhoods (Larson et al. 2015, Ettinger and

HilleRisLambers 2017), and disturbance history (Lenoir et al. 2010, Wason and Dovčiak 2017), are gaining attention in efforts to reduce uncertainty persistent in distribution forecasting (Thuiller 2004, Buisson et al. 2010). Likewise, recent research has demonstrated species responses to shifting climate patterns, not just average climate changes, associated with global warming (Parmesan et al. 2000, Knapp et al. 2008). Nonetheless, models of species distributional shifts tend to ignore these confounds and distinctions (Clark et al. 2011). In particular, the commonly used space-for-time substitution approaches (SFT) assume that species distributions are driven primarily by average climate changes (Elith and Leathwick 2009, Blois et al. 2013). However, species sensitive to climate extremes, such as increased annual drought compared to site averages (Easterling et al. 2000, Condit et al. 2004, Allen et al. 2010), are more vulnerable to increasing drought associated with climate change (Walther 2003, Dai 2013, Das et al. 2013). These species are less able to escape the effects of climate change via migration because interannual variability exists across the entire range (Parmesan et al. 2000, Condit et al. 2004). Increasingly variable climate may therefore contribute to population declines and higher extinction risk (Lenoir and Svenning 2015), but remains unexplored by most distribution models (Clark et al. 2011, Fordham et al. 2012).

The primary approach to distribution forecasting utilizes space-for-time substitution (e.g., climatic niche models, Dynamic Global Vegetation Models [DGVMs]). These models compare average climate conditions across a species' range to make inferences about climate change-induced shifts in the future (Thuiller 2003). Contemporary relationships between species occurrences and average regional climate are extrapolated to predict future occurrences with climatological change over time.

Assumptions of SFT forecasts include: 1) species are in equilibrium with climatic and environmental factors; 2) phenotypic variability, evolutionary adaptation, biotic relationships, and disturbance regimes can be ignored (Franklin 2010); and 3) species will shift in tandem with the average climatic niche they currently occupy as it moves with changing climate.

While SFT models can be highly predictive over centennial timescales (Hijmans and Graham 2006, Blois et al. 2013), their usefulness in predicting species responses to climate over the shorter, decadal time frames necessary for managers to develop climate-adaptation strategies has been called into question (Franklin 2010, Brun et al. 2016). For instance, forest communities vary in their spatial patterns throughout geographic ranges, reflecting past community assembly processes (Freund et al. 2014, Birch et al. 2019), but SFT models are blind to population and community dynamics (Fordham et al. 2012, 2013). Importantly, model assumptions may be violated in a climate-change context, as no-analogue climates (Williams and Jackson 2007), novel community assemblages (Suttle et al. 2007, Gilman et al. 2010), and altered disturbance regimes (Littell et al. 2010, Franklin et al. 2016) can disrupt species-environment equilibria.

An alternative approach is longitudinal modeling, which correlates climatic fluctuations over time with observed temporal population trends to forecast climate-induced range shifts (Clark et al. 2011, Renwick et al. 2018). These models assume: 1) population responses to interannual climate can be extrapolated to long-term climate trends, and 2) phenotypic variability and evolutionary adaptation can be ignored. Unlike SFT, longitudinal models can operate across levels of biological organization to capture individual- and population-level responses to climate. Models able to consider climate

effects on individual organisms can disentangle the unique and perhaps contrasting responses of mortality, recruitment, and growth processes (Lutz et al. 2014, Wason and Dovčiak 2017) while controlling for variation in stand age or site productivity (Larson et al. 2008). Likewise, individualized information can increase the power of statistical tests due to replication being at the level of the individual and thus detect relationships that may not be apparent with population-level datasets (but see Tredennick et al. 2017). Despite these benefits, limited data and computational power often relegate longitudinal models to describing net demographic patterns at the population scale rather than underlying biological processes.

Space-for-time and longitudinal models alike often recognize climate impacts as range shifts down a climate gradient (i.e. to cooler, wetter climates associated with higher elevations or latitudes; a “warming fingerprint”)(Parmesan and Yohe 2003). This pattern is identified via positive species responses (e.g., population increase) at the leading edge of species distributions (i.e. cooler, wetter locations in SFT models; cooler, wetter years in longitudinal models) and/or negative responses at the trailing edge (Gedir et al. 2015, Lenoir and Svenning 2015). When opposite trends are observed, including no distributional shifts or equal shifts up and down the climate gradient (Harsch et al. 2009, Chen et al. 2011, Rapacciuolo et al. 2014), it is concluded that species distributions are unlikely to shift with changing climate. Species’ ranges can shift dramatically, however, following die-offs associated with climate extremes (Thomas et al. 2004, VanDerWal et al. 2013). This is particularly evident in forests, where altered drought regimes reduce performance of trees adapted to cooler/wetter sites and those adapted to warmer/drier sites alike, even if mean annual climate stays constant (Walther 2003, Knapp et al. 2008,

Anderegg et al. 2013).

We add to ongoing efforts to improve vegetation components of earth system models (Moorcroft 2006, Purves and Pacala 2008) by quantifying the potential for bias in forecasts utilizing climate means to estimate species range shifts. We develop a forecasting ensemble that synthesizes data from a Smithsonian Forest Global Earth Observatory site (ForestGEO; Anderson-Teixeira et al. 2015) and region-wide forest monitoring sites to decouple uncertainty associated with temporal scale of climate effect (relative or average climate differences) from uncertainty related to model formulation. The prediction ensemble: 1) compares predictions of longitudinal and SFT models to determine whether species' responsiveness to climate extremes may preclude detection of an average climate effect using the subcanopy gymnosperm, *Taxus brevifolia*, as an example; and 2) assesses climate effects at the individual and population scales to characterize species responses in terms of biological processes and net demographic change. No model prediction ensemble of which we are aware has compared individual- and population-scale longitudinal models to SFT models, presenting the unique opportunity to also decouple uncertainty related to scale of biological organization from that related to scale of climate effect. We then critically examine the disparate ecological interpretations of each model to identify primary sources of uncertainty in forecasts of distributional change, thereby improving our ability to recognize climate change impacts and forecast future species distributions.



## Methods

### Species and Site Data

Pacific yew (*Taxus brevifolia* Nutt.) is a near-threatened tree species (Thomas 2013) with considerable ecological, social, and economic value. Recent reports show that mortality rates for *Taxus* in southern Washington State, USA have increased three- to four-fold within the past eighty years (Franklin and DeBell 1988, Busing et al. 1995, Larson and Franklin 2010, Lutz et al. 2014). Shade-tolerant understory tree species like *Taxus* may be particularly sensitive to extreme drought, as these species are adapted to low light levels and low vapor deficits of the understory microclimate and espouse lower water-use efficiencies than drought-tolerant pioneer species (Harrington and Reukema 1983, Lassoie et al. 1985). In the absence of acute disturbances, diminishing *Taxus* populations may therefore be an early indicator of broader forest responses to warming and drying climate trends (HilleRisLambers et al. 2015).

We combined two long-term, spatially explicit datasets spanning 690 m elevation to examine *Taxus* populations within the *Pseudotsuga-Tsuga* (Douglas-fir/western hemlock) forest zone (Franklin and DeBell 1988) of the Pacific Northwest, USA (Table 2.1; Fig. 2.1). In both datasets, all trees  $\geq 5$  cm diameter at breast height (DBH; 1.37 m) were mapped relative to neighboring trees and revisited at roughly 5-yr intervals to track individual survival and sapling recruitment. This protocol enabled the assessment of *Taxus* survival and population growth over time while accounting for competitive dynamics occurring in local tree neighborhoods. The Wind River Forest Dynamics Plot (WFDP)(Lutz et al. 2013) dataset included 23 years within 4 hectares of mature forest in

the T.T. Munger Research Natural Area in Washington State, USA. The Pacific Northwest Permanent Study Plot (PSP)(Acker et al. 1998) dataset comprised nineteen 1-ha to 2-ha, mature forest stands containing at least two live *Taxus* stems in the year of establishment and spanning 24 to 35 years of study (Table 2.1). All twenty stands have temperate maritime climates (cool, wet winters; warm, dry summers) with a strong elevational gradient: higher elevations experience colder, longer winters and cooler, shorter summers compared to lower elevations (Table 2.1, Fig. A.6).

For each stand, we developed population growth summaries: 1) annual population growth rate, calculated as the net change in abundance of *Taxus* stems  $\geq 5$  cm DBH over the study duration; and 2) local extinction time, defined as the number of years from the study end date until fewer than one *Taxus* tree  $\text{ha}^{-1}$  would be expected per the observed population growth rate.

$$(1) \quad L_j = P_{0,j} e^{r_j t}$$

This was found by solving for the time parameter ( $t$ ) of a simple exponential growth model (Eq. 1) for each stand,  $j$ , where  $P_0$  is *Taxus* abundance  $\text{ha}^{-1}$  in the final study year,  $r$  is the observed population growth rate, and  $L$  is the local extinction threshold, which we set to 0.99 (less than one tree  $\text{ha}^{-1}$ ).

### Ensemble Structure

Our prediction ensemble included six models representing one parametric and one non-parametric model each of: individual-level longitudinal, population-level longitudinal, and population-level SFT models (Table 2.1). We compared parametric and non-parametric formulations to distinguish between those constrained by distributional

and homoscedasticity assumptions (parametric) and those more powerful when underlying distributions are unknown (non-parametric). These six model forms have been commonly applied throughout the biogeography and ecology forecasting literature, allowing generalizability to prior research. The ensemble estimated three parameters related to *Taxus* demography: 1) individual mortality probability / instantaneous mortality probability (both individual-level longitudinal models); 2) population growth (one population-level longitudinal model); and 3) population abundance (both population-level spatial models, one population-level longitudinal model; see *Model Formulations*).

All models counted trees that were present at study establishment and trees that recruited during the study period (including year of recruitment for longitudinal models). Individual- and population-level comparisons were only possible using longitudinal models, as SFT models are unable to consider the individual scale. The primary difference between individual and population models was that population-level models quantified abundance or net population growth (i.e. the balance of recruitment and survival), while individual-scale models quantified survival of individual trees. Comparison between the two model types identified how individual survival processes scale up to the population. Agreement between models would suggest that survival (not recruitment) was the predominant process governing population growth and abundance; this is often the case in systems with long-lived species (Silvertown et al. 1993).

We validated models using 10-fold cross-validation following the methods of Cutler et al. (2007), which randomly selects 90% of the data for training at each of ten iterations, allowing all datapoints to be used once for training and once for testing. Using the out-of-sample predictions, we computed: 1) model accuracy (variance explained or

classification accuracy, where applicable); and 2) mean absolute deviance/mean ratios (MADMR)(Kolassa and Schütz 2007), which is mean absolute deviance divided by the mean observed response value. MADMR is an alternative to mean absolute percent error (MAPE) that is better suited to handling zeros while remaining scale-free, therefore allowing a direct comparison of error between models built using different units or response values. All statistical analyses were performed using the R version 4.0.2 statistical software (R Core Team 2020).

### Model Parameters

#### *Climate*

We analyzed *Taxus* responses to changes in biologically meaningful measures of climate to address recent criticisms of the temperature-driven approach (Stephenson 1998, VanDerWal et al. 2013). Interactions between temperature and precipitation can be important determinants of plant photosynthetic rates and survival (Daniels and Veblen 2003). We therefore used climatic water balance models to calculate drought-related climate covariates of physiological importance to plants (Stephenson 1998, Lutz et al. 2010): snowpack and climatic water deficit (Deficit). In this region, low snowpack has not historically been concomitant with high Deficit, and vice versa. In years when low snowpack and high Deficit happen to cooccur, tree mortality can be increased (Germain and Lutz 2022). Climatic water balance models were made for each site using monthly temperature and precipitation time series from the Parameter-elevation Regression on Independent Slopes Model (PRISM) data set (Daly et al. 2008) at an 800-m spatial resolution following the methods of Hostetler and Alder (2016) and McCabe and

Markstrom (2007). Climate values differed between stands but were the same for all trees within a stand.

Longitudinal models captured climate extremes by using maximum modeled annual Deficit anomaly (maximum Deficit) and minimum modeled annual snowpack anomaly (minimum snowpack), which were chosen due to known effects of drought on tree physiology and survival (McDowell et al. 2008, Lian et al. 2020). These values were found by: 1) standardizing annual Deficit and snowpack relative to the long-term (1970 to 2017), stand-level averages, thus controlling for different climate averages among sites and expressing climatic extremes relative to those averages, then 2) selecting the maximum Deficit anomaly and minimum snowpack anomaly within each time interval between measurement years per stand.

Space-for-time models captured average climate differences between stands by using mean modeled annual Deficit and mean modeled annual snowpack over the study duration for each stand (Table 2.1). These values were standardized across all stands to generate climatic units that would be comparable with longitudinal models. We also ran SFT models with maximum Deficit anomaly and minimum snowpack anomaly observed during the study timeframe (calculated by the same methods as for longitudinal models) to ensure that standardization procedures did not change model inferences (no meaningful differences; Tables A.1, A.2).

#### *Abiotic and Biotic Covariates*

To isolate the effects of climate, all six models controlled for the effects of elevation (m) and biotic interactions among forest trees, and individual-level models additionally included log-transformed tree DBH to control for density-independent size

asymmetries in survival. Elevation was standardized across the range to express relative differences between stands; elevation was measured at the stand scale and was therefore considered to be the same for each tree within the same stand (i.e. for individual-level models).

To control for prevailing biotic interactions, we calculated woody species richness (number of species) and the Hegyi crowding index (Eq. 2)(Hegyi 1974, Biging and Dobbertin 1995), which quantifies the potential for competitive interactions among trees. The Hegyi index,  $H$ , is the distance- and diameter-weighted sum of all tree neighbors,  $j$ , within a 10-m radius of focal tree,  $i$ . The 10-m radius for calculating the Hegyi index and species richness was chosen based on previously identified interaction distances in similar forests (Das et al. 2008, Lutz et al. 2014, Das et al. 2018).

$$(2) \quad H_i = \sum \frac{DBH_j}{(1+Distance_{ij})(DBH_i)}$$

Separate Hegyi values were calculated for conspecific neighbors and heterospecific neighbors based on previous research indicating these have distinct effects (Lutz et al. 2014, Germain and Lutz 2022). For individual-level models, neighborhood covariates were standardized per stand to express relative differences between individuals within each stand over time, and to control for site-specific differences in productivity; for population-level longitudinal models, these were standardized across all stands to express relative differences between stands over time across the entire geographic range; for SFT models, we chose the maximum neighborhood covariate values observed per stand over the study timeframe, then standardized across all stands to express relative differences between stands (but not changing over time).

Model Formulations

*Individual-level Longitudinal Models*

We tested generalized linear mixed models (parametric) and Cox survival analysis (semi-parametric). For both models, the interaction between maximum Deficit and minimum snowpack was tested and retained if significant at  $\alpha = 0.05$ . Though our analysis included stand-level (not individual-tree level) climate values, tree-specific Hegyi and richness parameters produced functional sample sizes equal to tree abundance per model (see sample sizes below).

To model individual mortality probabilities, we created generalized linear mixed models (GLMM; Eq. 3; lme4 package; Bates et al. 2015):

$$(3) \quad \hat{p}_{i,j} = \frac{e^{\beta_{0,i} + X'_{1,i,t} \times \theta_1 + X'_{2,j,t} \times \theta_2 + X_{3,j} \times \theta_3 + X_{4,i,t} \times \theta_4}}{1 + e^{\beta_{0,i} + X'_{1,i,t} \times \theta_1 + X'_{2,j,t} \times \theta_2 + X_{3,j} \times \theta_3 + X_{4,i,t} \times \theta_4}}$$

where  $\hat{p}$  is a Bernoulli distributed random variable representing tree mortality probability for individual,  $i$ , at site,  $j$ , which is related (using the Logit link) to sets of tree neighborhood ( $X'_1$ ) and climate covariates ( $X'_2$ ) at time,  $t$ , plus elevation ( $X_3$ ), and tree DBH ( $X_4$ ); with corresponding vectors of coefficients ( $\theta$ ) describing the individual effects of each covariate on survival probability. We included tree-specific random effects to allow intercepts to vary for each individual (i.e. accounting for repeated measures over time;  $n = 1256$ ). Validation metrics were calculated using a classification threshold of 0.053, which was obtained by optimizing sensitivity and specificity of model predictions (Fig. A.1).

To model individual mortality hazard (left-censored, meaning that non-zero

mortality hazard existed for a period before the study conception), we used a Cox analysis (Eq. 4; rms and simPH packages; Gandrud 2015, Harrell Jr. 2020):

$$(4) \quad \lambda_{i,j,t} = \lambda_{0,i,t} e^{X'_{1,i,t} \times \theta_1 + X'_{2,j,t} \times \theta_2 + X_{3,j,t} \times \theta_3 + X_{4,i,t} \times \theta_4}$$

where instantaneous mortality probability (i.e. mortality hazard;  $\lambda$ ) for individual,  $i$ , at time,  $t$ , is a function of the linear combination of time-specific neighborhood, climate, elevation, and DBH covariates scaled by an unspecified baseline hazard function,  $\lambda_0$ . Because Cox regression is a time-to-event model, we ensured that data availability did not bias this model by restricting the dataset to trees residing in the eleven stands with exactly six discrete time steps, between which the number of years spanned 4 to 6 (mode = 5; total timespan = 24 to 30 years). Generalized estimating equations were used to create robust standard errors and account for repeated measures of each tree over time ( $n = 888$ ) (Therneau et al. 2013). Repeated measures were present because all time-series were combined into a single risk set to allow individual tree mortality hazard to be calculated in the context of all observed climate covariate values over time.

#### *Population-level Longitudinal Models*

We compared an autoregressive linear mixed model (AR1; parametric) with Random forests (non-parametric). To model population abundances (continuous variable), we built an autoregressive linear mixed model (Eq. 5; lme4 package; Bates et al. 2015):

$$(5) \quad y_{j,t} = y_{j,t-1} + X'_{1,j,t} \times \theta_1 + X'_{2,j,t} \times \theta_2 + X_{3,j} \times \theta_3$$

where  $y$  is tree abundance per hectare within each forest stand,  $j$ , for year,  $t$ , modeled as a



function of tree abundance in the previous year ( $y_{t-1}$ ) plus tree neighborhood, climate, and elevation covariates ( $n = 20$ ). The interaction between maximum Deficit and minimum snowpack was tested and retained if significant at  $\alpha = 0.05$ . We allowed the intercept and slope of tree abundance in the previous year ( $y_{t-1}$ ) to vary randomly with tree stand to account for disparate initial population sizes at each stand, thus preventing dynamics at stands with the highest *Taxus* abundances from driving model outcomes.

To model population growth (expressed categorically as increasing, stable, or decreasing), we used Random forests (randomForest and rfPermute packages; Liaw and Wiener 2002, Archer 2020). Random forests is a machine learning extension of Classification and Regression Trees (CART) that creates an ensemble of many classification trees (or regression trees, if response is continuous;  $n = 5000$ ). The ensemble is created by: 1) bootstrap aggregation of data to create parallel trees, then 2) random permutation of predictor covariate placements at each tree node, where predictors at earlier tree nodes are assumed to have a stronger relationship with the response than predictors placed at later nodes. Interactions between covariates are captured implicitly by the branching structure of each tree. The predictive abilities of covariates are quantified by variable importance ranks, which are established on the basis of percent decrease in classification accuracy (or in regression, percent increase in mean squared error) when predictors are placed at earlier nodes along decision trees (i.e. modeled having stronger relationship with response variable). Total classification accuracy (or in regression, variance explained) by Random forests refers to the ensemble model. P-values for covariates were attained by permuting the response variable 100 times to produce a null distribution of variable importance, against which the importance metric

generated by the original tree ensemble was compared and assessed at  $\alpha = 0.05$ .

### *Population-level Space-for-time Models*

We compared a simple linear model (parametric) with Random forests (non-parametric). Because no time component was considered by these models, the response variable was maximum tree abundance per hectare that was observed over the study timeframe (though minimum and mean were tested and produced similar results).

To model population abundances (continuous variable), we used a simple linear regression model (Eq. 6):

$$(6) \quad y_j = X'_{1,j} \times \theta_1 + X'_{2,j} \times \theta_2 + X_{3,j} \times \theta_3$$

where  $y$  is maximum tree abundance per hectare within each forest stand,  $j$ , over the study period modeled as a function of tree neighborhood, climate, and elevation covariates. The interaction between mean Deficit and mean snowpack was tested and retained if significant at  $\alpha = 0.05$  (stats package; R Core Team 2020).

To model population abundances (continuous variable), we used Random forests (randomForest and rfPermute packages; Liaw and Wiener 2002, Archer 2020). Rather than building classification trees, we regressed *Taxus* maximum abundance at each site on the site-specific climatic, neighborhood, and elevation covariates (described in *Population-level Longitudinal Models*, above). Total variance and P-values were obtained as previously described.

## Results

### Summary

#### *Climate*

Between 1977 and 2017, all sites showed increasing modeled annual Deficit, decreasing modeled annual snowpack, and high interannual variability for both (Fig. A.6;  $P < 0.05$  for all sites' climatic trends). These trends are projected to continue with warmer temperatures and more variable precipitation (Littell et al. 2010, Dalton et al. 2013). Climatic anomalies showed roughly similar trends as annual Deficit and snowpack, but statistical significance was equivocal among sites at  $\alpha = 0.05$  (increasing high Deficit anomaly: 5% sites; decreasing low snowpack anomaly: 25% sites). Overall, Deficit became higher on average, with higher extremes in the most recent decade, while snowpack became lower on average and with generally lower extremes (Fig. A.6).

#### *Tree Populations*

Average *Taxus* abundance declined overall (mean annual population growth rate = -0.09%, SD = 1.46%). The highest declines (-2.4% to -2.7% yr<sup>-1</sup>) were evident at the WFDP and Ohanapecosh River, Washington (Fig. 2.1, Table 2.1), where *Taxus* is projected to become locally extinct within 189 and 26 years, respectively. *Taxus* distributions did not show a clear warming fingerprint: stands at the leading edge of the mean climate gradient (i.e. higher elevations and latitudes) did not have higher population growth rates than those at the trailing edge (Tables 2.1, 2.3). However, two of the three highest elevation sites (>1000 m) showed positive population growth (Table 2.1), and individual tree survival was enhanced at higher elevations (Table 2.3).

Climate extremes (i.e. anomalies) were more important than climate means for predicting *Taxus* individual survival and population growth. Longitudinal models showed that climatic extremes had strong negative relationships with *Taxus* survival and population growth, which appear to have obscured a relationship with average climate that may otherwise have been evident in SFT models. Consequently, *Taxus*' relationship with climate was only apparent in longitudinal models. The relative climate, individual-scale Cox models had the highest predictive accuracy of the six models tested (81.8%; Table 2.2) and among the lowest error rates (MADMR = 0.08; Table 2.2).

### Ensemble Details

#### *Individual-level Longitudinal Models*

Individual-tree mortality probability (GLMM) and mortality hazard (Cox) were increased by low elevations, high conspecific and heterospecific neighbor density (Hegyí indices), high Deficit, and low snowpack (Table 2.3). Even after accounting for tree density and elevation (i.e. average climate) effects, high Deficit and low snowpack extremes increased mortality. In both models, an interaction between snowpack and Deficit showed that survival was highest when snowpack was high and Deficit was low (Figs. A.2, A.3), but that high snowpacks could not ameliorate Deficit effects after Deficit surpassed  $\sim 2.7$  SD. Predictive accuracy was 14% higher for Cox models than GLMM (Table 2.2). Models showed similar significance and direction of effects for each variable, except for species richness (increased mortality probability but not hazard).

### *Population-level Longitudinal Models*

In agreement with individual-level models, the AR1 population model identified that small *Taxus* populations were related to higher maximum Deficit (Table 2.3). Though not significant at  $\alpha = 0.05$ , Random forests reflected the pattern of *Taxus* population decline with moderately high Deficits (1-3 SD) and at lower elevations (<0 SD; Fig. A.4). In contrast with individual-level models, small *Taxus* populations were related to low species richness and low heterospecific neighbor density. Random forests accuracy was comparable to that of individual-level GLMM at 70.6%. AR1 accuracy overall was highest ( $R^2 = 99.5\%$ ; Table 2.2), but this came almost entirely from random effects (autoregression; conditional  $R^2 = 99.0\%$ ) and predictive abilities of fixed effects was low (i.e. climate, neighborhood, and elevation covariates; marginal  $R^2 = 1.8\%$ ).

### *Population-level Space-for-time Models*

Average climate covariates were not predictive in either model. SLM and Random forests agreed that small *Taxus* populations were associated with low species richness and low conspecific neighbor density (Fig. A.5). Predictive accuracy was 6% higher for Random forests than SLM, but both SFT models had lower accuracy than longitudinal models (Table 2.2).

## **Discussion**

Our study highlights the importance of ensemble forecasting by demonstrating how different models can lead to contradicting inferences: because *Taxus* was more sensitive to climate extremes than climate means, SFT models suggested stable *Taxus* demography, while longitudinal models predicted population declines with continued

climate change. Conclusions drawn from longitudinal models are most consistent with observed *Taxus* declines in recent decades (Table 2.1). These findings illustrate how sensitivity to climate extremes creates uncertainty in species distribution models relying on climate means by obscuring unidirectional shifts along a geographic climate gradient (Lenoir et al. 2010, Boisvert-Marsh et al. 2014). Considering the many oversimplifications and assumptions that are violated by SFT models in a climate change context (Williams and Jackson 2007, Franklin 2010, Fordham et al. 2013), longitudinal model predictions that account for climatic variability and allow explicit consideration of biological mechanisms are likely to be more useful for developing species conservation and climate change mitigation strategies (Iverson and McKenzie 2013).

Though we used a temperate tree species as an example, climate extremes can induce population declines across taxa (George et al. 1992, Parmesan et al. 2000, Carey and Alexander 2003, Matthews and Marsh-Matthews 2003). Conclusions about SFT forecasting methods are thus generalizable to the extent that other species share vulnerabilities with *Taxus*, including thermo-sensitivity, low phenotypic plasticity, sessility, and dispersal limitation (Svenning et al. 2008, Bertrand et al. 2011, HilleRisLambers et al. 2015). For example, abundance declines are most often observed for non-vagile and thermo-sensitive animals (e.g., lizards and amphibians; Carey and Alexander 2003, Dubos et al. 2020), whereas distributions of highly motile animals (e.g., birds) often shift in accordance with a warming fingerprint (Lenoir and Svenning 2015). Likewise, species lacking the phenotypic plasticity required to rapidly respond to short-term fluctuations can less effectively acclimate to climatic extremes (Agrawal 2001, Chevin et al. 2013). When these species are also sessile or dispersal-limited, populations

across the range are likelier to succumb to the negative effects of climate extremes (Coulson et al. 2001, Urban 2015).

Observed tree species' range shifts disproportionately fail to show a strong warming fingerprint, suggesting that these *Taxus* dynamics may represent other temperate tree species particularly well. For instance, the leading edges of a majority (79%) of terrestrial plant ranges have expanded with their changing climate envelope (Lenoir and Svenning 2015), while only half (52%) of treelines have done the same (Harsch et al. 2009, Zhu et al. 2012). Trees are often subject to lagged responses that are asynchronous with the rate of warming (Bertrand et al. 2011), likely due to species interactions (Suttle et al. 2007, Das et al. 2018), recruitment or dispersal limitations (HilleRisLambers et al. 2015), and disturbance legacies (Wason and Dovčiak 2017). We add to this body of work to show there is potential for widespread declines if species with these characteristics are also sensitive to climate extremes over regional scales. These factors together support the interpretation that tree range expansion is unlikely to keep pace with climate warming (Grabherr et al. 1995). It is therefore inappropriate to conclude that species ranges will remain stable with climate change based on SFT model outcomes incongruent with a warming fingerprint, as instead, we might expect range-wide crashes due to increasingly variable climate patterns (Neumann et al. 2017).

Synchronous responses across scales of biological organization support the interpretation that sensitivity to climate extremes may promote range-wide declines. Individual mortality processes were manifest as population declines at the stand scale, even after accounting for elevation gradients and biotic relationships. Recruitment of young trees was not sufficient to offset the increased mortality observed during periods of

drought (HilleRisLambers et al. 2015), highlighting the importance of mortality processes in driving demography of long-lived and/or recruitment-limited species, particularly in temperate forests (Silvertown et al. 1993, Lutz and Halpern 2006, Bertrand et al. 2011). Sensitivity to climate extremes suggests stronger local competition during drought (Clark et al. 2011, Das et al. 2011, Urban et al. 2012, Furniss et al. 2020), which was supported by increased individual mortality with high neighbor crowding (Hegyí indices; Table 2.3). Sensitivity to Deficit could also suggest limited drought tolerance of established individuals (Voelker et al. 2018), resulting in physiological stress and concomitant vulnerability to forest pests (Mattson and Haack 1987, McDowell et al. 2008, Gaylord et al. 2013). In the absence of disturbances such as fire and pest epidemics that can accelerate forest decline (Bentz et al. 2010, Davis et al. 2019), these factors may together explain gradual declines that occur despite species being well-adapted to average climatological conditions (Bréda et al. 2006).

*Taxus* decline predicted by our longitudinal models joins the growing body of work demonstrating negative impacts of increasing drought in forests globally (Breshears et al. 2005, Hutyra et al. 2005, Allen et al. 2010, Neumann et al. 2017). Though not as dramatic as rapid die-offs, gradually declining survival rates can substantially reduce carbon sequestration capacity across forested landscapes (Das et al. 2016). Moreover, increasingly frequent and severe drought in the future (Field et al. 2012, Dai 2013) may result in more rapid population crashes compared to the declines of recent decades (Zhu et al. 2012, Lenoir and Svenning 2015). By ignoring climatic variability and extreme events, reliance on SFT models likely contributes to the growing problem of underestimating habitat loss with changing climate (VanDerWal et al. 2013, Allen et al.



2015).

Reliance on climate means in distribution models creates uncertainty that propagates to estimations of global ecosystem functionality with changing climate (Pan et al. 2013, Allen et al. 2015). In addition to anticipating future habitat for much of terrestrial biodiversity, accurately forecasting forest responses to climate change is necessary to obtaining realistic estimates of climate change itself due to strong regulation of global carbon and hydrological cycles by forests (IPCC 2019). Though some terrestrial components of coupled global climate models are rightly beginning to consider wildfire (Fisher et al. 2018), leading models continue to ignore the possibility of drought-induced population crashes (e.g., maximum stress mortality rate = 1%; Levis et al. 2004, Sitch et al. 2008). Nonetheless, forest loss due to increasing climatic variability may destabilize climate and associated habitat production at regional and global scales (Adams et al. 2010, Stark et al. 2016). Such feedbacks have been noted for western temperate forests in particular (i.e. within the range of *Taxus*; Garcia et al. 2016, Swann et al. 2018), which tout some of the highest biomass carbon densities in the world (Smithwick et al. 2002, Keith et al. 2009, Lutz et al. 2018, Sillett et al. 2018). Climate extremes-associated *Taxus* decline support the interpretation that current carbon sinks could become carbon sources with increasingly variable climate (Cox et al. 2000).

## **Conclusions**

Our study corroborates the growing understanding that SFT models built on climatic means cannot be relied upon to accurately forecast climate change effects in forests. SFT datasets may still be valuable tools, but individual-based, longitudinal data appear to be better suited to biogeographical forecasting amidst modern climate change.

It is increasingly important to supplement SFT datasets with a longitudinal component that reflects underlying biological mechanisms, whether that be observational or experimental (Lutz 2015). If this is not possible, SFT study results could be evaluated by explicitly testing whether climate means are indeed the best predictors of biological responses to changing climate. This could be done by comparing predictive accuracy between: 1) SFT models using differences in mean climate across the geographic range as a proxy for longitudinal climate change, and 2) SFT models using differences in variability metrics as the proxy, which may better reflect local climate extremes (e.g., coefficients of variance or derivatives). In either case, reliable forecasts of future species distributions require examination of species responses to average and relative climate changes.

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## Tables

**Table 2.1.** Site details for the research natural areas (RNA) and experimental forest (EF) permanent study sites containing at least two live *Taxus brevifolia* stems. Timespan indicates the duration over which tree data were collected. Maximum *Taxus* ha<sup>-1</sup> indicates the population abundance used as a response variable in space-for-time models; population growth (%) indicates annualized net change in *Taxus* abundance over the study timespan; and local extinction time extrapolates the observed population growth rate using an exponential growth model to determine the number of years until *Taxus* abundance would be fewer than one tree ha<sup>-1</sup> following the last year of measurement (final year of timespan) given future climates comparable to historical climates. Overall, populations are gradually declining across the sampled range (mean growth rate = -0.9%, SD = 1.5%).

Identity	Location	Stand Age (yr)	Plot Size (ha)	Elevation (m)	Aspect (deg)	Slope (deg)	Maximum <i>Taxus</i> ha <sup>-1</sup> (n)	Population Growth (% yr <sup>-1</sup> )	Local Extinction Time (yr)	Study Timespan
AB08	White River, WA	750	1	1050	300	11	2	2.5	-	1977-2006
AG05	Nisqually River, WA	650	1	950	260	9	54	0.5	-	1977-2009
AV02	Ohanapecosh River, WA	1000	1	850	125	0-6	2	-2.7	26	1977-2009
RS01	H.J. Andrews EF, OR	460	1	510	225	35	26	-0.7	467	1977-2012
RS02	H.J. Andrews EF, OR	460	1	520	315	20	33	-0.8	438	1978-2009
RS03	H.J. Andrews EF, OR	460	1	950	225	10	70	1.2	-	1978-2009
RS23	H.J. Andrews EF, OR	450	1	1020	45	3-29	79	2.7	-	1978-2009
RS24	Hagan Creek, OR	90	1	610	350	24-31	4	0	-	1978-2011
RS27	H.J. Andrews EF, OR	450	1	790	180	3-9	78	0.2	-	1978-2011
RS28	H.J. Andrews EF, OR	459	1	1060	180	10	8	-0.9	232	1978-2011
RS29	H.J. Andrews EF, OR	450	1	800	355	27-40	24	0	-	1978-2011
RS30	H.J. Andrews EF, OR	450	1	870	355	3	43	0.8	-	1978-2012
RS31	H.J. Andrews EF, OR	450	1	900	140	0-3	11	-1.8	134	1978-2012
RS34	H.J. Andrews EF, OR	450	2	820	90-279	3-31	64	1.4	-	1979-2013
RS35	Hagan Creek, OR	130	2.1	460	180-360	19-45	7	1.6	-	1980-2009
RS37	Hagan Creek, OR	130	1	475	90-270	3-35	10	-1.8	128	1981-2009
RS38	H.J. Andrews EF, OR	450	2.4	500	varied	varied	75	-0.6	721	1984-2012
TA01	Ohanapecosh River, WA	250	1	670	270	3-9	14	-0.9	294	1987-2012
TO04	Nisqually River, WA	750	1	640	flat	0	5	0	-	1990-2014
WFDP	T.T. Munger RNA, WA	525	4	368	0-360	0-21	93	-2.4	189	1994-2017

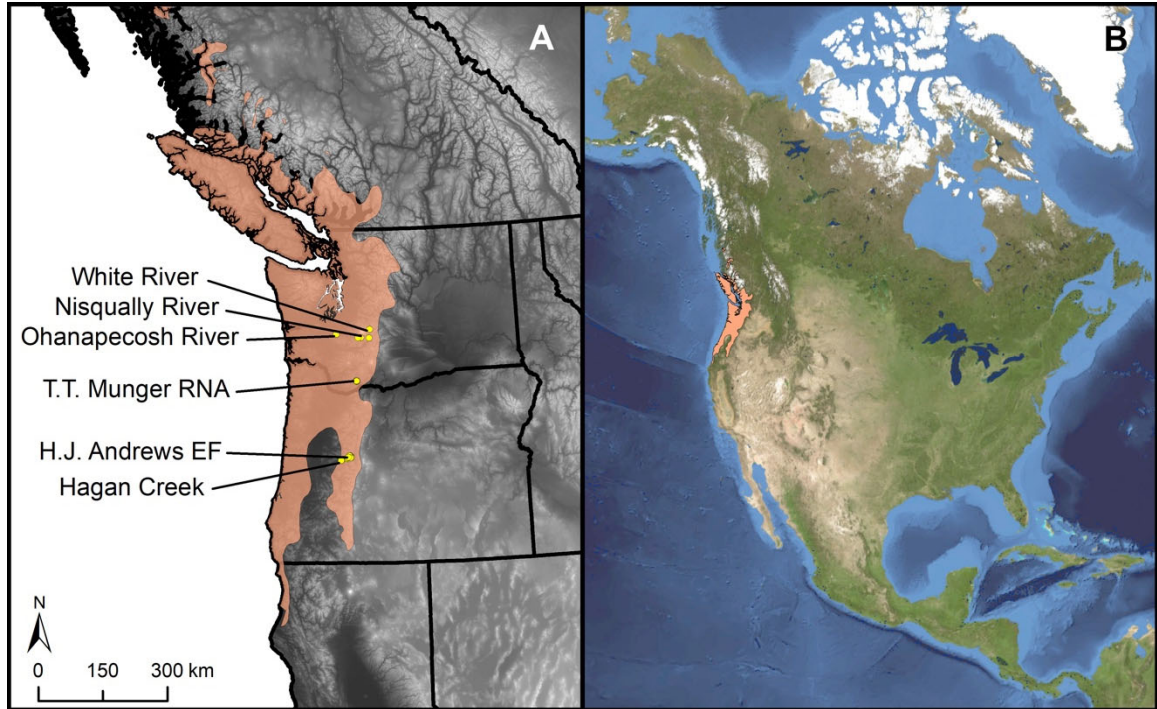
**Table 2.2.** Results of 10-fold cross-validated model performance for generalized linear mixed model (GLMM; individual scale), Cox survival analysis (Cox; individual scale), 1<sup>st</sup> order autoregressive linear mixed model (AR1; population scale), simple linear model (SLM; population scale), and Random forests (population scale). Accuracy is classification accuracy (GLMM, Random forests<sub>a</sub>), concordance (Cox), or percent variance explained (i.e. R<sup>2</sup>; AR1 and Random forests<sub>b</sub>). Two accuracy metrics are given for the AR1 model: marginal R<sup>2</sup> (first number; related to fixed climate and competition effects) and conditional R<sup>2</sup> (second number; related to random autoregressive effects). Mean Absolute Deviance/Mean Ratio (MADMR) is scaled by the units of each model's response variable to allow direct comparison of error between models (lower numbers indicate less error).

Model	Validation				
	MADMR	Accuracy (%)	Mortality (n)	Survival (n)	Sample Size (n)
<u>Longitudinal</u>					
GLMM	1.84	67.8	314	942	1256
Cox	0.08	81.8	250	638	888
AR1	0.06	1.8 / 99.0	-	-	20
Random forest <sub>a</sub>	1.05	70.6	-	-	20
<u>Space-for-Time</u>					
SLM	0.66	53.0	-	-	20
Random forest <sub>b</sub>	0.48	59.0	-	-	20

**Table 2.3.** Model coefficients for generalized linear mixed model (GLMM; individual scale), Cox survival analysis (Cox; individual scale), 1<sup>st</sup> order autoregressive linear mixed model (AR1; population scale), simple linear model (SLM; population scale), and Random forests (population scale). Coefficients for Random forests<sub>a</sub> indicate mean decrease accuracy, and percent increase mean squared error for Random forests<sub>b</sub>, for each variable. Species richness and Hegyi values were calculated within a 10-m radius of each tree; for population-scale models, maximum Hegyi and richness values were chosen to represent each stand. Deficit and snowpack values indicate climate extremes for longitudinal models (i.e. anomalously high Deficit or low snowpack observed within each timestep), and climate means over the entire study for space-for-time models. P-values are represented as follows: < 0.1°, < 0.05\*, < 0.01\*\*, and < 0.001\*\*\*. Dashes indicate variable was not included in models.

Model	<u>Covariates</u>							
	Elevation	Diameter	Species Richness	Conspecific Hegyi	Heterospecific Hegyi	Deficit	Snowpack	Deficit*Snowpack
<u>Longitudinal</u>								
GLMM	-0.456***	0.111	0.126*	0.287***	0.148*	0.895***	-1.807***	0.578**
Cox	-0.886***	0.202	0.121	0.382***	0.202*	0.518°	-2.895***	1.768***
AR1	0.626	-	1.438*	0.441°	0.871*	-0.718**	0.181	-
Random forest <sub>a</sub>	14.808°	-	17.491°	11.256	10.706	4.558	-5.892	-
<u>Space-for-Time</u>								
SLM	-0.986	-	25.769*	39.546*	10.318	-1.675	-5.831	-
Random forest <sub>b</sub>	-12.160	-	35.153**	51.614**	18.381°	-2.123	0.470	-

## Figures



**Figure 2.1.** Locations of Pacific Northwest permanent study sites (a) within North America (b), including those located within research natural areas (RNA) and experimental forest (EF). Study sites contained between one and six individual forest stands (Table 2.1), which were analyzed if least two live *Taxus brevifolia* stems were present in the stand, for a total of 20 stand locations. Orange shading indicates coastal *Taxus brevifolia* distributional range within the *Pseudotsuga-Tsuga* (Douglas-fir/western hemlock) forest zone.



CHAPTER III  
CLIMATE WARMING MAY WEAKEN STABILIZING MECHANISMS  
IN OLD FORESTS<sup>2</sup>

**Abstract**

Plant competition may intensify with climate warming, but whether this will occur equally for conspecific and heterospecific competition remains unknown. Competitive shifts have the potential to instigate community change because the relative strengths of conspecific and heterospecific negative density dependence mediate the stabilizing mechanisms underpinning species coexistence. We examined a mature temperate forest to assess both direct and indirect climate effects at multiple scales: individual species, interspecies relationships, and community stability mechanisms. Our coupled approach 1) quantified tree mortality risk dependence on the interactive effects of competition, climatic water deficit, snowpack, and soil moisture for 28,913 trees over eight years (3,149 mortalities), then 2) used a climate-projection ensemble to forecast changes in conspecific and heterospecific competition from 2020 to 2100. We predict that projected climate warming will destabilize the foundational forest community by increasing the strength of heterospecific competition at a greater rate and to a greater degree than conspecific competition for four of five abundant tree species, particularly on dry microsites. Modeling showed that these findings were most pronounced after the year 2038, at which point snowpacks were projected to be too small to ameliorate the effects of drought on competitive interactions. Our finding that heterospecific competition is

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<sup>2</sup> This chapter was published in *Ecological Monographs* on January 27, 2022, and should be cited as: Germain, S. J., and J. A. Lutz. 2022. Climate warming may weaken stabilizing mechanisms in old forests. *Ecological Monographs* 92(2): e1508. <https://doi.org/10.1002/ecm.1508>

more sensitive than conspecific competition to climate warming may indicate impending loss of ecosystem functioning. We join the growing body of work showing a predominance of indirect drought effects, yet coupled climate models still fail to consider how changing community dynamics may impact forest cover and, in turn, disrupt forest–climate carbon feedbacks. Ecosystems sharing characteristics with our example forest – those with low species richness and thus a limited biodiversity insurance effect – may be similarly vulnerable to climate-mediated destabilization. In such communities, increased heterospecific competition among even a small number of species can more easily destabilize communities without recourse from redundant species. This study of an overlooked but vital mechanism of community change can be adapted by researchers in a range of ecosystems to improve understanding of climate change consequences.

## **Introduction**

The issue of stability in vegetation communities has been long debated (Broekman et al., 2019; Chesson, 2000; Connell & Slatyer, 1977), but what has been less investigated is whether the underlying mechanisms of stability are changing. Differing degrees of conspecific and heterospecific competitive responses during drought have the potential to alter community dynamics (Adler et al., 2006; Chesson & Huntly, 1997) and drive community change (Gilman et al., 2010; Lancaster et al., 2017). Theoretical studies have shown increasing drought due to climate change may either increase community stability by reducing dominant competitive relationships (Adler et al., 2006; Lloret et al., 2012) or destabilize communities by increasing competitive exclusion of less-adapted species (Chesson & Huntly, 1997; Holt, 1985). Empirical studies of forests, however, have primarily focused on direct, physiological drought effects (Williams et al., 2013)

and drought-mediated disturbance processes (Furniss et al., 2020; Seidl et al., 2017). Here, we investigate the extent to which climate warming may create novel competitive relationships by using a spatially mapped, annually resolved time-series of mortality for 28 913 forest trees (3 149 mortalities) overlaid on soil resource distribution maps. Our temporally and spatially explicit dataset allows the necessary testing of multi-way interactions to resolve theoretical contradictions and determine whether forest communities will be stabilized or destabilized by warmer climates.

Global warming galvanizes forest change (Allen et al., 2010; Breshears et al., 2005) through thermophilization of regional species pools (Chen et al., 2011) and intensified competition (Urban et al., 2012) during drought. In future climate scenarios, communities are likely to be stabilized if conspecific negative density dependence (CNDD) remains greater than heterospecific negative density dependence (HNDD) (Adler et al., 2006; Comita et al., 2010; Uriarte et al., 2004). Here, stability refers to the long-term persistence of species in a community marked by resistance to competitive exclusion (Broekman et al., 2019; Chesson, 2000). Negative density dependence can stabilize coexistence by allowing rare species to invade resident neighborhoods when  $CNDD > HNDD$  (Hubbell et al. 2001, Uriarte et al. 2004; but see Stump and Comita 2018). This is primarily moderated by competition for shared limiting resources (Tilman, 1982) and natural enemies (Connell, 1971; Janzen, 1970). Conversely,  $CNDD < HNDD$  among adults (i.e., density-dependent mortality) can signify asymmetric heterospecific competition (Lutz et al., 2014), resulting in destabilization – i.e., exclusion of weaker competitors – particularly if equal rates of sapling recruitment do not follow adult mortality (Connell et al., 1984). Importantly, it is likely that CNDD and HNDD vary

independently with climate, as climate variability alters competition intensity differently among species (Williams & Jackson, 2007). Empirical studies have largely ignored this possibility and have instead examined total competition (Klanderud, 2005) or pairwise species competition (see Levine et al., 2017). We directly address these research needs by forecasting how the relationship between tree survival and neighboring trees may be altered by changing climate in a mature, multi-species, and structurally heterogeneous forest community (Franklin et al., 2002).

Modern coexistence theory often recognizes stabilizing processes as those giving any species a population growth advantage when rare (Chesson, 2000; Ellner et al., 2019). This perspective canonically refers to recruitment (i.e., invasion growth rate). Coexistence research in forests has therefore focused largely on tree seedlings (e.g., Bachelot et al., 2015; Comita et al., 2010; Harms et al., 2000), as long-term coexistence may be stable given positive seedling recruitment. In mixed-conifer temperate forests, however, an exceedingly large proportion of seedlings perish before becoming reproductive (>99%; Lysgaard et al., 2020), providing little balance to increasing overstory mortality with warming climate (Breshears et al., 2005; Lindenmayer et al., 2012). Mature tree (>50 yrs) mortality rapidly removes large amounts of reproductive biomass (Das et al., 2016; Stephenson et al., 2014) and can dramatically alter ecosystems over short timeframes (Silvertown et al., 1993; Swann et al., 2018). Moreover, compensatory tree recruitment amidst climate change is highly uncertain (HilleRisLambers et al., 2015; Kroiss & HilleRisLambers, 2015). It is consequently unknown when, or if, functions provided by mature trees in old forests will be restored in the novel climates and communities of the future (Walther, 2003; Williams & Jackson,

2007).

To address these ecological concerns, we focus on community stability among mature cohorts of foundational tree species: the locally abundant and regionally common purveyors of ecosystem functioning (Dayton, 1972). Here, the stabilizing process giving species a population growth advantage when rare hinges upon the persistence of extant individuals capable of maintaining ecological function. Destabilization among foundational species, particularly those attaining large diameters (Lutz et al., 2018), can degrade ecosystem function by altering forest structure, removing reproducing individuals, and reducing biodiversity (Ellison et al., 2005, 2019). Yet, the stability of existing foundational communities has been broadly ignored by the many coexistence studies focused on recruitment and rarity (e.g., LaManna et al., 2017; Schreiber et al., 2019). Identifying which species should be considered foundational can be difficult, particularly given the low species diversity and low functional redundancy in temperate forests (compared to tropical forests; Lamanna et al., 2014): the unique contributions of foundational species may be enigmatic amidst similarly critical functions provided throughout the community. Instead of single species, then, temperate forests may be particularly suited to an emerging paradigm recognizing that multiple species can act synergistically as a foundational community to stabilize ecosystem function (Angelini et al., 2011). Accordingly, our focus is not on forest community assembly in the theoretical sense, but on climate-related perturbations to existing forest communities that have tangible consequences over decadal to centennial timescales. By examining the stability of extant foundational communities, we investigate a previously ignored avenue by which climate change may disrupt the continuation of ecosystem functioning currently provided

by the mature cohort of trees.

Community dynamics can contribute to structural, compositional, and functional change in forests because competitive exclusion is more likely when interactions among species become destabilized (CNDD < HNDD; Chesson, 2000; Hubbell et al., 2001; Johnson et al., 2012; Uriarte et al., 2004). The resulting changes in background mortality rates can reduce carbon sequestration and production within forested ecosystems (Das et al., 2016), even if long-term coexistence is projected to remain stable (i.e., due to compensatory recruitment over many centuries). Yet, many predictive models of forest change, such as Dynamic Global Vegetation Models within coupled global climate models (e.g., Lawrence et al., 2019), only consider physiological climate effects on individuals or populations (e.g., carbon starvation, reduced photosynthetic rates). Though some of these models are beginning to include disturbance effects (Fisher et al., 2018), simplified background mortality dynamics continue to ignore how changing climate may alter interactions between species and give rise to novel emergent properties within the broader forest community. Consequently, there remains substantial uncertainty in estimates of forest vulnerability to climate change, with a bias towards underestimation of forest loss (Allen et al., 2015; Germain & Lutz, 2020; Luo & Chen, 2013; VanDerWal et al., 2013) that propagates to the coupled global climate models relied upon for predictions of future climate change itself.

Our objective was to reduce these uncertainties by creating comprehensive models of climate-mediated community change that assess both direct and indirect climate effects at multiple scales: individual species responses, interspecies relationships, and community dynamics. To do this, we used a coupled approach that combined Cox

survival analysis (Cox, 1972) with a community-level forecast ensemble derived from a temperate rainforest. Although we examine one example ecosystem here, the underlying modern coexistence framework facilitates generalization of our methodology across many plant, microbial, and animal ecosystems (e.g., Butler & Chesson, 1990; Ellner et al., 2019; Letten et al., 2021). We first quantified the magnitude of CNDD and HNDD responses to spatial and temporal variability for mature trees belonging of the dominant foundational community comprising four gymnosperm and one angiosperm tree species that together represent 90.4% of all woody stems in the forest. We then used a climate-projection ensemble to forecast CNDD and HNDD of each species, and the community as a whole, through the end of the 21<sup>st</sup> century along existing spatial resource gradients.

## Materials and Methods

### *Study Area*

The Wind River Forest Dynamics Plot (WFDP; plot center 45.819834°N 121.957125°W) is a 27.2-ha permanent research site (of which, 25.6 ha analyzed here) located in the T.T. Munger Research Natural Area of the Gifford Pinchot National Forest in Washington State, USA (Fig. 3.1; see Lutz et al. 2013 for full description). The WFDP is in an approximately 525-year-old *Pseudotsuga-Tsuga* (Douglas-fir/western hemlock) forest (Franklin & DeBell, 1988) encompassing five of six vegetation associations from the *Tsuga heterophylla* Zone that span a moisture spectrum (e.g., from dry to moist: *Pseudotsuga menziesii* / *Holodiscus discolor*; *Tsuga heterophylla* / *Rhododendron macrophyllum* / *Gaultheria shallon*; *Tsuga heterophylla* / *Polystichum munitum*; Franklin & Dyrness, 1988). Disturbances are primarily local windthrow events and endemic bark

beetle activity (Germain & Lutz, 2021; Lutz et al., 2021). Soils in the WFDP are volcanically derived and consist of deep, well-drained Vitric Hapludands (Stabler Series; Shaw et al., 2004) with elevations ranging between 352.4 m and 384.5 m. Climate is characterized by cool moist winters and warm dry summers, with annual mean temperature of 9.3° C and 2,297 mm mean annual precipitation that falls primarily as rain during the winter months (i.e., November through March; 30-yr climate normals 1981-2010; 800-m resolution; PRISM Climate Group, 2019).

Dominant tree species in the WFDP are gymnosperms (in order of decreasing basal area): *Tsuga heterophylla* (Rafinesque) Sargent, *Pseudotsuga menziesii* (Mirbel) Franco, *Thuja plicata* Donn ex D. Don, *Abies amabilis* Douglas ex J. Forbes, and *Taxus brevifolia* Nuttall. Subdominant angiosperm trees and tall shrubs, similarly ordered, include: *Acer circinatum* Pursh, *Cornus nuttallii* Audubon, *Corylus cornuta* ssp. *californica* (A. de Candolle) E. Murray, and *Alnus rubra* Bong (Tables 3.1, B.1). Nomenclature follows Flora of North America Editorial Committee (1993+)(Flora of North America Editorial Committee, 1993). Of these, we analyzed all tree species with n > 500, mortality n > 30, and quadrat frequency > 15%. These included two canopy-emergent, moderately drought-tolerant gymnosperms (*Pseudotsuga* and *Tsuga*); two subcanopy, less drought-tolerant gymnosperms (*Abies* and *Taxus*); and one subcanopy, mesophilic to riparian, clonal angiosperm (*Acer*).

### *Field Sampling*

The field methods for the WFDP are those of the Smithsonian ForestGEO network (Davies et al., 2021; Lutz, 2015). A 20-m reference grid was surveyed using total stations during the summer of 2010, with the original vegetation survey conducted



in 2010-2011. We identified, mapped, tagged, and measured diameter of all woody stems  $\geq 1.0$  cm at breast height (DBH; 1.37 m). In these late-seral, light-limited forests, understory growth is very slow and even small trees (1–4 cm DBH) can be old and reproductive, albeit at low rates (Antos et al., 2005; Parish & Antos, 2006). The field methods prioritize high relative accuracy of short inter-tree distances for the purpose of quantifying competitive interactions (0-2 m distance:  $\sim 10$  cm;  $> 2$  m distance: 10-25 cm accuracy). In the summer of 2016, we conducted a full re-measurement of the WFDP wherein we re-measured DBH of each live stem. In early summer of each year from 2012 to 2019, we revisited each tree to ascertain survival and conducted pathology exams of newly dead trees (Lutz, 2015), including identification of multiple factors associated with mortality, including fungal pathogen or bark beetle species when applicable (for full details, see Germain and Lutz [2021] their Appendix S1: Table S6).

#### *Site and Climatological Data*

Preliminary analyses tested which environmental components formed the primary axes of differential tree clustering and mortality (Table B.2, Figs. B.1, B.2). Elevation above maximum spring water table (water table; m) was chosen as our primary environmental covariate, calculated as the difference in elevation (generated from a 1-m<sup>2</sup> lidar surface model) between individual trees and the nearest point along a vernal stream (i.e., the maximum water table at soil surface). The water table was allowed to slope, as observed by the stream slope, to reflect the subsurface basalt layer on which the water table rests known to be present in the WFDP. Elevation above water table ranged between less than 0 (those areas that are wet for most of the year; hereafter, moist microsites) to 18.4 m (upland sites with dry conditions for at least part of the year;

hereafter, dry microsites; Table B.3).

Climatic water balance models were built at an 800-m spatial resolution following the methods of Hostetler and Alder (2016) and McCabe and Markstrom (2007) using temperature and precipitation time series from the 30 arc second Parameter-elevation Regression on Independent Slopes Model (PRISM) data set (Daly et al., 2008) for the period spanning January 2011 to December 2019. Water balance models included continuous measures of monthly snowpack and climatic water deficit (Deficit; mm H<sub>2</sub>O). Climatic water deficit incorporates seasonal hydrology, soil water-holding capacity, and energy inputs to quantify drought as felt by plants: it is the unmet water demand, calculated as the difference between potential transpiration (PET; how much plants would have transpired given optimal temperature and precipitation levels) and actual evapotranspiration (AET; how much plants were able to transpire given observed temperature and precipitation). The eight mortality years of our study (2012 to 2019) covered a range of Deficit / snowpack combinations, as Deficit and snowpack are not tightly correlated in this maritime climate compared to continental climates (Fig. B.3)(Lundquist et al., 2013).

### *Demography*

We calculated vital rates using the 5-6 yr remeasurement period (2010/2011 to 2016) to allow comparison among recruitment, growth, and mortality rates. First, we computed annually compounded radial growth rates (%) for live trees (Eq. 1; Lutz et al., 2014) by comparing 2016 DBH measurements to those attained during plot establishment (5-yr span for west side of plot, 6-yr span for east side) or during the year of tree recruitment into the 1-cm DBH cohort (1- to 4-yr span):

$$(1) \quad \textit{Radial Growth} = 100 \times \left[ \left( \frac{DBH_b}{DBH_a} \right)^{\frac{1}{y}} - 1 \right]$$

where  $DBH_a$  is establishment (or recruitment, if not present at establishment) diameter,  $DBH_b$  is 2016 diameter, and  $y$  indicates the number of years between measurements.

Annual recruitment (Eq. 2; Lutz et al., 2014) and mortality (Eq. 3; Lutz & Halpern, 2006) rates between 2011 and 2016 were also calculated per species (Table 3.1):

$$(2) \quad \textit{Recruitment} = 100 \times \left[ \left( \frac{N_0 + N_r}{N_0} \right)^{\frac{1}{y}} - 1 \right]$$

$$(3) \quad \textit{Mortality} = 100 \times \left[ 1 - \left( \frac{N_0 - N_m}{N_0} \right)^{\frac{1}{y}} \right]$$

where  $N_0$  is the initial population,  $N_r$  is the number of trees that recruited,  $N_m$  is the number of trees that died during the study period, and  $y$  is once again the time interval in years dictated by year of tree establishment (5-yr span for west side of plot, 6-yr span for east side) or recruitment into the 1-cm DBH cohort (1- to 4-yr span).

### *Mortality model – Phase I: Parameterization*

#### *Tree Neighborhoods*

To assess density-dependent mortality, we calculated the Hegyi competition index (Eq. 4; Biging & Dobbertin, 1995; Hegyi, 1974), a distance- and size-weighted sum of neighbors,  $j$ , for each focal tree,  $i$ :

$$(4) \quad H_i = \sum \frac{DBH_j}{(1 + \textit{Distance}_{ij})(DBH_i)}$$

The Hegyi index reflects a mechanistic understanding of tree relationships: it is diameter-weighted in order to account for size-asymmetrical competitive outcomes among trees, which are well documented in forest studies (Das et al., 2018; Lutz et al., 2014); and

distance-weighted to allow diminishing interaction effects across space without prematurely eliminating the disproportionate effects of large-diameter trees (see Sensitivity Analyses). We calculated Hegyi values separately for conspecific neighbors and heterospecific neighbors. We included all heterospecific neighbors rather than considering pairwise relationships between species due to potential interaction chains and feedbacks among multi-species competitive communities (Levine et al., 2017); we therefore sought to capture net heterospecific effects on each focal individual. See Appendix B: Section S1 for more Hegyi index specifications.

There was strong collinearity between tree diameter and the Hegyi index, due in part to the clustering tendency of small trees (Lutz et al., 2014). Though clustering indeed causes elevated competitive stress, the objective of the study was to estimate how changing climate will alter existing competitive relationships (despite if competition is currently strong, as may be expected for small clusters of trees, or weak, as may be expected for well-spaced large-diameter trees). We chose to do this because trees are long-lived and recruitment is often slow (Clark et al., 1999; HilleRisLambers et al., 2015), so the individuals being modeled are overwhelmingly the same individuals subject to oncoming climatic changes. To account for these effects and allow all trees (not just the smallest) to equally inform models, we standardized indices by species and diameter using the z-transformation (Eq. 5):

$$(5) \quad Z_{abcd} = \frac{H_{abcd} - \mu_{H_{bcd}}}{\sigma_{H_{cd}}}$$

where  $H_{abcd}$  is the observed Hegyi (conspecific or heterospecific denoted by b) for tree, a, belonging to the population of species, c, and diameter class, d; where  $\mu_{H_{bcd}}$  is the population mean; and  $\sigma_{H_{cd}}$  is the population standard deviation of the total neighborhood

index (i.e., not divided into conspecifics and heterospecifics) to ensure that the units of heterospecific and conspecific values remain comparable.

This standardization 1) controls for the existing spatial arrangement of trees, which reflects centuries of recruitment and mortality dynamics, in order to isolate current drivers of mortality (Goreaud & Pélissier, 2003; Larson et al., 2015; Tuck et al., 2018); 2) prevents mortality dynamics of the much more numerous (and often clustered) small trees from driving model outcomes; 3) quantifies relative ecological effects of crowded neighborhoods. Without standardization, for instance, a Hegyi index value of  $H=2$  might be extremely competitive for large trees but relatively non-competitive for small trees; and 4) allows a direct comparison of the magnitudes of conspecific and heterospecific Hegyi effects, which can be more clearly interpreted and generalized than the original distance- and size-weighted units of density.

We focused on the magnitude and direction of neighborhood effects because the true values of CNDD and HNDD are notoriously difficult to quantify directly, especially in natural ecosystems (Detto et al., 2019 ; but see Sensitivity Analyses below and Considerations of Bias in Appendix B: Section S2). After standardization, values  $> 0$  indicate denser neighborhoods than would be expected for trees of a particular species and diameter class (that is to say, denser in terms of distance-adjusted relative basal area, not simply stem quantity) and values  $< 0$  indicate sparser neighborhoods. Models therefore tested the following hypothesis: independent of diameter and species, trees with more crowded environments (than would be expected given the existing spatial structure of trees) have a higher mortality risk. This allows our results to be interpreted at the whole-forest scale.

### *Tree Mortality*

We created individual Cox survival models for each common tree species ( $n > 500$ ) that was present throughout the WFDP ( $20 \text{ m} \times 20 \text{ m}$  quadrat frequency  $> 15\%$ ) with a sufficient number of mortality events ( $n > 30$ ) and capable of attaining at least 10 cm DBH. This resulted in models for five species: *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Acer circinatum*. Together, these species constituted 92.6% of total basal area and 90.4% of the stems in the WFDP at plot establishment (2011; Tables 3.1, B.1), which is representative of the *Tsuga heterophylla*–*Pseudotsuga menziesii* zone (Fig. 3.1; Franklin & Dyrness, 1988). This assemblage comprises three taxonomic families (Pinaceae, Taxaceae, and Sapindaceae), spans a gradient of drought tolerance, and includes canopy dominant, co-dominant, and subcanopy species (Erickson et al., 2014; Franklin & Dyrness, 1988; Lassoie et al., 1985). Trees were omitted that died of plausibly climate- and competition-independent causes (e.g., crushing;  $n = 1056$ ).

Cox models (Eq. 6; Therneau, 2015) calculate mortality hazard (i.e., risk)  $\lambda$  at time,  $t$  as a function of the exponentiated linear combination of tree neighborhood ( $X'_1$ ) and climate covariates ( $X'_2$ ), with vectors of coefficients related to effects of neighborhood ( $\theta_1$ ) and climate ( $\theta_2$ ), all scaled by an unspecified baseline hazard function  $\lambda_0(t)$ .

$$(6) \quad \lambda_t = \lambda_{0,t} e^{(X'_{1,t} \times \theta_1 + X'_{2,t} \times \theta_2)}$$

Cox models are time-to-event survival analyses: hazard represents instantaneous mortality probability at time,  $t$ . Cox models are semi-parametric: the parametric component relates to the assumption of normally distributed residuals, and the non-

parametric component requires no distributional assumptions for predictor and response (time-to-event) variables.

Mortality models included main effects for six continuous variables: elevation above spring water table (i.e., soil moisture), total modeled Deficit from the growing season directly preceding mortality (March through October), maximum modeled snowpack from the non-growing season directly preceding mortality (November through February; total modeled snowpack also examined, with similar results), conspecific Hegyi and heterospecific Hegyi indices, and tree diameter (DBH) to control for density-independent size asymmetries in survival. We included all two-, three-, and four-way interactions between Deficit, snow, soil moisture, and the two Hegyi indices (conspecific Hegyi / heterospecific Hegyi interaction not included). Our analysis featured unique climate values for eight mortality years (2012-2019), though climate interactions with tree-specific Hegyi and topographic parameters produced functional sample sizes equal to tree abundance per model (Table B.4).

Cox model coefficients can be exponentiated to allow interpretation as hazard ratios (HR), or the change in hazard between time  $t$  and  $t + 1$  for each unit increase in the predictor, where a  $HR = 1$  would indicate no change,  $HR < 1$  indicates the predictor reduces mortality hazard, and  $HR > 1$  means the predictor increases the hazard. The HR for main effects in the interaction model (i.e., taking into consideration interactive effects) were calculated by Eq. 7:

$$(7) \quad HR_i = e^{n*[\beta_i + (\beta_{i,k}X_k) + (\beta_{i,j}X_j) + (\beta_{i,j,k}X_jX_k)]}$$

where  $\beta_{i,j,k}$  is the model coefficient estimate for the highest-order significant interaction involving predictor 1 (in this example, a 3<sup>rd</sup> order interaction),  $\beta_{i,k}$  and  $\beta_{i,j}$  are coefficient

estimates for all lower-order component interactions of the highest-order interaction containing predictor 1 (even if not significant), and  $\beta_i$  is the primary effect for predictor 1;  $n$  is the number of unit changes of interest for hazard ratio interpretation (default = 1). For interpretation of main effects, all interacting factors were held at mean values (after centering, mean = 0 so interactions are eliminated). For interpretation of interactions, we permuted minimum (< 2 SD), mean, and maximum (> 2 SD) values of interacting factors to calculate HR related to all possible combinations of factors.

Model performance was assessed using Wald tests (establishes overall model significance compared to a null model using robust scores to account for repeated measures) and predictive ability assessed via concordance values (Gönen & Heller, 2005)(i.e., proportion of tree pairs for which the tree with higher modeled mortality risk died rather than its lower-risk counterpart). Parameter model uncertainty was quantified using robust standard errors and a predictor error analysis (see Sensitivity Analyses, below). See Appendix B: Section S1 for accounting of variable transformations, treatment of repeated measures, and model assumptions.

#### *Mortality model – Phase II: Forecasts*

To interpret Cox regression results in the context of changing climate, we projected potential trends in Deficit- and snowpack-related mortality risk 80 years following study establishment (2020-2100). Projected Deficit and snowpack were modeled following the methods of Hostetler and Alder (2016) and McCabe and Markstrom (2007), using temperature and precipitation data from six NASA Earth Exchange U.S. Downscaled Climate Projections (NEX US-DCP30)(Thrasher et al., 2013): CCSM4, GFDL-CM3, GFDL-ESM2M, GFDL-ESM2G, HadGEM2-CC,



HadGEM2-ES. Data were obtained from Alder et al. (2013) at 800-m spatial resolution for Representative Concentration Pathway 8.5 (Meinshausen et al., 2011). NEX data were derived from General Circulation Models conducted under the Coupled Model Intercomparison Project Phase 5 (Taylor et al., 2012). Original climate data were from the NEX-DCP30 dataset, prepared by the Climate Analytics Group and NASA Ames Research Center using the NASA Earth Exchange, and distributed by the NASA Center for Climate Simulation (NCCS). Our selection of both climate and earth system models captures a range of sensitivities, with the selection weighted towards North American models due to the study site location. The six projections were averaged to create a mean climate model, upon which we used generalized least squares models (to account for the auto-regressive structure of time series data) to describe linear climate trends (Fig. 3.1).

The six climate projections were used to create an ensemble of potential future annual mortality hazard ratios. We calculated future annual hazard using Eq. 7 for each of the five species where projected annual Deficit and snowpack values interacted with local edaphic and biotic elements as defined by coefficient estimates produced by study-parameterized models (see Parameterization, above). Community-level hazard was calculated as a weighted average of the five species, where weights were the basal areas of each species relative to total woody stem basal area in the forest. Projection model uncertainty was quantified using this six-model projection ensemble (Fig. 3.1) and a climate scenario sensitivity analysis (see Sensitivity Analyses, below). All statistical analyses were performed using the ‘survival’ package in R version 3.4.3 statistical software (R development core team, 2019; Therneau, 2015).

*Sensitivity Analyses*

Because the eight-year analysis period was relatively short compared to the projection time period, we conducted three sensitivity analyses to test whether our inferences remained robust to uncertainty in historical and future climate. The first analysis (SA1) assessed sensitivity of the parameterization model to uncertainty in historical climate data (i.e., uncertainty arising from the downscaling method, stochastic interannual variability, or measurement error). Using the 1981–2010 climate normals, we first calculated the SE of Deficit (10 mm H<sub>2</sub>O) and snowpack (26 mm H<sub>2</sub>O). Then we reparameterized models to reflect low, moderate, and high levels of uncertainty ( $\pm 0.5$ ,  $\pm 1$ , and  $\pm 1.5$  standard error, respectively; 999 simulations each). Within each simulation, annual climate data were allowed to vary the amount of the uncertainty level from the observed value, where the decision to add or subtract SE was treated as a Bernoulli random trial (50% probability).

The second analysis (SA2) assessed sensitivity of community forecasts to uncertainty in future climate scenarios. We created community forecasts using simulated climate scenarios that deviated moderately ( $\Delta 25\%$ ) to extremely ( $\Delta 100\%$ ) from the mean ensemble projection. All scenarios maintained the rate of increasing Deficit and decreasing snowpack demonstrated by the ensemble projection. The third analysis (SA3) assessed sensitivity of study conclusions to uncertainty arising from the sample sizes of mortality and climate datasets. We considered stepwise additions of annual data by performing all analyses with each of the following mortality and climate data ranges: 2012 to 2017; 2012 to 2018; and 2012 to 2019. We then compared final conclusions among models built at each of the three timescales.

Due to potential for bias in NDD estimations (Adler et al., 2018; Damgaard &

Weiner, 2017; Detto et al., 2019; Rinella et al., 2020; Teller et al., 2016; Tuck et al., 2018), we conducted two further sensitivity analyses to assess error in the crowding index predictors. Sensitivity analysis four (SA4) compares three competition kernels to quantify sensitivity of study conclusions to the choice of NDD proxy. For all three kernels, we sum over neighboring trees (Adler et al., 2010; Uriarte et al., 2004) rather than using annuli (Teller et al., 2016), as trees are regularly shaped compared to shrub genet polygons, and centroid-to-centroid distances work well. It is still unknown to what extent flexible competition kernels (e.g., Teller et al. 2016) may be particularly subject to small sample size errors, overfitting, and reduced generalizability, so we instead compare three commonly used distance decay curves. All of these consider size asymmetries due to vastly differently sized trees in our forest (1- to 200-cm DBH). We compare geometric distance decay (Eq. 4) with exponential (Eq. 8) and gaussian (Eq. 9) decay functions, all calculated to a maximum 50-m radius for neighbors,  $j$ , per focal tree,  $i$ . All metrics were standardized by species and diameter to meet objectives described above.

$$(8) \quad E_i = \sum \frac{DBH_j}{(DBH_i) (e^{1+Distance_{ij}})}$$

$$(9) \quad G_i = \sum \frac{DBH_j}{(DBH_i) (1 + Distance_{ij})^2}$$

Sensitivity analysis five (SA5) creates a simulated null model of random mortality to test robustness of NDD estimates (and their interactions) when using the preferred NDD proxy. Though similar to random labelling methods used in point pattern analysis, (Goreaud & Pélissier, 2003; Wiegand & Moloney, 2004), we are able to retain the strengths of our dynamic, annual tree mortality assessment by conducting this test on the full dataset rather than a static point pattern (Detto et al., 2019). Mortality was assigned randomly to trees in equal proportion to the observed total mortality rate per species;

then, parameterization models were re-run using observed predictor values (i.e., DBH, climate, topography, chosen competition kernel) and simulated mortality. We completed 999 of these simulations to create a simulation envelope representing a null model of random mortality where null model coefficients are centered on zero, assuming no effect, and envelope width quantifies uncertainty for each parameter. Coefficients generated by the null and empirical models were compared to assess whether observed NDD could be distinguished from randomness (i.e., whether detected NDD was in fact the result of stochastic processes). NDD estimates are considered robust when competition parameters fall outside the simulation envelope.

## **Results**

We found evidence for climate-mediated forest change at all three levels of organization: population declines for 17 of 26 forest species, increasing density-dependent mortality, and forecasts of HNDD exceeding CNDD after snowpacks become rare mid-century, though this was moderated by local topography. Our finding that HNDD is more sensitive than CNDD to climate warming for a majority of common species indicates that climate change may weaken stabilization mechanisms and expedite forest change.

Cox analysis showed that direct and interactive effects of the six biotic and abiotic factors considered were highly predictive (mean 67.3% concordance; Table B.4) of individual-tree instantaneous mortality probability (i.e., risk). Most covariates formed at least one 2-way, 3-way, or 4-way interaction (Table B.4), so we held interacting variables at mean values to describe individual effects below (Table B.5). Hereafter, we use the term “denser” neighborhoods synonymously with higher Hegyi index (i.e., higher

distance-adjusted relative basal area of neighboring trees), where negative density dependence is indicated by higher mortality risk in denser neighborhoods *than would be expected given the existing spatial pattern* of trees.

### *Individual Species Responses*

Our eight years of annual mortality covered a large range of mortality rates and causes expected for old temperate forests (Table B.6, Figs. B.4, B.5)(Busing & Fujimori, 2002; A. J. Das et al., 2016). From 2011 to 2019, populations declined for all eight gymnosperms and nine of 18 angiosperms (Table 3.1). *Taxus* declined the most, exhibiting little recruitment while sustaining a 2.7% mortality rate yr<sup>-1</sup>. Recruitment and growth of surviving trees offset biomass reductions due to mortality losses for only three of 26 species (i.e., increased basal area despite loss of stems; Table B.1). Smaller-diameter trees (< 10 cm DBH) had higher mortality rates than larger trees (2.2% yr<sup>-1</sup> vs 1.3% yr<sup>-1</sup>; 82% total mortality; Fig. B.4).

After accounting for interactions, density-independent, direct effects of Deficit and snowpack were negligible (<1% change) for all species. Dry microsites increased density-independent mortality risk of the understory species, *Abies*: +5.1% and *Acer*: +2.5% per mm H<sub>2</sub>O. In contrast, dry microsites decreased density-independent risk of the pioneering species, *Pseudotsuga*: -0.06% and *Tsuga*: -1.1% per mm H<sub>2</sub>O (Tables B.4, B.5); dry microsites also decreased density-independent mortality risk of understory species, *Taxus* -3.0% per mm H<sub>2</sub>O, likely reflecting greater fungal pathogen pressure on *Taxus* at moist sites (Fig. B.5).

### *Interspecies Relationships*

When holding water balance parameters constant at average values (assuming average competitive interactions for water), denser conspecific neighborhoods increased mortality risk for *Abies*: +64.5%, *Tsuga*: +52.4%, and *Acer*: +1.9% per SD increase Hegyi, and decreased risk for *Pseudotsuga*: -27.7%, and *Taxus*: -49.1% per SD (Tables B.4, B.5). Denser heterospecific neighborhoods primarily increased risk (*Abies*: +38.8%; *Acer*: +15.2%; *Tsuga*: +26.6% per SD), though decreased *Pseudotsuga* risk -5% per SD.

Microsite effects on biotic interactions were evident for all species except *Taxus*, with heterospecific interactions generally more site-dependent for gymnosperms, and conspecific interactions more site-dependent for the angiosperm, *Acer* (Fig. 3.2). Given the observed climate, denser heterospecific neighborhoods produced precipitously increasing mortality risk for *Abies* and *Tsuga* on dry sites compared with moist sites (HR > 2); for *Pseudotsuga*, denser heterospecific neighborhoods increased mortality risk on moist microsites, but were often facilitative on dry sites. Conspecific neighbors were facilitative on moist and dry microsites for *Pseudotsuga*, and often facilitative for *Acer* across microsites as well.

### *Community Stability*

We found that 1) conspecific and heterospecific interactions do not respond equally to climate; and consequently, 2) stabilization mechanisms within the existing tree community are unlikely to be favored by climate change. Throughout the coming century, the strength of stabilizing mechanisms (i.e., the difference between mortality hazard ratios produced by conspecific and heterospecific neighborhoods; CNDD – HNDD) was forecasted to decrease or remain low for all species when averaged across

all microsites (Fig. B.6). On dry sites specifically, four of five species did not satisfy the stabilization condition of  $CNDD > HNDD$  (Fig. 3.2). This was not compensated for by the fifth species, resulting in net community  $CNDD < HNDD$  and suggesting destabilization on dry sites (Fig. 3.3). That is, our data more closely align with the outcome that *stabilization cannot happen because both  $\alpha\alpha_{11} > \alpha\alpha_{12}$  AND  $\alpha\alpha_{22} > \alpha\alpha_{21}$  are false* (Box 1).

The most dramatic shifts in NDD occurred at approximately decade 2040, when snow offset was projected to become negative (Fig. B.7). Variations in the strength of interactions between climate variables, soil moisture, and the two Hegyi indices produced different rates and directions of change for CNDD relative to HNDD, with generally greater HNDD sensitivity to increasing Deficit and decreasing snowpack (Figs. 3.2, 3.3). *Abies* and *Tsuga* were forecasted to destabilize (Fig. 3.2) at dry sites but not moist sites. *Acer* stability became higher on moist sites but remained unstable at dry sites; for *Pseudotsuga*, stability became neutral on dry sites but remained unstable at moist sites. *Taxus* remained unstable and did not interact with climate (no change over time). Community-level trends showed decreasing stability on dry sites but not moist sites, with positive stability on moist microsites slowing the rate of forecasted instability when aggregated across all microsites (Fig. 3.3; Table B.1).

#### *Climate projections*

The ensemble of six International Panel on Climate Change (IPCC) climate projections showed modeled Deficit increasing and snowpack decreasing over time (Fig. 3.1, Appendix B: Section S2). Deficit increased  $1.2 \text{ mm H}_2\text{O yr}^{-1}$  on average ( $R^2 = 0.61$ ,  $P < 0.001$ ) and snowpack decreased  $2.9 \text{ mm H}_2\text{O yr}^{-1}$  on average ( $R^2 = 0.42$ ,  $P < 0.001$ ).

All six models predicted more years during which there will be zero winter snowpack (mean 4 years decade<sup>-1</sup> after 2040) compared to historical snowpack (no years with zero snowpack before 2010), resulting in an “offset” < 0 where offset is the difference between Deficit and snowpack quantity per year (Fig. B.7). Although snowpack was able to positively offset Deficit historically, projections indicate that offset will become negative approximately after the year 2038; at this point, annual water surpluses provided by large snowpacks are expected to reduce to the point of net annual deficit. With snow offset negative, the ability of snowpacks to reduce the effect of Deficit was nullified in models and dramatic mortality risk increases were observed (Fig. 3.2). Projection model uncertainty primarily arose from disagreement between models regarding the exact years of highs and lows (giving the impression of wide ensemble envelopes; Fig. B.6), though all models agreed that Deficit is growing and snowpack is shrinking (Fig. 3.1; Fig. B.7). The mean models used here for inference therefore represent a conservative estimate of annual climate change, with the highest confidence pertaining to decadal to centennial trends.

### *Sensitivity Analyses*

Models exhibited low sensitivity to input uncertainties, suggesting that inferences were robust despite the relatively limited eight-year parameterization period. SA1 showed that models were not greatly affected by historical climate uncertainty, though several species-specific parameter sensitivities were identified (e.g., direct effects of CNDD for *Pseudotsuga*; Fig. B.8). Point estimates for these variables could perhaps be refined through additional study. Deficit and snowpack were not sensitive, likely because both had relatively small effect sizes. SA2 complimented our climate projection results



by identifying how much future climate would have to differ from mean climate projections for our inferences to change. SA2 showed that inferences of stability–climate change relationships were robust to feasible future climate variability (Fig. B.9). For four of five species, climate thresholds necessary for  $CNDD < HNDD$  were extreme (100% more snowpack; 95% less Deficit) and well outside confidence bounds for future climate (Fig. 3.1).

The ranges of annual Deficit and snowpack captured by our eight-year study exceeded mean climate differences estimated by the projection ensemble (Table B.3; Appendix B: Section S2). Stability–climate change conclusions remained consistent across a range of annual climate and mortality sample sizes. SA3 showed that smaller samples contributed to larger NDD effect sizes, with relatively modest point estimates shown by the largest dataset reported here (Fig. B.10). SA1 and SA2 run at each of the three sample sizes indicated reduced model sensitivity with increasing sample size, with the largest sample size converging on low model sensitivity (Figs. B.8, B.10). The magnitude of climate-mediated NDD was most uncertain on moist microsites (most dependent upon sample size), while dry microsites consistently showed large reductions to community stability ( $>2 HNDD : 1 CNDD$ ). We therefore expect that additional years of study would produce mortality risk estimates no less extreme than those described here (Fig. B.10). Though point estimates varied, models built on each of sample sizes agreed on conclusions emphasized here: 1)  $CNDD$  and  $HNDD$  do not respond equally to climate; and 2) stabilization mechanisms within the existing tree community are unlikely to be favored by climate change.

SA4 found that model conclusions were sensitive to the functional form of

competition metrics (Fig. B.11), yet the three metrics produced very similar model fitness (Wald test P-values  $< 0.001$ ; mean concordance  $\Delta 2.4\%$ ; Table B.7). This underscores the importance of a well-supported *a priori* and mechanistic understanding when choosing competition kernel form, as model fitness alone is not always the best judge. Importantly, only weak HNDD was detected for four of the five species when using the exponential function, resulting in inflated community-level CNDD (compared to the other metrics) across moist and dry microsites alike; this supports recent criticisms that erroneous NDD underestimation can be severe for heterospecific effects, and suggests that the exponential function may be particularly subject to such biases. Large neighbor effects rapidly approached zero when exponential decay was assumed, compared to slightly longer interaction distances with a gaussian kernel, and the longest distances shown by a geometric kernel (Fig. B.12). Biased NDD estimates may result from the inability of the exponential function to capture asymmetric competitive effects of large-diameter trees (Lutz et al., 2013, 2014, 2018); for example, it is extremely unlikely that a 100-cm tree has no effect on a 10-cm tree at 5-m distance, because crown spread (and thus, competition for light) is typically much larger than 5 m (Ishii & Wilson, 2001). Geometric decay allowed for the strongest large-diameter tree effects, though may overestimate competition at greater distances; this supports the conventional practice to set maximum interaction radii of 10-, 15-, or 20-m (depending on forest type) when using a geometric decay function, or as done here, to use a radius informed directly by prior research (Lutz et al. 2014). We report results from the 10-m Hegyi due to the known importance of large-diameter competitors in this region, and to facilitate generalizability to the wealth of forest ecology and silviculture literature utilizing a similar function (e.g.,

Uriarte et al. 2004, Das 2012, Slack et al. 2017, Maher et al. 2018).

Density dependence estimates using the 10-m Hegyi were well distinguished from the simulated null model of random mortality and were therefore unlikely to be the result of erroneous pattern detection. Broad simulation envelopes for *Pseudotsuga* were corroborated by our original Wald Test P-values  $> 0.05$  for the direct effects, but not interactive effects, of competition shown by SA5 (Table B.4, Fig. B.13). Simulation envelopes were generally narrow for interaction parameters, reflecting low uncertainty but small effect sizes; nonetheless, many interactions were still detectable from randomness, lending credence to their perceived significance (i.e., small P-values derived from Wald Tests). Indeed, there was high agreement between Wald Tests and simulation envelopes, as virtually all parameters that were considered to be significant predictors of mortality by Cox models were also distinguishable from random mortality. Agreement between these tests indicates it is extremely unlikely that our findings of NDD are spurious.

## **Discussion**

Climate change may fundamentally alter community coexistence dynamics because conspecific and heterospecific relationships do not respond equally to warming climate (Fig. 3.2). Our forecasts show that density-dependent mortality associated with heterospecifics (HNDD) will become more likely than density-dependent mortality associated with conspecifics (CNDD) for most species, and for the community as a whole, before the end of the 21<sup>st</sup> century (Figs. 3.2, 3.3). The shift from primarily CNDD to HNDD among extant individuals appears to be driven by increasing drought frequency and severity (i.e., increased Deficit and decreased snowpack) predicted by the climate

projection ensemble. This finding is in line with our hypotheses: density-dependent dynamics are not as strongly determined by successional processes in late-seral forests, being at more of an equilibrium (Franklin et al., 2002; Lutz et al., 2014), so variability in NDD is more likely to correspond closely to seasonal and interannual climate fluctuations (Condit et al., 2004). We build upon previously described studies of direct drought effects and stronger total competition and suggest that indirect, density-dependent drought effects and subsequent climate-altered community dynamics may contribute meaningfully to forest change (Allen et al., 2010; Breshears et al., 2005).

Climate change and associated impacts are often forecasted to become more extreme over time (Easterling et al., 2000). We found that stabilization mechanisms were favored under warmer conditions projected in the near term (2010–2040), as many species had similar strengths of CNDD and HNDD (Figs. 3.2, 3.3). However, predictions of extremely low snowpack values limited this effect in the long term (2040–2100): the risk of exclusion (CNDD < HNDD) increased precipitously by mid-century when annual snowpacks reached low value thresholds (snowpack offset < 0; Fig. B.3; Reyer et al., 2015). High snowpacks in the winter reduce continued competition for water during late fall and early spring months following a severe summer drought (Peterson & Peterson, 2001) and therefore preclude trees from reaching physiological thresholds of drought-induced mortality (McDowell et al., 2008). As years with low snowpack become more common due to climate change, increasingly severe and frequent summer drought (Dai, 2013) may become an unmitigated driver of instability. Our finding that HNDD will exceed CNDD at only dry microsites (Fig. 3.2) for three of the four species illustrates that spatial heterogeneity of soil moisture niches (Chesson, 2000) may maintain community

stability at landscape scales (Fig. 3.4; Adler et al., 2010; Chesson, 2000; Clark & McLachlan, 2003): though we may expect disproportionate persistence of drought-tolerant species like *Pseudotsuga* on dry sites, for example, this will likely be met by foundational community stability on moister sites where  $CNDD > HNDD$ .

Stabilization signifies the presence of niche differences, or differences in the most limiting factors, between species (Adler et al., 2010; Chesson, 2000). Hence, changes in the strength of community stability suggest underlying changes in species' most limiting factors as warming temperatures shift the range of environmental variability further from historical conditions. Given historically abundant water resources, for example, nitrogen availability may be most limiting for one species, while insect herbivores most limiting for another, and these differences stabilize communities by causing species to limit themselves more than heterospecifics (Broekman et al., 2019; Chesson, 2000). With climate change, however, limiting factors of the five species tested here appeared to converge on the singularly most limiting resource of water, producing elevated density-dependent mortality during drought on dry sites where water availability dropped most dramatically. Our forecasts suggest that the once stabilizing effect of climatic variability (Adler et al., 2006; Chesson & Huntly, 1997) may become weakened as climate change brings novel – and increasingly extreme – ranges of drought variability (Germain & Lutz, 2020). This interpretation is in line with predictions that species will migrate to follow their moving climatic niche to track cooler/moister sites as climate change brings warmer/drier conditions (Chen et al., 2011; Root et al., 2003). Stability trends reported here are therefore likely to be more extreme at the hotter, drier bounds of species' ranges where water is most limiting (e.g., southern latitudes, lower elevations; Jump et al.,

2006), or in younger forests (Luo & Chen, 2013) where competitive interactions can be very strong (Franklin & Dyrness, 1988).

Climate-induced destabilization is likely to be most pronounced in ecosystems that have low species richness and thus a limited insurance effect of biodiversity (McCann, 2000; Yachi & Loreau, 1999). With fewer interacting species, each species represents a greater proportion of the inequality underlying the community-level stabilization condition (Eqn. 12). Consequently, synchronous climate responses and increased competition among even a small number of species can more easily destabilize the community by shifting the product of species-level inequalities (Eqn. 13) without recourse from redundant species (Loreau & de Mazancourt, 2013). Though our example ecosystem is located in western North America, low species richness is a characteristic that is shared by boreal forests, temperate forests, and woodlands across the globe (Lamanna et al., 2014). Indeed, we are already observing climate-induced dieback in many of these other forests (Allen et al., 2010; Baltzer et al., 2014). Even in non-forested ecosystems, communities lacking adequate biodiversity are uniquely vulnerable to climate perturbations (e.g., Duffy et al., 2016; Pires et al., 2018). Our findings support the interpretation that ecosystem functionality may be reduced in low-richness systems as a consequence of climate-mediated destabilization (de Bello et al., 2021).

It is necessary to point out that we did not test all requirements for stable coexistence here, namely the effects that individual species may have *on* their conspecific and heterospecific neighbors (i.e., a measurement of fitness differences; see Broekman et al., 2019). We therefore cannot draw decisive conclusions about whether coexistence will remain stable under future climate regimes. Because stabilization is a necessary condition

of stable coexistence, however, our findings of weakened stabilization suggest that climate change may likewise reduce the likelihood of stable coexistence within the foundational tree community on dry sites (Chesson 2000, Broekman et al. 2019): *there can be no stable coexistence in a fundamentally destabilized community*. Yet, stable coexistence canonically refers to long-term persistence of multiple competing species, so recruitment and growth must be considered in addition to the climate-regulated density-dependent mortality assessed here. We found no evidence that recruitment and growth were sufficient to compensate for increasing mortality in the foundational community during the study period (Tables 3.1, B.1); at best, the observed recruitment and growth rates indicate an incredibly long lag time between overstory mortality and replacement of these stems by growth of younger or smaller stems. Indeed, recruitment of seedlings and saplings into the cohort of large, old trees can take a long time in temperate mixed-conifer forests, often spanning multiple centuries for this forest type (Antos et al., 2005; Parish & Antos, 2006). Over these time scales, coexistence may be stabilized by recruitment and changing forest spatial patterns despite the destabilization trend shown here.

Nevertheless, shorter-term destabilization and elevated mortality of large trees portends a temporary loss of ecosystem functionality, particularly of reduced carbon sequestration (Keith et al., 2009; Lutz et al., 2021), that has the potential to trigger cascading climate feedbacks and preclude long-term community stability altogether (Garcia et al., 2016; Swann et al., 2018). Without stabilizing mechanisms, competitive exclusion is expected to proceed rapidly if fitness differences are large (Adler et al., 2010); prior research in this forest type indicates large fitness differences by way of

strong asymmetric competition (Lutz et al., 2014), particularly among the species comprising the foundational community (e.g., *Tsuga*). Changing patterns of CNDD and HNDD thereby have the potential to reduce biodiversity (Angelini et al., 2011; Ellison et al., 2019; Wright, 2002) and lead to novel community assemblages (Hobbs et al., 2009; Millar & Stephenson, 2015; Williams & Jackson, 2007), particularly if recruitment is also low as reported here (Bertrand et al., 2011; Grabherr et al., 1995; Kroiss & HilleRisLambers, 2015). These findings highlight a growing predominance of indirect drought effects, yet currently, no coupled climate models consider how changing forest community dynamics may impact forest cover and, in turn, disrupt forest–climate feedbacks. Coupled models’ focus on direct drought effects (i.e., trees’ physiological responses) at the population scale are therefore likely to overestimate the stability of some forested ecosystems, and potentially, the related stability of the global climate system (Cox et al., 2000; Germain & Lutz, 2020). Climate and vegetation models alike will benefit from further refinement of modeled relationships between forest community dynamics and climate variability.

Observed patterns of density-dependent mortality reflect the net effects of positive and negative interactions within the broader forest community. These include not only the plant species, but plant enemies and mutualists as well (Cobb et al., 2010; Holt, 1985; Vandermeer, 1990). Even multispecies models that explicitly compute the interactions among multiple plant species are unable to fully account for these multitudinous trophic interactions (e.g., Saavedra et al., 2017). For informing management decisions, then, the most comprehensive way to predict forest changes is to examine net effects which represent the observed products of many complex ecosystem interactions. We found net



negative heterospecific effects with climate warming, suggesting that any underlying positive interactions (e.g., shared mycorrhizal networks; Bennett et al., 2017) were unable to completely offset increasingly negative interactions among the tree species.

Silvicultural interventions that cultivate enhanced facilitation among heterospecifics (Germain & Lutz, 2021; Jactel & Brockerhoff, 2007) may be able to counteract negative interactions and conserve forest community stability.

Given the recent wave of literature showing bias in coexistence studies, it has become increasingly important to transparently show how biases have been prevented in NDD analyses. Collectively, the following have been identified as potential sources of bias in NDD research: temporal heterogeneity (i.e., dynamic data)(Damgaard, 2019; Damgaard & Weiner, 2017), spatial heterogeneity (Rinella et al., 2020), influence of past ecological processes (Tuck et al., 2018), and predictor errors (Detto et al., 2019). Recent critiques have taken aim at analyses that are not comprehensive in nature, as few if any papers have addressed all of these sources of bias simultaneously. We present the first study of mature tree mortality for which all of these objections have been addressed to the maximum extent possible with an empirical approach: our longitudinal dataset captures temporal climate heterogeneity characteristic of the region; we quantify how NDD differs along the primary axis of spatial heterogeneity (soil water); we control for existing tree spatial patterns (i.e., those arising from past ecological processes) by standardizing the crowding index by species and diameter; and finally, we present sensitivity analyses for four types of error and examine only abundant species to avoid overestimation of NDD by error-prone proxies (see *Considerations of Bias* in Appendix B: Section S2 for a full discussion of our considerations).

## Conclusions

The forecasted increase of HNDD with continuing climate change is likely to have a destabilizing effect that results in local species exclusion in existing old forests, especially on dry sites. Moreover, none of the examined species showed compensatory rates of recruitment, foreshadowing changes to ecosystem functioning that are unlikely to be recovered by novel species assemblages (as yet unknown) for many centuries. Efforts to preserve environments most likely to favor continued stable coexistence of existing foundational assemblages (here, moist sites) will be critical to protecting ecological functioning and biodiversity amidst global change (Ellison et al., 2019).

We present a methodological framework for addressing how climate change can alter coexistence mechanisms, which has the capacity to 1) inform climate-adaptation research in plant communities globally, and 2) improve global climate models to refine predictions of future climate change. Projections show a first indication of community instability in forests, the magnitude of which will require refinement of climate models and climate–mortality interactions. Nonetheless, these empirically informed risk forecasts show that future community dynamics can be predicted when models simultaneously consider temporal climate variability, spatial niche heterogeneity, and demographic processes at the local scale (Chesson & Huntly, 1997; Levine et al., 2017). We demonstrate that the leading stabilization mechanism underpinning stable coexistence is strongly linked to climate, where growing HNDD relative to CNDD portends reduced stability in the future. Because interspecies relationships can override individual species responses to climate (Suttle et al., 2007), it is imperative that future research consider climate change impacts on community dynamics.

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### Box 1. Stabilization conditions for the five-species model

Under the two-species Lotka–Volterra model, the condition for stabilization is that total community-level CNDD > HNDD:

$$(10) \quad \alpha\alpha_{11} \alpha\alpha_{22} > \alpha\alpha_{12} \alpha\alpha_{21}$$

where the underlying species-level inequalities are shown by:

$$(11a) \quad \alpha\alpha_{11} > \alpha\alpha_{12}$$

$$(11b) \quad \alpha\alpha_{22} > \alpha\alpha_{21}$$

As summarized by Broekman et al. (2019), satisfying either one of these species-level inequalities is a *sufficient* but not *necessary* condition for stabilization. That is, stabilization can be present even if one of the underlying inequalities is not satisfied, provided the other inequality compensates to satisfy the community-level stabilization condition:

*stabilization can happen if either  $\alpha\alpha_{11} > \alpha\alpha_{12}$  AND/OR  $\alpha\alpha_{22} > \alpha\alpha_{21}$  are true*

However, if neither species-level condition is satisfied, then the product of the two conditions produces the opposite of the community-level stabilization condition, indicating a lack of community-level stabilization:

*stabilization cannot happen if both  $\alpha\alpha_{11} > \alpha\alpha_{12}$  AND  $\alpha\alpha_{22} > \alpha\alpha_{21}$  are false*

In our five-species model, we test whether effects of conspecifics are more negative than effects of heterospecifics for the five-species community, altering the stabilization condition to state:

$$(12) \quad \alpha_{con} > \alpha_{het}$$

We combine all heterospecific effects, effectively treating them as the second species that represents the net effects of many directly and indirectly interacting species (*sensu* Comita et al. 2010; Johnson et al. 2012), because the sum of pairwise heterospecific interactions is not sufficient to capture true heterospecific effects in multispecies communities (Levine 2017, Barabas et al. 2016). Though there are limitations to this methodology (e.g., it does not allow definitive conclusions for any two-species subset; Broekmann et al. 2019), this approach was sufficient to achieve our objective of assessing survival consequences of net effects arising from interactions among all community members.

Thus, the underlying species-level conditions for stabilization are shown by:

$$(13a) \quad \alpha\alpha_{11} > \alpha\alpha_{1,het}$$

$$(13b) \quad \alpha\alpha_{22} > \alpha\alpha_{2,het}$$

$$(13c) \quad \alpha\alpha_{33} > \alpha\alpha_{3,het}$$

$$(13d) \quad \alpha\alpha_{44} > \alpha\alpha_{4,het}$$

$$(13e) \quad \alpha\alpha_{55} > \alpha\alpha_{5,het}$$

We expect stabilization if the product of these five inequalities meets the community-level stabilization condition (Eqn. 10), even if any  $n$  number of species-level responses are themselves unsatisfied (Eqn. 13). Conversely, we expect destabilization if the product of these five inequalities does not meet the community-level stabilization condition, particularly if the majority or all species-level responses indicate CNDD < HNDD.

## Tables

**Table 3.1.** Demographic rates of all woody species reaching 1 cm diameter at breast height in the Wind River Forest Dynamics Plot between 2011 and 2016 (the remeasurement census interval). Frequency indicates the proportion of 20 m × 20 m quadrats (out of 640) occupied by at least one live stem in 2016. All vital rates refer to the 2011 to 2016 period. Of these, we analyzed: *Abies amabilis*, *Acer circinatum*, *Pseudotsuga menziesii*, *Taxus brevifolia*, and *Tsuga heterophylla*.

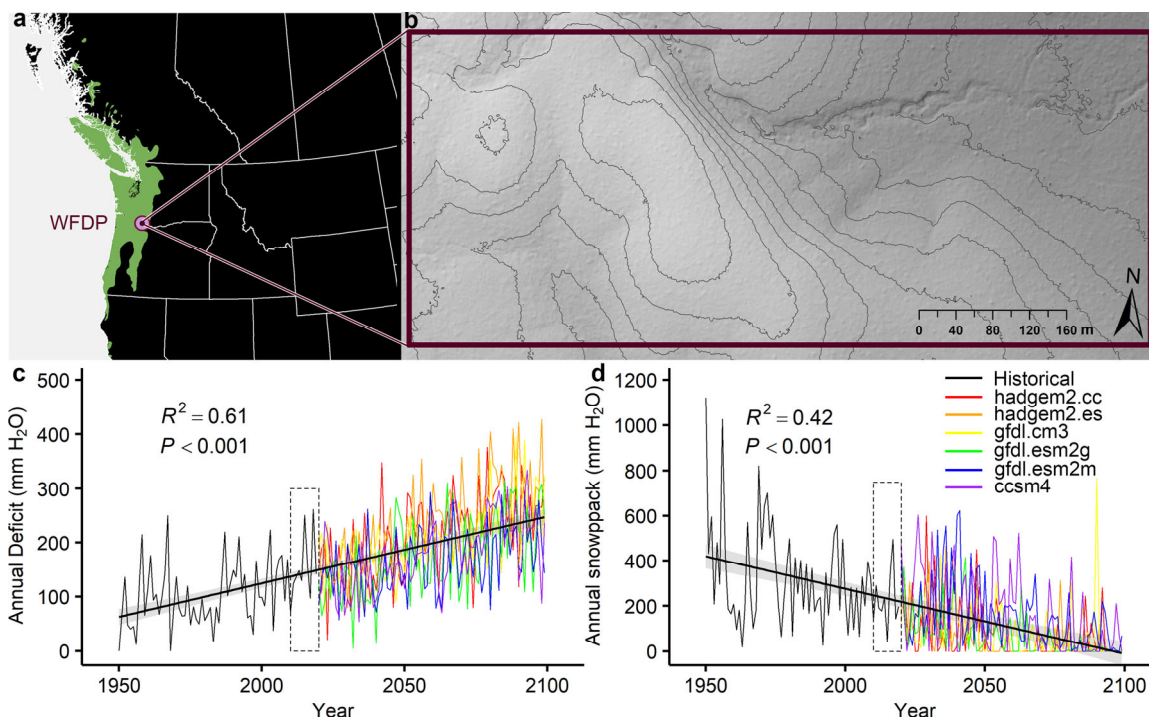
	Family	Frequency (%)	Growth (%)	Stems (n)		Recruitment		Mortality	
				2011	2016	Trees (n)	Rate (% yr <sup>-1</sup> )	Trees (n)	Rate (% yr <sup>-1</sup> )
<b>Gymnosperms</b>									
<i>Abies amabilis</i>	Pinaceae	84.4	2.50	4504	4496	345	1.49	350	1.60
<i>Abies grandis</i>	Pinaceae	7.5	1.46	68	59	1	0.29	10	3.13
<i>Abies procera</i>	Pinaceae	1.9	0.21	14	13	0	0.00	1	1.47
<i>Pinus monticola</i>	Pinaceae	0.6	-0.08	6	5	1	3.13	2	7.79
<i>Pseudotsuga menziesii</i>	Pinaceae	47.2	0.16	573	546	0	0.00	27	0.96
<i>Taxus brevifolia</i>	Taxaceae	81.9	0.14	2113	1843	1	0.01	271	2.71
<i>Thuja plicata</i>	Cupressaceae	16.9	0.56	200	194	1	0.10	7	0.71
<i>Tsuga heterophylla</i>	Pinaceae	100.0	1.70	10001	9809	365	0.72	553	1.13
All Gymnosperms		100.00	0.83	17479	16965	714	0.80	1221	1.44
<b>Angiosperms</b>									
<i>Acer circinatum</i>	Sapindaceae	97.8	1.32	11480	10365	259	0.45	1362	2.49
<i>Acer glabrum</i>	Sapindaceae	0.2	0.71	1	1	0	-	0	0
<i>Alnus rubra</i>	Betulaceae	0.9	2.12	9	8	0	-	1	2.33
<i>Amelanchier alnifolia</i>	Rosaceae	0.8	0.12	9	8	1	2.13	2	4.90
<i>Corylus cornuta</i>	Betulaceae	16.4	3.13	650	667	104	3.01	86	2.80
<i>Cornus nuttallii</i>	Cornaceae	17.5	0.68	178	150	3	0.33	31	3.75
<i>Frangula purshiana</i>	Rhamnaceae	0.2	1.30	1	1	0	-	0	0



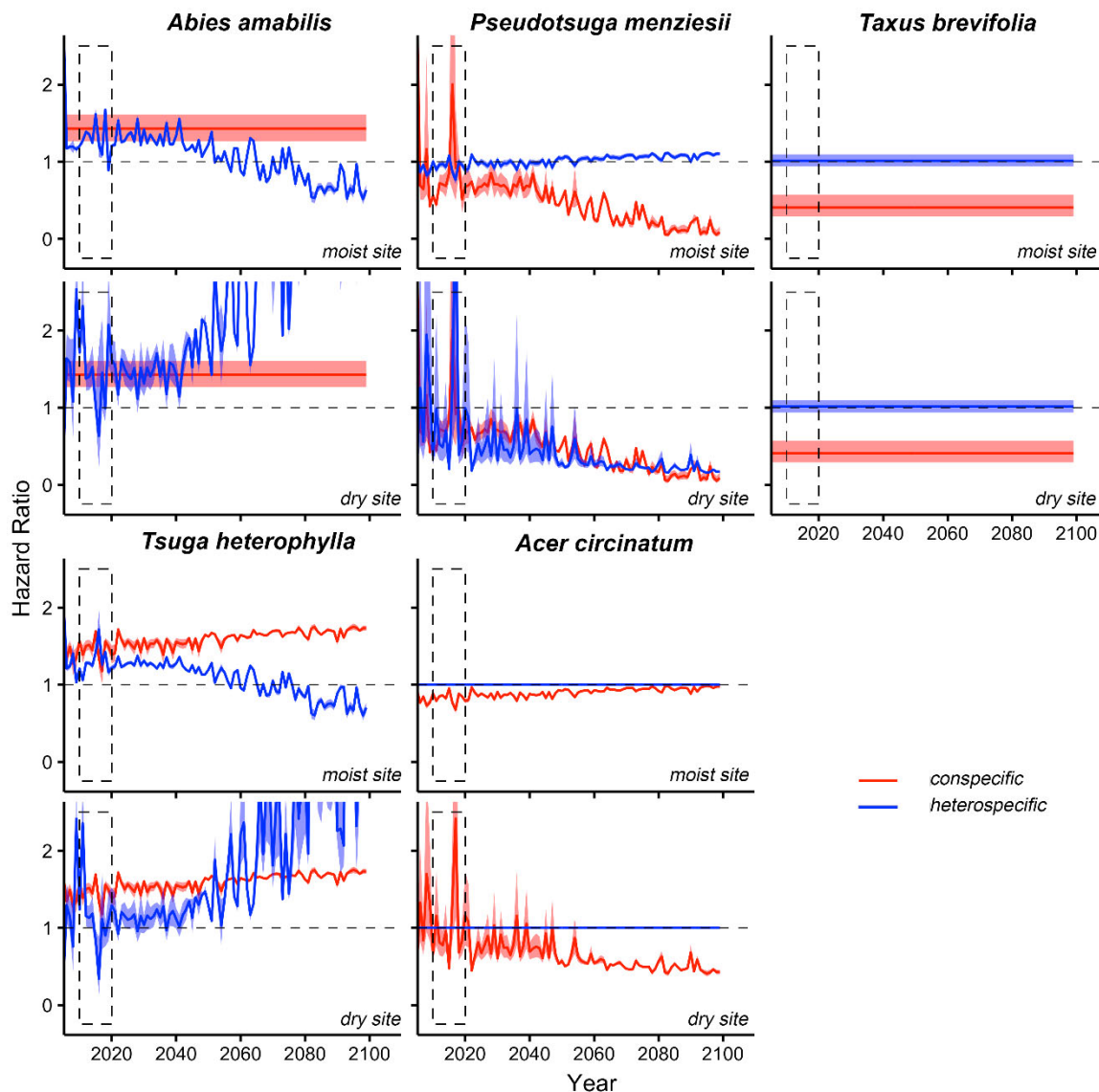
Table 3.1. Continued.

<b>Angiosperms</b>	Family	Frequency (%)	Growth (%)	Stems (n)		Recruitment		Mortality	
				2011	2016	Trees (n)	Rate (% yr <sup>-1</sup> )	Trees (n)	Rate (% yr <sup>-1</sup> )
<i>Gaultheria shallon</i>	Ericaceae	1.1	2.2	14	13	3	3.96	4	6.51
<i>Holodiscus discolor</i>	Rosaceae	1.7	2.85	27	26	3	2.13	4	3.16
<i>Lonicera ciliosa</i>	Caprifoliaceae	0.2	2.02	1	1	0	-	0	0
<i>Menziesia ferruginea</i>	Ericaceae	1.1	-1.24	20	18	0	-	2	2.09
<i>Oemleria cerasiformis</i>	Rosaceae	0.2	3.13	2	2	0	-	0	0.00
<i>Rhododendron macrophyllum</i>	Ericaceae	3.0	3.35	477	472	42	1.70	47	2.05
<i>Rosa gymnocarpa</i>	Rosaceae	0.2	6.99	1	1	0	-	0	0
<i>Rubus spectabilis</i>	Rosaceae	0.2	3.28	1	3	2	24.57	0	0
<i>Vaccinium ovalifolium</i>	Ericaceae	4.5	2.10	66	76	17	4.69	5	1.56
<i>Vaccinium parvifolium</i>	Ericaceae	52.0	1.70	1312	1314	179	2.59	167	2.69
All Angiosperms		100.00	2.10	14249	13126	613	0.85	1711	2.53
All Species		100.00	1.70	31728	30091	1327	0.82	2932	1.92

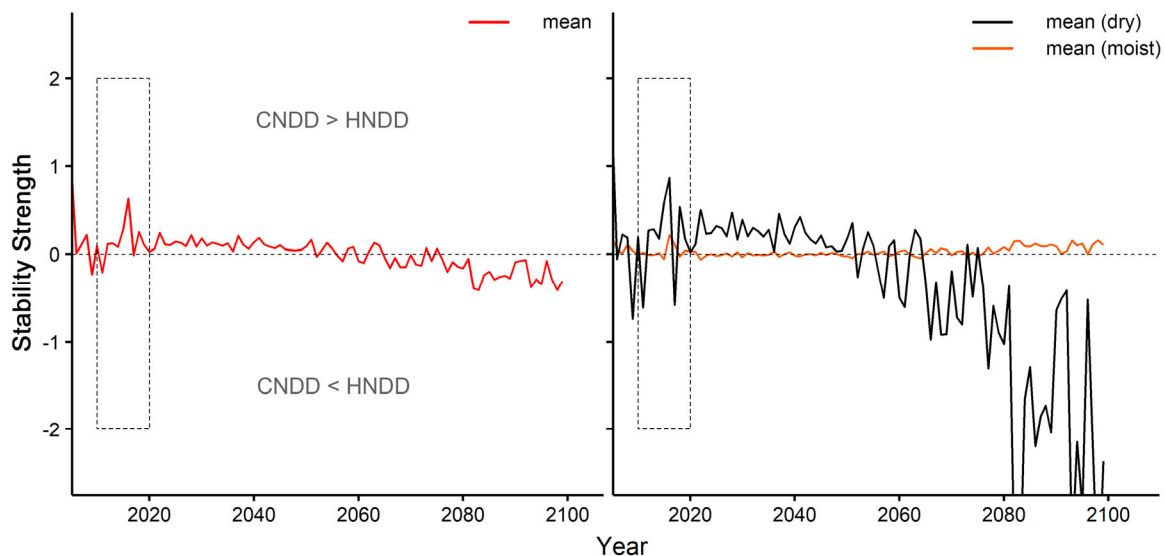
## Figures



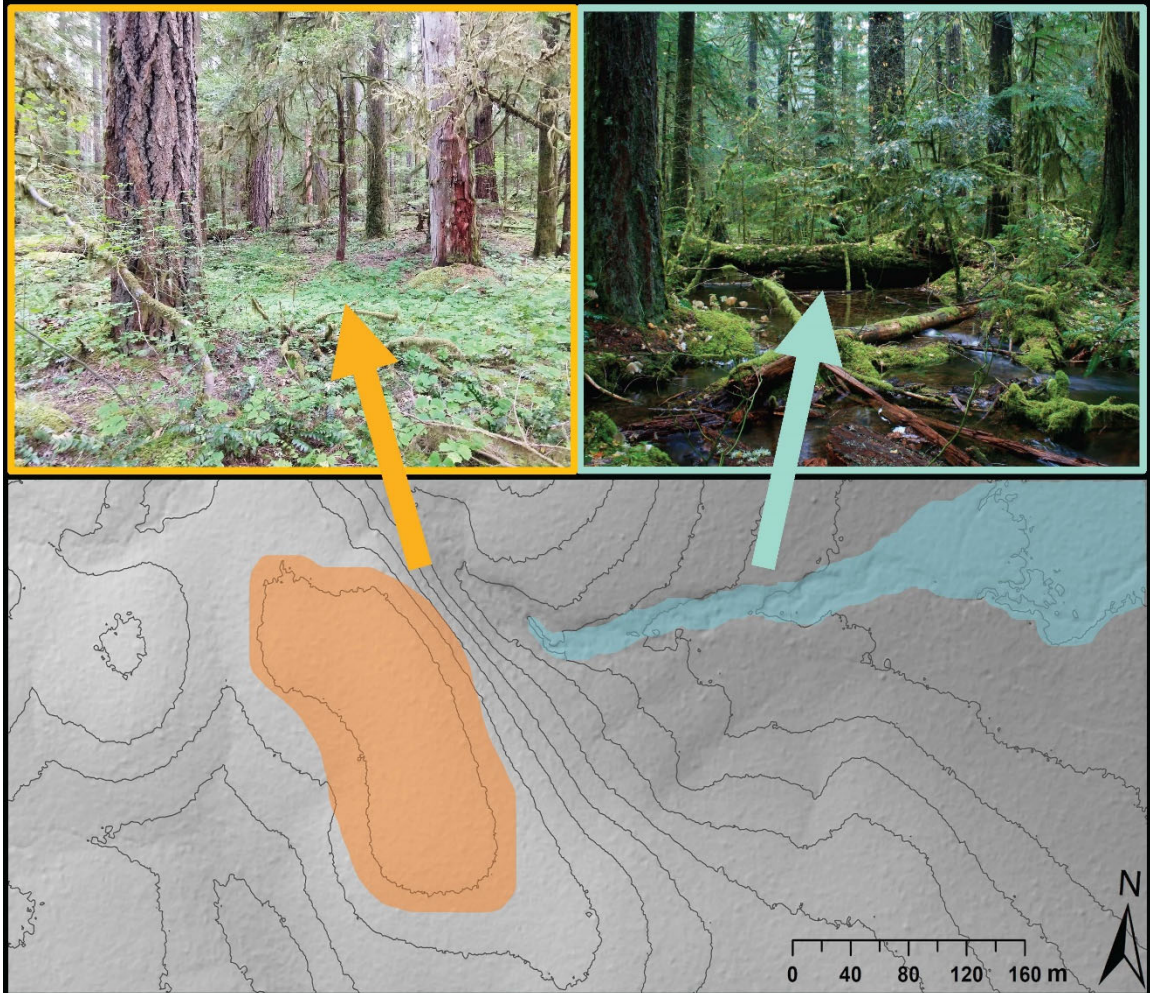
**Figure 3.1.** Geographic and climatic setting. (a) Location of the Wind River Forest Dynamics Plot (WFDP), with green shading depicting the *Tsuga heterophylla* – *Pseudotsuga menziesii* forest zone. (b) LiDAR-derived topographic map (3-m contour lines) of WFDP. (c) Modeled total annual Deficit and (d) modeled maximum annual snowpack in the WFDP, with generalized least squares regressions conducted on mean climate models created from six climate projections (colored lines) to show trends (95% confidence envelope in grey). Dotted rectangles indicate the period of demographic sampling.



**Figure 3.2.** Parameter Uncertainty. Forecasted hazard ratios (i.e., risk) for mortality produced by conspecific and heterospecific neighborhoods at dry and moist microsites. Curves of forecasted hazard ratios represent risk calculated from the mean climate model. Shaded portions indicate  $\pm 1$  standard error. Dotted horizontal line indicates a hazard ratio = 1, at which there is no effect on mortality risk. Hazard ratio  $> 1$  indicates mortality is increased; hazard ratio  $< 1$  indicates mortality is decreased; mortality risk doubles at hazard ratio = 2, above which mortality is precipitously increased (see *Tsuga* and *Abies*, dry sites). Dotted rectangles capture the period of demographic sampling. Flat curves indicate that the Hegyi index had no significant interactions with snowpack or Deficit, meaning the effect of neighborhood was not projected to change over time.



**Figure 3.3.** Forecasted strength of stabilizing mechanisms (i.e., the difference between mortality hazard ratios produced by conspecific and heterospecific neighborhoods) at the community level, either averaged across all microsites (red curve) or stratified by soil moisture levels (black and orange curves). Community-level hazard ratios represent the relative basal area-weighted average of species-specific hazard forecasts of dominant tree species: *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Acer circinatum*. Curves of forecasted hazard ratios represent risk calculated from the mean climate model. Horizontal dotted lines represent no difference between conspecific and heterospecific effects on mortality risk. Differences greater than 0 indicate higher net mortality risk increase from conspecific neighborhoods; differences less than 0 indicate higher net mortality risk increase from heterospecific neighborhoods. Dotted rectangles capture the period of demographic sampling.



**Figure 3.4.** Climate refugia in the Wind River Forest Dynamics Plot. The blue polygon represents moist areas (elevation above maximum spring water table  $< 0$  m). The orange polygon represents dry areas (elevation above maximum spring water table  $> 15$  m). Moist areas acted as climate refugia by maintaining sufficient soil water to temper the effects of increasing drought; this ameliorated competition, increased tree survival, and ultimately led moist areas to demonstrate stronger future community stability than dry areas (Figure 3.3). Contour lines: 3-m.

## CHAPTER IV

STAND DIVERSITY INCREASES PINE RESISTANCE AND RESILIENCE TO  
COMPOUND DISTURBANCE<sup>3</sup>**Abstract**

Drought, fire, and insects are increasing mortality of pine species throughout the northern temperate zone as climate change progresses. The synergistic effects among these factors make compound disturbances uniquely damaging, especially in forests with a history of fire exclusion. Study of the mechanisms promoting pine resistance and resilience provides actionable information to maintain these important carbon stores. We examined annual demography of large-diameter *Pinus lambertiana* in a canonical mixed-species forest in California, USA to characterize how the centennial-scale balance of growth and defense relate to bark beetle susceptibility in the presence of reintroduced fire and drought. Dendroecological analysis of growth rates and defensive resin ducts allowed us to quantify spatially explicit mechanisms of associational resistance (AR) and associational susceptibility (AS) over five years of drought-fire-beetle disturbances: AR and AS occur when stand characteristics, like structure and composition, either increase or decrease tree survival, respectively. In the historical era of frequent, mixed-severity fire (pre-1900), bark beetle-resistant and -susceptible trees showed similar growth and defenses as measured by axial resin duct traits. During the era of fire exclusion (1900-2013), however, susceptible trees demonstrated growth-defense tradeoffs, where growth was sacrificed to maintain defenses; and following fire re-entry in 2013, both growth and defense declined precipitously, leading to fatal bark beetle attack for susceptible trees.

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<sup>3</sup> This chapter was submitted to *Global Change Biology* on August 1, 2022.

Spatial analysis showed that monodominant crowding by shade-tolerant competitors contributed to the long-term stress that prevented susceptible trees from recuperating defenses quickly following fire re-entry. Yet, trees in species-rich communities had higher growth rates pre-fire, promoting resilience of growth and defenses following fire that helped trees resist bark beetle attack and reduced attack rates overall. This associational resistance outweighed associational susceptibility effects (+8.6% vs. -6.4% change in individual tree survival odds), ultimately allowing a majority of large pines to survive the compound disturbance (58%). Given the phylogenetically conserved nature of growth and physical defense responses in the genus *Pinus*, these findings will inform conservation of pine across the northern temperate region. Our results demonstrate how tree diversity can increase forest resistance and resilience to climate-amplified disturbances. Management that increases diversity, therefore, can be expected to increase forest carbon storage.

## **Introduction**

Compound disturbances involving fire, drought, and bark beetle epidemics are becoming more pervasive due to climate change, contributing to widespread forest decline in recent years (Van Mantgem et al. 2009, Jenkins et al. 2014, Millar and Stephenson 2015). The possibility that tree survival may be enhanced by species diversity is attractive to land managers seeking to promote forest health and maintain carbon stores in the midst of these disturbances (Roberts and Gilliam 1995, Hooper et al. 2005). Associational resistance (AR; Barbosa et al. 2009) refers to the observation that trees growing in species-rich stands are often less susceptible to host-specific mortality agents, such as bark beetles (Huber and Borden 2001, Jactel and Brockerhoff 2007, Himanen et

al. 2010). Historically, however, there has been considerably greater focus on how tree neighbors increase mortality risk through bark beetle attraction, fire effects, or competition (i.e., associational susceptibility; AS; Tilman 1982, Churchill et al. 2013, Furniss et al. 2022). A focus on AS instead of AR can have important management implications: AS would suggest that thinning decreases competition and subsequent bark beetle attack (Feeney et al. 1998, D'Amato et al. 2013), whereas AR would suggest that thinning may be ineffective, and instead, increasing diversity is necessary for bark beetle resistance (Germain and Lutz 2021a). Because of the potential consequences of these different approaches, it is important to understand the relative importance of AS and AR.

Associational resistance can emerge through many mechanisms (Jactel et al. 2021). Forest species diversity can reduce host-specific insect *attack* rates by masking the visual and chemical cues relied upon by insect to find preferred hosts (plant apparency hypothesis; Castagneyrol et al. 2013). Reduced insect attack is also observed in diverse stands due to reduced host frequency (resource concentration hypothesis; Kareiva 1983) and accumulation of insect natural enemies (enemies hypothesis; Russell 1989). Forest diversity can also influence insect *success* rates by moderating resource abundances via competitive and mycorrhizal interactions, therefore mediating the tree growth and defense capacities necessary to combat insect attack (Bennett et al. 2005, Slack et al. 2017). Moreover, active bark beetle attack itself can induce defenses (DeRose et al. 2017), creating a possible indirect effect of forest diversity on tree survival as well. Because trees' ability to defend can be compromised by water stress during drought (Gaylord et al. 2013, Stephenson et al. 2019), pathways of associational resistance that prevent bark beetle attack may be increasingly important as drought severity and



frequency increase due to climate change (Dai 2013). However, studies decoupling attack vs. success mechanisms of associational resistance are rare and have not been adequately explored in fire-excluded forests where bark beetle outbreaks are uniquely damaging.

Susceptibility to bark beetles depends, ultimately, on trees' ability to defend. The primary line of conifer defense against bark beetles is oleoresin (i.e., resin), which creates a physical barrier to entry and contains terpenoids that are toxic to insects and microbes (Phillips and Croteau 1999, Raffa 2014). Resin is crucial for combatting attack by bark beetles and their fungal symbionts (Ferrenberg et al. 2014, DeRose et al. 2017), and can also prevent pathogen invasion following physical damage (e.g., post-fire; Bonello et al. 2006, Hood et al. 2015). The genus, *Pinus*, constitutively produces large amounts of resin stored throughout a network of resin ducts in the primary and secondary xylem (Wu and Hu 1997) and can also be induced to produce resin systemically upon bark beetle attack (Lombardero et al. 2000). This abundance of defense capacity likely reflects *Pinus*' coevolution with herbivorous insects, such as *Dendroctonus* and *Ips* bark beetles, two of the most destructive insect genera worldwide (Raffa et al. 2008, Mason et al. 2019); and fire, as many *Pinus* genera grow in drier, fire-prone forests (Kolb et al. 2007). As such, *Pinus* is at the crux of drought, fire, and insect compound disturbances and has been consequently declining across the northern temperate region (Lutz et al. 2009, Haynes et al. 2014, García de la Serrana et al. 2015, Sangüesa-Barreda et al. 2015, Li et al. 2020). Identifying pathways that protect large-diameter *Pinus* from future outbreaks will provide actionable information to maintain these important carbon stores (Lindenmayer et al. 2012, Stephenson et al. 2014).

The growth-differentiation balance (GDB) hypothesis posits that the antagonistic demands of growth and defense for plant metabolites, particularly amidst limited resources, manifests as a negative relationship between growth and defense (Herms and Mattson 1992, Züst and Agrawal 2017). Though many aspects of plant growth and defense are phylogenetically conserved (Wu and Hu 1997, Six et al. 2021), factors such as forest community composition, drought, and fire can regulate resource availability that, consequently, alters defense expression (Hood et al. 2015, Slack et al. 2017). When environmental conditions are favorable, growth tends to receive resource priority over defense (Herms and Mattson 1992). For example, added nitrogen can decrease constitutive resin flow by promoting growth, reflecting that constitutive resin production depends on the carbohydrate pool size remaining after growth is maximized (Warren et al. 1999, Lombardero et al. 2000). The same pattern, however, is not evident for induced resin flow, suggesting that growth and induced defenses may be similarly prioritized when defense needs are high (Lerdau et al. 1994, Lombardero et al. 2000). The complex relationships between GDB and environmental conditions – in addition to the differing responses of constitutive and induced defenses – has led to equivocal empirical evidence for GDB in the field (Reid and Watson 1966, Kane and Kolb 2010, Ferrenberg et al. 2014, Slack et al. 2017).

Field observations indicate that moderate stress can promote resin production (Hood et al. 2015, Anderegg et al. 2015), while severe stress can reduce both growth and resin production (Lombardero et al. 2000, Gaylord et al. 2013). Likewise, diverse neighborhoods may have less prominent facilitative effects during drought years due to increased competition for water and water-soluble nutrients (Urban et al. 2012,

Castagneyrol et al. 2018), and this may be most evident for trees suffering from fire damage (Ryan 2000, Varner et al. 2009). On the other hand, fire-suppressed forests suffer from increased stress due to high densities (i.e., stronger competition; van Mantgem et al. 2004, Barth et al. 2015), leaving open the possibility that fire re-entry releases trees from stress, promoting growth and inducing defenses regardless of diversity levels (Feeney et al. 1998). Determinations of whether, and over what time frame, diversity is able to mediate tree responses to compound disturbances can inform management endeavoring to promote forest resilience to fire, drought, and bark beetle disturbances.

We examine the direct and indirect effects of fire, climate, and bark beetles in a previously fire-suppressed forest to identify 1) mechanisms governing associational resistance and susceptibility, and 2) conditions regulating the relative dominance of these opposing processes over the span of a compound disturbance. We address these questions by studying the mechanisms and spatiotemporal variability of growth-defense trade-offs in Yosemite National Park, CA, USA. We investigated how two potential mechanisms of associational resistance and susceptibility, growth and axial resin duct production, depend on forest diversity and density for *Pinus lambertiana* Douglas, an iconic gymnosperm residing in historically fire-prone montane forests of the Sierra Nevada. We then identified environmental thresholds governing emergence of growth-defense trade-offs by assessing growth and defense over variability in forest structure, climate, and disturbances. Finally, we assessed whether growth or defense benefits to *Pinus* growing in diverse communities, if they exist, translate into enhanced survival.

## Materials and Methods

### Study Area and Data Characterization

#### *Study Area*

The study area was the Yosemite Forest Dynamics Plot (YFDP), located in Yosemite National Park, California, USA (Lutz et al. 2012, 2013). The YFDP is part of the Smithsonian ForestGEO network (Anderson-Teixeira et al. 2015, Davies et al. 2021), with every tree  $\geq 1$  cm diameter at breast height (DBH) mapped and identified. Since 2011, the YFDP has served as a natural experiment for compound disturbances by tracking growth and survival of 34,458 trees within a 25.6-ha contiguous area exposed to overlapping fire, drought, and bark beetle disturbances. The fire regime at the YFDP prior to Euro-American settlement was one of low- to moderate-severity fires occurring at a mean fire return interval of 30 years in the YFDP (Barth et al. 2015). This return interval was longer than characteristic for this vegetation type (12 years; Scholl and Taylor 2010), most likely because of its generally north-facing aspect. The last fire to burn through the YFDP prior to the onset of fire exclusion was in the year 1900 (Barth et al. 2015).

The YFDP is located in the *Abies concolor* / *Pinus lambertiana* vegetation zone of the central Sierra Nevada, where the distribution and abundance of woody vegetation is jointly determined by climate and fire (Lutz et al. 2010, van Wagtenonk et al. 2020). Common tree species include the gymnosperms *Abies lowiana* (Gordon) A. Murray (previously *Abies concolor* (Gordon & Glendinning) Hildebrand; shade tolerant, subdominant), *Calocedrus decurrens* (Torrey) Florin (shade tolerant, co- to subdominant), and *Pinus lambertiana* Douglas (shade intolerant, dominant); and

subdominant angiosperms *Cornus nuttallii* Audubon and *Quercus kelloggii* Newberry. Prominent shrubs include *Arctostaphylos patula* Greene, *Ceanothus cordulatus* Kellogg, *Ceanothus integerrimus* Hooker & Arnott, *Ceanothus parvifolius* Trelease, *Chrysolepis sempervirens* (Kellogg) Hjelmquist, *Corylus cornuta* ssp. *californica* (A. de Candolle) E. Murray, and *Prunus emarginata* (Douglas) Eaton. Nomenclature follows Flora of North America Editorial Committee (1993+)(Flora of North America Editorial Committee 1993).

The YFDP experienced severe drought spanning 2012 to 2015: In spring of 2015, the snow water equivalent was at 5% of its historical average, a level that has not been observed for over 3000 years (Belmecheri et al. 2016, Furniss et al. 2020). Coinciding with drought, the YFDP burned in September 2013 in a management-ignited backfire set to control the spread of the Rim Fire (Lutz et al. 2017). The satellite-derived fire severity within the YFDP showed mostly a mixture of low- to moderate-severity (Blomdahl et al. 2019) generally characteristic of fires in Yosemite since 1975 (van Wagendonk and Lutz 2007). Within the YFDP, fire severity was generally indistinguishable from the majority of the Rim Fire footprint within Yosemite (Kane et al. 2015), but much less severe than the high-severity effects on the adjacent Stanislaus National Forest (Lydersen et al. 2014). Surface fuel consumption, including consumption of duff mounds near larger-diameter trees was approximately 90% (Cansler et al. 2019), but completely unburned surface area in patches  $\geq 1 \text{ m}^2$  was 5% (Blomdahl et al. 2019). Elevated bark beetle activity coincided with fire and drought (Raffa et al. 2008), and reached incipient-epidemic levels in the YFDP between the years 2014-2016 (Furniss et al. 2020, 2022).

Trees were measured for diameter in 2009-2010, 2014, and 2019. We revisited each tree annually from 2011 to 2019 (Lutz 2015) and conducted pathology exams of newly dead trees (i.e., no live foliage), including identification of the multiple factors associated with mortality (species recorded if a biotic agent) and documentation of additional factors affecting mortality (e.g., crushing; Germain and Lutz 2021a, their Appendix S1). Our immediate post-fire pathology exams in May 2014 measured direct fire effects (crown and bole scorch, fire mortality), and subsequent pathology exams from 2015 to 2019 captured delayed fire- and bark beetle-related mortality.

### *Sampling Design*

We randomly selected 80 bark beetle-resistant and 80 beetle-susceptible *Pinus* trees that were  $\geq 80$  cm DBH in 2019 from which to sample annual growth and defense. Selected trees met all the following criteria: resistant trees were those still alive in the summer of 2019; susceptible trees were those that were alive in 2014 (immediately post-fire) but that died due to bark beetles (*Dendroctonus ponderosae* Hopkins and/or *Dendroctonus valens* LeConte) between 2015 and 2019; though these trees may have endured fire damage, annual surveys in the five years following fire indicated these trees survived the fire and that bark beetles were the most proximate cause of mortality. Of resistant trees, 19% showed evidence of bark beetle attack during the 5 years post-fire (pitching, bark beetle frass, entry and exit holes, bark beetles). Trees were not sampled from rocky ridges or riparian draws to avoid possibly confounding effects of unique water status, nutrients, and altered fire intensity in these areas (North et al. 2009, van Wagtenonk et al. 2020). Topographical strata were determined by calculating 50-m<sup>2</sup> topographic position index (TPI; Fig. 4.1), then defining ridges as  $>80^{\text{th}}$  percentile (2.2

TPI) and draws as < 20<sup>th</sup> percentile (-2.3 TPI). We verified that this stratification controlled for prevailing edaphic controls on tree neighborhoods through additional soil and topographic tests (Appendix C: Section S1).

An increment borer was used to extract one, 5.15-mm wide × 30-cm long core from each sampled tree, approximately 1 m above the soil surface. Cores were visually inspected upon sampling and trees were re-sampled if initial cores were too rotten to identify rings. Increment borers were cleaned with steel wool and disinfected with a diluted Lysol solution between each tree to prevent disease transmission. At the time of coring, we remeasured tree DBH and fire injury (proportion of basal circumference scorched, maximum scorch height) for consistency. Cores were dried, mounted, and sanded progressively from 220 grit to 30 microns using standard dendrochronological techniques (Speer 2010). Mounted cores were scanned as high-resolution images (3000 dpi).

### *Climate*

We obtained monthly drought time series from the TerraClimate dataset via Google Earth Engine at a 4-km spatial resolution (Abatzoglou et al. 2018). Monthly TerraClimate spanned the years 1958 to 2019 and included snow water equivalent (SWE), climatic water deficit (deficit), and the Palmer Drought Severity Index (PDSI). We also tested monthly climate time series from the Parameter-elevation Regression on Independent Slopes Model (PRISM) data set (Daly et al. 2008) at a 4-km spatial resolution with grid cell interpolation. Monthly PRISM climate spanned the years 1895 to 2019 and included precipitation, temperature (minimum, maximum, and mean), and

vapor pressure deficit (VPD; minimum and maximum). See Appendix C: Section S1 for details on each of these variables.

Two preliminary analyses compared cumulative metrics of drought (SWE, deficit, PDSI, VPD) with precipitation and temperature to determine which parameter best predicted tree growth, defense, and survival. We examined total SWE; maximum monthly deficit of the current and previous year (separately); minimum and mean monthly PDSI for each growth year (October of previous year to September of current year); and minimum, mean, and maximum temperature, precipitation, and VPD. For PRISM variables, we first conducted univariate sliding window analyses (SWA) to detect the time period over which annual tree growth and resin duct area were most strongly affected by monthly climate variables within the 1895 to 2019 climate data period (climwin; Bailey and Pol 2016). We then performed a multivariate moving correlation function analysis (CFA; treeclim; Zang and Biondi 2015) for growth and resin duct area relationships with the aggregate climate parameters chosen by SWA; this examined how associations between climate and growth/defense changed over time and determined which parameters were most relevant to the study time frame. All analyses were performed in R statistical software [version 4.1.2] (R development core team 2019).

### *Growth*

Of the originally sampled 160 trees, 30 cores could not be crossdated due to severe stem rot (final live  $n = 80$ , dead  $n = 50$ ). Ring boundaries were assigned and radial growth measured to  $\pm 0.001$  mm accuracy using Cybis' CooRecorder and CDendro software [version 9.6] (Larsson and Larsson 2017). All cores were visually crossdated before being evaluated for possible errors using the package dpLR [version 1.7.2] (Bunn



2008). The final year of live tree growth was the year of sampling (2019). Live trees were used to crossdate dead trees and determine their final year of growth. Dead trees produced terminal growth rings between 0 and 3 years preceding evidence of death observed in the field, which was deduced from annual mortality surveys (Germain and Lutz 2021a, their Appendix S1).

We compared our master chronology (robust biweight mean of live and dead trees built on pre-whitened ring widths; Germain and Lutz 2021b, 2021c) with five *Pinus* chronologies and one *Calocedrus decurrens* (Torrey) Florin chronology to verify crossdating accuracy (all pre-whitened; Table C.1). We then interactively detrended our master chronology to find the best detrending method (chosen: 2/3 smoothing spline) using the package dplR [version 1.7.2] (Bunn 2008). Our detrended and pre-whitened chronology had a Pearson's intercorrelation of 0.57 (i.e., COFECHA or overall correlation;  $n = 130$ ) and the average correlation between series (RBAR) was 0.33. The expressed population signal (EPS) was 0.96, static to noise ratio (SNR) was 24.4, mean first-order autocorrelation of raw ring widths across all series was 0.73, first-order autocorrelation of the detrended and pre-whitened master chronology was -0.09, and mean sensitivity was 0.17 (but see Bunn et al. 2013). Ring width was converted to basal area increment (BAI;  $\text{mm}^2 \text{yr}^{-1}$ ) to control for temporal variability in tree diameter. Likely because of the mature stature of the trees, combined with the fact that our coring depth did not hit pith, we observed no age-related growth trends, and therefore did not further detrend growth data for analysis.

## *Defense*

To assess defense, we identified and measured annual resin ducts in core images using the ellipse tool in ImageJ software [version 1.53e] (Rasband 2012). We delineated a 350-px-wide area down the center of each core within which to measure resin ducts to control for slightly different core widths. We cross-verified resin duct measurements twice for consistency and accuracy and calculated seven metrics of resin duct production: duct number per annual ring (no. yr<sup>-1</sup> and no. ring mm<sup>2</sup>), duct area per annual ring (mm<sup>2</sup> yr<sup>-1</sup> and mm<sup>2</sup> ring mm<sup>-2</sup>), and average area per duct (mm<sup>2</sup> and mm<sup>2</sup> ring mm<sup>-2</sup>; Hood and Sala 2015).

Growth-defense trade-offs were assessed over the whole chronology (years 1591–2019) using linear mixed models predicting duct production (total annual area, total annual density, and annual average duct size) as a function of interacting BAI and tree survival, where tree individuals were included as random effects to account for repeated measurements. Growth and defense were standardized to reflect high and low values relative to the average for each tree. We also investigated the effect of drought by including the three-way interaction between drought, BAI, and survival. Climate data limited this analysis to the years 1959–2019. To ensure that model results were not biased by data availability post-fire, we tested all 5 and 10-year aggregations during exclusion and historical periods to determine whether any period matched the pattern observed following re-entry. We also tested bole scorch to disentangle the effects of fire and drought. We tested multiple measurements of drought based on SWA and CFA preliminary analyses: summer maximum temperature (May-August), winter minimum temperature (November-February), total annual SWE, maximum monthly deficit in the current or the previous year, and minimum or mean monthly PDSI. Welch's T-tests were

performed on unstandardized, mean values for growth and defense (see Results: *Growth and Defense*) to compare live and dead trees for descriptive statistics.

### *Tree Neighborhoods*

We calculated live density and basal area of each individual tree species present in the stand. Shrubs, heterospecifics, and neighbors were each categorized collectively. We examined the effect of neighbor size by including the density and basal area of large ( $DBH \geq 60$  cm), medium ( $10 \text{ cm} \leq DBH \leq 30$  cm), small ( $1 \text{ cm} \leq DBH < 10$  cm), and all neighbors ( $DBH \geq 1$  cm). Additionally, we calculated density and basal area of large and small individuals of each of the gymnosperm tree species. We measured the nearest distance to a susceptible *Pinus* and resistant *Pinus*, the proportion of neighboring *Pinus* that were killed by bark beetles, and basal area of bark beetle-killed *Pinus* in the neighborhood. Finally, we characterized species and structural diversity using the number of different woody species (richness) and the standard deviation of tree DBH within each neighborhood (i.e., old-growth index; Spies et al. 1991). We used a mirrored edge correction to account for edge effects.

Each of these density, basal area, distance, and diversity metrics were calculated at 5, 10, 20, and 30-m radii from focal trees, where focal trees were the 130 cored *Pinus*. We conducted two preliminary analyses using Random forests to determine 1) the optimal radial distance within which to quantify neighborhoods, and 2) which of the neighborhood variables were most predictive of *Pinus* survival. Final combinations of neighborhood variables were chosen through classification accuracy and AIC comparisons of GLM models. We verified that final neighborhood variables were not collinear through additional tests (Appendix C: Section S1). Welch's T-tests were

performed to compare live and dead trees for descriptive statistics (*Neighborhoods*, below).

### *Management-oriented Models*

We built generalized linear models (GLM) based on pre-fire and post-fire data to inform management taking place either before or after fire re-entry. These prioritized landscape-level management, assumed that data related to tree growth and defense were unavailable, and omitted climate as it is not a directly manageable parameter. Remaining neighborhood-related covariates were selected using Random Forests importance rankings, model AIC, and model accuracy (assessed through 10-fold cross validation). Two- and three-way interactions among chosen variables were tested. Preliminary variable importance tests showed that the old-growth index was moderately important for *Pinus* survival, but the effect was highly non-linear (intermediate levels associated with increased survival). Thus, this measure of structural diversity was omitted from linear models.

The resulting pre-fire model assessed survival of cored *Pinus* as a function of neighboring species richness (30-m), small living *Abies* density (1 cm  $\leq$  DBH < 10 cm; 10-m), and large living *Pinus* density (DBH  $\geq$  60 cm; 10-m). The post-fire model assessed the largest *Pinus* survival as a function of neighboring species richness (30-m), medium living *Abies* density (10 cm  $\leq$  DBH  $\leq$  30 cm; 10-m), large living *Pinus* density (DBH  $\geq$  60 cm; 10-m), bark beetle-killed *Pinus* basal area (10-m), and bole scorch height as a proxy for fire severity.

*Mechanism-oriented Models*

We built a multilevel moderated mediation structural equation model (SEM) that tested the serially mediated mechanisms by which forest composition and structure directly and indirectly altered bark beetle success rates (i.e., tree survival) across heterogeneous drought and fire disturbances. As an extension of linear regression, SEM allows greater flexibility to examine interactions between variables through moderation and mediation. Much like interactions in simple linear models, moderators alter the direction or strength of a relationship between two variables. Conversely, mediators characterize the mechanism by which an indirect effect occurs between two variables. Serial mediation refers to an indirect effect that is mediated by two or more variables, and moderated mediation happens when an indirect relationship is also moderated. The multilevel structure reflects within-tree variability sampled by growth, defense, and drought over time, while between-tree variability was sampled by tree neighborhoods and fire damage. All mediated relationships were cross-level interactions.

We built the SEM iteratively to assess interaction sensitivities. The first model included no moderation, assessing only the mediation effects of biotic variables on tree survival (i.e., average mediation effects across all fire and drought levels). We then added single moderators, testing the individual moderation effect of fire damage and drought. At this step, we tested multiple measurements of drought based on preliminary analyses: summer maximum temperature (May-August), winter minimum temperature (November-February), total annual SWE, maximum monthly deficit in the current or the previous year, and minimum or mean monthly PDSI.

Preliminary tests showed that close-range ( $\leq 10$  m) bark beetle dispersal from beetle-killed conspecifics nullified the effect of close-range competition from large live

conspecifics on *Pinus* mortality (see results for *Management-oriented Models*, below). Our mechanistic model therefore considered competition in terms of *Abies* densities and allowed the *Pinus* effect to be defined by bark beetle-killed basal area. The final SEM predicted bark beetle success rates (indicated by tree survival) as a function of 1) the direct effects of biotic factors in the five years following fire: 30-m post-fire woody species richness, 10-m post-fire *Abies* density, 10-m post-fire basal area of bark beetle-killed *Pinus* (proxy for beetle attack rates), BAI (growth), and resin duct area (defense); 2) the indirect effects of single and serial mediation processes among these five factors, and 3) the moderation of each direct and indirect effect by drought (i.e., maximum monthly deficit) and fire damage (bole scorch). Variables were standardized across all trees using the z-score transformation. Analyses were performed using the `semEff` package [version 0.6.0] (Murphy 2021) with standard bootstrapping (1000 samples) and cross-verified using the `piecewiseSEM` package [version 2.1.2] (Lefcheck 2016).

## Results

Direct mortality from the Rim Fire reduced total stand density by 72.4% (1402.8 stems ha<sup>-1</sup> in 2013 to 387.4 stems ha<sup>-1</sup> in 2014), and delayed fire effects over the 5 years post-fire further decreased density by 28.4% (277.4 stems ha<sup>-1</sup> in 2019). The stand density in 2019 was still more than double the estimated historical density (i.e., pre-1900; historical = 109.5–114.1 stems ha<sup>-1</sup>; Barth et al. 2015 their Table B.1). However, including delayed effects, the fire returned large *Pinus* and small *Abies* densities to historical levels: *Pinus* ≥100 cm DBH dropped from 13.4 stems ha<sup>-1</sup> to 7.2 stems ha<sup>-1</sup> (historical = 6.9–8.0 stems ha<sup>-1</sup>) and *Abies* ≤10 cm DBH dropped from 612.2 stems ha<sup>-1</sup> to 14.3 stems ha<sup>-1</sup> (historical = 9.4–14.3 stems ha<sup>-1</sup>). Of the *Pinus* with DBH >80 cm (the

coring cohort), 1.8% died pre-fire; 1.8% were killed during the fire; and 42.3% were killed in the 5 years post-fire.

### *Climate*

Maximum monthly deficit and, secondarily, total winter SWE emerged as the strongest correlates of tree growth, defense, and survival. Hereafter, the *p* subscript denotes a month in the previous year, and a *c* subscript denotes a month in the current year. On average over the series (SWA), drought metrics predicted resistant and susceptible tree annual growth better than did temperature or precipitation alone. Both resistant and susceptible trees' growth was reduced by higher maximum deficit (October<sub>p</sub> – June<sub>c</sub>). Resistant trees' growth decreased with higher spring SWE (Feb<sub>c</sub> – Apr<sub>c</sub>), while susceptible trees' growth decreased with higher summer deficit (Jun<sub>c</sub> – Sep<sub>c</sub>). Both groups' growth was increased by higher spring PDSI (Live: Dec<sub>p</sub> – Apr<sub>c</sub>; Dead: Feb<sub>c</sub> – Jun<sub>c</sub>). Resistant trees' duct area was increased by higher minimum VPD in spring and summer (Nov<sub>p</sub> – Apr<sub>c</sub> and Jun<sub>c</sub> – Oct<sub>c</sub>), and with warmer summer temperatures (Jun<sub>c</sub> – Oct<sub>c</sub>). Susceptible trees' duct area was increased by higher spring deficit (Dec<sub>p</sub> – Apr<sub>c</sub>).

The CFA found that resistant and susceptible tree growth responded similarly to fluctuations in deficit, SWE, and PDSI over time; this was true for raw values and those standardized to reflect the average per tree (used here: standardized; Fig. C.1). Although the SWA showed that resistant trees' duct area did not correlate well with drought metrics over the series on average, the CFA showed that higher duct production was observed mid-century during high SWE (Fig. C.2). We chose deficit to use in statistical models because this correlated well with the most factors (resistant and susceptible tree growth, susceptible tree defense). Because SWA showed the period of deficit aggregation

to differ between resistant and susceptible trees, and between growth and defense, we used the maximum monthly deficit unconstrained by season for statistical models (which tended to fall in early- to mid-summer).

### *Growth and Defense*

Growth differed the most between groups during the most recent fire-suppressed century: trees that ultimately died from bark beetles following the 2013 Rim Fire and concomitant drought were the trees that responded poorly to fire suppression following the 1900 fire (less growth; Fig. 4.2). Susceptible trees showed massive growth declines following the Rim Fire. On average over the series, susceptible trees had 17% smaller median ring width and 8% smaller BAI compared to resistant trees (Fig. 4.2). Within-series growth variability was similar for both groups (Table 4.1), but there was greater inter-series variability for susceptible trees than resistant trees (Fig. C.3). Cores contained between 69 and 427 rings. Susceptible trees had greater variance in ring number (SD = 76.5 vs 53.9 rings, respectively), generally having more numerous, smaller rings. At the time of sampling, tree DBH ranged from 80.1 to 170.6 cm, meaning the 30-cm long cores sampled between 18% and 37% of total tree diameter. There were no detectable differences in DBH between resistant and susceptible groups at the time of sampling.

Both resistant and susceptible trees increased duct density, with parallel increases in total duct area, during the era of fire exclusion (1900–2013; Fig. 4.3). Resistant trees showed slightly more resin ducts than susceptible trees, but density converged in the past three decades. Susceptible trees' ducts tended to be larger than those of resistant trees, but this difference also converged. Differences in duct density and size struck a balance such that resistant and susceptible trees produced similar total annual duct area. Because



susceptible trees had lower annual growth but equal duct area as resistant trees in the years following the Rim Fire (2014–2019), susceptible trees showed higher relative annual duct area ( $P = 0.007$ ) and relative area per duct ( $P < 0.001$ ). These relative metrics were driven by differences in ring width, yet our goal was to model the separate effects of disturbance and stand structure on growth and defense. We therefore included annual duct area (the best synthesis of duct density and size) and growth separately in statistical models.

Historically and during the period of fire exclusion, all trees demonstrated annual growth-defense tradeoffs by producing more ducts, larger ducts, and greater total duct area during years with the least relative amount of growth (Fig. 4.4). However, this was only true pre-fire: following fire re-entry, bark beetle-susceptible trees showed a positive relationship between growth and defense. This was primarily driven by low growth and low defenses occurring in the same years, and intermediate levels occurring in the same years; there were no post-fire years of high growth and high defenses. Many bark beetle-susceptible trees produced no growth nor defenses in the one to two years post-fire and preceding mortality. Susceptible trees produced less duct area with severe fire damage; resistant trees produced higher defenses independent of fire damage. Differences between resistant and susceptible trees' growth-defense trade-offs were not observed over any other aggregation of time prior to re-entry, including during years with comparable drought levels to the re-entry period (Fig. C.4). Over the long-term, resistant trees maintained high growth rates and duct production, while susceptible trees sacrificed growth to maintain defenses at levels equal to resistant trees (Fig. 4.2).

### *Tree Neighborhoods*

Close-range basal area of bark beetle-killed *Pinus* (10 m) was associated with subsequent *Pinus* mortality, while basal area of live *Pinus* at a close range was not (Fig. C.5). Within a 10-m radius, lower densities of small-diameter *Abies* ( $1 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ ), large-diameter *Pinus* ( $\text{DBH} \geq 60 \text{ cm}$ ), and lower total basal area and density ( $\text{DBH} \geq 1 \text{ cm}$ ) during the pre-fire period were associated with *Pinus* post-fire survival; moreover, though large-diameter *Pinus* density decreased with fire at the stand scale, little change was observed at the 10-m scale (Fig. C.6). Within a 30-m radius, neighborhood species richness was higher for resistant trees pre- and post-fire; along with higher *Cornus* and shrub pre-fire density (Fig. C.7; high variability). Structural diversity (old-growth index) did not differ between resistant and susceptible trees during the fire exclusion nor post-fire periods (Fig. C.7). Richness was not correlated with total density, large *Pinus* density, large *Pinus* BA, nor *Abies* density, but was associated with slightly higher small *Abies* density (Appendix C: Section S1).

### *Management-oriented Models*

The pre-fire model had moderate accuracy (correctly classified = 62.3%; sensitivity = 62.0%; specificity = 62.5%). The best pre-fire management action to mitigate large-diameter *Pinus* mortality following fire re-entry was to preserve large-scale species richness (30-m) and reduce nearby small *Abies* density (10-m). For every reduction of 10 small *Abies* within 10-m of the largest *Pinus*, this increased *Pinus* survival odds by 28%. At the stand scale, our models indicate the largest *Pinus* post-fire survival would have increased by 27.4% if small *Abies* density had been reduced by half (306 trees ha<sup>-1</sup>). Reducing small *Abies* to historical densities (median 12 trees ha<sup>-1</sup>) did not

further influence *Pinus* survival. Richness at the 30-m scale increased *Pinus* survival odds on average (8.5% per additional species), while large neighboring conspecifics (10-m) decreased survival odds on average (1047% per tree). However, an interaction showed that increasing richness ameliorated negative conspecific effects: having five or more woody species within 30 meters completely offset the effect of having between 1 and 7 large neighboring *Pinus* within 10 m (Fig. C.8).

The post-fire model had high accuracy (correctly classified = 86.9%; sensitivity = 86%; specificity = 87.5%). The best post-fire management action to mitigate large-diameter *Pinus* mortality following fire re-entry was to prevent aggregated bark beetle activity in high-density *Pinus* areas (reduce bark beetle-killed BA) and reduce nearby medium *Abies* density (10-m). This was true for all levels of bole scorch (no interactions). The largest *Pinus* were more likely to die with higher bole scorch (24% lower survival odds per vertical meter). *Pinus* survival odds decreased by 1037% per m<sup>2</sup> of bark beetle-killed BA within a 10-m radius, and decreased by 47% for each medium *Abies* stem within a 10-m radius. After accounting for the effects of shared enemies (bark beetle-killed BA), greater densities of large-diameter *Pinus* within a 10-m radius increased survival odds on average (99% per tree). Richness within a 30-m radius also increased survival odds on average (31% per additional species). An interaction showed that having one to seven additional woody species within 30 m aided the largest *Pinus* survival when one or more other large *Pinus* was nearby (Fig. C.8). Richness was unable to modify bark beetle effects (no interaction with beetle-killed BA or distance to nearest beetle-killed *Pinus*).

*Mechanism-oriented Models*

SEM predicted tree survival with very high accuracy (94.6% specificity, 94.0% sensitivity, 94.6% total accuracy). As expected, indirect effects outweighed direct effects of tree neighborhoods on *Pinus* survival (Fig. 4.5, Tables C.4, C.5). On average, associational resistance (i.e., total richness effects) increased survival by 8.6%, while associational susceptibility (i.e., *Abies* total density effects) decreased survival by 6.4%. Trees that grew faster survived, regardless of duct area produced. The highest bark beetle attack rates were near fire-damaged trees in low-diversity, high *Abies* density neighborhoods (bad for survival). The most growth was during non-drought years in trees with low bark beetle attack, few *Abies* neighbors, and high diversity neighborhoods (good for survival). The highest defenses were in trees with low fire damage, low bark beetle attack, few *Abies* neighbors, and high diversity neighborhoods (no effect on survival).

Fire strengthened the ability of diverse neighborhoods to reduce bark beetle attack, leading to increased growth and survival for burned trees when diversity was high. Conversely, fire damage led to greater bark beetle attack, less growth, and lower survival when trees were in monodominant neighborhoods. Drought and *Abies* density decreased growth directly. Drought and higher *Abies* density also increased bark beetle attack rate, indirectly reducing growth and survival. Higher diversity decreased bark beetle attack, indirectly increasing growth (except during drought) and survival.

Duct area was not predictive of tree survival, but varied as a function of drought, fire, bark beetle attack, and neighborhoods. *Abies* density increased bark beetle attack, which increased defenses (only during drought). For trees without fire damage, diversity increased bark beetle attack, indirectly increasing defenses (only during drought). For trees with fire damage, diversity decreased bark beetle attack, indirectly decreasing

defenses (especially during drought). See Appendix C: Section S1, Fig. C.9 for more details on SEM structure and underlying hypotheses.

## Discussion

Climate change is causing more frequent and extreme drought (Dai 2013), more frequent and severe wildfire (Westerling et al. 2006), and greater fecundity and success of bark beetles (Bentz et al. 2010). The synergistic effects among these factors make compound disturbances uniquely damaging to forests (McDowell et al. 2011, Anderegg et al. 2015, Furniss et al. 2020), especially in those with a history of fire exclusion (Stephens et al. 2018). One of the most dominant genera to occupy northern temperate forests, *Pinus*, has been at the center of these disturbance-mediated declines (Yan et al. 2005, Klos et al. 2009, Van Mantgem et al. 2009, Pandit et al. 2020).

We add to previous work of tree mortality during compound disturbances (van Mantgem et al. 2013, Van Mantgem et al. 2018) by identifying multiple interacting mechanisms responsible for *Pinus* susceptibility to bark beetle attack and, ultimately, beetle success. Less than 2% of large-diameter pines died due to fire alone, whereas nearly half of large pines were killed by bark beetles following fire. Mechanisms pertaining to survival during this post-fire phase are therefore the most important targets of management action. We show that associational susceptibility was characterized as excessive crowding by shade-tolerant competitors due to fire exclusion, which likely contributed to long-term stress preventing trees from recuperating defenses quickly following fire re-entry and drought damage (e.g., cavitation; Sevanto et al. 2014). In other words, the dramatic decline in growth and defense in susceptible trees following fire could indicate carbon starvation following fire damage and drought (Sevanto et al. 2014),

as pre-fire reserves appear to have been lower for susceptible trees than resistant trees (i.e., lower growth rates). This stress culminated in succumbence to bark beetle kill within five years post-fire. As we expected, however, competitive costs were offset by benefits of increased vigor and reduced bark beetle attack when crowding comprised a more diverse assemblage of species, providing evidence for associational resistance. Moreover, AR total effects were larger than AS effects, resulting in survival of a slim majority of *Pinus* during the outbreak. Associational resistance was even maintained for burned trees during drought, contrasting with previous findings focused on AS alone (Castagneyrol et al. 2018, Stephenson et al. 2019) and providing hope for conservation of large-diameter *Pinus* in vulnerable temperate forests (Lutz et al. 2018).

These findings join the growing body of work showing that 1) species interactions have the potential to counteract negative climate change effects (Suttle et al. 2007), and, as such, 2) community-level climate responses may hold the key to more comprehensively predicting, mitigating, and adapting to the climate crisis (Germain and Lutz 2021a, 2022). Without accounting for these indirect and interactive effects, models are unlikely to fully anticipate climate change impacts in forests (Allen et al. 2015, Clark et al. 2021, Germain and Lutz 2022). In particular, models reliant on simplistic depictions of delayed fire effects likely overpredict survival of large-diameter trees (Furniss et al. 2019), leading to a concurrent overprediction of carbon storage capacity in mature forests (Stephenson et al. 2014, Pioniot et al. 2022). The first step to addressing these weaknesses is to integrate models capable of more ecological complexity into projections of future disturbance regimes under climate change (Hessburg et al. 2005, Kasischke et al. 2013). Our SEM results contrasted with simple linear models that suggested richness

did not ameliorate the effects of bark beetles and competition following fire re-entry. This discrepancy arose because linear models are only capable of considering moderation interactions and are unable to quantify indirect effects (i.e., mediation) that SEM revealed to be important. Taken together, models show that diversity did not moderate the direction or strength of the relationship between bark beetle attack and survival following fire; higher attack rates always decreased survival odds. Yet, diversity decreased bark beetle attack rates themselves, which in turn, improved survival. The ability of complex models like SEM to quantify these indirect mechanisms will be especially useful to managers and ecologists alike when forecasting the future of community interactions and forest disturbances.

Managers are increasingly reliant on wildland fire use over large areas in an attempt to restore historic conditions (van Wagtenonk 2007), but it is clear that first re-entry fire does not erase the legacy effects of fire exclusion (Becker and Lutz 2016, Lutz et al. 2020). In many cases, fire reintroduction can elevate bark beetle attack, even after initial thinning (Youngblood et al. 2009, Stark et al. 2013, Steel et al. 2021). Although the Rim Fire returned small *Abies* densities to historic levels, for example, the long-term stress caused by these competitors during the century of fire exclusion reduced *Pinus*' resilience to bark beetles post-fire (Van Mantgem et al. 2018). Instead, mechanical thinning pre-fire can promote resilience to compound stressors in fire-suppressed forests by decreasing fire severity and increasing resistance to drought and bark beetles (Agee and Skinner 2005, Fettig et al. 2007, Hood et al. 2016). Whether and how quickly trees can reverse declining trajectories and resist bark beetles following thinning depends on the forest type in question and is still largely unexplored (Harrington and Reukema 1983,

Hood et al. 2016, Zald et al. 2022). For Sierra Nevada mixed-conifer forests, our pre-fire management models quantified thresholds for thinning small-diameter *Abies* and identified less vigorous large-diameter *Pinus* as sources of aggregated bark beetle attack. Yet, our findings join others in urging discretion when thinning forests in order to maintain pathways of associational resistance that promote tree vigor and defenses: composition, not just density, should be considered (Baleshta et al. 2005, Germain and Lutz 2021a).

Associational resistance operated along two distinct pathways: decreased bark beetle attack and decreased bark beetle success. For individual trees, bark beetle attack rates depend on patch-scale beetle population density, which is directly proportional to the basal area of nearby large-diameter trees killed by bark beetles: higher basal area reflects more available phloem area and thus a greater number of emerging bark beetles (Cole and Amman 1969, Amman 1972). Bark beetles proceed to attack nearby living hosts after emerging from killed trees, resulting in spatially aggregated beetle activity (Furniss et al. 2020, Howe et al. 2022). We found that diversity at a larger spatial scale than conspecific clustering (30-m vs. 10-m) prevented this aggregated attack activity (e.g., due to host apparency, resource concentration, or natural enemies). For trees that were attacked, survival then depended on vigor, which was also aided in diverse communities. Bark beetles may have chosen not to attack nearby healthy trees based on olfactory cues suggesting strong defenses (Wallin and Raffa 2000), but evidence from field observations indicates that many resistant trees were attacked and survived. Enhanced vigor in diverse communities therefore appears to have also decreased bark beetle success. Higher richness was not correlated with more productive sites, nor with



reduced stem density; and moreover, the benefit of diversity emerged at the community level. It is therefore unlikely that rich communities reflect differences in local abiotic conditions. These factors together support the interpretation that, during the era of fire exclusion, diverse communities provided greater resource access through a mechanism independent of competitive interactions or site productivity, such as shared mycorrhizal networks (Germain and Lutz 2021a), that promoted long-term tree vigor and sustained defenses post-fire.

Evidence for whether bark beetles target fast- or slow-growing trees is equivocal and appears to depend on species (Ferrenberg et al. 2014), diameter (Buonanduci et al. 2020), and beetle populations (Boone et al. 2011, Howe et al. 2022). The prevailing paradigm is that slow growth can be an indicator of long-term stress that makes trees more susceptible to bark beetles (Hard 1985, Franklin et al. 1987, Nesmith et al. 2015, Cailleret et al. 2017). Yet, bark beetles may target fast-growing, healthy trees because these represent greater nutritive value (Huberty and Denno 2004). This latter hypothesis would also support the GDB prediction that slower-growing trees are better defended (Herms and Mattson 1992). Indeed, recent work has indicated that faster-growing trees can be more susceptible to bark beetle-kill (Six et al. 2021), particularly when beetle populations reach incipient levels (Boone et al. 2011, de la Mata et al. 2017, Howe et al. 2022) or during drought (Stephenson et al. 2019). Our findings support the decline spiral hypothesis (Manion 1981), however, which is surprising because we would expect bark beetles to attack and kill healthy trees during the coinciding drought and incipient beetle outbreak observed during the study. This is among the first studies to delineate how

associational resistance can prevail even amidst higher risk levels inherent to compound disturbances.

Theory predicts there should be a strong relationship between growth and defense, and that tradeoffs should occur when resources are limited (Züst and Agrawal 2017). The trees examined here were exposed to multiple, synergizing stressors: increased tree densities due to a century of fire suppression (Barth et al. 2015), physical damage following fire re-entry, water stress from extreme drought (Williams et al. 2013), and incipient-epidemic bark beetle attack (Furniss et al. 2020). Though both resistant and susceptible trees showed some evidence of annual G-D trade-offs during the historical and fire exclusion eras, only resistant trees showed sustained growth and defenses over the long term and following fire re-entry. Moreover, we show that these responses arose not just from the genetic lottery (e.g., Six et al. 2018), but specifically because trees were growing in species-rich communities. The effect of biotic elements on growth and defense, both in terms of other trees and bark beetle attack rates, could help explain why evidence for G-D trade-offs is sometimes elusive in observational studies.

The presence of sustained duct production through G-D trade-offs pre-fire did not translate to reduced susceptibility during compound disturbance, leading to the conclusion that physiological defense characteristics cannot necessarily be used to anticipate tree resistance to bark beetles. Susceptible and resistant trees produced virtually equivalent resin duct size, density, and annual area over the two centuries prior to mortality. Indeed, resin duct density and area even increased over the past 200 years: it is unlikely that increasing CO<sub>2</sub> concentrations are associated with these trends, though rising temperatures may be important (Kilpeläinen et al. 2007). Though the exact

mechanisms explaining increasing duct area were not identified here, we found that pre-fire defenses were less important to survival than was pre-fire growth. Examination of resin ducts prior to compound disturbance would have erroneously concluded that susceptible and resistant trees were equally likely to survive bark beetle attack, when in fact, long-term stress precluded the resilience of tree defenses following first re-entry fire. More accurate predictions of tree survival during compound disturbances might be captured through simultaneous assessments of tree vigor and chemical defenses, such as terpene concentrations (Delorme and Lieutier 1990), resin flow (Warren et al. 1999), and volatile cues (Gray et al. 2015). Chemical defenses are allocated independently from physical defenses (Mason et al. 2019) and may therefore better reflect tree stress (e.g., Hood and Sala 2015; but see Reichardt et al. 1991). Though resin ducts may be associated with tree survival in some cases (Kane and Kolb 2010, Ferrenberg et al. 2014, Hood and Sala 2015, Slack et al. 2021), we found the strength of this relationship is conditioned on the combined effects of disturbance history, forest structure and composition, and the presence of synergizing stressors.

## **Conclusions**

We show that the interactive effects of drought, fire, competition, and bark beetles together were responsible for unexpectedly large volumes of biomass loss through delayed mortality of the largest pines in the five years following first fire re-entry. Growth and defense declines in susceptible trees immediately post-fire were not entirely explained by higher fire damage: though more severely burned trees had higher mortality probability on average, burned trees maintained growth, defense, and survival in species-rich neighborhoods. Likewise, post-fire growth and defense declines were not explained

by drought alone, as similar declines were not observed during pre-fire periods of severe drought; and competitive stress did not coincide with high bark beetle kill pre-fire. It was only the combined, interactive effects of simultaneous fire damage, water stress, and a history of competition that together governed susceptibility to bark beetles.

Complementing the wealth of literature identifying associational resistance in other forest types, ours is the first study to show tree diversity can reduce insect attack in a fire-excluded forest during compound disturbance. In fact, associational resistance effects outweighed associational susceptibility, ultimately protecting the majority of large-diameter *Pinus* that may have otherwise been targeted by bark beetles post-fire. We highlight that the indirect mechanisms of associational resistance predominated: richness did not directly increase tree survival, but indirectly did so by increasing tree vigor pre-fire and reducing bark beetle attack post-fire. Future research can build upon these findings to evaluate the balance of AR and AS in different forest types. Given the phylogenetically conserved nature of growth and defense responses in the genus *Pinus*, particularly those that reside in drier, low-elevation forests, these findings will inform conservation of pine across the temperate region. Building forest resilience to compound disturbances hinges on both conserving biodiversity and reducing competitor densities before fire to promote the multiple complementary pathways promoting tree survival.

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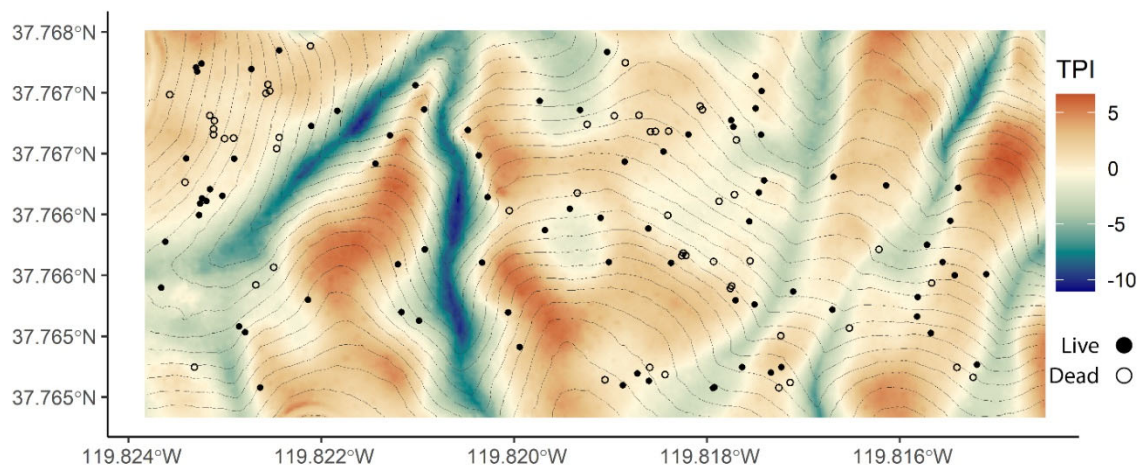
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## Tables

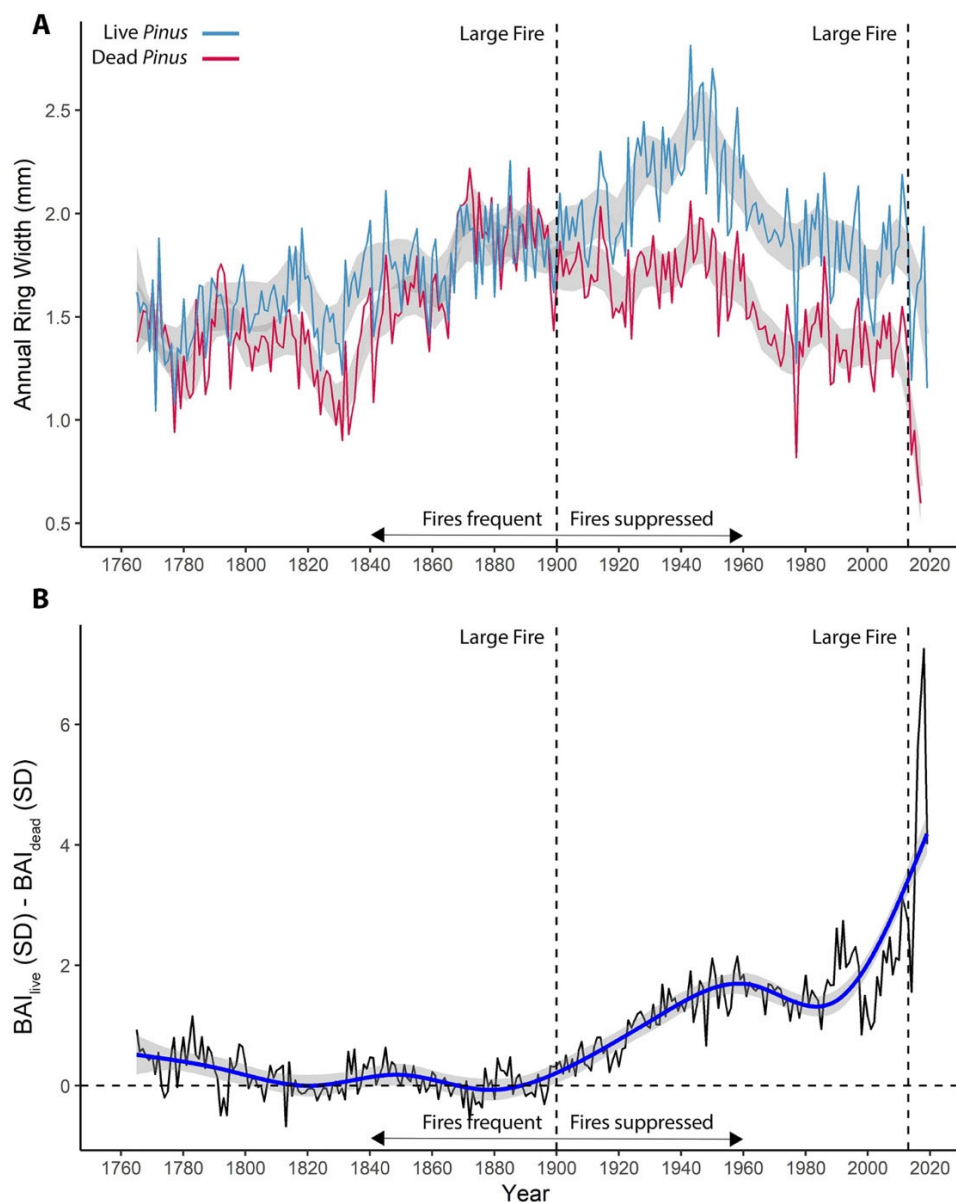
**Table 4.1.** Summary of growth and defense metrics obtained from dead and live tree cores. Anomalies are the z-score of relative duct area per ring, per tree. Basal area increment and annual duct area were used for growth and defense metrics in statistical models.

	Live				Dead			
	Min	Median	Max	SD	Min	Median	Max	SD
Core Sample (yrs)	1709	1874	2019	53.9	1591	1848	2019	76.5
Diameter at Breast Height (cm)	80.1	111.0	171.0	23.0	84.6	121.1	154.6	19.3
Ring Width (mm)	0.10	1.79	9.17	0.69	0.42	1.47	7.10	0.67
Basal Area Increment (mm <sup>2</sup> )	1.3	47.4	348.7	17.2	1.4	40.6	191.2	15.5
Duct Density (n yr <sup>-1</sup> )	0	1	14	1.4	0	1	10	1.3
Duct Size (mm <sup>2</sup> n <sup>-1</sup> )	0.004	0.260	0.100	0.008	0.005	0.290	0.210	0.010
Duct Area (mm <sup>2</sup> yr <sup>-1</sup> )	0	0.039	0.306	0.040	0	0.034	0.339	0.040
Relative Duct Density (n ring-mm <sup>-2</sup> )	0	0.26	5.24	0.33	0	0.25	32.16	0.45
Relative Duct Size (mm <sup>2</sup> n <sup>-1</sup> ring-mm <sup>-2</sup> )	0.0005	0.0047	0.0710	0.0028	0.0005	0.0064	0.2388	0.0047
Relative Duct Area (mm <sup>2</sup> ring-mm <sup>-2</sup> )	0	0.0068	0.1540	0.0093	0	0.0073	0.9550	0.0135

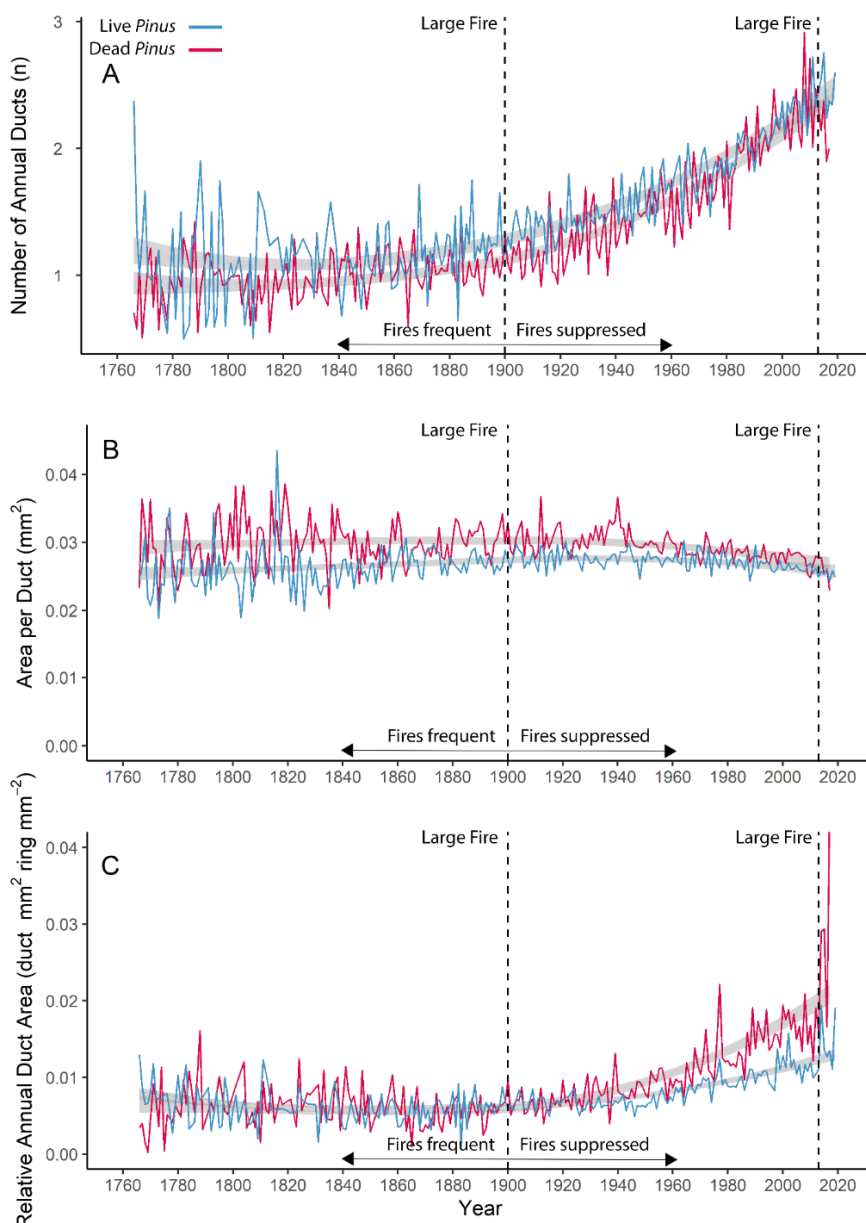
## Figures



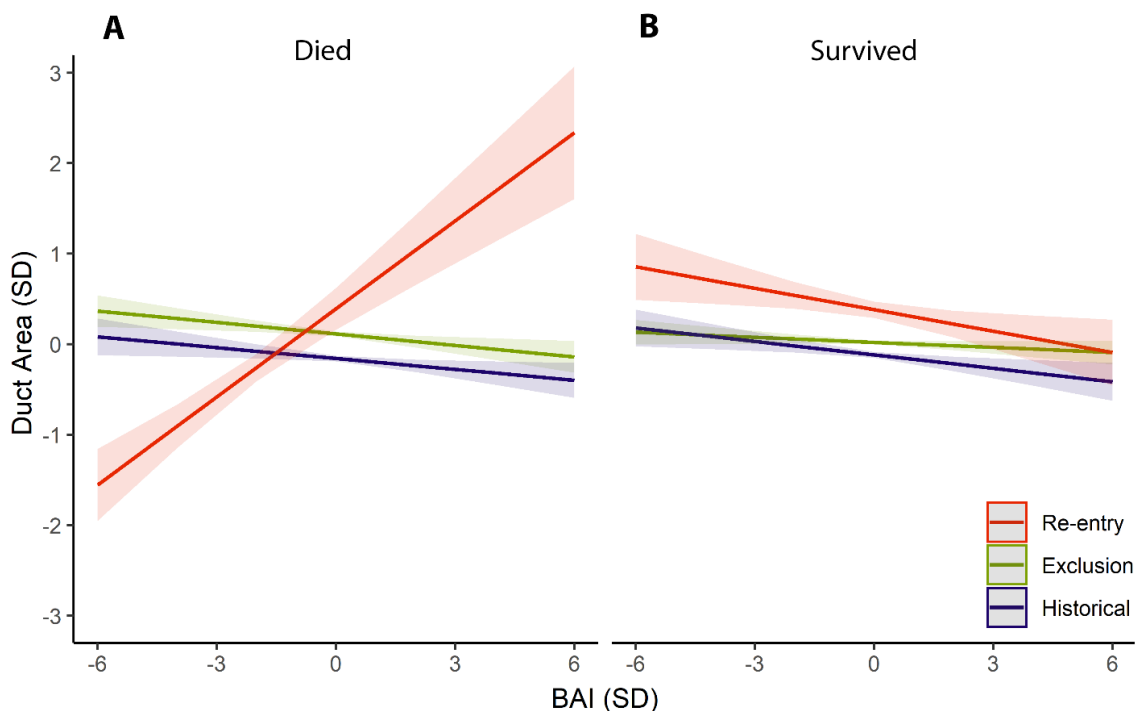
**Figure 4.1.** Map of the Yosemite Forest Dynamics Plot from which *Pinus lambertiana* was sampled, where a low topographic position index (TPI) represents concavity and high TPI represents convexity. *Pinus* was not sampled from ridges (>80th percentile; 2.2 TPI) or draws (< 20th percentile; -2.3 TPI). Lines represent 5-m contours.



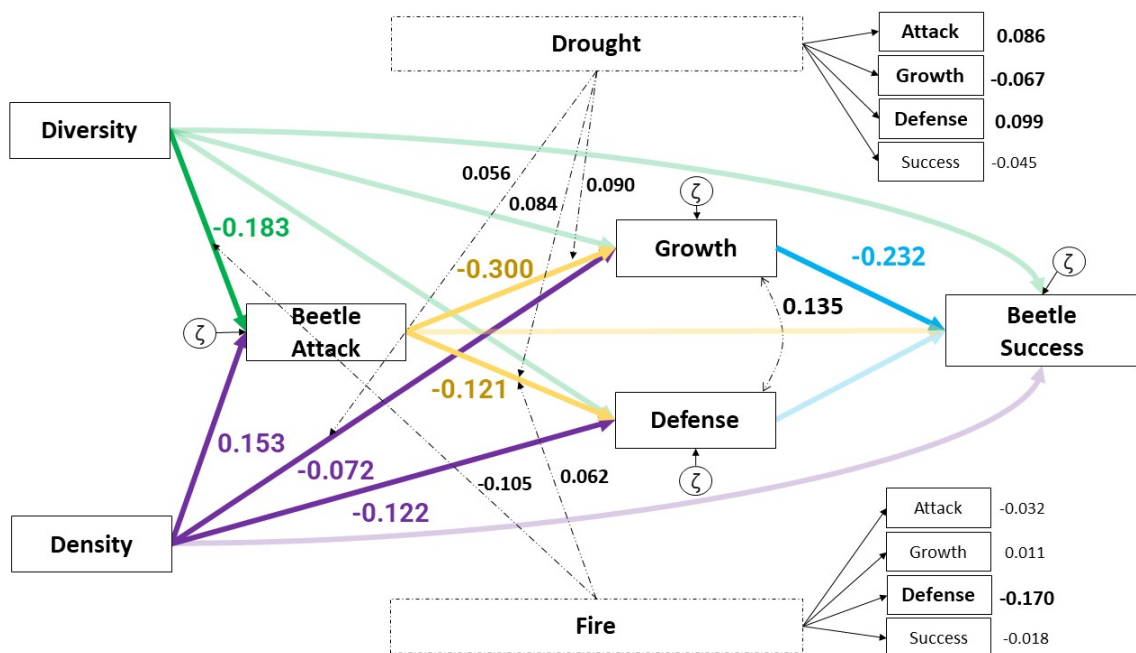
**Figure 4.2.** *Pinus lambertiana* ring width chronologies for live and dead trees (A) and the difference between z-scores of live and dead tree basal area increment (BAI; B), where each was standardized by BAI during their respective historical period (pre-1900). Curves falling above zero in B indicate higher than average BAI in live compared with dead trees. Live and dead tree growth was similar during the pre-1900 period when historic frequent fire regime was still intact (mean fire return interval 30 years). The last large fire in 1900 marked the beginning of fire suppression efforts. During this post-1900 era of fire suppression, trees that would ultimately die from bark beetles following the 2013 Rim Fire grew more slowly than trees that would survive, indicating less resilience to the structural and compositional changes resulting from fire suppression. Curves begin at 1765, after which sampling depth was  $\geq 10$  individuals per live and dead category. Mean fire return intervals derived from Barth et al. (2015). 95% confidence intervals are shown in grey.



**Figure 4.3.** *Pinus lambertiana* annual resin duct density (A), area per duct (B), and annual relative resin duct area (C) with 95% confidence intervals shown in grey. Duct density has been increasing over the past 260 years for live and dead trees alike. Duct area (not shown) follows the same trajectory as duct density. Relative duct area was similar between dead and live trees during the pre-1900 period when historic frequent fire regime was still intact (mean fire return interval 30 years). During the post-1900 era of fire suppression (mean fire return interval 65 years), trees that would ultimately die from bark beetles following the 2013 Rim Fire sacrificed growth in order to sustain resin duct production, resulting in a higher duct area:ring width ratio (C). At the time of tree death following the Rim Fire, live and dead trees did not differ in duct density, area, or area per duct; they only differed in relative duct area due to the smaller ring sizes of dead trees. Curves begin at 1765, after which sampling depth was  $\geq 10$  individuals per live and dead category.



**Figure 4.4.** Annual growth-defense relationships for bark beetle-susceptible trees (A) and resistant trees (B). Growth and defense were standardized relative to the mean of each tree. Trees that resisted bark beetles demonstrated growth-defense trade-offs following fire re-entry: basal area increment (BAI) was negatively correlated with duct area, whereas susceptible trees showed positive growth-defense relationships counter to the growth-differentiation balance hypothesis. Over no aggregation of time during fire exclusion – including comparably droughty years – did growth-defense relationships become as extremely positive as those observed for bark beetle-susceptible trees following fire re-entry (Fig C.4). This effect was driven by years with simultaneously low or intermediate growth and defense. No years of both high growth and high defense were observed for susceptible trees following fire. Shaded regions indicate 95% confidence intervals.



**Figure 4.5.** Results from the multilevel moderated mediation structural equation model testing the mechanisms underpinning bark beetle attack/success and tree constitutive/induced defenses in a compound disturbance environment. Paths represent hypothesized causal relationships. Bark beetle success rate is measured as *Pinus* survival or mortality due to bark beetles. Bark beetle attack rate is approximated by total bark beetle-killed *Pinus* BA within a 10-m radius. Density is *Abies concolor* within 10-m radius, and diversity is species richness within a 30-m radius. Dashed lines connecting two factors indicate a covariance. Dashed lines connecting a factor to a path (i.e., drought and fire effects) indicate a moderation interaction. Drought and fire moderated paths independently from one another, though this is not depicted in the figure for aesthetic parsimony. Within-tree variability (level 1) was sampled by growth, defense, and drought over time; between-tree variability (level 2) was sampled by all other factors. Thus, all mediated (i.e., indirect) relationships are represented as cross-level interactions. Transparent arrows indicate a non-significant effect. To calculate the total moderation effect, direct effects of moderators are also shown for each variable (bold if significant, but even non-significant values needed for calculations of a significant interaction term).

## CHAPTER V

SHARED FRIENDS COUNTERBALANCE SHARED ENEMIES IN OLD FORESTS<sup>4</sup>**Abstract**

Mycorrhizal mutualisms are nearly ubiquitous across plant communities. Yet, it is still unknown whether facilitation among plants arises primarily from these mycorrhizal networks or from physical and ecological attributes of plants themselves. Here, we tested the relative contributions of mycorrhizae and plants to both positive and negative biotic interactions to determine whether plant-soil feedbacks with mycorrhizae neutralize competition and enemies within multitrophic forest community networks. We used Bayesian hierarchical generalized linear modeling to examine mycorrhizal guild- and mortality cause-specific woody plant survival compiled from a spatially and temporally explicit dataset comprising 101,096 woody plants from three mixed-conifer forests across western North America. We found positive plant-soil feedbacks for large-diameter trees: species-rich woody plant communities indirectly promoted large tree survival when connected via mycorrhizal networks. Shared mycorrhizae primarily counterbalanced apparent competition mediated by tree enemies (e.g., bark beetles, soil pathogens) rather than diffuse competition between plants. We did not find the same survival benefits for small trees or shrubs. Our findings suggest that lower large-diameter tree mortality susceptibility in species-rich temperate forests resulted from greater access to shared mycorrhizal networks. The interrelated importance of above-ground and below-ground biodiversity to large tree survival may be critical for counteracting increasing pathogen,

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<sup>4</sup> This chapter was published in *Ecology* on July 26, 2021, and should be cited as: Germain, S. J., and J. A. Lutz. 2021. Shared friends counterbalance shared enemies in old forests. *Ecology*, 102(11): e03495. <https://doi.org/10.1002/ecy.3495>



bark beetle, and density threats.

## Introduction

Mycorrhizal mutualisms between trees and fungi form the primary pathways for nutrient acquisition and are therefore central to facilitation dynamics in forests (Simard et al. 1997, Smith and Read 2008). Despite known benefits of mycorrhizae, positive outcomes of interactions among trees are often credited to the trees themselves rather than to plant-soil feedbacks with fungal mutualists (Brooker et al. 2008). Enhanced survival of trees growing in more species-rich forest stands (Jactel and Brockerhoff 2007), for instance, has been attributed to proportionally lower host abundances (Kareiva 1983), non-host pheromones (Huber and Borden 2001), and novel tree silhouettes (Mayfield and Brownie 2013). Yet, forests support diverse mycorrhizal networks as well (Jones et al. 1997, Twieg et al. 2007, Beiler et al. 2010, Lang et al. 2011, Karst et al. 2014), which promote tree survival by bolstering nutrient uptake (Baxter and Dighton 2001, Köhler et al. 2018) and defenses (Bennett et al. 2005, Wehner et al. 2010). Here, we decouple the effects of above-ground and below-ground biotic interactions to explore the possibility that species-rich forests indirectly promote tree survival through shared mycorrhizal networks.

Ecological research has long sought to model the complexity of diffuse interactions in multi-species communities (Holt 1977). Diffuse interactions capture the indirect effects of many interacting individuals or species in a community, which can overwhelm direct effects observed in pairwise interactions alone (Vandermeer 1990, Levine et al. 2017). Diffuse *trophic* interactions arise when interacting individuals belong to different trophic levels (e.g., primary producers, consumers, decomposers). Two trees

may appear to be competing, for example, but the negative effect actually derives from trophic interactions between individual trees and a shared herbivore (apparent competition; Janzen 1970, Connell 1971, Cobb et al. 2010, Chaneton et al. 2010). In contrast, trees may appear to be facilitating one another, but the positive outcome is actually an indirect effect arising from attraction of a shared mutualist, such as pollinators or mycorrhizal fungi (apparent facilitation; Johnson et al. 2003, Sargent and Ackerly 2008).

Indirect positive interactions that connect plant communities above-ground with mycorrhizal fungi communities below-ground are a primary source of positive plant-soil feedbacks (+PSF; Bennett et al. 2017). Some mature trees, for instance, indirectly facilitate seedling establishment through accumulation of shared mycorrhizal fungi near the parent tree (Teste and Simard 2008, Liang et al. 2015, Johnson et al. 2018). The extent to which +PSF occur among mature trees themselves remains largely unexplored; instead, it is often assumed that diffuse interactions among many individual trees produce apparent facilitation through non-trophic suppression of a strong competitor, such as a large neighboring tree (diffuse competition; Peterson and Squiers 1995, Levine 1999, Lutz et al. 2014). These interactions, however, are confounded with mycorrhizal effects due to the close spatial correlation between mycorrhizal fungi assemblages and plant assemblages (Hausmann and Hawkes 2009, Lang et al. 2011, Karst et al. 2014). To accurately parse the relative contributions of different taxonomic groups in large community networks, it is first necessary to disentangle the effects of above- and below-ground communities.

Mycorrhizae form the crux of multitrophic interactions in forests by linking

above-ground and below-ground communities. Mycorrhizae enhance nutrient uptake (Baxter and Dighton 2001, Köhler et al. 2018); transfer nutrients directly between plants (Francis and Read 1984, Simard et al. 1997); regulate genetic expression to systemically bolster constitutive defenses (Liu et al. 2007, Kanekar et al. 2018); prime defenses to allow more rapid induced-defense responses (Jung et al. 2012, Pastor et al. 2013); facilitate inter-plant communication to quickly mount defense responses if an enemy is detected in the network (Gorzalak et al. 2015); and can directly compete with pathogenic microbes to protect plants from attack (Marx 1972). Importantly, different fungi can confer unique defense capabilities (Wehner et al. 2010, Roger et al. 2013, Lewandowski et al. 2013), meaning plants colonized by a diversity of fungal networks may be better defended against a wider array of enemies (van der Heijden 2001, Wehner et al. 2010). Nonetheless, survival consequences of shared mycorrhizal networks have not been adequately described for mature trees. For long-lived woody forest plants, survival is the vital rate most directly associated with sustained ecological functioning (Silvertown et al. 1993), as mature tree mortality (>50 yrs) rapidly removes large amounts of reproductive biomass (Stephenson et al. 2014, Das et al. 2016) and can dramatically alter ecosystems over short timeframes (Lutz et al. 2018, Swann et al. 2018). We therefore tested whether mycorrhizal benefits were able to change survival outcomes amidst competition and apparent competition in the above-ground plant community (Bennett et al. 2005, Teste and Simard 2008, Gehring and Bennett 2009, Liang et al. 2015).

We synthesized existing gradients of above-ground woody plant richness with spatial patterns of mycorrhizal guilds to investigate facilitation mechanisms in mature forests. To do this, we combined conventional forest mensuration techniques quantifying

plant crowding with long-term monitoring techniques tracking individual plant fates through time (Hegyí 1974, Lutz 2015). Plant crowding is most commonly utilized as a singularly competitive metric (e.g., Biging and Dobbertin 1995), but here we test the possibility that crowding also provides access to nearby mycorrhizal networks (Beiler et al. 2010). Notably, woody plants are expected to have access to survival benefits provided by surrounding mycorrhizal networks only to the extent that neighboring plants are members of the same mycorrhizal guild (Martin et al. 2016): arbuscular mycorrhizal (AM), ectomycorrhizal (EM), or ericoid mycorrhizal (ErM; Fig. 5.1). Plants tend to form mycorrhizae with multiple fungal species, and fungi are likewise often able to colonize a multitude of plant species, within each of these guilds (Molina and Trappe 1982, Moeller and Neubert 2015). Some mycorrhizas are specialized, however, such that neighboring plants of the same guild are not guaranteed to share mycorrhizal networks (van der Linde et al. 2018); and conversely, some plants form dual associations that allow connection with both neighboring AM and EM species (Malloch and Malloch 1981, Neville et al. 2002). We therefore tested mycorrhizal guild affiliation of woody species for which this may be uncertain: (1) ErM fungi have been shown to form EM with non-Ericaceous species (Vrålstad 2004), so we tested whether Ericaceous species should be categorized as ErM or EM; and (2) for dual-hosting species able to form both EM and AM (either simultaneously or ontogenetically stratified), we tested whether these should be categorized as EM, AM, or a separate guild altogether (both-forming; AM/EM; see Appendix D for an extended discussion of study assumptions and limitations).

Our objective was to develop an improved framework for investigating diffuse multitrophic interactions by elucidating the role of mycorrhizal networks in observed

facilitation dynamics among plants. Our temporally and spatially variant dataset provided the opportunity to identify the forest structural and compositional conditions that promote +PSF and neutralize negative forest interactions. We found evidence of +PSF for large trees across all three forest types. Increasing above-ground richness reduced negative effects of only the mycorrhizal guild-sharing neighbors, suggesting that below-ground mycorrhizal networks were able to counteract diffuse interactions among these trees and their enemies. Mycorrhizae primarily reduced apparent competition (i.e. mortality mediated by indirect interactions between trees and shared enemies) rather than direct competition between plants, suggesting that shared mycorrhizae reduced large-diameter tree susceptibility to shared enemies. Our finding of +PSF in mature forests indicates that mutualisms and facilitation may be key counterbalances to increasingly negative trophic interactions threatening western forests (Stachowicz 2001, Bastolla et al. 2009, Huxham et al. 2010, Van Nuland et al. 2017).

## **Materials and Methods**

### *Data Acquisition*

We assessed woody plant survival patterns in three spatially and temporally explicit forest dynamics plots spanning the western USA: Wind River, WA (WFDP; Lutz et al. 2014; 27.2 ha; 352–384 m elevation; 45.82° N, 121.95° W;  $n = 35,531$ ), Yosemite, CA (YFDP; Lutz et al. 2012; 25.6 ha; 1774–1911 m elevation; 37.77° N, 119.82° W;  $n = 38,104$ ), and Cedar Breaks, UT (UFDP; Furniss et al. 2017; 13.2 ha; 3039–3169 m elevation; 37.66° N, 112.85° W;  $n = 27,461$ ). These three sites represent three distinct climatic zones in western North America: the WFDP has a temperate maritime climate

(warm, dry summers and cool, wet winters) where most precipitation falls as winter rain; the YFDP climate is Mediterranean (hot, dry summers and cold, wet winters) where most precipitation falls as winter snow; and the UFDP has a subalpine continental climate (cool, wet summers and cold, wet winters) where most precipitation falls as winter snow, with additional monsoonal rains during the short growing season.

All woody stems  $\geq 1$  cm diameter at breast height (DBH; 1.37 m) were identified to species, mapped, and DBH measured (Anderson-Teixeira et al. 2015). Newly recruited stems were recorded and mapped on an annual basis after reaching 1 cm DBH. Woody species included both trees and shrubs: we defined trees as species with singular boles that do not regenerate vegetatively, while shrubs were defined as multi-stemmed species that are capable of vegetative regeneration (e.g., resprouting, root suckering; Table D.1). From these definitions, all trees were wind-pollinated gymnosperms, while shrubs included gymnosperms and angiosperms that tended to be shorter-statured than tree species. Each group captured a range of plant statures: there was variability in maximum DBH potential for shrubs (e.g., *Vaccinium* vs. *Populus*) as well as trees (e.g., *Taxus* vs. *P. lambertiana*). We therefore utilized species-specific DBH percentiles in analyses described below (Table 5.1).

To measure trophic interactions between forest plants and their enemies, we revisited each stem annually and conducted pathology exams for newly dead stems to assess survival since 2010, 2011, and 2015 respectively per plot, through 2020 (further details in Appendix D: Section S1; Table D.3; Figs. D.6, D.7). Survival assessments took place during the same month in each plot to control for seasonal phenological differences (YFDP: May; WFDP: June; UFDP: July). Individuals were considered dead if no live

foliage, buds, or photosynthetic stems were evident; we then exposed phloem and sapwood of the stem and roots, which allowed detailed identification of mortality factors to species (e.g., *Dendroctonus ponderosae*). The YFDP burned in the 2013 Rim Fire, so we considered only pre-fire mortalities and post-fire mortalities that were not directly caused by the fire.

Because most mycorrhizal fungi are generalists in these forests (Molina and Trappe 1982, Birch et al. 2021a), we assessed diffuse trophic interactions between forest plants and mycorrhizal fungi at the guild-level (AM, EM, ErM, or both AM/EM). Mycorrhizal guilds were designated at the smallest taxonomic unit described in the literature (23% of plant species were designated at the family level; 67% at genus level; 10% at species level; Table D.1). Guild designations were confirmed with the MycoDB (Chaudhary et al. 2016) and FungalRoot databases (Soudzilovskaia et al. 2020; see also *Sensitivity Analyses*).

### *Quantifying Diffuse Interactions*

We represented the effects of diffuse plant-plant interactions using the crowding and species richness of mycorrhizal guild-specific above-ground plant neighborhoods. Individuals were counted as neighbors that were rooted within a 20-m radius of the focal individual, which envelopes previously identified interaction distances for mycorrhizal networks and competition among trees (Das et al. 2008, Beiler et al. 2010, Johnson et al. 2018). We used a distance-diminished, diameter-weighted crowding index to quantify the effective density of neighbors,  $j$ , for focal individual,  $i$ . In other words, the crowding index collapses information about the density, spatial pattern, and relative diameters of neighboring woody plants into a single, quantitative measurement of the plant

neighborhood. The geometric distance decay function assumes decreasing interaction effects with decreasing proximity to neighbors (Das et al. 2008). The diameter-weighting procedure reflects the observation that larger trees are often hubs of mycorrhizal connectivity (Beiler et al. 2010), but are also strong competitors (Lutz et al. 2013, 2014) and enemy attractants (Barbosa et al. 2009, de la Mata et al. 2017).

$$(1) \quad C_i = \sum \frac{DBH_j}{1 + Distance_{ij}}$$

Correlations between plant survival and crowding capture the *net effects* of many diffuse interactions occurring among members of the community, which include both positive and negative interactions. Crowding indices can be leveraged to identify thresholds at which forest neighborhoods have a net positive effect on individual survival, particularly when refined to include information about neighborhood composition and mycorrhizal affiliation. To do this, we calculated crowding separately for conspecific neighbors, heterospecific guild-sharing neighbors (*HGS*), and heterospecific guild-disparate neighbors (*HGD*); crowding was then allowed to interact with species richness of *HGS* and *HGD* neighbors in survival models (see *Modeling Approach*).

Differences in observed crowding across species and diameters reflect vestiges of processes past (dispersal, recruitment, and pre-study mortality events), particularly in late-seral forests (Lutz et al. 2014, Furniss et al. 2017, 2020); it was therefore necessary to decouple these from the recent spatially explicit survival processes of interest. We controlled for the existing spatial structure of trees to isolate *a posteriori* survival (Goreaud and Pélissier 2003, Larson et al. 2015) by centering the crowding index on the



mean per species and diameter (Germain and Lutz 2020). After centering, values  $> 0$  indicate more crowded neighborhoods than would be expected for trees of a particular species and diameter and values  $< 0$  indicate less crowded neighborhoods. Standardizing by species and diameter (described above) allows crowding effects to be assessed at the plot level without being overly sensitive to the responses of single species (see *Modelling Approach*, below). Models therefore tested whether plants with more crowded environments had higher mortality risk than would be expected given the existing spatial structure for stems of that particular species and diameter.

### *Modelling Approach*

Because plant survival tends to depend on plant size, statistical tests were performed separately for trees and shrubs belonging to each diameter class (small or large; Table 5.1). Large was defined as individuals having  $DBH \geq 90^{\text{th}}$  percentile per species, and small was defined as individuals having  $DBH \leq 10^{\text{th}}$  percentile per species. We tested a range of percentiles: both  $5^{\text{th}} - 95^{\text{th}}$  and  $15^{\text{th}} - 85^{\text{th}}$  options produced results with the same interpretation as the  $10^{\text{th}} - 90^{\text{th}}$ . Here, we utilize the  $10^{\text{th}} - 90^{\text{th}}$  for parsimony (allowed larger sample size than  $5^{\text{th}} - 95^{\text{th}}$ , but reflects the large-small dichotomy better than  $15^{\text{th}} - 85^{\text{th}}$ ). We performed all analyses for all diameters combined as well during preliminary phases of the study: the strongly divergent responses of large and small individuals nullified each other's effects in these combined models. The resulting interpretation was misleading, so we do not report findings from these combined models.

Individuals with the following characteristics were included in crowding/richness calculations but omitted from survival analyses to preserve interpretability of prevailing

PSF dynamics: 1) those that died of mechanical crushing or direct fire damage ( $n = 28,589$ ); 2) species with fewer than two individuals per plot ( $n = 10$ ); and 3) individuals recruited in the final year of study ( $n = 4878$ ). Trees located at plot perimeters (0 to 20 m inside edge) were omitted to prevent edge effects ( $n = 9994$ ). Therefore, we analyzed survival for 57% of the 101,096 individuals utilized for crowding calculations (WFDP  $n = 29,417$ ; YFDP  $n = 8,178$ ; UFDP  $n = 20,030$ ), which comprised 73% of the forests' total basal area (Table 5.1).

We used a Bayesian hierarchical generalized linear model to estimate the effects of above-ground crowding and below-ground mycorrhizal network access on individual survival over the course of the study (perfect observation of survival was assumed). We modeled survival probability,  $S$ , of individual,  $i$ , in plot,  $j$ , as a Bernoulli random variable with probability,  $p$ , related to a linear combination of covariates using a logit link (Eq. 2). The annual resolution of sampling provided the opportunity to accurately assess mortality causes, though analyses were conducted on final survival outcomes at the study end (i.e. no repeated observations). Linear effects varied randomly by plot (random intercept;  $n = 3$ ) to 1) account for differing study timeframes among plots (WFDP: 2010–2020, YFDP: 2011–2020, UFDP: 2015–2020); and 2) facilitate model generalizability to mixed-conifer temperate forests across western North America.

$$(2) \quad S_{ij} \sim \text{Bernoulli}(p_{ij})$$

$$\text{logit}(p_{ij}) = \beta_{0j} + \beta_1 * CC_i + \beta_2 * HSC_i + \beta_3 * HDC_i + \beta_4 * HSR_i + \beta_5 * HDR_i + \beta_6 * HSC_i * HSR_i + \beta_7 * HDC_i * HDR_i$$

Fixed effects variables were the three crowding indices: conspecific, heterospecific guild-sharing, and heterospecific guild-disparate neighbor crowding

(notated *CC*, *HSC*, and *HDC*, respectively); heterospecific guild-sharing and heterospecific guild-disparate species richness (notated *HSR* and *HDR*, respectively); and interactions between richness and crowding for both heterospecific neighborhood parameters. We tested the interaction between crowding indices and neighborhood richness to determine whether the composition of above-ground neighbors, not just their relative densities and spatial structure, modified the effect of mycorrhizal network access. Because conspecific crowding is monospecific, we did not test its interaction with richness.

Positive relationships between crowding and survival indicate a net facilitative effect, while negative relationships indicate a net harmful effect. Harmful effects were further delineated as competition or apparent competition through assessment of the causes of mortality established during pathology exams. If facilitation mechanisms were primarily mediated by above-ground plant attributes (e.g., diffuse plant competition, crown form), then we expect increasing plant richness to ameliorate negative interactions among both guild-sharing and guild-disparate neighbors (Fig. 5.1). On the other hand, we expect increasing plant richness to reduce negative effects of only the guild-sharing neighbors if facilitation primarily arose through +PSF. Thus, positive interactions between *HSC* and *HSR*, in the absence of positive interactions between *HDC* and *HDR*, would indicate that diverse above-ground communities indirectly promoted plant survival via mycorrhizal networks.

Models contained diffuse normal priors for all covariates, where random plot intercepts were drawn from a shared normal distribution (Eq. 3). Priors were normally distributed to allow the possibility of both negative and positive effects within a logistic

model framework (i.e. with a logit link). We chose to keep priors diffuse because there is currently no study in temperate mixed-conifer forests comparing mycorrhizal guild-level neighborhood effects from which we could have attained justifiable informed priors (particularly for the interaction terms of interest). Of prior studies investigating guild-specific survival, the forest types were dissimilar; saplings rather than mature trees were studied; and/or differences in analytical approach minimized availability of useful information (e.g., spatial point patterns of recruitment in hardwood forests; Johnson et al. 2018). Consequently, informed priors would have had to be derived from only tangentially related datasets examining conspecific vs. heterospecific interactions in similar forest types (e.g., Slack et al. 2017), which risk biasing models because mycorrhizal guilds were not designated and too few species were considered. Diffuse priors allowed our large dataset to objectively inform model outcomes, and conversely, our use of a large, data-rich census minimizes sensitivity to priors (Depaoli et al. 2017, Thorson and Cope 2017).

$$(3) \quad \beta_{0j} \sim \text{Normal}(\mu \sim \text{Normal}(0, 1), \sigma \sim \text{Uniform}(0, 1)) \\ [\beta_1: \beta_7] \sim \text{Normal}(0, 0.33)$$

Models were built using five chains of 20,000 iterations: the first 3,000 iterations of each chain were discarded as burn-in and no thinning was conducted, resulting in 51,000 posterior samples of each parameter. We assessed convergence of chains through  $\hat{R}$  values, where  $\hat{R} \leq 1.1$  indicates acceptable convergence, and visual inspections of trace plots. We assessed model accuracy using mean parameter estimates to predict survival, which was then compared to observed survival to calculate classification accuracy (sensitivity and specificity: percent of observations correctly classified as live or dead,

respectively, when using the optimal survival probability threshold for classification) and Area Under the ROC Curve (AUC; measures model performance of live/dead classification across all classification thresholds, where  $AUC = 1$  indicates perfect classification). Analyses were performed using JAGS v. 4.3.0 (Plummer 2003) called from R v. 3.6.0 (R development core team 2019) with package jagsUI v. 1.5.1 (Kellner 2016).

### *Sensitivity Analyses*

Our model selection process was founded on two sensitivity analyses that together addressed the following uncertainties: (1) do ErM- and both AM/EM-forming species share mycorrhizae with other EM and/or AM species? (2) do mycorrhizal and competitive interactions differ as a function of which woody species and diameters are analyzed? (3) do complex or simplified density metrics (i.e. distance- and diameter-weighted density vs. raw density) better capture these interactions? (4) at what distances are interactions most evident?

Sensitivity Analysis one (SA1) addressed all four uncertainties by investigating the sensitivity of model accuracy (measured by area under curve [AUC] and deviance information criterion [DIC]) to factorial combinations of mycorrhizal guild designation, woody plant diameter, neighborhood radius, and density metric. Combinations were tested for all-species, tree-specific, and shrub-specific models ( $n = 288$  models). We permuted mycorrhizal guild designations for ErM- and both AM/EM-forming species, where ErM species were considered (1) guild-sharing for both ErM and EM heterospecifics, or (2) guild-sharing amidst other ErM species only; and AM/EM species were considered (1) guild-sharing for both AM and EM heterospecifics, or (2) guild-

sharing amidst other AM/EM species only. Tests were performed for either the smallest individuals ( $DBH \leq 10^{\text{th}}$  percentile), the largest individuals ( $DBH \geq 90^{\text{th}}$  percentile), or all diameters combined. We tested neighborhood radii at 5-, 10-, 15-, and 20-m away from focal individuals. The neighborhood density metric at each radius was either simple density (number of stems; more parsimonious) or distance- and diameter-adjusted density (i.e. crowding; more biologically representative; Eq. 1). We then conducted a more refined Sensitivity Analysis two (SA2) that targeted Uncertainties 2–4 by investigating the sensitivity of parameter estimates to woody plant diameter, neighborhood radius, and density metric. We chose guild designations indicated by SA1 to be most predictive, then permuted diameter, neighborhood radius, and density metric as described for SA1. We calculated sensitivity of model parameters' posterior distributions to neighborhood radii of 5-, 10-, 15-, and 20-m. This test was performed for all-species, tree-specific, and shrub-specific models ( $n = 72$  models).

Sensitivity Analysis one found higher predictive accuracy for the tree-specific models, and lower accuracy for shrub-specific models, compared to models combining both functional types. Crowding generated higher accuracy (AUC) than density for all-species and trees models, but density was more predictive for shrubs. After controlling for species and diameter, however, differences in AUC were negligible (mean  $\Delta$  AUC as a function of density metric = 0.3 percentage points). Model DIC was more sensitive to permutations in neighborhood radius and density metric than was AUC (mean  $\Delta$  DIC as a function of density metric = 22). In all-species, tree, and shrub models alike, the 20-m neighborhood radius yielded the lowest DIC scores (Table D.2). After controlling for species, diameter, and neighborhood radius, DIC was often minimized ( $\Delta$  DIC > 10) by

designating ErM and both AM/EM forming species separate, independent guilds (as opposed to designating ErM as EM, or both AM/EM-forming species as either EM or AM). Sensitivity Analysis two found greater parameter sensitivity to neighborhood distances than density metric. Regardless of density metric chosen, point estimates and credible intervals were very similar; however, the more complex crowding metric tended to produce tighter credible intervals (higher confidence in point estimates).

## **Results**

Based on findings of two sensitivity analyses (Table D.2, Fig. D.4), final models had the following qualities: (1) plant species forming ericoid mycorrhizae and those forming both AM/EM were considered distinct guilds and were not assumed to share mycorrhizae with other EM and/or AM species; (2) mycorrhizal and competitive interactions differed substantially depending both on species and diameter, so we report results from small and large shrubs and trees separately; (3) complex and simplified density metrics performed similarly in terms of AUC, but we chose the more complex distance-diminished, diameter-weighted crowding index (Eq. 1) as it substantially reduced DIC and posterior distribution credible intervals, particularly for tree models; (4) plant–plant interaction distances were 20-m, which minimized DIC.

### *Quantifying Diffuse Interactions*

Annual woody plant survival rates were highest in Cedar Breaks, UT (99.6%), intermediate in Wind River, WA (98.6%), and lowest in Yosemite, CA (95.4%; Table 5.1). Small-diameter annual survival was 1% and 5.5% lower than large-diameter annual survival in Wind River and Yosemite, respectively, but roughly equal in Cedar Breaks.

Above-ground neighborhood species richness, particularly of guild-sharing neighbors, generally increased shrub and tree survival (Fig. D.3). Higher conspecific crowding increased large shrub survival and decreased small tree survival. Shrub and small tree mortality was dominated by suppression (i.e. competition for light from larger trees). Large tree mortality was dominated by native bark beetles in Cedar Breaks and Yosemite, and native fungal pathogens/saprophytes in Wind River (Table D.3, Fig. 5.2; see also Lutz et al. 2021, their Fig. 7).

As predicted, we found positive interactions between *HSC–HSR* and an absence of positive interactions between *HDC–HDR* (Fig. 5.3): together these indicate that diverse above-ground communities indirectly promoted plant survival via mycorrhizal networks. Crowded neighborhoods increased tree survival when *HSR* was high, but reduced tree survival when *HSR* was low (Fig. 5.3). We found the opposite interaction for crowded guild-disparate neighborhoods (low *HDC*), which increased tree survival only when *HDR* was low. The presence of facilitation among only the guild-sharing species supports our hypothesis of +PSF in more species-rich neighborhoods. Beneficial mycorrhizal effects were driven primarily by large EM tree species, while negative interactions between guild-disparate crowding and richness were driven primarily by large AM tree species (Fig. D.5). It is worth noting that large AM tree sample size ( $n = 245$ ) and mortality  $n$  were small ( $n = 19$ ) compared to large EM trees ( $n = 3801$ ; mortality  $n = 357$ ) and may be subject to higher type II error. No +PSF were detected for shrubs or small trees.

### *Model Performance*

Tree models were good classifiers (large tree AUC = 0.72; small tree AUC =



0.90) and the shrub models were moderate (large shrub AUC = 0.67; small shrub AUC = 0.94; Table D.2). Likewise, correct classification of dead individuals was higher for trees (large tree specificity = 0.67; small tree specificity = 0.79) than shrubs (large shrub specificity = 0.64; small shrub specificity = 0.63). For all models, Markov chains converged and trace plots indicated well-sampled posterior distributions for all parameters.

## **Discussion**

Early work on facilitation largely overlooked the role of plant-soil feedbacks involving mycorrhizae and instead assumed facilitation arose primarily from direct plant-plant interactions (summarized by Callaway 1995). Despite its simplicity, this body of work was pivotal during an era of ecological study that was otherwise focused on competitive interactions (Tilman 1982, Brooker et al. 2008). Though there have since been substantial gains in the understanding of mycorrhizal networks in forests (Simard et al. 2012), the significance of how mycorrhizae mediate plant–enemy relationships is only recently coming into focus (Bennett et al. 2005). Beyond the conventional understanding that mycorrhizae mediate plant competitive relationships by controlling nutrient acquisition (Teste and Simard 2008), our findings suggest that mycorrhizae can also reduce large trees’ susceptibility to native enemies (Franklin et al. 1987, Das et al. 2011; Fig. 5.2). The prominence of +PSF for these trees indicates that positive interactions among forest plants cannot be solely attributed to physical or chemical attributes of trees themselves (e.g., crown form or chemical volatiles; summarized by Barbosa et al. 2009). Though the strength of +PSF may differ along gradients of environmental variability (e.g., Lodge 1989, Benning and Moeller 2021), large tree dynamics converged across

different site-level topographic positions (captured by large plot sizes) and regional-scale climatological contexts (captured by the three distinct sampling areas). Findings from these temperate mixed-conifer forests join the growing body of evidence demonstrating the interconnected importance of above-ground and below-ground biodiversity to tree survival (Clark and McLachlan 2003, Teste et al. 2017, Schuldt et al. 2018).

Large-diameter trees rarely die of competition alone, but instead succumb to interactive processes of enemy attack, climatic stress, physical damage, and competition (Fig. 5.2, Table D.3; Franklin et al. 1987, McDowell et al. 2011, Larson et al. 2015). Thus, conspecific crowding-dependent mortality prevailed for small trees (CNDD; Chesson 2000, Chen et al. 2018), while heterospecific crowding-dependent mortality prevailed for large trees in low-richness neighborhoods (HNDD; Larson et al. 2015). Informed by our in-depth pathology exams, this HNDD primarily reflected the activity of biotic enemies (Fig. 5.2). Unlike in many tropical forests (e.g., Janzen 1970), native fungal pathogens and saprophytes found in temperate mixed-conifer forests tend to be generalists (host family- to division-specific), while the insect herbivores are often more specialized (host species- to genus-specific). As such, heterospecific neighborhoods – not just conspecific – are important sources of accumulated shared enemies (Uriarte et al. 2004, Riihimäki et al. 2005, Jactel and Brockerhoff 2007).

Large trees' shift from negative to positive HDD given sufficiently high guild-sharing species diversity (see also Teste and Simard 2008, Liang et al. 2015) supports the interpretation that mycorrhizae counteracted negative plant-soil feedbacks being operated by generalist pathogenic fungi, such as *Armillaria ostoyae* (Romagnesi) Herink (Table D.3, Fig. D.7; Marx 1972, Baleshta et al. 2005). Yet, the notable prominence of +PSF for

large-diameter EM trees presents the additional possibility that mycorrhizae counteracted genus-specialized bark beetles as well (e.g., *Scolytus ventralis* on *Abies* spp.; Figs. D.2, D.5, D.6; Pineda et al. 2010, Raffa 2014, Kanekar et al. 2018). Benefits of above-ground woody plant diversity (Kareiva 1983, Huber and Borden 2001, Yamamura 2002, Jactel and Brockerhoff 2007, Mayfield and Brownie 2013) likely synergize with benefits of below-ground mycorrhizal diversity (Baxter and Dighton 2001, Wehner et al. 2010, Köhler et al. 2018) to vastly increase pest resistance of large trees growing in species-rich, mycorrhizae-connected communities (Fig. 5.3). This complex balancing act between tree density, plant-soil feedbacks, and enemies could help explain contradictions in the literature regarding the directionality of density dependence (or lack thereof) among large-diameter trees in temperate forests (Das et al. 2008, Larson et al. 2015, Lintz et al. 2016, Furniss et al. 2020, Jiang et al. 2020).

Decoupling above-ground and below-ground facilitation quantifies the relative importance of mechanisms governing enemy attack vs. predisposing factors contributing to enemy success. Above-ground tree richness can reduce enemy *attack rates* by obfuscating host detection via non-host pheromones (Huber and Borden 2001) and novel tree silhouettes (Mayfield and Brownie 2013). If above-ground richness had been the dominant mechanism of facilitation, however, both guild-disparate and guild-sharing plant richness would be expected to counteract negative crowding effects (Fig. 5.3). Though some below-ground mycorrhizal networks can also reduce enemy attack rates by suppressing pathogenic soil microbes (Marx 1972, Wehner et al. 2010), mycorrhizae are more broadly recognized for reducing enemy *success rates* (Gehring and Bennett 2009, Pineda et al. 2010; but see Roger et al. 2013). Access to shared mycorrhizal networks can

reduce trees' susceptibility to enemies post-attack, both *indirectly* by reducing the net effects of competition (Baxter and Dighton 2001, Teste and Simard 2008, Bastolla et al. 2009, Köhler et al. 2018) and *directly* by enhancing plant defenses (van der Heijden 2001, Wehner et al. 2010, Kanekar et al. 2018). The strong mycorrhizal effect shown here indicates that mycorrhizae-mediated defense pathways may be critical for reducing large-diameter tree susceptibility to native enemies in temperate mixed-conifer forests.

Distinct responses of large and small trees suggest the presence of ontogenetic differences in the importance of +PSF. Large-diameter trees tend to grow in neighborhoods with lower diversity and density than smaller trees (Lutz et al. 2014, Das et al. 2018) due to a history of size-asymmetric competition (Lutz et al. 2014, Das et al. 2018) and persistence through antecedent disturbances (Furniss et al. 2020). In support of this interpretation, we found that small trees succumbed to competitive exclusion in crowded, monodominant guild-sharing neighborhoods (e.g., those near large trees); but inversely, crowding by a species-rich consortium of guild-sharing neighbors increased large tree survival (Fig. 5.3). These results together suggest that +PSF for large trees is built upon –PSF for small trees. Indeed, larger trees show a higher degree of mycorrhizal connectivity than their smaller neighbors and are the primary mediators of resource transfer in forests (Beiler et al. 2010). In turn, we found that a more diverse assemblage of neighbors provided large trees with greater benefit, perhaps due to a concomitantly wider array of fungal partners providing multiple pest-defense capabilities (Jones et al. 1997, van der Heijden and Horton 2009, Wehner et al. 2010; but see Moeller and Neubert 2015). Studies of old forests increasingly show that large trees are key components of mycorrhizal networks that become more beneficial and efficient through ontogenetic

time.

The benefits of plant-soil feedbacks likely change over the course of forest succession as well (Horton et al. 2005). In contrast with dynamics evident in the largest, oldest trees only present in late-seral stages, we found no +PSF in forest patches recapitulating early-seral habitats (e.g., dense patches of shrubs and small-diameter trees; Hubbell et al. 1999, Franklin et al. 2002, Halpern and Lutz 2013). Instead, above-ground facilitation was more important here: small tree survival was increased by neighborhood richness (both *HSR* and *HDR*), while shrub survival was increased by conspecific crowding (conspecific positive density dependence). Despite sharing successional similarities, small tree and shrub dynamics represent two fundamentally different processes due to divergent below-ground life history traits. Shrubs are multi-stemmed species capable of vegetative regeneration, making crowding by conspecifics often synonymous with crowding by interconnected ramets of the same genetic individual. Beyond mycorrhizae, then, common root systems and habitat filtering offset shrubs' competitive effects by facilitating nutrient transfer between stems (Das et al. 2018), while differences in physical traits of heterospecifics (i.e. fitness differences) offset competition among small trees (Chesson 2000, Carroll et al. 2011). The distinct differences between shrub, small-tree, and large-tree facilitation dynamics portend a parallel temporal gradient of PSF effects throughout forest development: mycorrhizae may be less beneficial for survival in highly competitive, early stages dominated by shrubs and/or saplings, but become very beneficial in the less competitive, later stages containing large trees and complex mortality dynamics (Twieg et al. 2007, Larson et al. 2015).

The prevalence of generalist mycorrhizal mutualisms in temperate mixed-conifer

forests indicates that many of the plants tested here had the capacity to form multiple mycorrhizas if presented with the opportunity (Kropp and Trappe 1982, Molina and Trappe 1982, Vrålstad 2004, Horton et al. 2005, Gorzelak et al. 2015). However, some mycorrhizas are more specialized (Molina and Horton 2015, van der Linde et al. 2018, Birch et al. 2021a). The absent mycorrhizal effect for shrubs, for example, may reflect a higher degree of ErM specificity that precludes shrubs' access to additional benefits gained through multiple mycorrhizas. Contrarily, the mycorrhizal effect shown for large-diameter EM trees indicates that these individuals were able to access advantages in diverse guild-sharing neighborhoods; in the absence of a similar effect in diverse guild-disparate neighborhoods, the most plausible mechanism by which this may occur is through formation of multiple facilitative mycorrhizas. Prior studies have shown that the majority of EM species sampled from Cedar Breaks fungal communities (54.4%) occurred on more than one tree species and were capable of forming interspecific mycorrhizal networks (Birch et al. 2021a). Likewise, mycorrhizal connectivity among distantly related heterospecific trees is well-described in Douglas-fir forests like Wind River (Simard et al. 1997, Birch et al. 2021b). The evidence shown here constitutes a first approximation of multitrophic plant–enemy–mutualist dynamics in western forests, a basis for which future studies may conduct direct sampling of mycorrhizae and plant defensive chemistry to illuminate the complex relationship between plant diversity, fungal diversity, and plant mortality susceptibility.

## **Conclusions**

Our long-term study of spatially explicit, cause-specific forest plant mortality provided the opportunity to bridge above-ground and below-ground communities,

revealing that mycorrhizal networking can counterbalance apparent competition in forests. Importantly, the large permanent monitoring plot sizes enabled detection of large-diameter tree dynamics that are often undetectable over smaller sampling areas (Lutz 2015). Our finding that large trees of multiple species converged on similar facilitation dynamics – despite residing in distinct topographic positions, forest types, and climatological contexts – suggests a degree of significance not previously acknowledged by PSF research. Given the disproportionate ecological importance of large-diameter trees (Lutz et al. 2018), it is increasingly important that forest diversity is conserved to maintain mycorrhizal benefits as a countervailing force to rising rates of enemy attack (McDowell et al. 2011). Further study of +PSF mechanisms will offer pathways for adaptive management and conservation in temperate mixed-conifer forests.

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## Tables

**Table 5.1.** Demographics of woody stems considered as the response variable in survival analyses. Relative basal area is relative to total basal area across the three plots. Trace basal area (t) was < 0.1 m<sup>2</sup> (total) or < 0.01% (relative). Annual survival applies to only the stems analyzed (all, small, and large diameters separately). Study periods were nine, ten, and six years, respectively, for Wind River, Yosemite, and Cedar Breaks. There were 3424, 3080, and 487 total mortalities in Wind River, Yosemite, and Cedar Breaks, respectively. Total DBH is the mean percentile for small and large diameter bins. Growth form and mycorrhizal guild of each species in Table D.1.

Family	Species	All Diameters				Small Diameter			Large Diameter		
		Stems (n)	Basal Area (m <sup>2</sup> )	Basal Area (%)	Survival Rate (yr <sup>-1</sup> )	Stems (n)	Survival Rate (yr <sup>-1</sup> )	P <sub>10</sub> DBH (cm)	Stems (n)	Survival Rate (yr <sup>-1</sup> )	P <sub>90</sub> DBH (cm)
<b><u>Cedar Breaks</u></b>											
Adoxaceae	<i>Sambucus racemosa</i>	3	t	t	0.0%	0	-	-	0	-	-
Cupressaceae	<i>Juniperus communis</i>	161	t	t	99.2%	43	98.4%	1.1	18	100.0%	2.3
Cupressaceae	<i>Juniperus scopulorum</i>	3	0.1	t	100.0%	0	-	-	0	-	-
Grossulariaceae	<i>Ribes cereum</i>	67	t	t	97.9%	14	100.0%	1.0	8	95.3%	1.5
Pinaceae	<i>Abies bifolia</i>	14639	141.5	3.49%	99.6%	1525	99.7%	1.3	1476	99.2%	18.1
Pinaceae	<i>Abies concolor</i>	10	0.4	0.01%	100.0%	0	-	-	0	-	-
Pinaceae	<i>Picea engelmannii</i>	1053	23.0	0.57%	99.9%	115	99.9%	1.5	106	100.0%	28.6
Pinaceae	<i>Picea pungens</i>	424	29.7	0.73%	99.9%	43	100.0%	2.0	43	100.0%	50.3
Pinaceae	<i>Pinus edulis</i>	7	0.0	t	100.0%	0	-	-	0	-	-
Pinaceae	<i>Pinus flexilis</i>	761	38.0	0.94%	99.9%	82	99.8%	1.6	77	99.8%	43.8
Pinaceae	<i>Pinus longaeva</i>	697	85.9	2.12%	99.9%	72	100.0%	2.4	70	100.0%	65.0
Pinaceae	<i>Pseudotsuga menziesii</i> ssp. <i>glauca</i>	27	1.8	0.04%	99.4%	4	100.0%	2.0	3	93.5%	53.1
Rosaceae	<i>Cercocarpus ledifolius</i>	9	t	t	100.0%	0	-	-	0	-	-
Salicaceae	<i>Populus tremuloides</i>	2169	72.5	1.79%	99.2%	223	98.5%	1.4	217	99.7%	31.4
<b>Total:</b>		<b>20030</b>	<b>393.0</b>	<b>9.68%</b>	<b>99.6%</b>	<b>2121</b>	<b>99.6%</b>	<b>1.6</b>	<b>2018</b>	<b>99.4%</b>	<b>32.7</b>

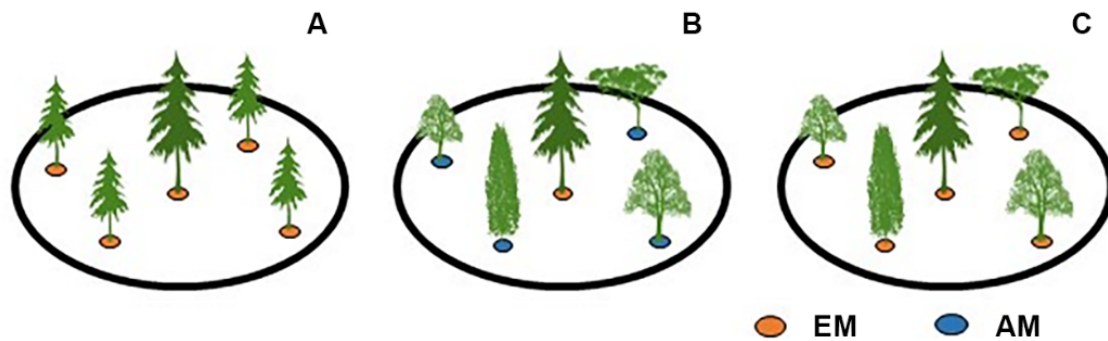
Table 5.1. Continued.

Family	Species	All Diameters				Small Diameter			Large Diameter		
		Stems (n)	Basal Area (m <sup>2</sup> )	Basal Area (%)	Survival Rate (yr <sup>-1</sup> )	Stems (n)	Survival Rate (yr <sup>-1</sup> )	P <sub>10</sub> DBH (cm)	Stems (n)	Survival Rate (yr <sup>-1</sup> )	P <sub>90</sub> DBH (cm)
<b>Wind River</b>											
Betulaceae	<i>Alnus rubra</i>	9	0.2	0.01%	98.7%	0	-	-	0	-	-
Betulaceae	<i>Corylus cornuta</i> ssp. <i>californica</i>	775	0.3	0.01%	98.3%	93	98.1%	1.1	79	99.1%	3.4
Cornaceae	<i>Cornus nuttallii</i>	170	0.9	0.02%	97.3%	17	94.3%	3.2	17	99.3%	12.0
Cupressaceae	<i>Thuja plicata</i>	190	95.7	2.36%	99.4%	20	95.3%	10.3	19	100.0%	127.0
Ericaceae	<i>Gaultheria shallon</i>	17	<i>t</i>	<i>t</i>	95.3%	3	88.5%	1.0	3	100.0%	1.4
Ericaceae	<i>Menziesia ferruginea</i>	16	<i>t</i>	<i>t</i>	96.9%	2	100.0%	1.1	2	92.6%	1.6
Ericaceae	<i>Rhododendron macrophyllum</i>	268	0.1	<i>t</i>	98.7%	31	99.3%	1.3	27	99.1%	3.8
Ericaceae	<i>Vaccinium ovalifolium</i>	90	<i>t</i>	<i>t</i>	98.7%	15	99.2%	1.1	12	98.0%	1.6
Ericaceae	<i>Vaccinium parvifolium</i>	1367	0.2	0.01%	98.7%	143	97.9%	1.0	150	98.4%	1.8
Pinaceae	<i>Abies amabilis</i>	4147	49.8	1.23%	98.8%	422	99.1%	1.6	417	98.0%	16.7
Pinaceae	<i>Abies grandis</i>	69	7.8	0.19%	97.9%	7	94.0%	2.3	7	100.0%	60.1
Pinaceae	<i>Abies procera</i>	16	6.7	0.17%	99.3%	2	100.0%	30.5	2	100.0%	97.0
Pinaceae	<i>Pinus monticola</i>	7	3.2	0.08%	91.0%	0	-	-	0	-	-
Pinaceae	<i>Pseudotsuga menziesii</i> ssp. <i>menziesii</i>	499	430.8	10.61%	99.3%	50	99.3%	68.0	50	99.8%	134.5
Pinaceae	<i>Tsuga heterophylla</i>	9313	815.8	20.10%	99.1%	939	98.2%	1.8	935	99.3%	64.8
Rosaceae	<i>Amelanchier alnifolia</i>	7	<i>t</i>	<i>t</i>	94.0%	0	-	-	0	-	-
Rosaceae	<i>Holodiscus discolor</i>	25	<i>t</i>	<i>t</i>	95.2%	3	95.6%	1.5	3	0.0%	3.7
Rosaceae	<i>Rubus spectabilis</i>	4	<i>t</i>	<i>t</i>	100.0%	0	-	-	2	100.0%	1.4
Sapindaceae	<i>Acer circinatum</i>	10580	14.3	0.35%	98.3%	1136	96.8%	1.4	1081	98.3%	6.4
Taxaceae	<i>Taxus brevifolia</i>	1848	39.7	0.98%	97.9%	187	95.3%	5.9	185	98.8%	24.3
<b>Total:</b>		<b>29417</b>	<b>1465.6</b>	<b>36.11%</b>	<b>98.6%</b>	<b>3070</b>	<b>97.7%</b>	<b>8.3</b>	<b>2991</b>	<b>98.7%</b>	<b>35.0</b>

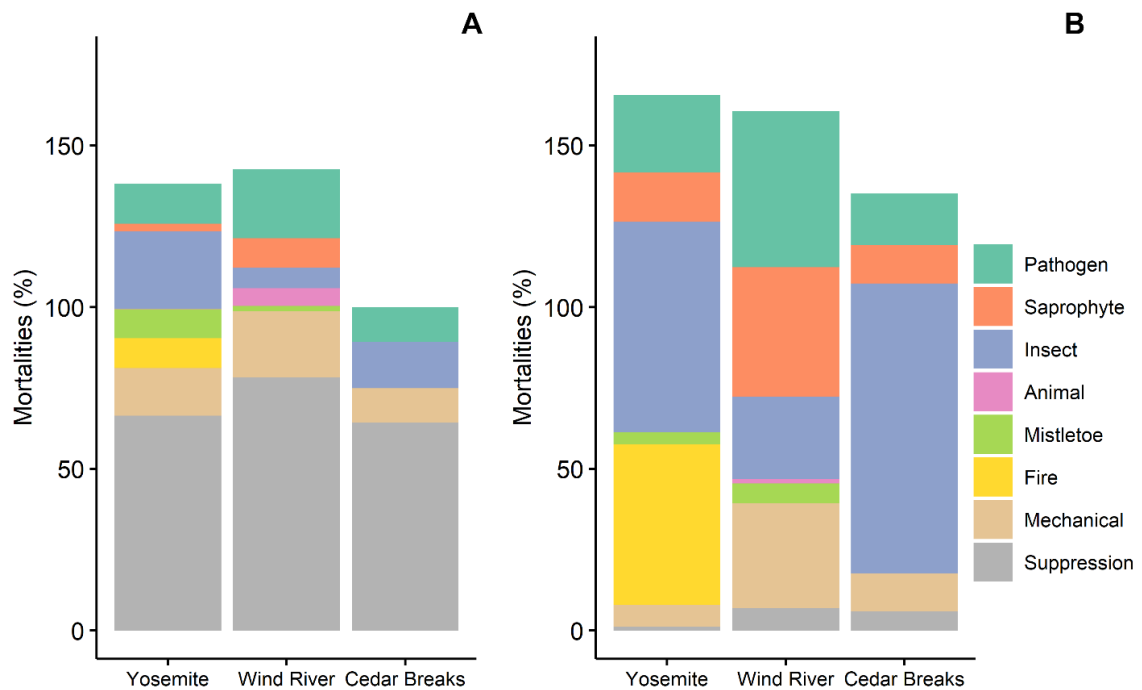
Table 5.1. Continued.

Family	Species	All Diameters				Small Diameter			Large Diameter		
		Stems (n)	Basal Area (m <sup>2</sup> )	Basal Area (%)	Survival Rate (yr <sup>-1</sup> )	Stems (n)	Survival Rate (yr <sup>-1</sup> )	P <sub>10</sub> DBH (cm)	Stems (n)	Survival Rate (yr <sup>-1</sup> )	P <sub>90</sub> DBH (cm)
<b>Yosemite</b>											
Adoxaceae	<i>Sambucus nigra</i> ssp. <i>caerulea</i>	13	<i>t</i>	<i>t</i>	98.3%	2	93.3%	1.1	2	100.0%	1.8
Betulaceae	<i>Corylus cornuta</i> ssp. <i>californica</i>	144	<i>t</i>	<i>t</i>	99.8%	15	100.0%	1.1	16	98.7%	2.4
Cornaceae	<i>Cornus nuttallii</i>	555	1.7	0.04%	98.8%	64	98.7%	1.5	56	99.1%	11.1
Cornaceae	<i>Cornus sericea</i>	152	0.1	<i>t</i>	99.8%	20	100.0%	1.3	21	99.5%	2.9
Cupressaceae	<i>Calocedrus decurrens</i>	408	72.1	1.78%	99.0%	42	95.7%	6.4	41	100.0%	84.6
Ericaceae	<i>Arctostaphylos patula</i>	81	<i>t</i>	<i>t</i>	99.8%	9	100.0%	1.6	11	99.1%	3.6
Ericaceae	<i>Rhododendron occidentale</i>	6	<i>t</i>	<i>t</i>	98.2%	2	100.0%	1.2	0	-	-
Fagaceae	<i>Chrysolepis sempervirens</i>	32	<i>t</i>	<i>t</i>	100.0%	4	100.0%	1.2	4	100.0%	2.6
Fagaceae	<i>Quercus kelloggii</i>	651	12.1	0.30%	99.5%	66	99.7%	1.4	67	99.2%	27.5
Pinaceae	<i>Abies concolor</i>	4714	476.5	11.74%	93.7%	485	88.7%	4.3	472	97.6%	57.5
Pinaceae	<i>Abies magnifica</i>	2	0.3	0.01%	100.0%	2	100.0%	42.3	2	100.0%	42.3
Pinaceae	<i>Pinus lambertiana</i>	1377	547.7	13.49%	93.6%	140	84.2%	4.6	141	94.5%	126.2
Pinaceae	<i>Pseudotsuga menziesii</i> ssp. <i>menziesii</i>	3	0.9	0.02%	96.0%	0	-	-	0	-	-
Rhamnaceae	<i>Ceanothus cordulatus</i>	2	<i>t</i>	<i>t</i>	93.3%	0	-	-	0	-	-
Rhamnaceae	<i>Ceanothus integerrimus</i>	6	<i>t</i>	<i>t</i>	100.0%	2	100.0%	1.3	0	-	-
Rhamnaceae	<i>Ceanothus parvifolius</i>	2	<i>t</i>	<i>t</i>	100.0%	0	-	-	0	-	-
Rhamnaceae	<i>Frangula californica</i>	3	<i>t</i>	<i>t</i>	100.0%	0	-	-	0	-	-
Rosaceae	<i>Prunus emarginata</i>	27	<i>t</i>	<i>t</i>	98.4%	6	98.2%	1.4	3	100.0%	2.8
<b>Total:</b>		<b>8178</b>	<b>1111.4</b>	<b>27.38%</b>	<b>95.4%</b>	<b>859</b>	<b>92.1%</b>	<b>5.1</b>	<b>836</b>	<b>97.6%</b>	<b>30.4</b>

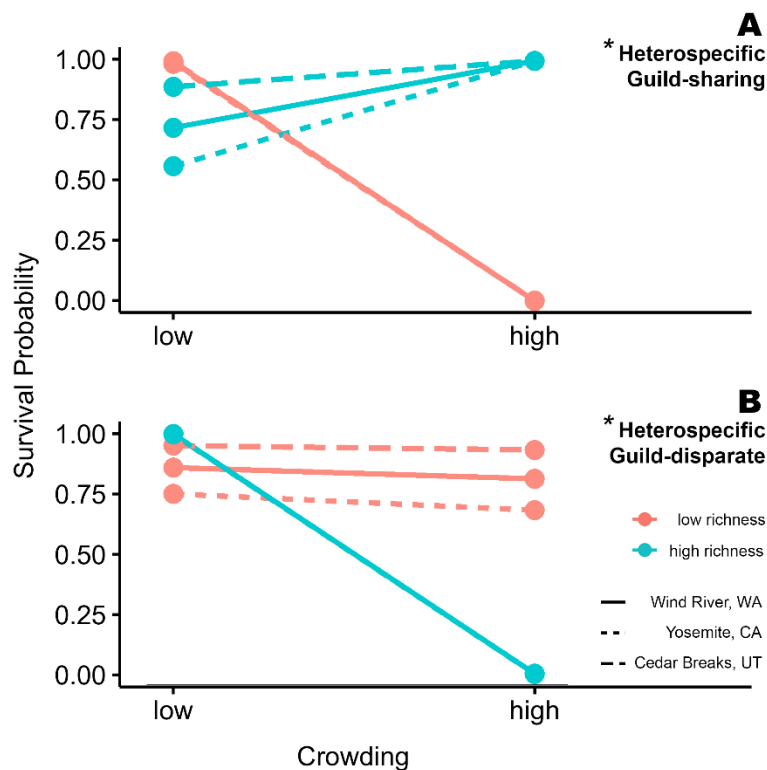
## Figures



**Figure 5.1.** Hypothetical forest communities that differ by tree species and mycorrhizal guild: ectomycorrhizal (EM) or arbuscular mycorrhizal (AM). We test these hypotheses: A) monodominant neighborhoods share mycorrhizal guild but likely have strong competition; B) species-rich, guild-disparate neighborhoods likely have weaker competition, but limited access to benefits of mycorrhizal network; C) species-rich, guild-sharing neighborhoods likely have weaker competition and access to benefits of mycorrhizal network. We expect that survival will be highest in neighborhood C.



**Figure 5.2.** Factors associated with mortality of small (A) and large (B) trees that died at each of three forest dynamics plots (small = DBH  $\leq$  10<sup>th</sup> percentile; large = DBH  $\geq$  90<sup>th</sup> percentile per species). Pathology exams were performed for newly dead individuals on an annual basis and multiple factors associated with mortality recorded (cumulative mortality > 100%; Table D.3). Biotic enemies included: fungal pathogens (parasitic fungi attacking live cambium and phloem cells), fungal saprophytes (decay fungi attacking dead xylem cells), insects (primarily bark beetles), animals (woodpeckers, large ungulates), mistletoe plant parasites, and suppression (i.e. light competition from neighboring trees). Predisposing factors (fire and mechanical damage, suppression, mistletoe) were not necessarily the most proximate causes of death but were recorded to provide further context for mortality. Trees for which fire or mechanical damage were the primary cause of mortality were omitted from analyses, so here, these processes represent predisposing factors only. For species-level mortality causes, see Fig. D.1.



**Figure 5.3.** Interaction between heterospecific guild-sharing species richness and heterospecific guild-sharing crowding in a 20-m radius of large-diameter trees (A), and the interaction between heterospecific guild-disparate species richness and heterospecific guild-disparate crowding in a 20-m radius of large trees (B). Overlapping lines indicate no difference between study sites (when dots, dashes, and lines overlap), but a present difference between high and low richness levels at all sites. Survival probabilities were assessed at the end of each study timeframe per plot (not annualized; WFDP: 2010–2020, YFDP: 2011–2020, UFDP: 2015–2020). Low heterospecific richness was the lowest observed number of different species within any large-diameter tree neighborhood (here,  $HSR_{\min} = 0$ ;  $HDR_{\min} = 0$ ), and vice versa for high richness ( $HSR_{\max} = 6$ ,  $HDR_{\max} = 10$ ). Heterospecific crowding was centered by diameter and species, so high and low categories reflect the *relative* effect of crowding. Low crowding was the smallest observed value within any large-diameter tree neighborhood, which after centering represented the lowest crowding that would be expected for any large-diameter tree species (here,  $HSC_{\min} = -37$ ;  $HDC_{\min} = -31$ ), and vice versa for high crowding ( $HSC_{\max} = 117$ ,  $HDC_{\max} = 105$ ). We held all other parameters at mean observed values so only the values for parameters of interest were permuted to create interaction slopes; this included using mean  $HDC/HDR$  when assessing the effect of guild-sharing interactions, and vice versa when assessing guild-disparate interactions. Survival probabilities were calculated using these observed values and the mean of posterior distributions for all coefficients in large-diameter tree models following Eq. 2. Compared to monodominant neighborhoods ( $HSR$  and  $HDR = 0$ ; red lines), increased species richness (blue lines) reduced the negative effects of crowding by guild-sharing neighbors (A) but increased the negative effects of crowding by guild-disparate neighbors (B). Though only linear effects were detected here, extremely high or low levels of crowding would likely produce nonlinear effects. Asterix (\*) indicates a significant interaction (95% credible intervals do not include zero).

## CHAPTER VI

### SUMMARY AND CONCLUSIONS

#### **The Role of Longitudinal Research**

The Smithsonian ForestGEO network is uniquely poised to identify major biotic and abiotic drivers of forest species distributions and coexistence (LaManna et al. 2017, Davies et al. 2021). The nature of the ForestGEO design – a network of large, single plots representative of key forest types across the planet – requires that analyses of any single plot are centered at the scale of individual trees, patches, and at most, the forest stand. An annual resolution of sampling can yield great insights into the mechanisms controlling tree individual and community dynamics and, thus, future forest change (Lutz 2015, Germain and Lutz 2021a, 2022). Yet, landscape-scale processes (e.g., disturbance heterogeneity and migration) and evolutionary processes (e.g., acclimation and adaptation) are likely to interact in unforeseen ways with the decadal dynamics observed within stands (Aitken et al. 2008, Alberto et al. 2013, Lenoir and Svenning 2015). For this reason, pairing ForestGEO sites with additional sample plots (Germain and Lutz 2020, Furniss et al. 2022), dendrochronological methods (Anderson-Teixeira et al. 2022, Germain and Lutz *Submitted*), or genetic sampling (Bishop et al. 2019) can increase the power of ForestGEO studies to anticipate the effects of changing climate in the world's forests.

Migration and adaptation operate over much longer timescales than the rapid pace of environmental change facing western forests today (Bréda et al. 2006, Harsch et al. 2009, Bertrand et al. 2011, Zhu et al. 2011, Alberto et al. 2013). If the earth system was not currently so precarious, such long time scales for forest recovery following currently



observed declines may not be alarming (e.g., Clark 1998). Given that anthropogenic activities have brought many elements of the earth system to the brink of destabilization (Steffen et al. 2015), however, we cannot afford to wait centuries for forests to recover: reduced carbon storage and sequestration in forests now can stimulate positive feedbacks with the climate system to trigger irrecoverable change (Adams et al. 2010, Pachauri et al. 2015, Swann et al. 2018). The annual to decadal dynamics that were the focus of this dissertation aim to answer pressing questions in ecology at the timescales relevant to mitigating forest loss and preventing further climate destabilization.

### **Oversimplifying Climate Impacts Underestimates Forest Loss**

The first section of this dissertation (Chapters II and III) examined the direct and indirect effects of climate change in forests of the Pacific Northwest, USA. These forests are globally distinguished for their carbon storage capabilities (Smithwick et al. 2002, Anderson-Teixeira et al. 2021) and their continued conservation is therefore critical to maintaining regional climate stability (Garcia et al. 2016, Swann et al. 2018). Climate is becoming hotter, drier, and more variable in this region, leading to more severe summer drought and snowpack declines (Germain and Lutz 2020, 2022). I found that, in the absence of fire, extreme weather events and indirect climate effects emergent at the community level dominate PNW forest responses to climate (Germain and Lutz 2020, 2022). Specifically, climate change may be weakening the mechanisms responsible for maintaining biodiversity (Germain and Lutz 2022): fitness differences (e.g., Voelker et al. 2018, Kulmatiski et al. 2020) led to stronger interspecific competition on dry, water-limited sites, resulting in stronger community stability and coexistence of a broader variety of species at wetter sites, but monodominance of only the most drought-tolerant

species on dry sites (Germain and Lutz 2022). This type of compositional shift, known as thermophilization, is being observed in forests across the planet (Duque et al. 2015). I am the first to show how altered community dynamics – not just population- and species-level responses – are responsible for these climate-instigated compositional shifts. Moreover, I found that tree migration may be challenged and local extinction favored by increasing climatic variability at even the typically cooler, moister sites, reducing thermophilization and thus the adaptive potential of forests (Germain and Lutz 2020). Such responses are broadly ignored in large-scale models of forest change, contributing to the ongoing problem of carbon storage overestimation (Allen et al. 2015, Germain and Lutz 2020).

The mechanisms underpinning direct climate effects on tree growth and mortality are perhaps more straightforward to scale from individual trees to landscapes than are complex indirect effects. For instance, warmer temperatures and CO<sub>2</sub> fertilization can alter growth rates (Battipaglia et al. 2020, Clark et al. 2021, Larysch et al. 2022) and many of these responses have been quantified for individual species (particularly commercially valuable trees; e.g., Hood and Sala 2015). Likewise, drought-induced tree mortality can be predicted as a greater probability for hydraulic failure (especially for species with anisohydric water use behavior) and carbon starvation (especially for species with isohydric water use behavior; McDowell et al. 2008, Sevanto et al. 2014). Simplistic growth and mortality responses such as these are commonly scaled to larger extents (e.g., Allen and Breshears 1998, Williams et al. 2013). Yet, because these forms of drought stress can make trees more vulnerable to biotic enemies (McDowell et al. 2011, Anderegg et al. 2015) and wildfire (van Mantgem et al. 2013), it is difficult to disentangle

the direct and indirect effects of climate in forests (but see Bentz et al. 2010, Chu et al. 2019). Consequently, large vegetation models appear to have concluded it too cumbersome to parse direct drought-induced mortality and growth declines from those mediated by insects, wildfire, disease, and competitive exclusion (Fisher et al. 2018, Anderegg et al. 2020).

Though indirect effects may be more complicated to model, I found that these vastly outweighed direct climate effects (Germain and Lutz 2022). Moreover, the different scales of climate effects undermine interchangeability or combination of these responses: growth rate fluctuations, hydraulic failure, and carbon starvation occur at the scale of individual trees; while insect activity, wildfire, and competitive interactions occur at the scale of forest communities. Moreover, spatially explicit feedbacks between these levels of organization (Slack et al. 2017, Furniss et al. 2022) render the omission of either scale a potential source of bias. Of course, it is unnecessary and perhaps counterproductive to include the maximum level of complexity in vegetation models (Astrup et al. 2008, Tredennick et al. 2017). My recommendations for the ongoing efforts to improve vegetation components of earth system models (Moorcroft 2006, Purves and Pacala 2008) are to 1) develop more robust predictions of population collapse by including severe weather and drought extremes in input climate datasets (i.e., rather than mean trends alone; Parmesan et al. 2000, Germain and Lutz 2020); and 2) integrate a more comprehensive suite of forest mortality mechanisms to include drought responses of prominent natural enemies (Bentz et al. 2010), competition (Young et al. 2017), and fire (Fisher et al. 2018, Abatzoglou et al. 2021); and 3) allow forest cover and species composition to vary as a function of these additions (Duque et al. 2015, Germain and

Lutz 2022).

### **Biodiversity in Western Forests: Small Yet Mighty**

Findings from the second section of this dissertation (Chapters IV and V) join the growing body of evidence demonstrating the interconnected importance of aboveground and belowground biodiversity to tree survival (e.g., Schuldt et al. 2018). Temperate coniferous forests may have fewer woody species than their tropical counterparts (Turner 2004, Lamanna et al. 2014), but I found that even small increments of increased woody species diversity provided protection against natural enemies, drought, and competition (Germain and Lutz 2021b, *Submitted*). These findings add to the known benefits of biodiversity (Hansen et al. 1991, Jactel and Brockerhoff 2007, Schuldt et al. 2018) by showing that higher woody species richness can not only decrease pathogen and bark beetle attack rates (Jactel and Brockerhoff 2007, Germain and Lutz 2021b, *Submitted*), but also increase trees' ability to resist bark beetles following attack (Germain and Lutz *Submitted*). These mechanisms underly a positive relationship between diversity and carbon stocks (e.g., Steur et al. 2022). Despite diversity benefits, I also found that climate change may be weakening the mechanisms responsible for maintaining forest biodiversity (Germain and Lutz 2022), making it essential that managers take more active measures to conserve biodiversity in forests (Hylander et al. 2021).

An emerging theme of this work is that forest biodiversity is important in western temperate forests, despite and due perhaps to lower functional redundancy and therefore greater individual impact of each species compared with diverse tropical forests (Ellison et al. 2019). Unfortunately, great expanses of land have been converted to commercially valuable tree monocultures for timber production (Brown et al. 2018, Franklin and

Donato 2020). Not only are these stands more vulnerable to bark beetles and disease (Jactel and Brockerhoff 2007, Jactel et al. 2009), but my work also suggests that correspondingly reduced plant-soil feedbacks (Karst et al. 2014, Teste et al. 2017) and elevated competitive stress (Pretzsch et al. 2013, Chen et al. 2018) in these forests may predispose trees to mortality following drought and fire with continued climate change (Germain and Lutz *Submitted*). These findings support efforts to increase production tree diversity and conserve native forests (Schroth et al. 2002, Felton et al. 2010, Waring et al. 2020), both of which being necessary to maintain carbon storage while increasing forest resilience to climate change.

The insurance effect of biodiversity sits opposing to foundational species theory: the former states species rich communities maintain ecosystem functioning amidst stress, recuperating the functions lost by any one sensitive species (Yachi and Loreau 1999, Hooper et al. 2005, Loreau and de Mazancourt 2013); whereas the latter states that individual species may make contributions to ecosystem functioning that are disproportionate to their own abundances, the loss of which cannot be recovered by other species (Dayton 1972, Stachowicz 2001, Ellison et al. 2005). In fact, biodiversity and foundational species create feedbacks to maintain one another: biodiversity can help protect individual species that may be considered foundational (Baxter and Dighton 2001, Germain and Lutz 2021a, *Submitted*), and in turn, foundational species often cultivate community-level biodiversity (Angelini et al. 2011, Baiser et al. 2013, Ellison et al. 2019). For instance, foundation species may be identified in forests following an obligately facilitative model of succession (Connell and Slatyer 1977) where the presence of the subsequently more diverse forest community is precluded upon presence of a

single pioneering facilitator (e.g., Chapin et al. 1994, Baumeister and Callaway 2006). I build upon this concept to add that, in mature western forests with vast structural heterogeneity (Franklin et al. 2002), cohorts of large-diameter trees may behave as the foundational assemblage by providing functions disproportionate to their abundances (Lutz et al. 2013, 2018, Germain and Lutz 2022).

Representing the intersection between these themes, others have acknowledged that multiple species may act as a foundational assemblage (Angelini et al. 2011). In species-depauperate forests, biodiversity benefits therefore begin to converge with foundational assemblage benefits: an assemblage may behave as foundational (i.e., dominant providers of ecosystem functioning), and when that assemblage contains multiple species, the benefits of biodiversity become yet another function being provisioned. Though I found that diversity benefits existed even with a relatively few number of species (Germain and Lutz 2021b, *Submitted*), these benefits are more precariously situated because there is a limited insurance effect being provided by additional, redundant species (Peterson et al. 1998). Preserving what biodiversity does exist in these forests and correctly identifying the foundational assemblage, not necessarily limited to be an individual species, can help managers prioritize areas for conservation and restore forests following disturbance (Hansen et al. 1991).

### **Harnessing Facilitation Mechanisms to Offset Climate Impacts**

This dissertation focused on how resistance and resilience scales from the individual tree and stand (Chapters III and IV) to landscape and regional scales (Chapters II and V). I found that individual tree resistance was marked by the ability to avoid or tolerate disturbance (e.g., reduced mortality from bark beetles and disease; Germain and

Lutz 2021b), and resilience was the ability to regain vigor following disturbance (e.g., defense recovery following fire; Germain and Lutz *Submitted*). At the stand scale, higher competition and apparent competition between trees resulted in reduced stand-level resilience to changing climate (i.e., increased competitive exclusion indicating impending compositional shifts; Germain and Lutz 2022). At the landscape scale, I found that low individual- and stand-level resistance to extreme drought (i.e., higher mortality and population declines) resulted in reduced landscape-scale resilience of the species, *Taxus* (i.e., inability to migrate with a changing climatic niche; Germain and Lutz 2020). Finally, synthesizing the net effects identified by each of these studies, I found that large trees comprising 17 common species from three forest types across the western region showed increased resistance to biotic disturbances and drought when patch-level diversity favored positive plant-soil feedbacks (Germain and Lutz 2021b).

Study of mature forests offers the perspective that endemic insects, disease, and wildfire are necessary elements of healthy, carbon-dense forests (Franklin et al. 2002, Kolb et al. 2007). My dissertation work expands upon this understanding to show how the future of carbon storage in western forests is not only predicated upon how fast trees are growing and dying (e.g., Hegyi 1974); but also upon how trees interact with each other (Germain and Lutz 2022), with their enemies and mutualists (Germain and Lutz 2021b), and how these synergistic effects are moderated by climate and fire (Germain and Lutz *Submitted*) to together govern tree survival. Contemporary management has begun to recognize the importance of these processes (Swanson and Franklin 1992, Churchill et al. 2013), but a cohesive, operationalized framework for maintaining forest

resilience to myriad climate change impacts has yet to fully materialize (Drever et al. 2006, Fettig et al. 2007, North et al. 2022).

More and more, it is appearing that climate change favors antagonistic relationships (Raffa et al. 2008, Weed et al. 2013, Abatzoglou et al. 2021) while weakening mutualistic relationships (Clark et al. 2011, Eklöf et al. 2012). My research suggests that managers would benefit forests by actively harnessing the aspects of ecological complexity that bolster mechanisms of facilitation (Simard and Austi 2010, Germain and Lutz 2021b) and offset increasingly stressful aspects of climate change (Bastolla et al. 2009). The two leading ways I found to do this is to 1) conserve woody species biodiversity (Hansen et al. 1991, Germain and Lutz *Submitted*) and 2) promote positive plant-soil feedbacks that enhance tree defenses to natural enemies (Germain and Lutz 2021b, Forero et al. 2021). Because the historical mechanisms supporting biodiversity may be weakening (Germain and Lutz 2022), failing to enact management to maintain these positive counterbalances may allow unmitigated climate change to instigate population collapse (Urban et al. 2012, Germain and Lutz 2020) and type conversion (Millar and Stephenson 2015, Davis et al. 2019, Coop et al. 2020).

## **Conclusions**

“When generalizing these findings to other mature forests, we highlight the importance of delineating the most limiting factor for large trees in that forest (e.g., fire, drought, beetles). Although these factors often co-occur (Franklin et al. 1987), identifying the most foundational and threatening factor can help put our findings into context. For instance, reducing tree density and removing ladder fuels is critically important in fire-suppressed Ponderosa pine forests that are otherwise susceptible to uncharacteristic



crown fires (D'Amato et al. 2013). In pinyon woodlands, where drought is increasingly limiting (greater incidents of embolism and hydraulic failure; Adams et al. 2009), thinning can reduce competition for water to increase forest health (D'Amato et al. 2013).

For mature forests that do not reside at these ends of the fire- and drought severity spectrums, such as those analyzed here, the next most limiting factors for large trees are biotic enemies (Bentz et al. 2010). Our results advise some prudence before reducing tree densities in these forests, as losing friends may unwittingly correspond with deleterious side effects. We show that forest composition, not just density, is essential to consider in order to maintain positive counterbalances for the large trees: if woody plant species richness was low, density also needed to be low for large trees to survive. Yet, the greatest survival effects for large trees were in denser, networked communities with high species richness. If the management objective is to increase forest resilience to bark beetles and pathogens, many of which are becoming more virulent with climate changes, then we must first ask: are neighboring trees acting primarily as enemies themselves, needing to be removed, or are they friendly purveyors of mycorrhizal networking critical to retaining resilience?

[This dissertation] demonstrates a promising— and actionable—mechanism by which... mutualisms may act as a key counterbalance to increasing threats in western forests... large trees of 17 common western coniferous species converged on similar facilitation dynamics across the decadal sampling period —despite residing in distinct topographic positions, forest types, and climatological contexts. The significance of these facilitation mechanisms deserves continued study to offer pathways for adaptive management and conservation.

Going forward, future research would benefit management the most by developing a process-based approach for addressing these complex issues in different forest types. To begin, we propose a greater effort to adapt the silvicultural paradigm to include not just how to remove negative dynamics, but also how to retain and even bolster positive dynamics in forests. There is a growing need for research and management action that considers existing facilitation mechanisms as tools to conserve forests amidst rapid environmental change. Continued discovery of big trees' fungal friends will help managers to protect old-growth forests and maintain the many ecosystem services provided by these trees and their symbionts. ForestGEO sites are vital conservation resources uniquely poised to serve this need, providing longitudinal datasets capable of disentangling multitrophic facilitation dynamics in forests across the globe.” (Germain and Lutz 2021b) <sup>5</sup>

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<sup>5</sup> This excerpt was published in the International Mycorrhiza Society Quarterly Newsletter in October, 2021, which should be cited as: Germain, S. J., and J. A. Lutz. 2021. Shared friends counterbalance shared enemies in old forests. *International Mycorrhiza Society Quarterly Newsletter*, 2(3): 9-13.

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APPENDICES

## APPENDIX A

## SUPPLEMENTARY MATERIAL FOR CHAPTER II:

## CLIMATE EXTREMES MAY BE MORE IMPORTANT THAN CLIMATE MEANS

## WHEN PREDICTING SPECIES RANGE SHIFTS

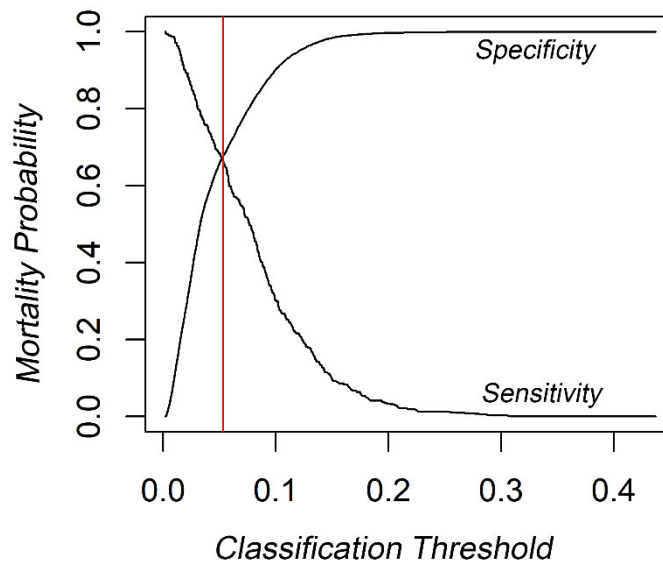
**Table A.1.** Results of 10-fold cross-validated model performance for the two space-for-time models using climate extremes (maximum Deficit anomaly and minimum snowpack anomaly observed during the study timeframe) rather than means per site. There was little difference in model outcomes compared to those using climate means (Table 2.2), likely because the space-for-time approach aggregates the climate value (whether mean or min/max) over the whole study timespan, thus washing out variability that can be captured by longitudinal models. Both the simple linear model (SLM) and Random forests were population-level models. Accuracy is percent variance explained (i.e.  $R^2$ ). Mean Absolute Deviance/Mean Ratio (MADMR) is scaled by the units of each model's response variable to allow direct comparison of error between models (lower numbers indicate less error).

Model	Validation				
	MADMR	Accuracy (%)	Mortality (n)	Survival (n)	Sample Size (n)
SLM	0.64	63.6	-	-	20
Random forest <sub>b</sub>	0.51	56.0	-	-	20

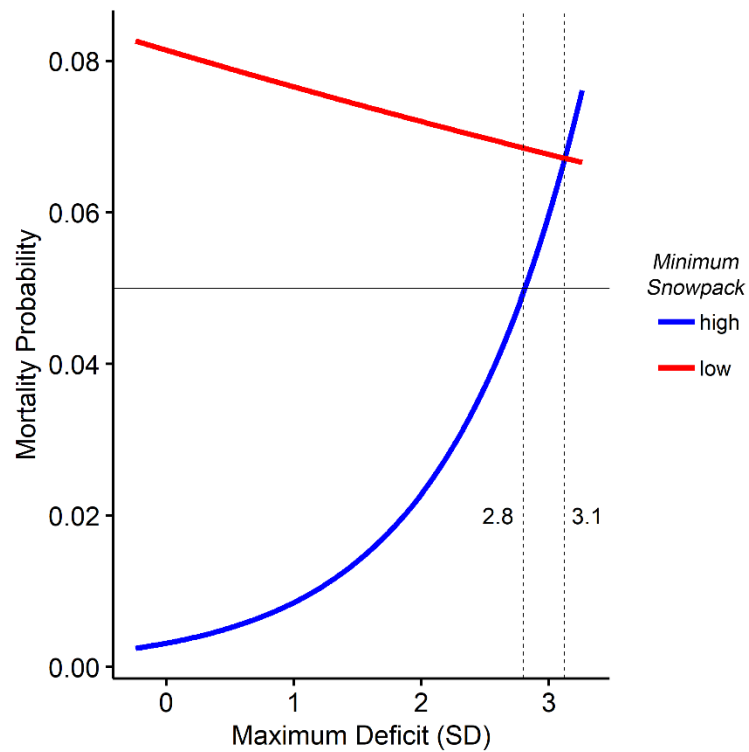
**Table A.2.** Model coefficients for the two space-for-time models using climate extremes (maximum Deficit anomaly and minimum snowpack anomaly observed during the study timeframe) rather than means per site. There was little difference in model outcomes compared to those using climate means (Table 2.2), likely because the space-for-time approach aggregates the climate value (whether mean or min/max) over the whole study timespan, thus washing out variability that can be captured by longitudinal models. Both the simple linear model (SLM) and Random forests were population-level models. Coefficients for Random forests indicate percent increase mean squared error for each variable. Species richness and Hegyi values were calculated within a 10-m radius of each tree. P-values are represented as follows: < 0.1°, < 0.05\*, < 0.01\*\*, and < 0.001\*\*\*. Dashes indicate variable was tested but not included in models.

Model	<u>Covariates</u>							
	Elevation	Diameter	Species Richness	Conspecific Hegyi	Heterospecific Hegyi	Maximum Deficit	Minimum Snowpack	Deficit*Snowpack
SLM	3.666	-	23.518*	37.145*	9.827	6.881°	-7.002	-
Random forests	-12.051	-	32.099**	49.744**	18.268°	2.972	-5.206	-

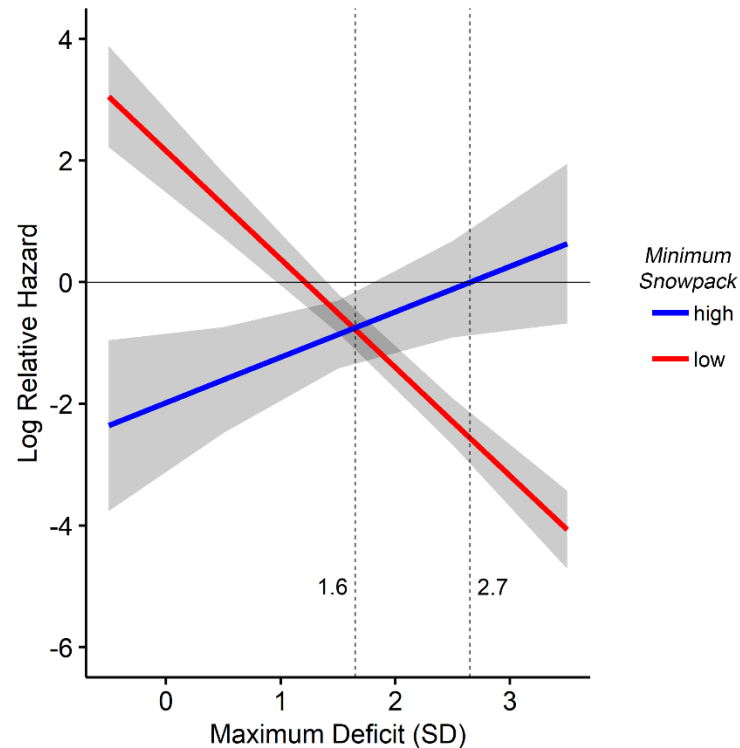




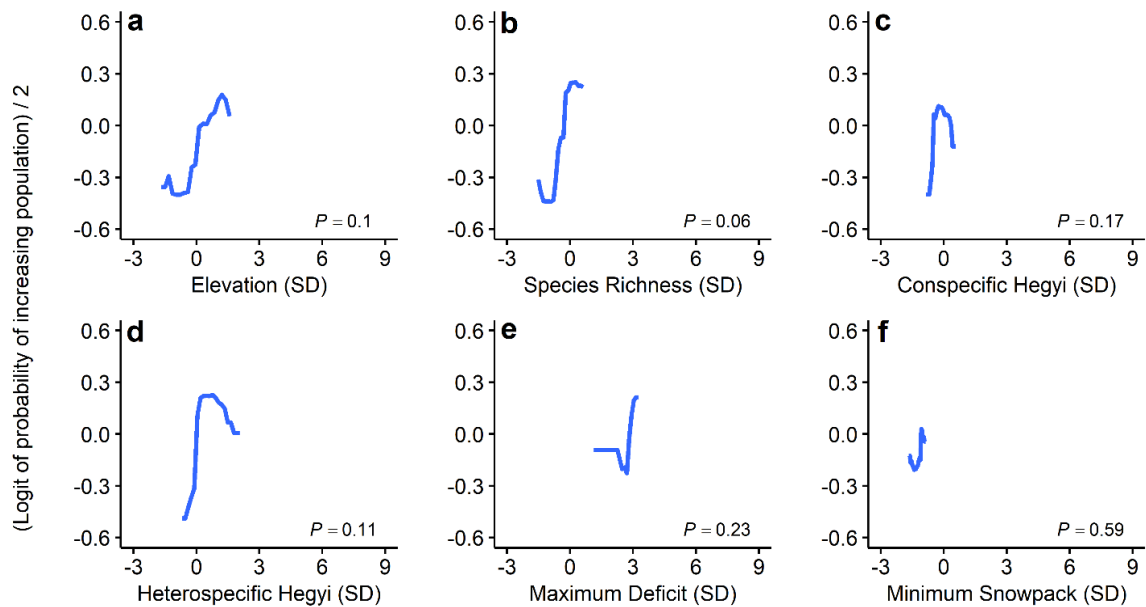
**Figure A.1.** The classification threshold for generalized linear mixed models (individual-level longitudinal) was obtained by optimizing model specificity (true negative rate) and sensitivity (true positive rate). This threshold was used during cross-validation to determine how accurately the model predicted out-of-sample mortality, where mortality probabilities above 0.053 were classified as “dead” and those below were classified as “live”.



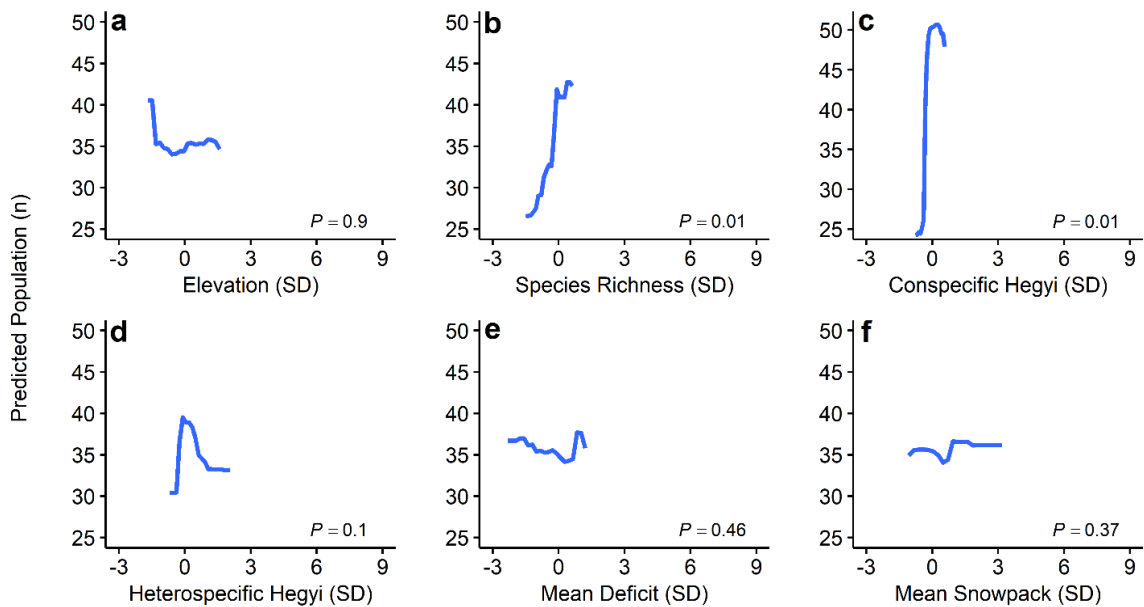
**Figure A.2.** The interaction between modeled maximum Deficit and modeled minimum snowpack observed in the generalized linear mixed model (individual-level longitudinal). Above the classification threshold, 0.053, indicates increased mortality probability, and below the threshold indicates decreased mortality probability. Mortality probability was minimized when Deficit anomaly was low and snowpack anomaly was high; however, high snowpacks could not offset the increased mortality effect of Deficit when Deficit anomaly was above 2.8 standard deviations (SD). Mortality probability was always above the threshold (classifying trees as dead) when snowpack anomaly was low, regardless of Deficit values.



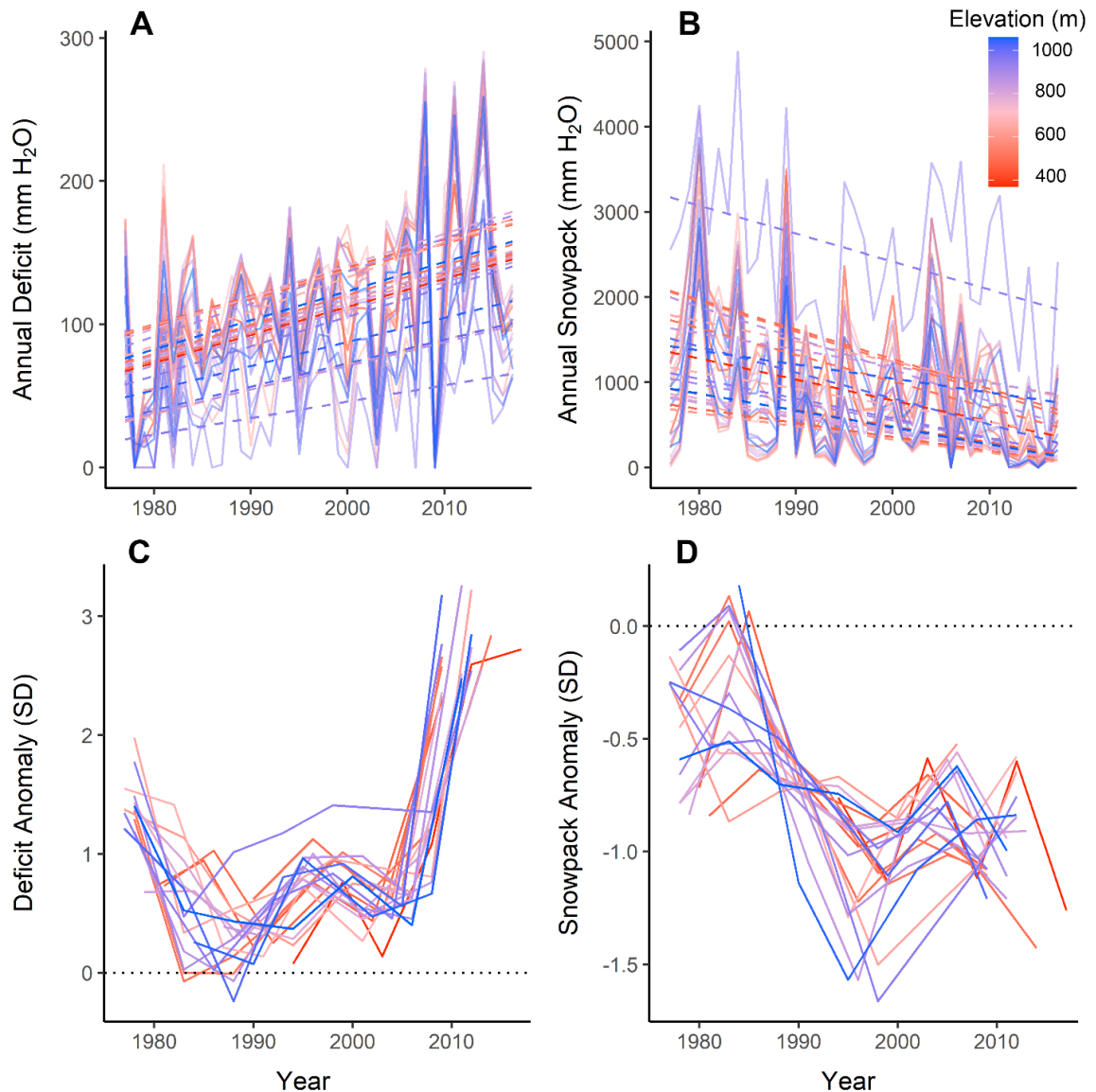
**Figure A.3.** The interaction between modeled maximum Deficit and modeled minimum snowpack observed in the Cox model (individual-level longitudinal). Above zero indicates increased mortality hazard (i.e. instantaneous mortality probability), and below zero indicates decreased mortality hazard. In agreement with the generalized linear mixed models (GLMM; Fig. D2), mortality hazard was low when Deficit anomaly was low and snowpack anomaly was high; likewise, high snowpacks could not offset the increased mortality effect of Deficit when Deficit anomaly was above 2.7 standard deviations (SD). In contrast to the GLMM, mortality hazard was also decreased when snowpack was low and Deficit was high.



**Figure A.4.** Partial dependence plots showing the marginal (i.e. individual) effects of each covariate included in longitudinal Random forests (population-level). The response variable, *Taxus* population growth, was expressed categorically as increasing, stable, or decreasing. Response values greater than zero indicate population increase is more probable, and values less than zero indicate population decrease is more probable. P-values for covariates were obtained by permuting the response variable 100 times to produce a null distribution of variable importance, against which the importance metric generated by the original tree ensemble was compared. The model indicates that probability of *Taxus* populations growth is expected to increase as species richness increases. Though not significant at  $\alpha = 0.05$ , Random forests reflected the pattern of *Taxus* population decline with moderately high Deficits (1-3 SD) and at low elevations (<0 SD).



**Figure A.5.** Partial dependence plots showing the marginal (i.e. individual) effects of each covariate included in space-for-time Random forests (population-level). Response values represent the predicted *Taxus* population abundance as a continuous variable. P-values for covariates were obtained by permuting the response variable 100 times to produce a null distribution of variable importance, against which the importance metric generated by the original tree ensemble was compared. The model indicates that *Taxus* abundance is expected to increase as species richness and conspecific neighbor density also increase. Climate covariates bore no relationship with *Taxus* abundance.



**Figure A.6.** Modeled annual climatic water Deficit (A) and modeled annual snowpack (B) at each of the twenty sites between 1977 and 2017; with Deficit anomalies (C) and snowpack anomalies (D) analyzed by longitudinal models. Climatic water balance models were made for each site using monthly temperature and precipitation time series from the Parameter-elevation Regression on Independent Slopes Model data set at an 800-m spatial resolution. Anomalies were calculated as the highest (Deficit) or lowest (snowpack) annual value within each time interval between measurement years (4-6 yrs) and expressed as standard deviations from long-term averages per site (1970 to 2017; dotted horizontal line); site-level anomalies represent the period of data in Table 2.1. Solid lines indicate modeled Deficit and snowpack; dashed lines show simple linear regression trends over the 40-yr study timespan; increasing Deficit and decreasing snowpack trends demonstrated by regression lines were significant at  $\alpha = 0.05$  for all sites.

APPENDIX B  
SUPPLEMENTARY MATERIAL FOR CHAPTER III:  
CLIMATE WARMING MAY WEAKEN STABILIZING MECHANISMS  
IN OLD FORESTS

**SECTION S1: SUPPLEMENTAL METHODS**

*Site and Climatological Data*

Preliminary analyses tested which environmental components formed the primary axes of differential tree clustering and mortality: we tested elevation above maximum spring water table (water table; m), soil nitrogen ( $\text{mg kg}^{-1}$ ), soil phosphorus ( $\text{mg kg}^{-1}$ ), and total exchangeable bases (TEB;  $\text{cmol kg}^{-1}$ ). We assessed 1) linear models showing the relationship between environmental components and each Hegyi index to test for differential tree clustering along soil resource gradients; 2) Cox models showing the relationship between environmental components and tree mortality hazard; and 3) Cox models that included all components to control for the possibility of ecological sorting along all four soil resource gradients. This final analysis was not parsimonious (too many variables for the number of mortality events) and appeared to be overfit, so results are not be reported here.

Water table was the most important environmental component structuring tree spatial patterns (Table B.2) and was thus chosen as our primary environmental variable. This is likely because the ranges of variability in N and TEB were fairly small compared to water table differences at our study site (Table B.3); additionally, N, P, and TEB distributions were more heterogeneous across the landscape than changes in water table

(Fig. B.2). By including water table in the final analysis, we control for the effects of ecological sorting along the existing moisture gradient (i.e. the primary axis governing spatial autocorrelation) to isolate NDD effects.

#### *Mortality model – Phase I: Parameterization*

In computing the Hegyi index, trees were included as neighbors that were rooted within a fixed radius of 10 m from the focal tree, based on previously identified interaction distances (Das et al., 2011a; Lutz et al., 2014). We used a mirrored edge correction where the perimeter of the plot (0 to 10 m inside edge) was mirrored (0 to 10 m outside edge) to allow calculation of Hegyi for trees growing within 10 m of the plot edge. We revised the Hegyi index by specifying distances between edges of the tree (face-face) rather than distances between tree centers (pith-pith). This revision accounts for closely growing trees with fused stems (those with pith-pith distances  $> 0$  and face-face distances  $\leq 0$ ), allowing us to distinguish between trees that were growing closely and are fused, thus providing direct evidence of shared cambium and resources, and those that were growing closely but not visibly fused above ground, thus experiencing potentially strong competitive interactions.

DBH was log-transformed to adjust right-skewed distributions; and water table, Deficit, and snowpack were each centered by subtracting the mean to reduce collinearity while retaining coefficient interpretability in original units (Dalal & Zickar, 2012). After variable transformations, predictor variables were roughly normal (verified by visual assessment of histograms and quantile-quantile normality plots); while the Cox model's non-parametric component does not have explicit distributional assumptions for covariates, this aided our ability to interpret predictor effects in terms of minimum and



maximum values. Generalized estimating equations were used (i.e. cluster variance; Therneau et al., 2013)) to create robust estimate of standard errors and account for repeated measures between years for each individual tree. Repeated measures were present because the entire time series was treated as a single risk set (rather than each year separately) to deal with climate covariates that differed year-to-year but not tree-to-tree within a given year; this allowed individual tree mortality risk to be calculated in the context of all observed climate covariate values.

The hazard ratio compares hazard between two points in time; as such, one of the fundamental assumptions of the standard Cox proportional hazards model is that HR (i.e. predictor effects) remain constant over time, where the change in hazard is assumed to be the same for  $t_0$  to  $t_1$  vs. for  $t_1$  to  $t_2$ , and so on. This assumption allows for consistent interpretation of predictor effects throughout the duration of the study. When models have non-proportional hazards, this means predictor effects changed throughout the study (i.e. hazard was reduced, increased, or fluctuated from year to year); in this case, an extension of the Cox model must be used to allow for time-varying coefficients (Therneau et al., 2013). Here, we used this extension and therefore employed a Cox model with time-varying coefficients rather than the more basic proportional hazards model. Deficit and snowpack often interacted in models, which is to say that the effect of Deficit changed over time with differing levels of snowpack and vice versa, thus constituting a time-dependent effect. We defined the time-varying coefficients for each of these terms (Deficit and snowpack) by the Deficit / snow interaction coefficient; this approach allowed us to make inferences about the time-dependent effects of Deficit and snowpack in terms of their effects on each other rather than with some unspecified

constituent of time. No other variables showed evidence of time-dependence.

### *Mortality model – Phase II: Forecasts*

We created mortality risk forecasts that are robust to climate model uncertainty by considering six different IPCC climate projections to estimate future snowpack and Deficit. We chose to use Representative Concentration Pathway (RCP) 8.5 climate scenarios for all projections because temperature and precipitation uncertainty stems primarily from process error rather than scenario error (i.e. difference between RCP scenarios; Hawkins & Sutton, 2009, 2011). The six climate projections agreed on long-term climate trends, but process uncertainty was evident in disagreement between annual Deficit and snowpack quantities. Thus, the six climate projections produced widely ranging annual ensemble estimates of future mortality risk for species with the greatest climate sensitivities (e.g., *Abies*). The unique components of each model contribute to annual disagreement: the HadGEM2-CC model is lacking the chemistry component present in the HadGEM2-ES model (Bellouin et al., 2011; Collins et al., 2011); the GFDL-ESM2M model uses Modular Ocean Model Version 4.1 with vertical pressure layers, while the GFDL-ESM2G model employs Generalized Ocean Layer Dynamics with a bulk mixed layer and interior isopycnal layers, with the result that the ESM2G better represents climate changes relating to the North Pacific ocean (Dunne et al., 2012, 2013); and all four of these consider the carbon cycle, which is absent from the uncoupled climate models GFDL-CM3 and CCSM4 (Donner et al., 2011; Gent et al., 2011). Mortality risk estimates produced from models more comprehensive (HadGEM2-ES) or specific to the Pacific Northwest region (GFDL-ESM2G) may therefore yield better predictions than our conservatively averaged ensemble.

## SECTION S2: SUPPLEMENTAL DISCUSSION

### *Considerations of Bias*

A recent resurgence of literature has emerged showing bias when detecting mechanisms of coexistence; namely, when quantifying density dependence. It is therefore necessary that studies such as ours, which aim to draw inferences from density-dependent interactions, carefully consider the pitfalls described by these publications. In the following sections, we address four prominent studies related to four primary considerations necessary of NDD research: temporal heterogeneity (Damgaard & Weiner, 2017), spatial heterogeneity (Rinella et al., 2020), influence of past ecological processes (Tuck et al., 2018), and proxy errors (Detto et al., 2019).

#### *Temporal Heterogeneity*

Damgaard and Weiner (2017) (also Damgaard, 2019) discuss the importance of dynamic ecological data. They show how using static “spatial variation to study processes of community ecology may lead to erroneous conclusions”, and more poignantly, contend that “inferences about processes...from static data are weak.” Our study design hinges on this understanding, and to our knowledge, ours is the longest study in the world of annualized tree survival across a contiguous spatial extent large enough to capture microsite heterogeneity (>4 ha). Our data are dynamic and, moreover, the statistical approach features a dynamic time-to-event model rather than a static model of tree mortality, such as GLM (without repeated measures) or univariate point-pattern analysis.

### *Spatial Heterogeneity*

Rinella et al. (2020) note that “model failures owe at least partly to heterogeneity in unmodeled factors (e.g., nutrients, soil pathogens).” We agree, and carefully considered the possibility for spatial heterogeneity in soil characteristics: our preliminary analysis of ecological sorting showed that soil moisture heterogeneity predicted tree mortality better than soil nutrients. We therefore allowed NDD effects to be flexible along a gradient of existing soil water variability, and show vastly different results between microsites that reinforce Rinella et al. (2020) findings. Conversely, the heterogeneous activity of mortality agents (e.g., soil pathogens) were not modeled individually due to the underlying relationship between such heterogeneity and the structure/composition of tree neighborhoods themselves (Barbosa et al., 2009; Franklin et al., 1987; Hansen & Goheen, 2000; Jactel & Brockerhoff, 2007); we preferred to let the data inform the extent to which tree neighborhoods moderated this mortality.

### *Past Processes*

Tuck et al. (2018) study of an annual plant community makes the assertion that “poor predictive ability is likely to be general in plant communities due to ‘the ghost of competition present’ that confines species to parts of the environment in which they compete best”. This may be especially true for long-lived trees and underlies our reasoning for 1) examining NDD along spatiotemporal gradients of soil water, and 2) standardizing the crowding index. For mature trees in old forests, density-dependent (and -independent) interactions occur for over many centuries; it is thus necessary to decouple *a priori* mechanisms of dispersal and recruitment from *a posteriori* mortality that is presently observable. Allowing NDD to vary along a gradient of water availability

captures how interactions differ along a primary axis of differentiation, rather than being biased by dynamics occurring primarily within preferred microsites. Importantly, standardizing our density metric expresses NDD relative to what would be expected for a tree of a given diameter and species, thus controlling for current spatial patterns and diameter distributions of trees (the “ghost of competition”) and isolating drivers of recent mortality.

### *Predictor Error*

Detto et al. (2019) discuss three sources of predictor error that can result in NDD bias: measurement error, incorrect scale, and incorrect metric/functional form. Due to high relative accuracy of our spatially explicit dataset, our annual survival censuses (not a sub-sample; repeated measures), and that our neighborhood metric was generated through direct measurements of trees rather than allometric equations, we assume asymptotically zero measurement error. Likewise, our choice of scale was informed directly by previous research of interaction distances at our study site (Lutz et al., 2014), plus corroborating findings in other western temperate forests (Das et al., 2008; Larson et al., 2015). Sensitivity Analysis four therefore quantified functional form uncertainty of the NDD metric, and Sensitivity Analysis five tested whether this metric could be used to distinguish random from density-dependent mortality.

Detto et al. (2019) state that incorrect metric/functional form error “can only be resolved by mechanistic understanding of the effects of conspecifics, in particular the nature and the range of the interaction”. Our final choice of metric is well-informed by mechanistic understanding, as we opted for a biologically and ecologically grounded metric of neighborhood crowding among mature trees that is substantiated by regional

literature (Biging & Dobbertin, 1995; Das et al., 2011b; Hegyi, 1974). The distance- and diameter-weighted metric like the Hegyi index reflects the understanding that large and small trees experience competition from neighborhoods of the same density very differently; importantly, this metric captures the disproportionately suppressive effects of large-diameter trees better than other commonly used competition kernels (Fig. B.12). Indeed, this is incredibly similar to the distance- and diameter-weighted metric used by Uriarte et al. (2004), which dictated a maximum interaction radius of 15-m (compared to our 10-m threshold). Our approach differs primarily by using an alternative to Uriarte's species-specific scaler: we standardize crowding effects by both species and diameter class (given the large range of diameters observed), and do so after calculating initial crowding values, rather than within the computation itself.

Detto et al. (2019) discuss how spuriously large CNDD effects, particularly for rare species, can arise because “[NDD] underestimation is more severe for abundant species and for heterospecific effects”. To remain conservative in our conclusions, we only considered abundant species; we did not compare the fates of rare and abundant species, and we did not attempt to link NDD with abundance or diversity. Furthermore, by pooling all heterospecifics together, we avoid sensitivities of individual heterospecific effects while capturing the net effects of multi-way interactions that occur in diverse communities (Levine et al., 2017). Detto et al. (2019) also propose that “[underestimation of HNDD] can explain why many studies observed... heterospecific effects to be disproportionately smaller than conspecific effects”. In contrast to this prediction, we observed very similar degrees of current heterospecific and conspecific effects, with differences between the two arising primarily as functions of microsite and annual

climate. Finally, Detto et al. (2019) explain that error-prone proxies are “common to all situations where the independent and response variables cannot be measured in the exact same location or time”, specifically warning of experimental designs dependent upon subsampling. In contrast, our study is a census (i.e. not a subsample) of precisely mapped neighborhood positions, where the timing of mortality (at a finer temporal resolution than past studies) is observed in the same time and location as the measured predictors.

### *Ecological Interpretations of NDD Patterns*

Across all microsites, density-dependent interactions during drought were stronger drivers of tree mortality than density-independent drought effects, and moreover, larger sources of interspecific variability. It is important to note that density dependence (i.e. crowding effects) does not refer exclusively to competition: the density and identities of surrounding trees can mediate survival by mechanisms independent of competition, or interacting with competition (Barbosa et al., 2009; Franklin et al., 1987), and thus still be density-dependent. For example, insect attack rates often depend on tree density (Bentz et al., 2010) and tree species composition (Jactel & Brockerhoff, 2007), and strong competition for water can reduce tree defenses against insect pests (Huberty & Denno, 2004). Even of processes often assumed to be density-independent, like windthrow, the close connection with root-rotting pathogens (e.g., *Phellinus weirii*) (Holah et al., 1997) can render these processes indirectly density-dependent in many cases as well (for full discussion, see Furniss et al., 2020). Of course, some mortality processes are truly stochastic and density-independent, such as lightning strikes, but none were observed in this dataset. The prevalence of indirect drought effects, operating through multitrophic density-dependent processes, demonstrates a need for models that incorporate multi-way

interactions among climate, topography, and community biota to comprehensively anticipate the effects of climate change.

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**SUPPLEMENTAL TABLES AND FIGURES**

**Table B.1.** Demographic rates per species in terms of basal area at the Wind River Forest Dynamics Plot (25.6 ha). Trace ( $< 0.01\% \text{ m}^2 \text{ ha}^{-1}$ ) indicated by t. All vital rates refer to the 2011 to 2016 time period.

Gymnosperms	Family	Basal area ( $\text{m}^2 \text{ ha}^{-1}$ )					
		2011	2016	Recruitment		Mortality	
				Trees	Rate (%)	Trees	Rate (%)
<i>Abies amabilis</i>	Pinaceae	57.04	54.74	0.07	0.025	5.22	1.90
<i>Abies grandis</i>	Pinaceae	7.88	7.52	t	t	0.59	1.54
<i>Abies procera</i>	Pinaceae	5.08	4.82	0	0	0.28	1.13
<i>Pinus monticola</i>	Pinaceae	3.24	1.19	t	t	2.00	17.48
<i>Pseudotsuga menziesii</i>	Pinaceae	492.11	475.93	0	0	21.46	0.89
<i>Taxus brevifolia</i>	Taxaceae	44.05	39.77	t	t	4.71	2.24
<i>Thuja plicata</i>	Cupressaceae	99.49	102.49	t	t	0.05	0.01
<i>Tsuga heterophylla</i>	Pinaceae	874.99	868.15	0.07	0.002	39.07	0.91
All Gymnosperms		1583.88	1554.61	0.14	0.002	73.38	0.94

Table B.1. Continued.

Angiosperms	Family	Basal area (m <sup>2</sup> ha <sup>-1</sup> )					
		2011	2016	Recruitment		Mortality	
				Trees	Rate (%)	Trees	Rate (%)
<i>Acer circinatum</i>	Sapindaceae	14.55	14.51	0.03	0.041	1.38	1.97
<i>Acer glabrum</i>	Sapindaceae	<i>t</i>	<i>t</i>	0	0	0	0
<i>Alnus rubra</i>	Betulaceae	0.21	0.23	0	0	<i>t</i>	<i>t</i>
<i>Amelanchier alnifolia</i>	Rosaceae	0.01	0.01	<i>t</i>	<i>t</i>	<i>t</i>	<i>t</i>
<i>Corylus cornuta</i> ssp. <i>californica</i>	Betulaceae	0.26	0.31	0.02	1.493	0.03	2.42
<i>Cornus nuttallii</i>	Cornaceae	0.94	0.86	<i>t</i>	<i>t</i>	0.12	2.69
<i>Frangula purshiana</i>	Rhamnaceae	<i>t</i>	<i>t</i>	0	0	0	0
<i>Gaultheria shallon</i>	Ericaceae	<i>t</i>	<i>t</i>	<i>t</i>	<i>t</i>	<i>t</i>	<i>t</i>
<i>Holodiscus discolor</i>	Rosaceae	0.01	0.01	<i>t</i>	<i>t</i>	<i>t</i>	<i>t</i>
<i>Lonicera ciliosa</i>	Caprifoliaceae	<i>t</i>	<i>t</i>	0	0	0	0
<i>Menziesia ferruginea</i>	Ericaceae	<i>t</i>	<i>t</i>	0	0	<i>t</i>	<i>t</i>
<i>Oemleria cerasiformis</i>	Rosaceae	<i>t</i>	<i>t</i>	0	0	0	0
<i>Rhododendron macrophyllum</i>	Ericaceae	0.22	0.26	<i>t</i>	<i>t</i>	0.02	1.89
<i>Rosa gymnocarpa</i>	Rosaceae	<i>t</i>	<i>t</i>	0	0	0	0
<i>Rubus leucodermis</i>	Rosaceae	<i>t</i>	0	0	0	<i>t</i>	<i>t</i>
<i>Rubus spectabilis</i>	Rosaceae	<i>t</i>	<i>t</i>	<i>t</i>	<i>t</i>	0	0
<i>Vaccinium ovalifolium</i>	Ericaceae	0.01	0.01	<i>t</i>	<i>t</i>	<i>t</i>	<i>t</i>
<i>Vaccinium parvifolium</i>	Ericaceae	0.19	0.21	0.02	2.022	0.03	3.38
All Angiosperms		16.4	16.41	0.07	0.085	1.58	2.01
All Species		1600.28	1571.02	0.21	0.003	74.96	0.95

**Table B.2.** Multivariate linear relationships between conspecific and heterospecific Hegyi indices and the soil resources tested in preliminary analyses of ecological sorting in the Wind River Forest Dynamics Plot. N, P, and TEB were log-transformed to meet distributional assumptions and elevation above the water table was centered about the mean.

	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>P value</b>
<u>Conspecific Hegyi</u>				
Elevation above water table	-0.032	0.001	-29.676	< 0.001
Nitrogen	-0.0002	0.008	-0.030	0.98
Phosphorus	-0.017	0.008	-2.174	0.03
Total exchangeable bases	-0.021	0.007	-3.143	0.002
<u>Heterospecific Hegyi</u>				
Elevation above water table	-0.012	0.001	-10.540	< 0.001
Nitrogen	-0.0003	0.008	-0.040	0.97
Phosphorus	0.008	0.008	1.085	0.28
Total exchangeable bases	0.011	0.007	1.558	0.12

**Table B.3.** Data ranges for competition (Hegyi), species richness (number of species), climatic water balance, and topography for analyzed trees in the Wind River Forest Dynamics Plot. Hegyi indices and richness were calculated within a 10-m radius of focal trees. Only trees with Hegyi indices  $\pm 4$  SD were considered for analyses. Species richness, nitrogen, phosphorus, and total exchangeable bases were assessed in preliminary analyses but not retained in final models.

	<b>Minimum</b>	<b>Mean</b>	<b>Maximum</b>	<b>Units</b>
Hegyi (conspecific)	-1.8	0	5.2	SD
Hegyi (heterospecific)	-2.3	0	9.4	SD
Richness	1	5	11	# species
Deficit	97	163	261	mm H <sub>2</sub> O
Snowpack	43	227	495	mm H <sub>2</sub> O
Elevation above maximum spring water table	-1.1	5.3	18.4	m
Nitrogen	0.55	1.14	2.5	mg kg <sup>-1</sup>
Phosphorus	1.2	7.8	26.13	mg kg <sup>-1</sup>
Total exchangeable bases	0.26	1	6.68	cmol kg <sup>-1</sup>

**Table B.4.** The  $\beta$  coefficients produced by Cox mortality models for all tree species with  $n > 500$ , mortality  $n > 30$ , and quadrat frequency  $> 15\%$ : *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Acer circinatum*. Asterisks represent corresponding p-values  $< 0.05$  (\*),  $< 0.01$  (\*\*), and  $< 0.0001$  (\*\*\*). Exponentiate coefficients to attain hazard ratios. DBH = Diameter at breast height; Deficit = total annual modeled climatic water deficit; snow = maximum annual modeled snowpack; watertable = elevation above maximum spring water table; Hegyi.con = conspecific Hegyi; Hegyi.het = heterospecific Hegyi; Hegyi indices were calculated within a 10-m radius of focal trees. Trace ( $t$ ) =  $< |0.001|$ .

	<i>Abies</i>	<i>Pseudotsuga</i>	<i>Taxus</i>	<i>Tsuga</i>	<i>Acer</i>
DBH	+ <b>0.285***</b>	- 0.065	- <b>0.638***</b>	- <b>0.338***</b>	- <b>0.589***</b>
Deficit	- <b>0.005***</b>	- <b>0.005*</b>	- <b>0.008***</b>	- <b>0.005***</b>	- <b>0.005***</b>
Hegyi.het	+ <b>0.328***</b>	- 0.038	+ 0.109	+ <b>0.242***</b>	+ <b>0.142***</b>
snow	+ <b>0.001***</b>	+ <b>0.002*</b>	+ $t$	+ <b>0.002***</b>	+ $t$
watertable	+ <b>0.05**</b>	- 0.004	- 0.03	- 0.011	+ <b>0.024***</b>
Hegyi.con	+ <b>0.498***</b>	- 0.325	- <b>0.675*</b>	+ <b>0.421***</b>	+ 0.033
Deficit:Hegyi.het	- 0.001	- 0.001	+ $t$	- 0.001	- $t$
Deficit:snow	+ $t^{***}$	+ $t$	+ $t$	+ $t^{***}$	+ $t^{***}$
Deficit:watertable	- <b>0.001**</b>	- $t$	+ $t$	- $t$	+ $t$
Hegyi.het:snow	- $t$	+ 0.002	+ $t$	- $t$	+ $t$
Hegyi.het:watertable	+ 0.021	- 0.021	+ 0.022	- 0.009	+ 0.01
snow:watertable	- $t$	- $t$	+ $t$	+ $t$	+ $t$
Deficit:Hegyi.con	+ $t$	+ $t$	- 0.001	+ $t$	- $t$
snow:Hegyi.con	- $t$	+ 0.002	+ 0.001	- 0.001	+ 0.001
watertable:Hegyi.con	+ 0.047	- 0.016	- 0.085	+ 0.01	+ 0.023
Deficit:Hegyi.het:snow	- $t$	+ $t$	+ $t$	- $t$	- $t$
Deficit:Hegyi.het:watertable	+ $t$	+ $t$	- $t$	- $t$	- $t$
Deficit:snow:watertable	- $t$	+ $t$	+ $t^*$	+ $t$	- $t$
Hegyi.het:snow:watertable	- $t$	+ $t^*$	+ $t$	- $t$	+ $t$

Table B.4. Continued.

	<i>Abies</i>	<i>Pseudotsuga</i>	<i>Taxus</i>	<i>Tsuga</i>	<i>Acer</i>
Deficit:snow:Hegy.con	+ <i>t</i>	+ <i>t</i> *	+ <i>t</i>	- <i>t</i>	+ <i>t</i>
Deficit:watertable:Hegy.con	- <i>t</i>	+ 0.001	- 0.001	- <i>t</i>	- <i>t</i>
snow:watertable:Hegy.con	+ <i>t</i>	- <i>t</i>	- <i>t</i>	+ <i>t</i>	+ <i>t</i> *
Deficit:Hegy.het:snow:watertable	- <i>t</i> *	+ <i>t</i>	- <i>t</i>	- <i>t</i> *	- <i>t</i>
Deficit:snow:watertable:Hegy.con	- <i>t</i>	- <i>t</i>	- <i>t</i>	- <i>t</i>	- <i>t</i>
<i>Mortality n</i>	474	38	336	664	1637
<i>Survival n</i>	4333	528	1672	9391	9840
<i>Concordance</i>	66.7%	62.3%	69.7%	70.3%	67.3%

**Table B.5.** Cox model results for mortality hazard ratio (HR), i.e. the change in instantaneous mortality probability over time. HR indicates individual effects while holding all interacting variables (if any; identified by Table B.3) constant at mean values. All reported HR are significant at  $\alpha = 0.05$  level. Deficit = total annual modeled climatic water deficit; snow = maximum annual modeled snowpack; watertable = elevation above maximum spring water table; Hegyi.con = conspecific Hegyi; Hegyi.het = heterospecific Hegyi. Hegyi indices were calculated within a 10-m radius of focal trees.

<b>Species</b>	<b>Predictor</b>	<b>Mean Hazard</b>
<i>Abies amabilis</i>	watertable	5.06%
<i>Abies amabilis</i>	Deficit	-0.54%
<i>Abies amabilis</i>	snow	0.15%
<i>Abies amabilis</i>	Hegyi.het	38.78%
<i>Abies amabilis</i>	Hegyi.con	64.46%
<i>Pseudotsuga menziesii</i>	watertable	-0.06%
<i>Pseudotsuga menziesii</i>	Deficit	-0.48%
<i>Pseudotsuga menziesii</i>	snow	0.22%
<i>Pseudotsuga menziesii</i>	Hegyi.het	-4.97%
<i>Pseudotsuga menziesii</i>	Hegyi.con	-27.72%
<i>Taxus brevifolia</i>	watertable	-2.99%
<i>Taxus brevifolia</i>	Deficit	-0.84%
<i>Taxus brevifolia</i>	snow	0.02%
<i>Taxus brevifolia</i>	Hegyi.con	-49.11%
<i>Tsuga heterophylla</i>	watertable	-1.11%
<i>Tsuga heterophylla</i>	Deficit	-0.53%
<i>Tsuga heterophylla</i>	snow	0.16%
<i>Tsuga heterophylla</i>	Hegyi.het	26.63%
<i>Tsuga heterophylla</i>	Hegyi.con	52.35%
<i>Acer circinatum</i>	watertable	2.46%
<i>Acer circinatum</i>	Deficit	-0.54%
<i>Acer circinatum</i>	snow	0.02%
<i>Acer circinatum</i>	Hegyi.het	15.22%
<i>Acer circinatum</i>	Hegyi.con	1.87%



**Table B.6.** Factors affecting death were recorded for newly dead trees during annual surveys in the Wind River Forest Dynamics Plot. Multiple factors may be recorded. Insect pest and fungal pathogen species were identified when possible (the majority of cases). No fire-related or lightning mortalities were observed between 2012 and 2019.

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**Factor Affecting Death**

Drought stress  
 Suppression  
 Animal damage (specify animal if possible)  
 Mistletoe  
 White pine blister rust  
 Rot (specify if possible)  
 Canker  
 Other disease (specify)  
 Unknown disease  
 Anthropogenic mortality (specify)  
 Tree not found two years in a row. Assumed dead.  
 Bark beetles (specify if possible)  
 Defoliating insect (specify if possible)  
 Other insect (specify)  
 Uprooted by falling tree or tree parts  
 Uprooted (note cause)  
 Broken stem by falling tree or tree parts (entire or partial crown loss)  
 Broken stem (entire or partial crown loss) (note cause)  
 Crown damage (stripped, broken branches, etc)  
 Crushed by falling tree or tree parts  
 Crushed (note cause)  
 Lightning  
 Other physical cause (specify)  
 Tree physically removed from plot (landslide)  
 Crown Scorch  
 Crown Combustion  
 Bole/stem Scorch  
 Bole/stem Combustion  
 Cambial Heating  
 Burned through at base (due to duff consumption)  
 Other Fire (see comments)  
 Fire induced mechanical failure.  
 Complete Consumption  
 Unknown

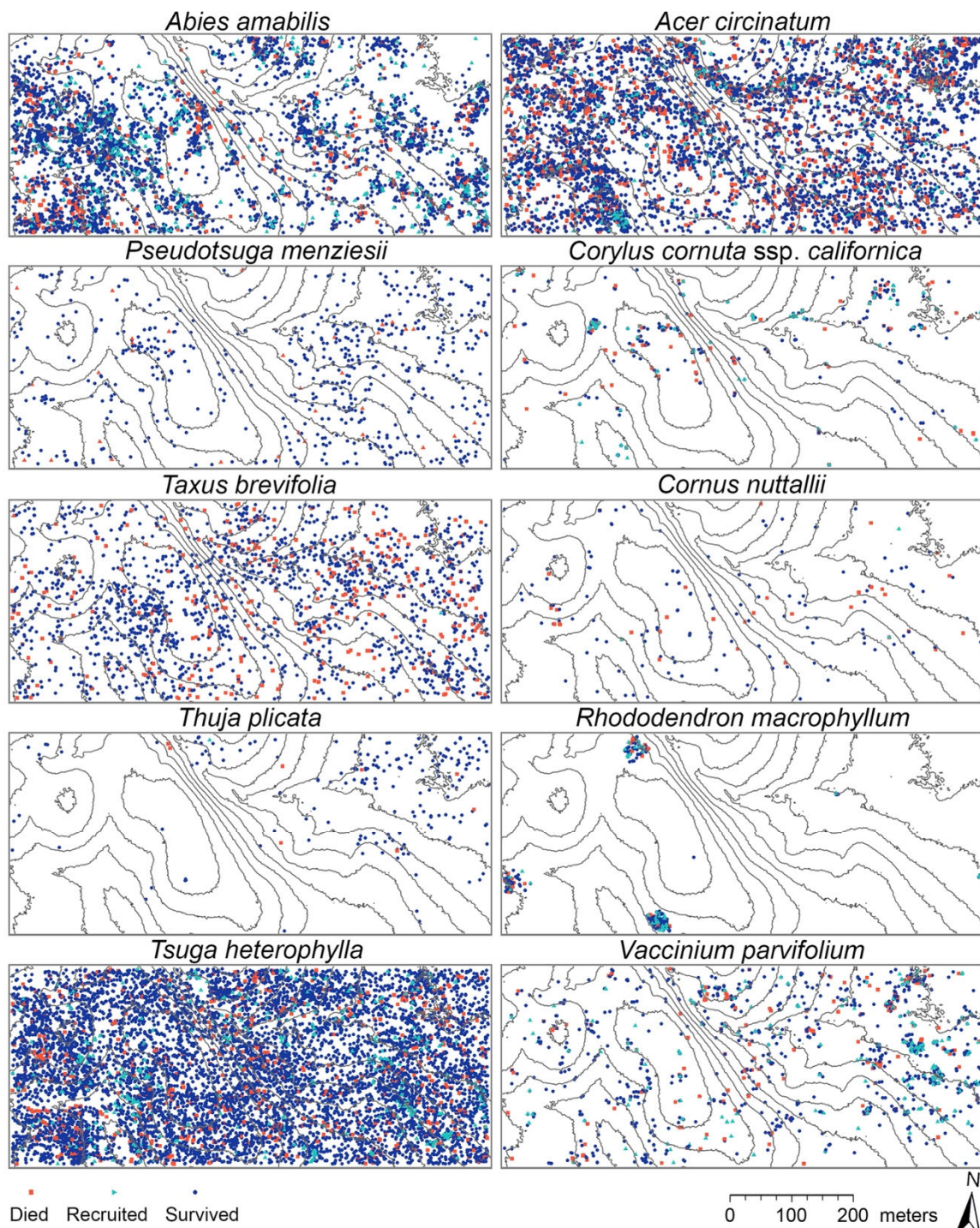
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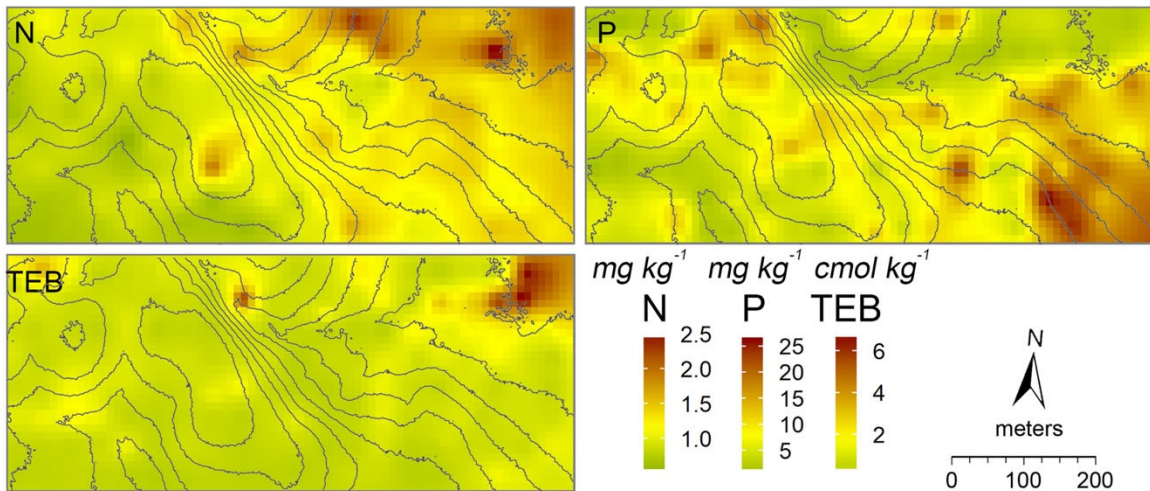
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**Table B.7.** Sensitivity Analysis 4 compared three competition kernels to quantify sensitivity of model fitness to the choice of NDD proxy: A) geometric decay (Hegyí index), B) exponential decay, and C) gaussian decay, all measured using a 50-m maximum radius. The chosen metric follows geometric decay capped at a 10-m radius. Fitness was roughly equivalent among the three functional forms and final metric chosen.

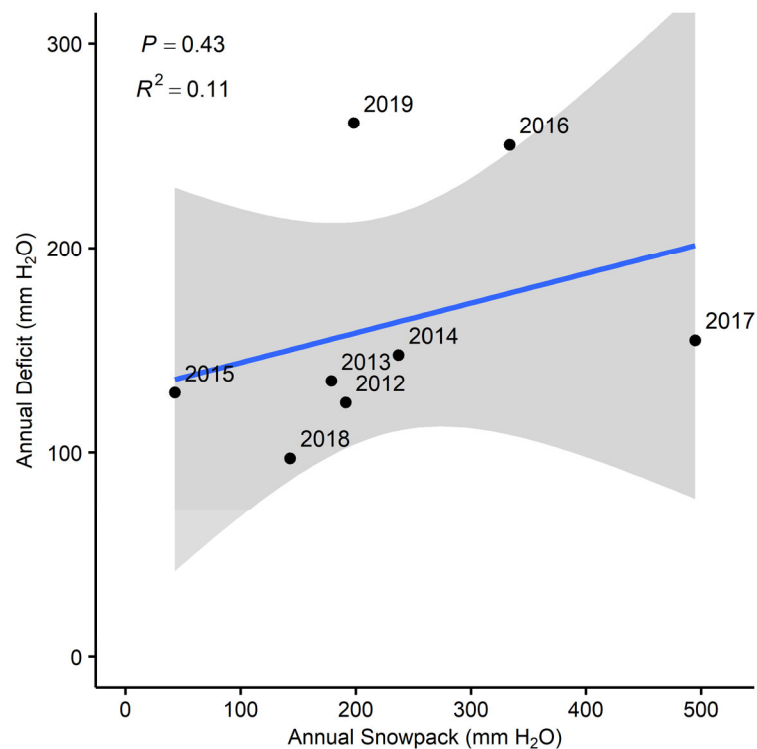
	<i>Exponential</i>	<i>Gaussian</i>	<i>Geometric</i>	<i>Chosen</i>
<i>Abies</i>	63.4%	66.7%	68.5%	66.7%
<i>Pseudotsuga</i>	62.8%	61.9%	71.0%	62.3%
<i>Taxus</i>	69.5%	70.0%	72.9%	69.7%
<i>Tsuga</i>	68.0%	69.4%	71.7%	70.3%
<i>Acer</i>	67.3%	67.5%	70.9%	67.5%



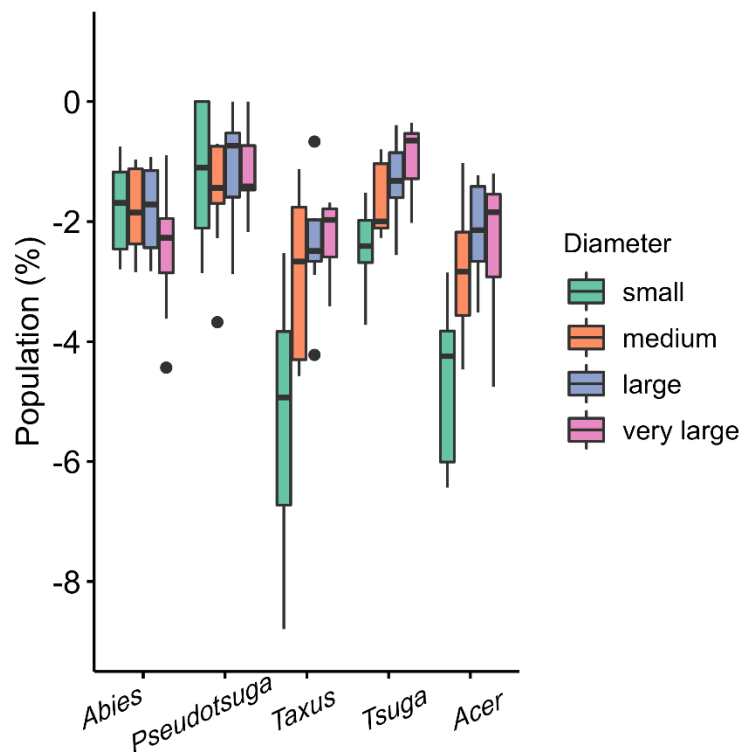
**Figure B.1.** Spatial distributions of the 10 species with >500 individual stems within the Wind River Forest Dynamics Plot. Contour lines: 3-m



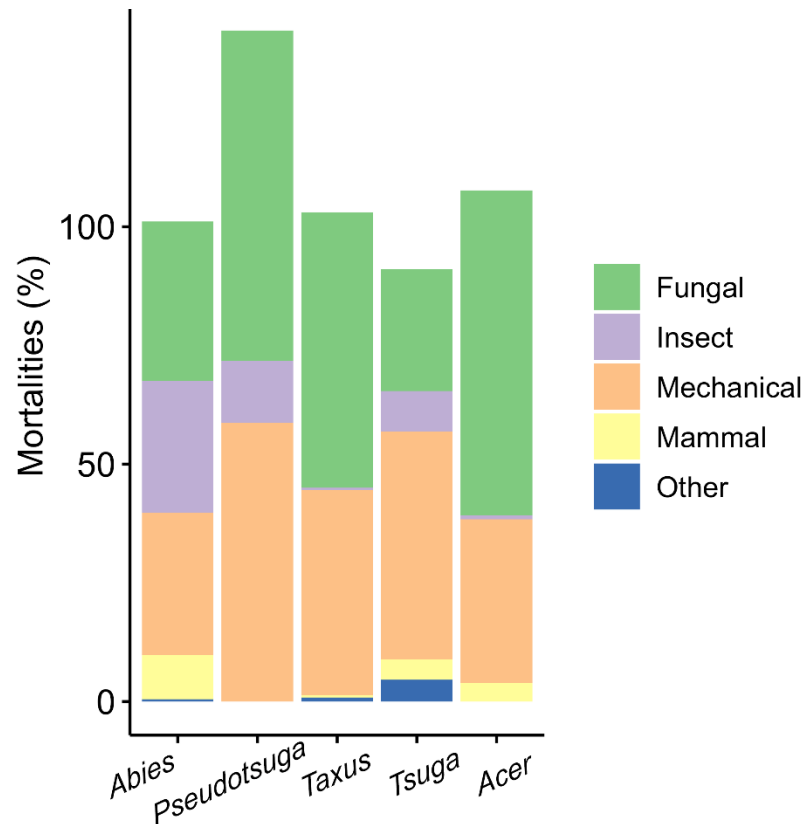
**Figure B.2.** Patchy soil resource distributions for nitrogen (N), phosphorus (P), and total exchangeable bases (TEB) within the Wind River Forest Dynamics Plot. These resources were considered in preliminary analyses but not retained in final models.



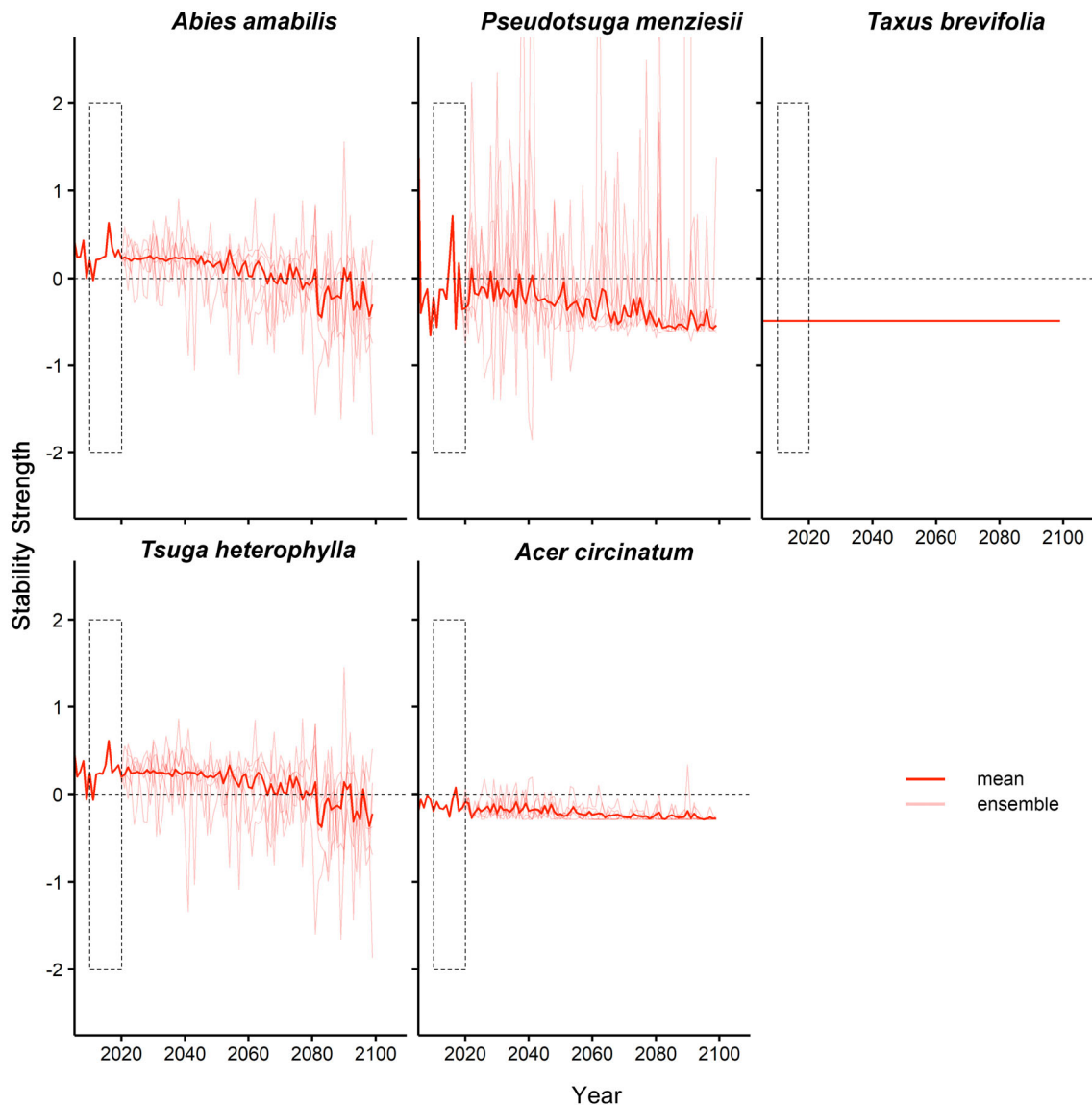
**Figure B.3.** Linear relationship between maximum annual winter snowpack (November through February) and total annual summer Deficit (March through October) in the Wind River Forest Dynamics Plot between 2012 and 2019. Linear relationship was not significant at  $\alpha = 0.05$  ( $P = 0.43$ ,  $R^2 = 0.11$ ). Snowpack melt times are variable due to relatively warmer winter and early spring temperatures compared to continental climates.



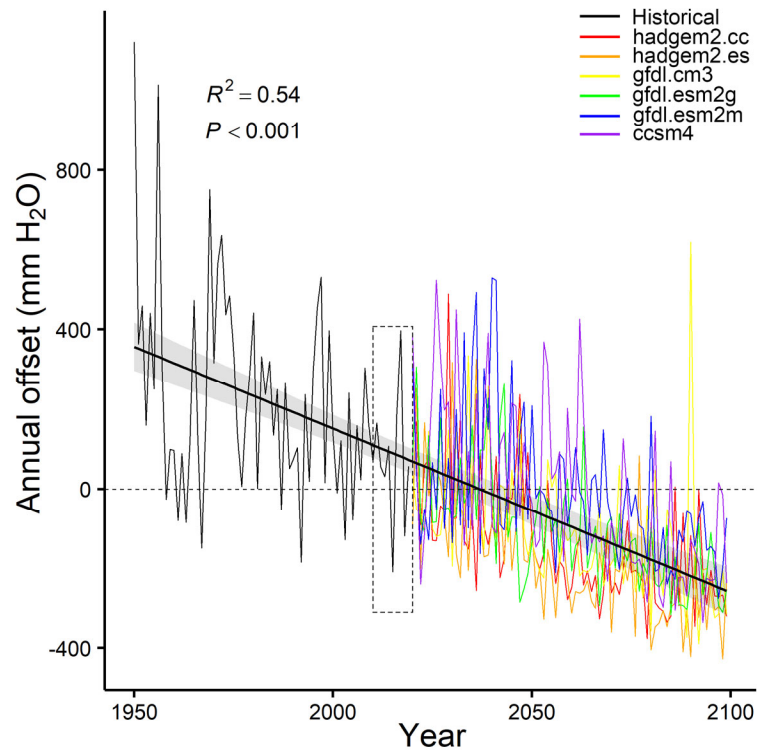
**Figure B.4.** Annual mortality rates by diameter class between 2012 and 2019 in the Wind River Forest Dynamics Plot for: *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Acer circinatum*. Boxplots reflect 25<sup>th</sup> to 75<sup>th</sup> quartiles, where whiskers span the full data range (excluding outliers, represented by dots); horizontal lines indicate the median. Diameter classes (small, medium, large, and very large) were defined by each species' diameter quartiles (0.25, 0.50, 0.75, 1.00). Diameter cut-offs (cm) for these quartiles are as follows: *Abies* (2.6, 4.5, 7.8, 8.5, 86.0); *Pseudotsuga* (86.2, 102.7, 101.7, 118.6, 184.0); *Taxus* (8.2, 12.3, 14.0, 17.4, 70.5); *Tsuga* (3.7, 10.0, 21.4, 28.9, 133.0); *Acer* (2.0, 3.2, 3.6, 4.7, 16.5).



**Figure B.5.** Factors associated with mortality between 2012 and 2019 in the Wind River Forest Dynamics Plot for: *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Acer circinatum*. “Fungal” mortality was evidenced by fruiting body identification and/or wood rot characteristics. “Insect” mortality refers to bark beetles for gymnosperms and foliar herbivores for angiosperms. “Mechanical” mortality refers either to physical crushing by adjacent trees or windthrow. “Mammal” mortality refers either to foliar herbivory (often the case for angiosperms) or physical damage from elk rubbing and scraping. “Other” mortality factors include lightning, mistletoe, or anthropogenic mortality. Many stems had multiple factors associated with mortality, hence >100% cumulative mortality for some species. All other mortality not shown (<100%) had unknown mortality factors (i.e. no evidence of fungal, insect, mechanical, mammal, or other damage was observable in the field).

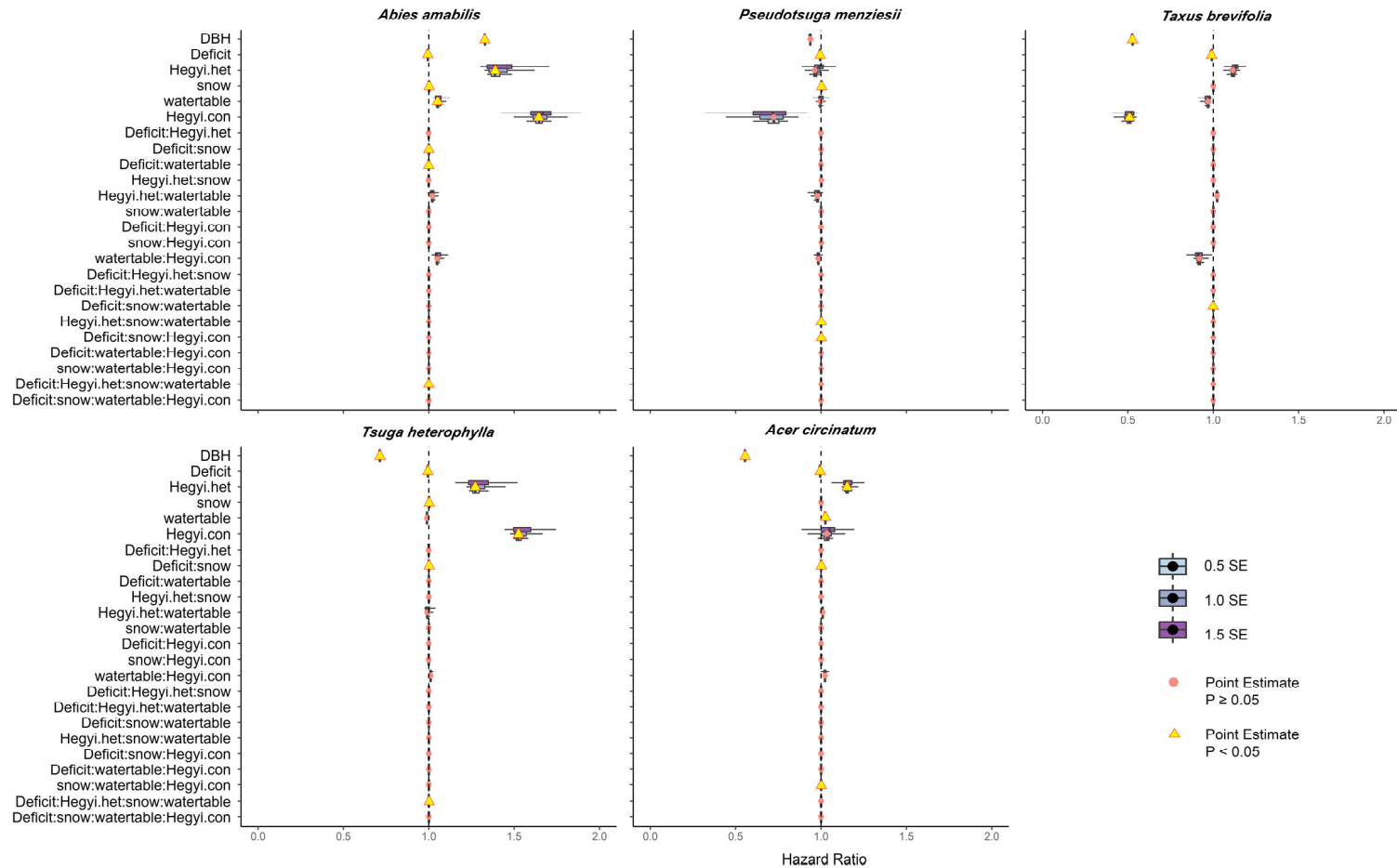


**Figure B.6.** Forecasted strength of stabilizing mechanisms (i.e., the difference between mortality hazard ratios produced by conspecific and heterospecific neighborhoods) at the species level at the average microsite. Curves of mean forecasted hazard ratios represent differences in the model mean, and ensemble curves are unique per each of six climate projections (CCSM4, GFDL-CM3, GFDL-ESM2M, GFDL-ESM2G, HadGEM2-CC, HadGEM2-ES). The horizontal dotted line represents no difference between conspecific and heterospecific effects on mortality risk. Differences greater than 0 indicate higher net mortality risk increase from conspecific neighborhoods; differences less than 0 indicate higher net mortality risk increase from heterospecific neighborhoods. Dotted rectangles capture the period of demographic sampling. Flat curves indicate that the Hegyi index had no significant interactions with snowpack or Deficit, meaning the effect of neighborhood was not projected to change over time.

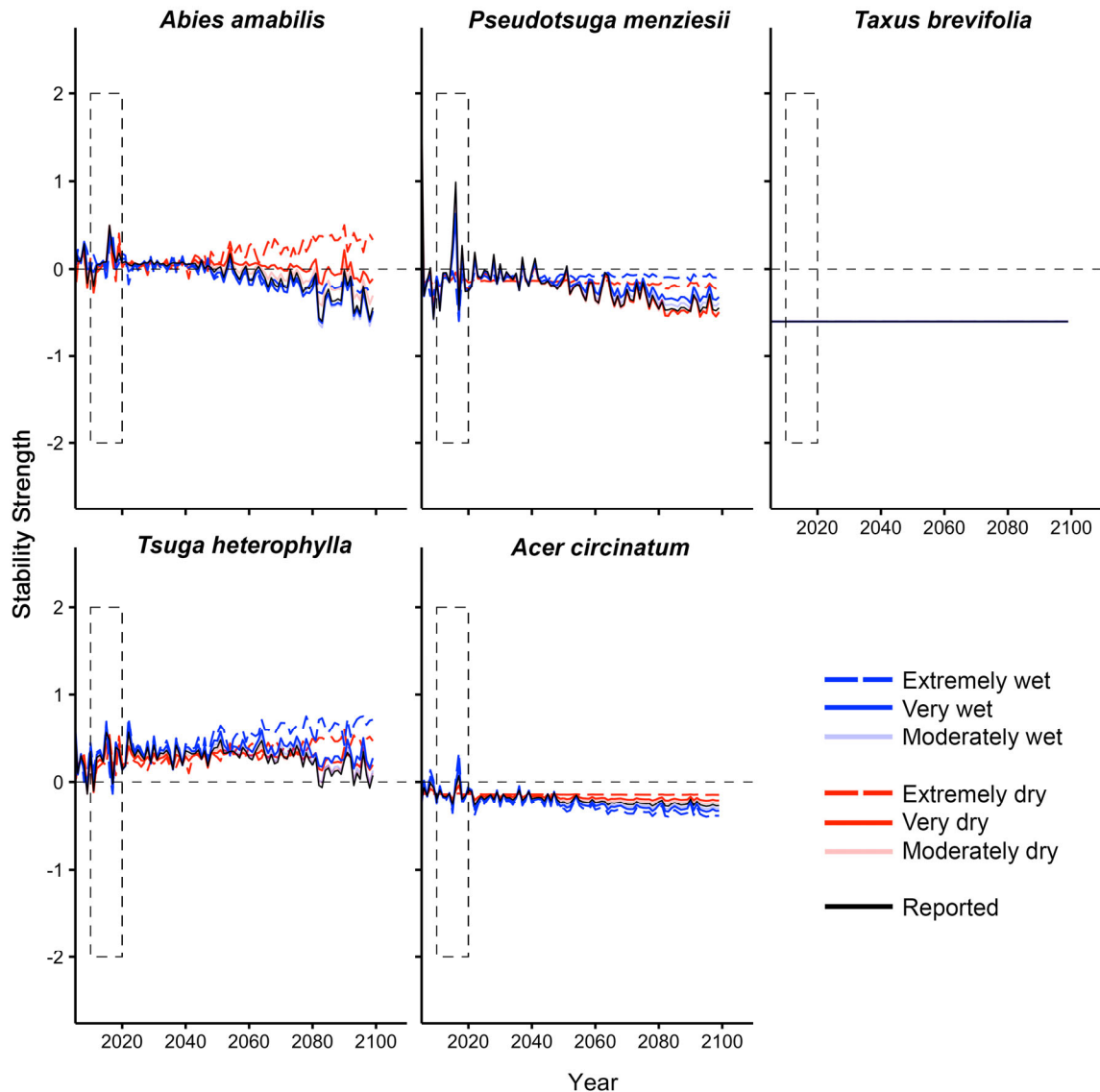


**Figure B.7.** Snow offset (difference between maximum snowpack and total Deficit) with generalized least squares regressions conducted on mean climate models created from six climate projections (colored lines) to show trends (95% confidence envelope in grey). Dotted rectangle encapsulates observations within the study period. Snow offset  $< 0$  (modeled to occur near year 2038) indicates annual water surpluses provided by large snowpacks are no longer present, resulting in net annual deficit.

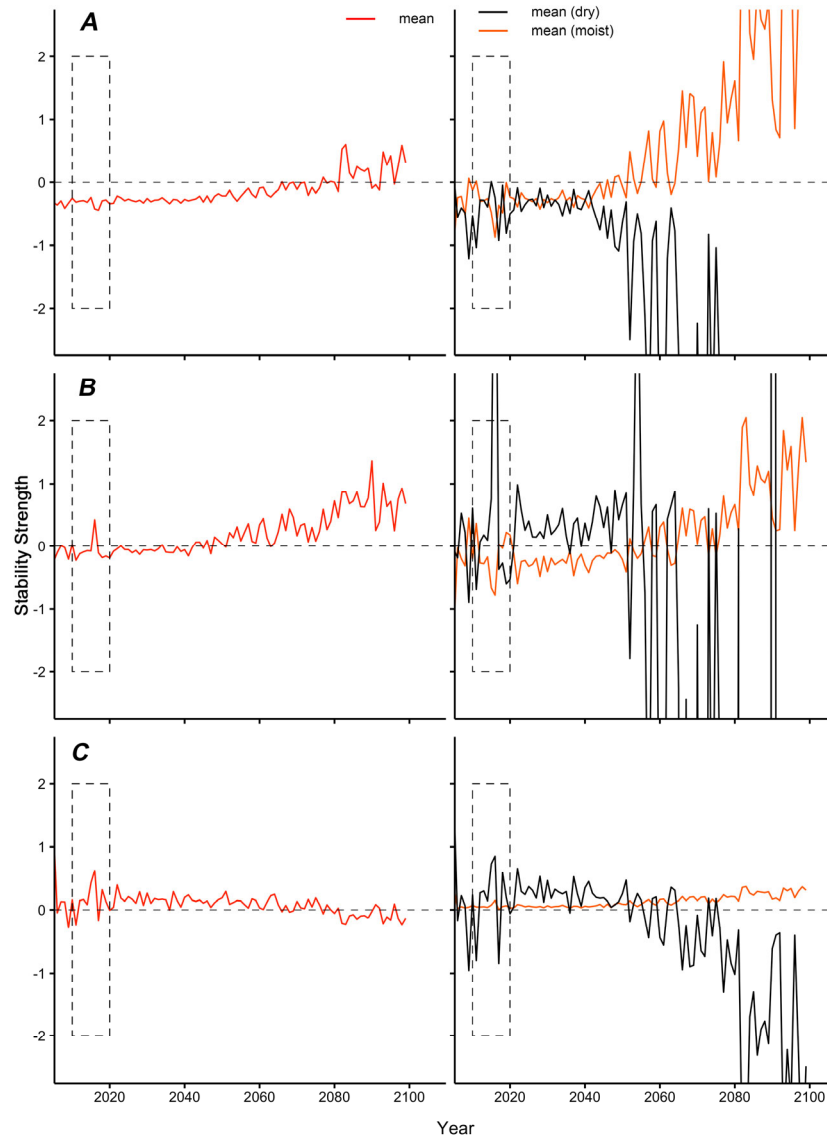




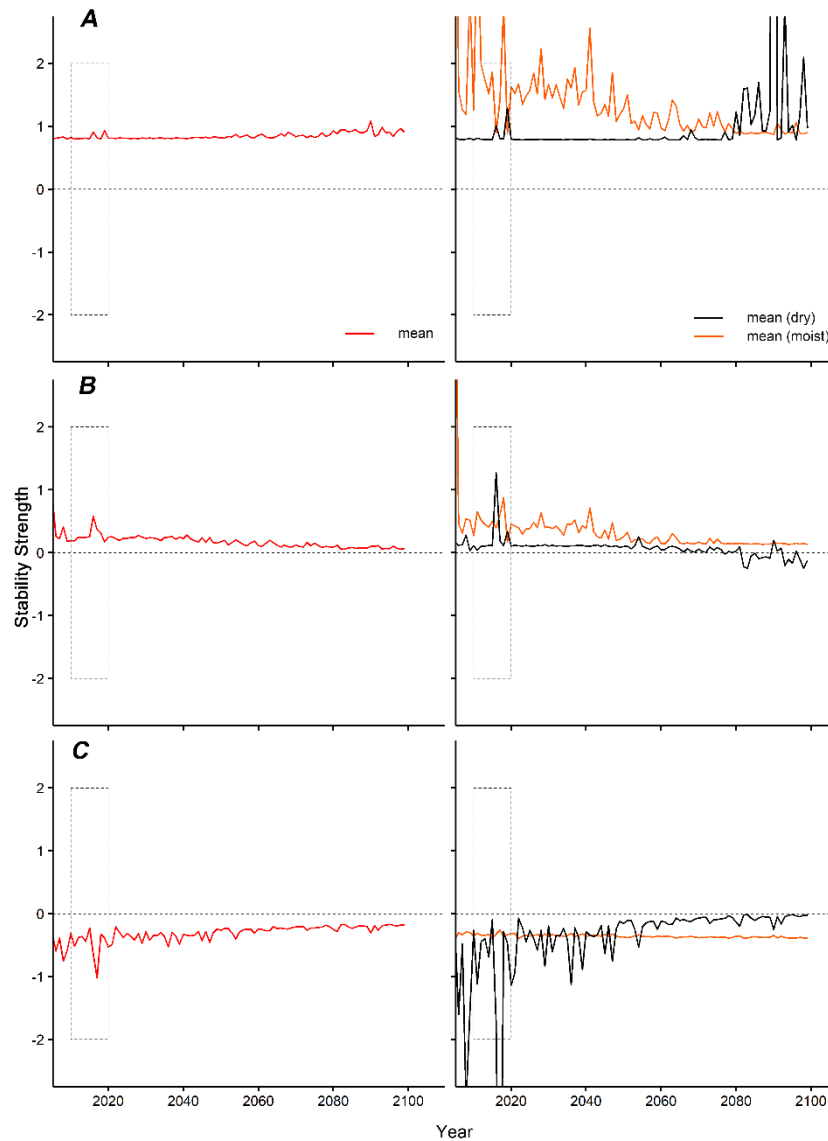
**Figure B.8.** Sensitivity Analysis 1 tested how three levels of historic climate uncertainty,  $\pm 0.5$ ,  $\pm 1$ , and  $\pm 1.5$  standard error (SE), altered parameter estimates (parameters listed on Y axis). Reported point estimates are represented by triangles (P-value < 0.05) or circles (P-value  $\geq 0.05$ ). Box plots indicate the 25th and 75th quartiles, and whiskers indicate  $\pm 1.5 \times \text{IQR}$  (interquartile range; 75th - 25th quartiles), for the 999 simulation models run at each uncertainty level. The vertical dotted line represents a hazard ratio of one, meaning no relationship between the predictor and mortality hazard (i.e. risk).



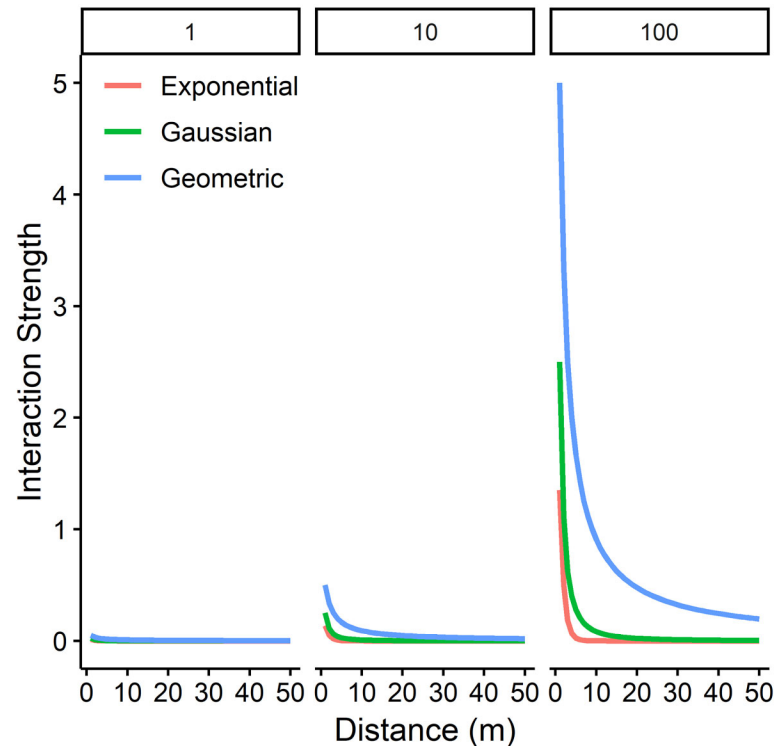
**Figure B.9.** Sensitivity Analysis 2 tested forecasted the strength of stabilizing mechanisms under six future climate scenarios: extremely dry (95% less snowpack, 100% more Deficit), very dry (50% less snowpack, 50% more Deficit), moderately dry (25% less snowpack, 25% more Deficit), extremely wet (100% more snowpack, 95% less Deficit), very wet (50% more snowpack, 50% less Deficit), and moderately wet (25% more snowpack, 25% less Deficit). The horizontal dotted line represents no difference between conspecific and heterospecific effects on mortality risk. Differences greater than 0 indicate higher net mortality risk increase from conspecific neighborhoods; differences less than 0 indicate higher net mortality risk increase from heterospecific neighborhoods. Dotted rectangles capture the period of demographic sampling. Flat curves indicate that the Hegyi index had no significant interactions with snowpack or Deficit, meaning the effect of neighborhood was not projected to change over time.



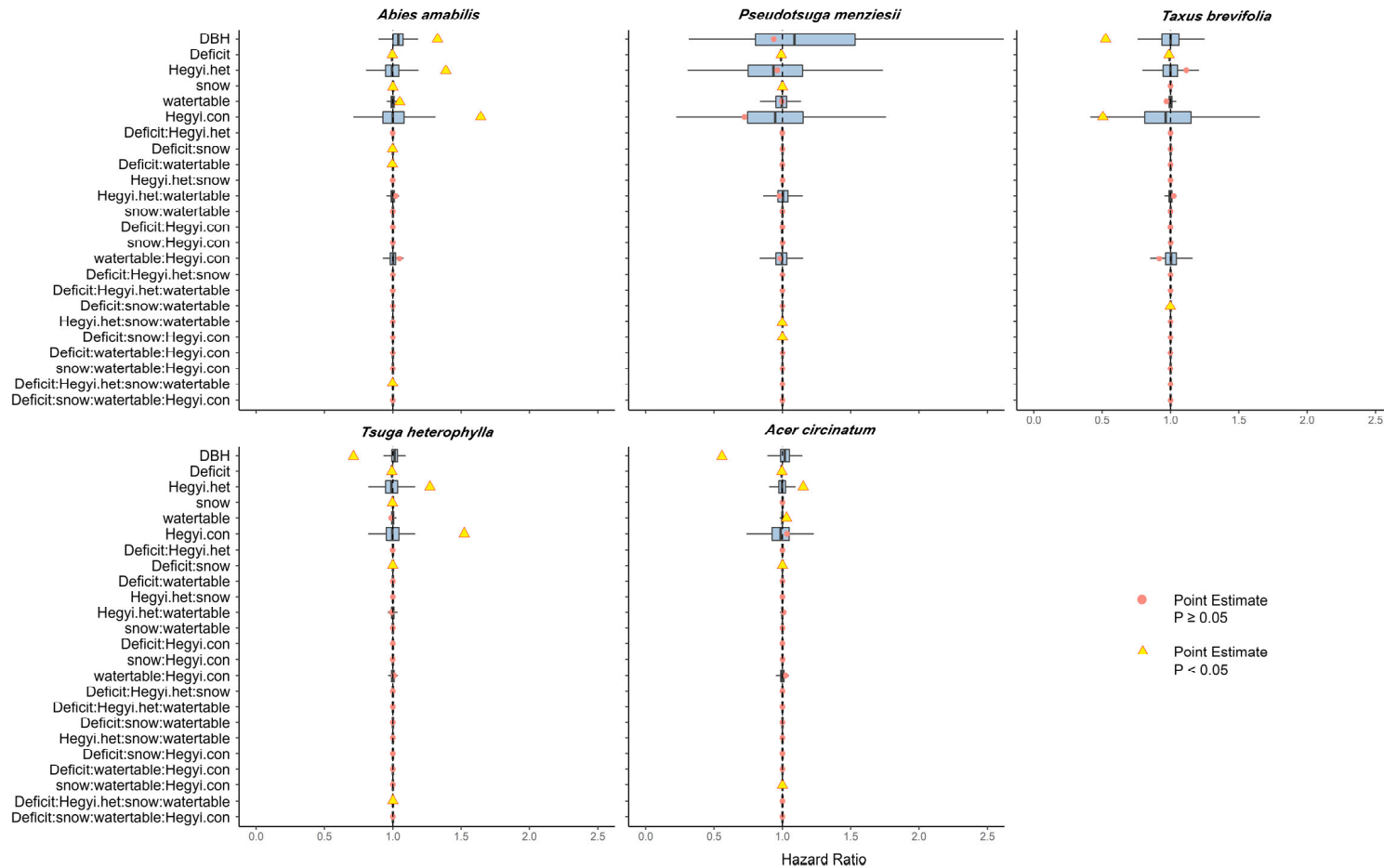
**Figure B.10.** Sensitivity Analysis 3 tested how sample size uncertainty relates to final conclusions drawn by the study, where panel A) 6-yr timespan; B) 7-yr timespan; and C) the reported 2012 to 2019 8-yr timespan. Curves indicate the forecasted strength of stability mechanisms (i.e. the difference between mortality hazard ratios produced by conspecific and heterospecific neighborhoods) at the community level, either averaged across all microsites (red curves) or stratified by soil moisture levels (black and orange curves). Community-level hazard ratios represent the relative basal area-weighted average of species-specific hazard forecasts of dominant tree species: *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Acer circinatum*. Curves of forecasted hazard ratios represent risk calculated from the mean climate model. Horizontal dotted lines represent no difference between conspecific and heterospecific effects on mortality risk. Differences greater than 0 indicate higher net mortality risk increase from conspecific neighborhoods; differences less than 0 indicate higher net mortality risk increase from heterospecific neighborhoods. Dotted rectangles capture the period of demographic sampling.



**Figure B.11.** Sensitivity Analysis 4 compared three competition kernels to quantify sensitivity of study conclusions to the choice of NDD proxy: A) exponential decay, B) gaussian decay, and C) geometric decay (Hegy index), all measured using a 50-m maximum radius. Curves indicate the forecasted strength of stability mechanisms (i.e. the difference between mortality hazard ratios produced by conspecific and heterospecific neighborhoods), either averaged across all microsites (red curves) or stratified by soil moisture levels (black and orange curves). Community-level hazard ratios represent the relative basal area-weighted average of species-specific hazard forecasts of dominant tree species: *Abies amabilis*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Tsuga heterophylla*, and *Acer circinatum*. Curves of forecasted hazard ratios represent risk calculated from the mean climate model. Horizontal dotted lines represent no difference between conspecific and heterospecific effects on mortality risk. Differences greater than 0 indicate higher net mortality risk increase from conspecific neighborhoods; differences less than 0 indicate higher net mortality risk increase from heterospecific neighborhoods. Dotted rectangles capture the period of demographic sampling.



**Figure B.12.** Sensitivity Analysis 4 compared three distance decay functions to quantify sensitivity of study conclusions to the choice of NDD proxy: geometric (Hegyi index), exponential, and gaussian decay of tree-tree interactions. Holding focal tree diameter at 10 cm at breast height (1.37 m; DBH), curves indicate tree interaction strength (i.e. the competition index) given a neighbor with DBH=1, 10, and 100 respectively per panel. The three competition kernels described similar relationships when neighbors were smaller (1) or when tree diameters were similar (10); however, competition from large-diameter neighbors (100) rapidly approached zero using the exponential decay function, compared to longer effective distances with a gaussian function, and the longest distances shown by geometric decay. Though somewhat better than the exponential, the gaussian kernel likewise does not fully capture the suppressive effects of large-diameter trees at close (<10 m) distances. The Hegyi index best reflects our mechanistic understanding of tree interactions in forests where large-diameter trees are present.



**Figure B.13.** Sensitivity Analysis 5 compared model estimates to a simulated null model of random mortality. Simulation envelopes (SE; box plots) indicate the 25th and 75th quartiles, and whiskers indicate  $\pm 1.5 \times \text{IQR}$  (interquartile range; 75th - 25th quartiles) for 999 simulations. The vertical line represents a hazard ratio of one, meaning no relationship between the predictor and mortality hazard. Point estimates inside SE are not well distinguished randomness (circles), while points outside SE indicate robust inferences; even point estimates very near to one can be considered robust, with weak effects, when outside simulation envelopes (triangles).

## APPENDIX C

## SUPPLEMENTARY MATERIAL FOR CHAPTER IV:

STAND DIVERSITY INCREASES PINE RESISTANCE AND RESILIENCE TO  
COMPOUND DISTURBANCE**SECTION S1: METHODS**Neighborhoods

We conducted multivariate multiple regression to test whether neighborhood effects were confounded with underlying variability in site conditions. Neighborhood variables were 30-m species richness and 10-m *Abies* density, as identified by preliminary tests for management and mechanistic models. Edaphic variables included topographic position (relative concavity or convexity of the site; used to stratify initial sampling), slope, aspect, soil nitrogen ( $\text{NH}_4 \text{ mg kg}^{-1}$ ), soil phosphorus ( $\text{mg kg}^{-1}$ ), total exchangeable bases ( $\text{cmolc kg}^{-1}$ ), and effective cation exchange capacity ( $\text{cmolc kg}^{-1}$ ; Tamjidi and Lutz 2020). Soil nutrients and slope were standardized using a z-score transformation; aspect was standardized using an offset cosine transformation to set northeast aspects at 1 and southwest aspects at -1; and the topographic position index was not standardized as this is already a relative metric. We then verified the predominant topographic controls had no effect on SEM conclusions by running the SEM with the residuals of richness and its topographic correlates. Separately, we also tested the correlation between species richness and neighborhood density metrics used in models.

Higher *Abies* densities were found on sites with slightly more nitrogen, while the highest richness was on slightly steeper slopes. Using the residuals of richness and slope,

there were no meaningful differences in SEM model output. Species richness at 30-m was not correlated with 10-m total density ( $p = 0.2$ ), *Abies* density ( $p = 0.9$ ), large *Pinus* density ( $p = 0.2$ ), or large *Pinus* living basal area ( $p = 0.1$ ). Small *Abies* density was slightly higher when richness was higher ( $p < 0.001$ ; +0.6 small *Abies* per additional species richness, maximum 7.8 more small *Abies*). Given that higher species richness was not associated with more favorable sites (more nutrients, more concave, or more northeasterly), and vice versa for *Abies* densities, we conclude that the effects of neighborhoods on tree survival are not the result of underlying edaphic gradients. Furthermore, the lack of relationship between richness and community densities suggests that richness effects were not the product of reduced competitive stress.

### Climate

Snow water equivalent (SWE) and climatic water deficit (Deficit) were extracted from TerraClimate, which calculated these metrics using a modified Thornthwaite-Mather climatic water-balance model and extractable soil water storage capacity data. Deficit represents the difference between potential and actual evapotranspiration, or the unmet water demand during the growing season. We also extracted TerraClimate's Palmer Drought Severity Index (PDSI), which is a standardized metric incorporating temperature and a physical water balance model to estimate relative dryness. The PRISM-calculated vapor pressure deficit (VPD) was calculated from based on observed precipitation and temperature. VPD measures the pressure difference between air water content and hypothetical air water content at saturation for a given temperature. As VPD increases, plant transpiration rates increase until a maximum threshold is reached (Grossiord et al. 2020), at which point plants may close stomata at the risk of carbon



starvation, or may continue photosynthesis at the risk of hydraulic failure (i.e., isohydric or anisohydric water use, respectively; Voelker et al. 2018). Winter drought is characterized by low SWE, while summer drought is characterized by high Deficit, high VPD, and annual drought captured by low PDSI.

We compared the associations between tree growth/defense (raw and standardized) and each of these metrics, temperature, and precipitation by using a sliding window analyses (SWA) on the live and dead chronologies. SWA uses linear regression and the Akaike information criterion (AIC) optimization to compare a base model to univariate models of each climate parameter, which are aggregated over all possible monthly intervals in the year prior to the month of growth sampling (set here to October, representing the end of the growing season). The growth base model was a first-order autoregressive model of BAI, and the defense base model assessed annual resin duct area as a function of annual BAI. Base models were then compared to climate models built across aggregation intervals of variable window width. For instance, precipitation could be aggregated over one month, multiple months, or up to one full year prior to observed annual tree growth. For each of these intervals, we tested the minimum, mean, and maximum (and sum, for precipitation) of the climate parameter.

We then performed a multivariate moving correlation function analysis (CFA) on the live and dead chronologies for the climate aggregations identified by SWA. Standard bootstrapping was used to calculate significance and confidence intervals. The moving window tested correlations with climate over 9-yr time intervals, which is the mean return interval for strong El Niño–Southern Oscillation events (ENSO; Enfield and Cid 1991). Static intervals were shifted consecutively by one from the first window (1896–

1904) to the last (2011–2019). This analysis identified decadal patterns in climate responses between dead and surviving trees to provide historical context to our subsequent models spanning shorter time intervals. That is, climate variables may have strong correlations during some decades (CFA) or over the whole series (SWA), but not necessarily during the study timeframe here (2010–2019). Therefore, we used the CFA to test SWA aggregations against *a priori* aggregations derived from the literature (e.g., maximum summer deficit, total winter SWE, mean annual PDSI).

### *Mechanism-oriented Models*

We performed piecewise SEM (i.e., confirmatory path analysis), which uses local estimation of each linear regression (i.e., path) rather than global estimation of all paths simultaneously (Lefcheck 2016). This allowed for the fitting of a wide range of variable distributions, including our binomial survival response and multilevel data structure. The hypotheses underlying each path and moderation (Fig. C.9) are described below:

#### *Stage 1 – Direct effects on survival*

Overall, we expect direct effects of tree neighborhoods on *Pinus* survival ( $\alpha_1, \beta_1$ ) to be less predictive than indirect effects. We expect tree survival (i.e., low beetle success rate) to depend on tree growth ( $\delta_1$ ) and defense ( $\epsilon_1$ ), which are in turn governed by direct and indirect biotic and abiotic factors (see single and serial mediation, below). The direct effects of beetle attack on tree survival represent mass attacks that overwhelm and thus circumvent tree defensive capacity ( $\gamma_2$ ). Negative covariance between growth and defense indicates a growth-defense trade-off. In the presence of such an observation, we expect that tree survival would be benefited by defense and harmed by growth. In the absence of

a growth-defense trade-off, however, we expect that tree survival would simultaneously benefit from defense and growth. We expect the relationships between tree growth/defense and survival to be moderated by drought and fire damage ( $\delta_1, \epsilon_1$ ): these two stressors may increase the relative importance of factors not considered by the model (e.g., hydraulic conductivity), thus weakening the relationship between tree defense and survival.

*Stage 2 - Single mediation of survival: neighborhood effect on survival mediated by tree growth & defense*

We expect tree neighborhoods to have direct effects on tree growth and defense: if there is lower competitive stress due to lower density of neighbors, *Pinus* will have higher photosynthetic rates to support increased growth ( $\beta_2$ ) and constitutive defenses ( $\beta_3$ ). We expect the relationships between neighborhoods and tree growth/defense to be moderated by drought and fire damage ( $\alpha_2, \beta_2, \alpha_3, \beta_3$ ): these two stressors may strengthen competitive interactions and weaken the facilitative effects of diversity, reducing growth and defenses as a result.

*Stage 3 - Serial mediation of survival: neighborhood effect on survival mediated by tree growth & defense, which is itself mediated by bark beetle attack rates*

We expect that tree neighborhood indirect effects on tree growth and defense are mediated by beetle attack rates: if there are fewer beetles attacking due to higher tree diversity ( $\alpha_4$ ), *Pinus* will be able to invest more carbon in growth ( $\gamma_2$ ), as less will be required for defense ( $\gamma_3$ ). We may expect the opposite to be true for density: if there are more beetles attacking due to vulnerability arising from competitive stress ( $\beta_4$ ), *Pinus* will be induced to allocate carbon to defense ( $\gamma_3$ ) rather than growth ( $\gamma_2$ ). We expect the

relationships between neighborhoods and beetle attack rates to be moderated by drought and fire damage ( $\alpha_4, \beta_4$ ): these two stressors may induce *Pinus* to emit an altered volatile chemical profile that increases beetles' detection probabilities (Jenkins et al. 2014), weakening the relationship between neighborhoods and beetle attack. Likewise, we expect the relationships between beetle attack rates and tree growth/defense to be moderated by drought and fire damage ( $\gamma_2, \gamma_3$ ): these two stressors may further induce *Pinus* to invest in defenses (Hood et al. 2015), strengthening the relationship between beetle attack rates and defense relative to growth.

**SECTION S2: SUPPLEMENTAL REFERENCES**

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**TABLES AND FIGURES**

**Table C.1.** Pearson’s correlations between the *Pinus lambertiana* chronology developed here (YFDP-PILA; Germain and Lutz 2021a, 2021b), three *Pinus* chronologies from Yosemite National Park (King and Graumlich 2002a, 2002b, 2002c), two *Pinus* chronologies from in the Sierra Nevada region (White 2002, Bigelow et al. 2014), and one *Calocedrus decurrens* chronology from the same study location (YFDP-CADE; Barth et al. 2014). Correlations were performed using a robust biweight mean and pre-whitened chronologies. Tuolumne Grove is <1 km northeast of the YFDP, with slightly lower elevation and wetter habitat. The Merced Grove is ~4 km south-southwest of the YFDP, with slightly lower elevation and wetter habitat. Hodgdon Meadows is ~5 km northwest of the YFDP, with lower elevation and drier habitat. Plumos County is ~260 km north-northwest of the YFDP in northern coastal California. Felkner Ridge is ~310 km northwest of the YFDP in the northern Sierra Nevada mountains.

	<b>YFDP- PILA</b>	<b>YFDP- CADE</b>	<b>Tuolumne</b>	<b>Merced</b>	<b>Hodgdon</b>	<b>Plumos</b>	<b>Felkner</b>
<b>YFDP-PILA</b>		0.67	0.35	0.7	0.42	0.47	0.28
<b>YFDP-CADE</b>			-0.09	0.05	0.24	0.21	0.04
<b>Tuolumne</b>				0.58	0.34	0.48	0.26
<b>Merced</b>					0.46	0.5	0.32
<b>Hodgdon</b>						0.66	0.27
<b>Plumos</b>							0.34
<b>Felkner</b>							

**Table C.2.** Results from the univariate sliding window analysis to determine the optimal monthly interval over which to aggregate each climate variable for growth. Growth was standardized per tree to reflect relative variability.

Response	Status	Climate Variable	Method	Window Open	Window Close	Base Coefficient	Base P-value	Climate Coefficient	Climate P-value	Adjusted R <sup>2</sup>	AIC	Group
Growth	Live	SWE	max	Feb	Apr	0.243	0.058	-0.002	0.006	0.13	69.84	A
		Deficit	max	Oct (prev)	May	0.225	0.078	-0.007	0.008	0.12	70.46	A
		PDSI	min	Dec (prev)	Apr	0.210	0.100	0.060	0.010	0.11	70.81	A
		SWE	sum	Feb	Feb	0.236	0.067	-0.002	0.011	0.11	71.05	A
		SWE	min	Feb	Feb	0.236	0.067	-0.002	0.011	0.11	71.05	A
		SWE	mean	Feb	Feb	0.236	0.067	-0.002	0.011	0.11	71.05	A
		PDSI	max	Oct (prev)	Jan	0.198	0.123	0.049	0.018	0.10	71.92	B
		PDSI	sum	Oct (prev)	Jan	0.196	0.130	0.012	0.031	0.08	72.91	B
		PDSI	mean	Oct (prev)	Jan	0.196	0.130	0.048	0.031	0.08	72.91	B
		Deficit	min	Nov (prev)	Dec (prev)	0.202	0.119	-0.039	0.031	0.08	72.94	B
		Deficit	sum	Oct (prev)	Oct (prev)	0.200	0.124	-0.004	0.044	0.07	73.59	B
		Deficit	mean	Oct (prev)	Oct (prev)	0.200	0.124	-0.004	0.044	0.07	73.59	B
		Temperature (min)	min	May	Sep	0.355	< 0.001	0.068	< 0.001	0.22	121.59	C
		Temperature (min)	mean	May	May	0.357	< 0.001	0.067	< 0.001	0.21	121.88	C
		Temperature (min)	max	May	May	0.357	< 0.001	0.067	< 0.001	0.21	121.88	C
		Temperature (mean)	mean	Dec (prev)	May	0.383	< 0.001	0.116	< 0.001	0.21	122.21	C
		Temperature (mean)	min	May	Oct	0.344	< 0.001	0.068	0.002	0.20	123.92	D
		Precipitation	sum	Oct (prev)	Dec (prev)	0.390	< 0.001	0.001	0.003	0.19	125.01	D
		Precipitation	mean	Oct (prev)	Dec (prev)	0.390	< 0.001	0.002	0.003	0.19	125.01	D
		Temperature (mean)	max	May	May	0.365	< 0.001	0.053	0.003	0.19	125.36	D
		Temperature (max)	mean	Dec (prev)	May	0.388	< 0.001	0.094	0.005	0.19	126.13	E
		Temperature (max)	min	May	Oct	0.357	< 0.001	0.049	0.008	0.18	126.97	E
		Precipitation	max	Oct (prev)	Nov (prev)	0.381	< 0.001	0.001	0.009	0.18	127.31	E
		VPD (max)	mean	Jun	Jul	0.369	< 0.001	-0.039	0.009	0.18	127.33	E
		VPD (max)	max	Oct (prev)	Jun	0.382	< 0.001	-0.029	0.019	0.17	128.66	F
		Temperature (max)	max	May	May	0.374	< 0.001	0.035	0.023	0.17	128.96	F
		Precipitation	min	Oct (prev)	Oct (prev)	0.386	< 0.001	0.002	0.028	0.17	129.30	F
		VPD (max)	min	Jun	Sep	0.388	< 0.001	-0.026	0.037	0.16	129.83	F
		VPD (min)	min	May	May	0.375	< 0.001	0.074	0.052	0.16	130.42	NA
		VPD (min)	mean	May	May	0.375	< 0.001	0.074	0.052	0.16	130.42	NA
		VPD (min)	max	May	May	0.375	< 0.001	0.074	0.052	0.16	130.42	NA

Table C.2. Continued.

Response	Status	Climate Variable	Method	Window Open	Window Close	Base Coefficient	Base P-value	Climate Coefficient	Climate P-value	Adjusted R <sup>2</sup>	AIC	Group
Growth	Dead	Deficit	max	Oct (prev)	Jun	0.958	< 0.001	-0.008	0.004	0.71	88.39	A
		PDSI	max	Feb	Jun	0.974	< 0.001	0.065	0.004	0.71	88.45	A
		Deficit	sum	Jun	Sep	0.934	< 0.001	-0.003	0.005	0.70	89.04	A
		Deficit	mean	Jun	Sep	0.934	< 0.001	-0.011	0.005	0.70	89.04	A
		PDSI	sum	Apr	Apr	0.967	< 0.001	0.062	0.006	0.70	89.38	A
		PDSI	min	Apr	Apr	0.967	< 0.001	0.062	0.006	0.70	89.38	A
		PDSI	mean	Apr	Apr	0.967	< 0.001	0.062	0.006	0.70	89.38	A
		Deficit	min	Jul	Jul	0.924	< 0.001	-0.008	0.008	0.70	89.91	A
		Temperature (max)	mean	Jun	Sep	0.745	< 0.001	-0.180	< 0.001	0.47	126.58	B
		Temperature (mean)	min	Jun	Sep	0.700	< 0.001	-0.109	< 0.001	0.47	127.27	B
		VPD (max)	mean	Jun	Sep	0.745	< 0.001	-0.087	< 0.001	0.47	127.94	B
		VPD (min)	max	Oct (prev)	Jun	0.631	< 0.001	-0.119	< 0.001	0.46	128.80	C
		Temperature (max)	min	Jun	Sep	0.734	< 0.001	-0.088	< 0.001	0.46	129.49	C
		Temperature (mean)	mean	Jun	Sep	0.695	< 0.001	-0.148	< 0.001	0.45	131.05	D
		VPD (max)	min	Jun	Sep	0.725	< 0.001	-0.049	< 0.001	0.45	131.34	D
		VPD (max)	max	Oct (prev)	Jun	0.713	< 0.001	-0.048	< 0.001	0.45	131.61	D
		Temperature (mean)	max	Jun	Jun	0.696	< 0.001	-0.081	< 0.001	0.45	132.77	D
		Temperature (min)	min	Jun	Sep	0.680	< 0.001	-0.086	< 0.001	0.44	133.37	E
		Temperature (max)	max	Jun	Jun	0.724	< 0.001	-0.067	< 0.001	0.44	133.71	E
		VPD (min)	min	Feb	Feb	0.705	< 0.001	-0.232	< 0.001	0.44	133.96	E
		VPD (min)	mean	Feb	Feb	0.705	< 0.001	-0.232	< 0.001	0.44	133.96	E
		Precipitation	sum	Oct (prev)	Sep	0.803	< 0.001	< 0.001	< 0.001	0.44	134.61	E
		Precipitation	mean	Oct (prev)	Sep	0.803	< 0.001	0.005	< 0.001	0.44	134.61	E
		Temperature (min)	max	Oct (prev)	Jun	0.678	< 0.001	-0.072	0.002	0.43	135.78	F
		Temperature (min)	mean	Jun	Jun	0.681	< 0.001	-0.070	0.002	0.43	135.90	F
		Precipitation	max	Oct (prev)	Nov (prev)	0.758	< 0.001	0.001	0.008	0.42	138.89	G
		Precipitation	min	Dec (prev)	Mar	0.772	< 0.001	0.002	0.016	0.41	140.09	G
		SWE	sum	Oct	Oct	0.910	<i>NA</i>	0.071	<i>NA</i>	0.67	95.43	<i>NA</i>
		SWE	min	Oct	Oct	0.910	<i>NA</i>	0.071	<i>NA</i>	0.67	95.43	<i>NA</i>
		SWE	mean	Oct	Oct	0.910	<i>NA</i>	0.071	<i>NA</i>	0.67	95.43	<i>NA</i>
		SWE	max	Oct	Oct	0.910	<i>NA</i>	0.071	<i>NA</i>	0.67	95.43	<i>NA</i>



**Table C.3.** Results from the univariate sliding window analysis to determine the optimal monthly interval over which to aggregate each climate variable for resin duct area. Duct area was standardized per tree to reflect relative variability.

Response	Status	Climate Variable	Method	Window Open	Window Close	Base Coefficient	Base P-value	Climate Coefficient	Climate P-value	Adjusted R <sup>2</sup>	AIC	Group
Defense	Live	VPD (min)	mean	Jun	Oct	0.116	< 0.001	0.078	< 0.001	0.35	-109.60	A
		Temperature (min)	mean	Jun	Oct	0.110	0.001	0.068	< 0.001	0.31	-102.87	B
		VPD (min)	max	Nov (prev)	Apr	0.124	< 0.001	0.110	< 0.001	0.30	-101.06	B
		Temperature (min)	min	Jul	Sep	0.111	0.001	0.046	< 0.001	0.28	-97.73	C
		VPD (min)	min	Jul	Sep	0.115	< 0.001	0.058	< 0.001	0.27	-95.64	D
		Temperature (min)	max	Sep	Oct	0.111	0.001	0.043	< 0.001	0.26	-94.11	D
		Temperature (mean)	mean	Jun	Sep	0.122	< 0.001	0.074	< 0.001	0.25	-91.90	E
		Temperature (mean)	max	Jul	Aug	0.118	< 0.001	0.055	< 0.001	0.21	-86.38	F
		Temperature (mean)	min	Jun	Sep	0.145	< 0.001	0.039	< 0.001	0.19	-82.50	G
		VPD (max)	min	Jan	Jan	0.128	< 0.001	0.024	0.004	0.15	-76.74	H
		VPD (max)	mean	Jan	Jan	0.128	< 0.001	0.024	0.004	0.15	-76.74	H
		VPD (max)	max	Jan	Jan	0.128	< 0.001	0.024	0.004	0.15	-76.74	H
		Precipitation	min	Oct (prev)	Nov (prev)	0.149	< 0.001	-0.001	0.023	0.12	-73.34	I
		Temperature (max)	mean	Jun	Sep	0.136	< 0.001	0.037	0.038	0.12	-72.50	I
		Temperature (max)	min	Jun	Sep	0.147	< 0.001	0.019	0.042	0.12	-72.28	I
		PDSI	sum	Nov (prev)	Nov (prev)	0.111	0.020	-0.018	0.020	0.11	-50.53	J
		PDSI	min	Nov (prev)	Nov (prev)	0.111	0.020	-0.018	0.020	0.11	-50.53	J
		PDSI	mean	Nov (prev)	Nov (prev)	0.111	0.020	-0.018	0.020	0.11	-50.53	J
		PDSI	max	Nov (prev)	Nov (prev)	0.111	0.020	-0.018	0.020	0.11	-50.53	J
		Deficit	mean	Jul	Sep	0.080	0.083	0.003	0.027	0.10	-49.96	J
		Deficit	sum	Jul	Sep	0.080	0.083	0.001	0.027	0.10	-49.96	J
		Temperature (max)	max	Dec (prev)	Dec (prev)	0.143	< 0.001	-0.013	0.071	0.11	-71.40	NA
		Precipitation	max	Mar	Sep	0.137	< 0.001	< 0.001	0.138	0.10	-70.31	NA
		Precipitation	sum	May	Oct	0.136	< 0.001	< 0.001	0.175	0.10	-69.94	NA
		Precipitation	mean	May	Oct	0.136	< 0.001	0.002	0.175	0.10	-69.94	NA
		Deficit	min	Jan	Jan	0.099	0.037	0.009	0.052	0.08	-48.75	NA
		Deficit	max	Jan	Jan	0.099	0.037	0.009	0.052	0.08	-48.75	NA
		SWE	sum	Jan	Jan	0.077	0.101	-0.001	0.132	0.06	-47.15	NA
		SWE	min	Jan	Jan	0.077	0.101	-0.001	0.132	0.06	-47.15	NA
		SWE	mean	Jan	Jan	0.077	0.101	-0.001	0.132	0.06	-47.15	NA
		SWE	max	Jan	Jan	0.077	0.101	-0.001	0.132	0.06	-47.15	NA

Table C.3. Continued.

Response	Status	Climate Variable	Method	Window Open	Window Close	Base Coefficient	Base P-value	Climate Coefficient	Climate P-value	Adjusted R <sup>2</sup>	AIC	Group
Defense	Dead	Deficit	sum	Dec (prev)	Apr	0.374	< 0.001	0.005	0.001	0.67	1.10	A
		Deficit	mean	Dec (prev)	Apr	0.374	< 0.001	0.023	0.001	0.67	1.10	A
		Deficit	max	Dec (prev)	Apr	0.371	< 0.001	0.006	0.002	0.66	2.63	A
		PDSI	max	Nov (prev)	Apr	0.353	< 0.001	-0.033	0.003	0.65	3.25	B
		PDSI	min	Apr	Aug	0.354	< 0.001	-0.032	0.004	0.65	3.79	B
		Deficit	min	Mar	Sep	0.348	< 0.001	0.017	0.005	0.65	4.00	B
		PDSI	sum	Apr	Sep	0.354	< 0.001	-0.005	0.005	0.65	4.18	B
		PDSI	mean	Apr	Sep	0.354	< 0.001	-0.030	0.005	0.65	4.18	B
		VPD (min)	max	Oct (prev)	May	0.218	< 0.001	0.115	< 0.001	0.25	22.43	C
		VPD (min)	mean	Aug	Oct	0.231	< 0.001	0.100	< 0.001	0.23	26.00	D
		VPD (min)	min	Oct (prev)	Oct (prev)	0.212	< 0.001	0.098	< 0.001	0.22	28.12	E
		Temperature (min)	mean	May	Oct	0.227	< 0.001	0.081	< 0.001	0.19	32.49	F
		Temperature (min)	min	Jul	Sep	0.208	< 0.001	0.054	< 0.001	0.19	32.94	F
		Temperature (mean)	mean	Jan	Oct	0.219	< 0.001	0.114	< 0.001	0.18	33.52	F
		Temperature (min)	max	Sep	Oct	0.204	< 0.001	0.051	< 0.001	0.18	34.37	F
		VPD (max)	min	Jan	Feb	0.179	< 0.001	0.056	0.002	0.16	37.23	G
		VPD (max)	mean	Jan	Apr	0.197	< 0.001	0.068	0.002	0.16	37.43	G
		Temperature (mean)	min	Aug	Sep	0.191	< 0.001	0.049	0.002	0.15	37.96	G
		Temperature (mean)	max	Sep	Oct	0.189	< 0.001	0.046	0.004	0.15	38.91	G
		VPD (max)	max	Oct (prev)	May	0.187	< 0.001	0.028	0.004	0.14	39.12	G
		Temperature (max)	mean	Jan	Sep	0.194	< 0.001	0.080	0.011	0.13	40.83	H
		Precipitation	max	Jan	Feb	0.174	< 0.001	< 0.001	0.018	0.13	41.70	H
		Temperature (max)	max	Oct (prev)	May	0.185	< 0.001	0.032	0.021	0.12	41.98	H
		Precipitation	min	Oct (prev)	Feb	0.174	< 0.001	-0.002	0.023	0.12	42.14	H
		Precipitation	sum	Jan	Apr	0.175	< 0.001	< 0.001	0.024	0.12	42.26	H
		Precipitation	mean	Jan	Apr	0.175	< 0.001	-0.001	0.024	0.12	42.26	H
		Temperature (max)	min	Jun	Sep	0.202	< 0.001	0.032	0.043	0.11	43.26	I
		SWE	min	Mar	Apr	0.363	< 0.001	-0.022	0.102	0.62	9.59	NA
		SWE	sum	Apr	Apr	0.361	< 0.001	-0.003	0.103	0.62	9.61	NA
		SWE	mean	Apr	Apr	0.361	< 0.001	-0.003	0.103	0.62	9.61	NA
		SWE	max	Apr	Apr	0.361	< 0.001	-0.003	0.103	0.62	9.61	NA

**Table C.4.** Serial mediation model coefficients (logit of mortality odds ratio) and change in mortality odds for the effects of each predictor on *Pinus* survival. Indirect effects were those mediated by a third and/or fourth variable, summarized by Mediation. Richness is number of species within a 30-m radius. *Abies* density is number of *Abies* within a 10-m radius. Beetle attack was measured as the basal area of bark beetle-killed *Pinus* within a 10-m radius. Asterisk (\*) indicates statistical significance at  $\alpha = 0.05$ .

		Coefficient	Mortality Odds
Richness	<b>Totals:</b>		
	Total Effects	-0.0860 *	-8.2%
	Total Direct	-0.0090	
	Total Indirect	-0.0760	
	<b>Mediation:</b>		
	Beetles	-0.0003	
	Growth	-0.0544	
	Defense	-0.0015	
	Beetles + Growth	-0.0188 *	-1.9%
	Beetles + Defense	-0.0011	
<i>Abies</i> Density	<b>Totals:</b>		
	Total Effects	0.0640 *	+6.6%
	Total Direct	0.0100	
	Total Indirect	0.0540	
	<b>Mediation:</b>		
	Beetles	0.0004	
	Growth	0.0252	
	Defense	0.0034	
	Beetles + Growth	0.0235 *	+2.4%
Beetles + Defense	0.0013		
Beetle Attack	<b>Totals:</b>		
	Total Effects	0.1260 *	+13.4%
	Total Direct	0.0020	
	Total Indirect	0.1240 *	+13.2%
	<b>Mediation:</b>		
Growth	0.1170 *	+12.4%	
Defense	0.0066		

**Table C.5.** Moderated mediation model coefficients for the effects of each predictor on each response variable in a serial mediation. Growth is basal area increment; defense is annual duct area; richness is number of species within a 30-m radius; *Abies* is number of *Abies* within a 10-m radius; attack is basal area of beetle-killed *Pinus* within a 10-m radius; fire is bole scorch height; deficit is maximum monthly climatic water deficit. Fire and deficit were moderators (interaction effect), whereas attack, growth, and defense were mediators (indirect pathways connecting richness, density, and tree survival). Asterisk (\*) indicates statistical significance at  $\alpha = 0.05$ .

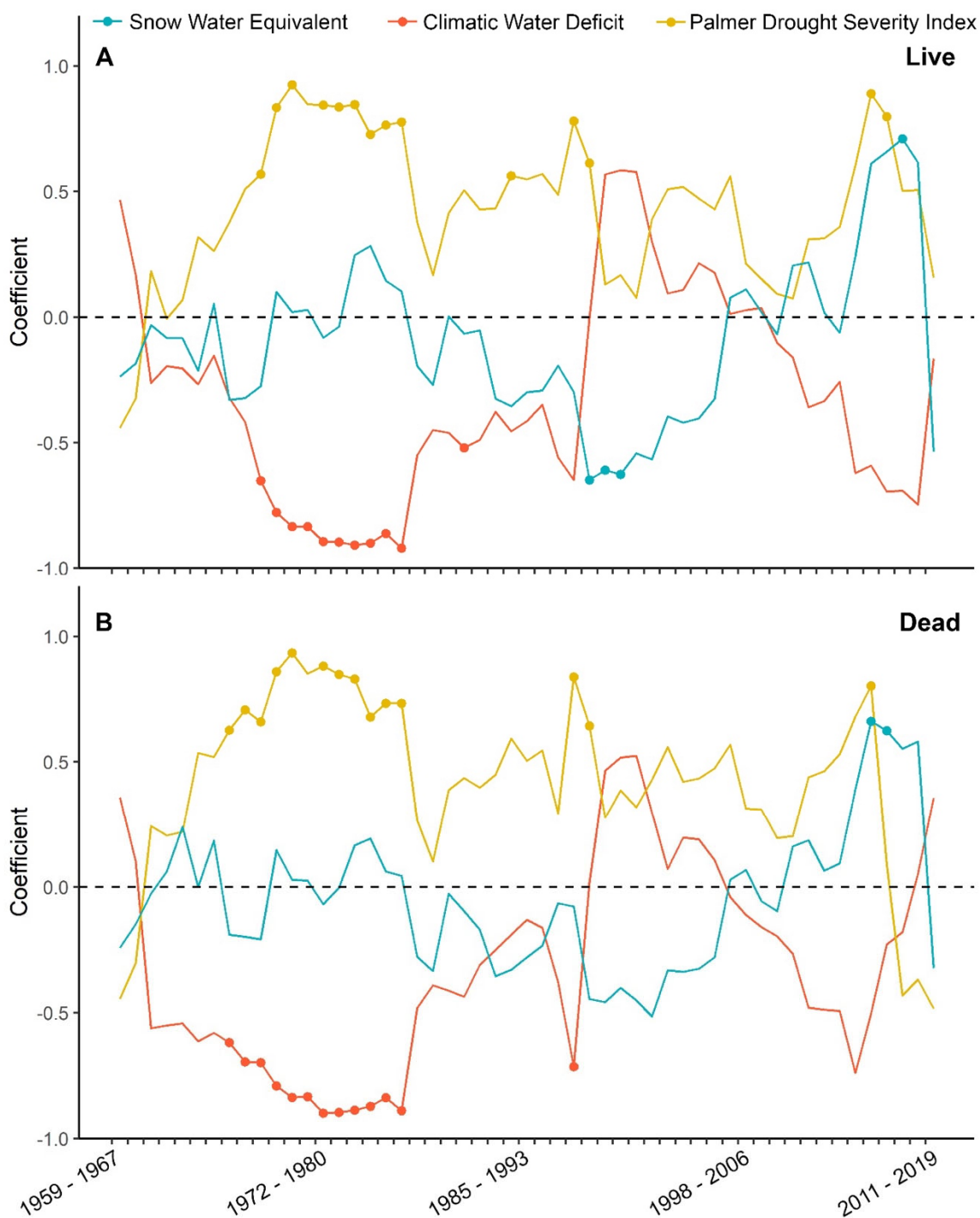
Response	Effect Type	Predictor	Coefficient
Survival	DIRECT	deficit	-0.045
		<i>Abies</i>	-0.008
		richness	0.009
		fire	-0.018
		growth:deficit	0.011
		deficit:defense	-0.027
		deficit: <i>Abies</i>	-0.045
		deficit:richness	0.039
		deficit:attack	-0.028
		growth:fire	-0.009
		defense:fire	-0.016
		<i>Abies</i> :fire	-0.001
		richness:fire	-0.015
		attack:fire	-0.021
	growth	-0.232*	
	defense	-0.047	
	attack	-0.013	
	INDIRECT	deficit	0.016*
		<i>Abies</i>	0.032*
		richness	-0.043*
		fire	0.004
		deficit: <i>Abies</i>	-0.013*
		deficit:richness	0.01
		deficit:attack	-0.025*
		<i>Abies</i> :fire	0.012
		richness:fire	-0.019
attack:fire		0.009	
attack		0.075*	

Table C.5. Continued.

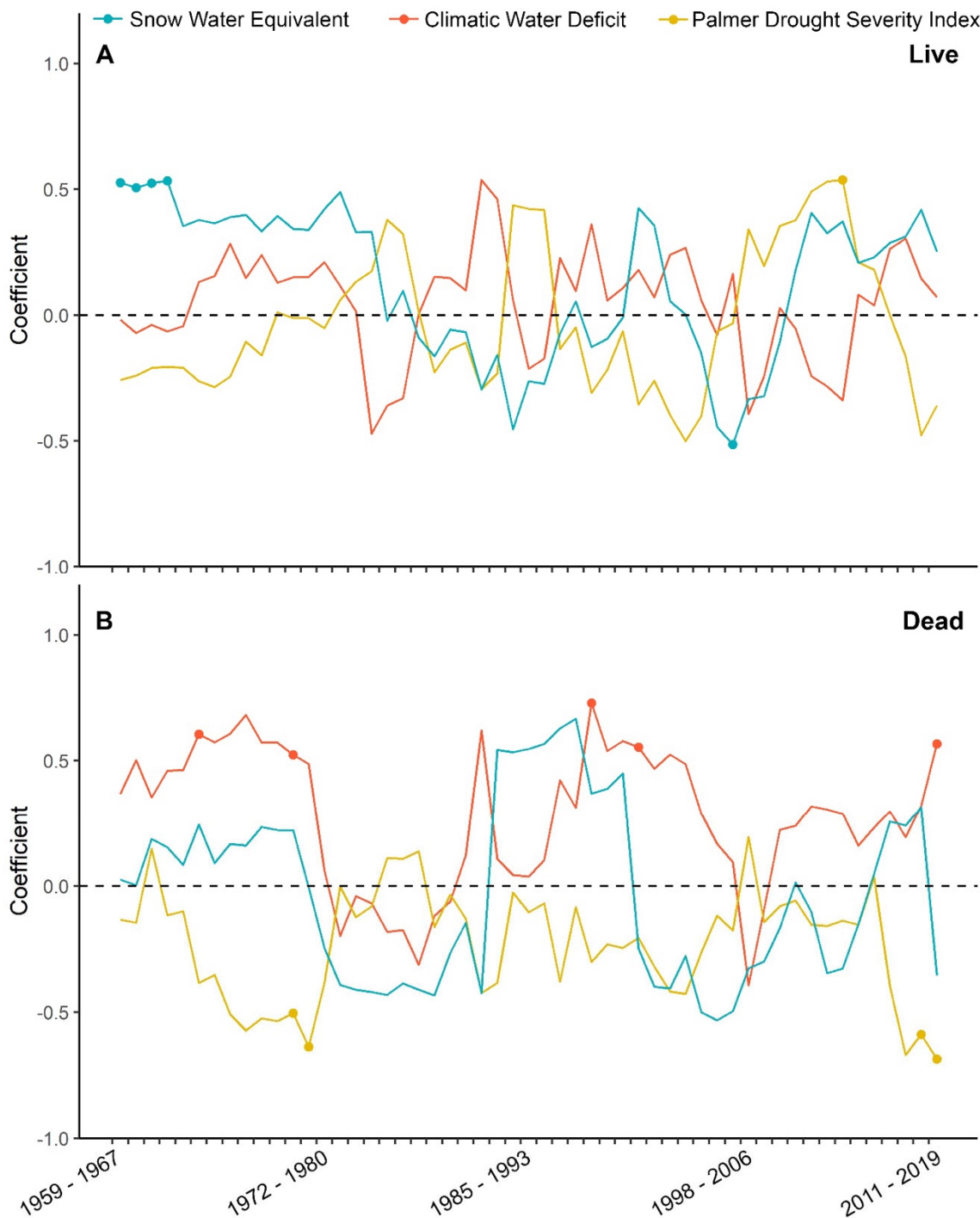
Response	Effect Type	Predictor	Coefficient	
Survival	TOTAL	deficit	-0.029	
		<i>Abies</i>	0.024	
		richness	-0.034	
		fire	-0.014	
		growth:deficit	0.011	
		deficit:defense	-0.027	
		deficit: <i>Abies</i>	-0.045*	
		deficit:richness	0.049	
		deficit:attack	-0.053	
		growth:fire	-0.009	
		defense:fire	-0.016	
		<i>Abies</i> :fire	0.01	
		richness:fire	-0.035	
		attack:fire	-0.011	
		growth	-0.232*	
		defense	-0.047	
		attack	0.062*	
		MEDIATORS	growth	0.05
			defense	0.007
			attack	-0.003
Growth	DIRECT	deficit	-0.067*	
		<i>Abies</i>	-0.072	
		richness	0.132	
		fire	0.011	
		deficit:richness	-0.033	
		deficit:attack	0.09*	
		<i>Abies</i> :fire	-0.039	
		richness:fire	0.044	
		attack:fire	-0.053	
		<i>Abies</i> :deficit	0.056*	
		attack	-0.3*	
		INDIRECT	deficit	-0.026*
			<i>Abies</i>	-0.046*
			richness	0.055*
			fire	0.01
			deficit: <i>Abies</i>	-0.003
			<i>Abies</i> :fire	-0.006
			richness:fire	0.032*
		richness:deficit	-0.001	
		TOTAL	deficit	-0.092*
	<i>Abies</i>		-0.118*	
	richness		0.187*	
	fire		0.02	
	deficit: <i>Abies</i>		-0.003	
		deficit:richness	-0.033	
		deficit:attack	0.09*	

Table C.5. Continued.

Response	Effect Type	Predictor	Coefficient	
Growth	TOTAL	<i>Abies</i> :fire	-0.045	
		richness:fire	0.076	
		attack:fire	-0.053	
		<i>Abies</i> :deficit	0.056*	
		richness:deficit	-0.001	
		attack	-0.3*	
	MEDIATORS		attack	0.015
	Defense	DIRECT	deficit	0.099*
			<i>Abies</i>	-0.122*
			richness	0.026
			fire	-0.17*
			deficit:richness	-0.043
			deficit:attack	0.084*
			<i>Abies</i> :fire	-0.027
richness:fire			0.052	
attack:fire			0.062*	
<i>Abies</i> :deficit			0.012	
attack		-0.121*		
INDIRECT		deficit	-0.01*	
		<i>Abies</i>	-0.019*	
		richness	0.022*	
	fire	0.004		
TOTAL	deficit: <i>Abies</i>	-0.001		
	<i>Abies</i> :fire	-0.002		
	richness:fire	0.013*		
	richness:deficit	0		
	deficit	0.089*		
	<i>Abies</i>	-0.141*		
	richness	0.048		
	fire	-0.166*		
	deficit: <i>Abies</i>	-0.001		
	deficit:richness	-0.043		
deficit:attack	0.084*			
<i>Abies</i> :fire	-0.029			
richness:fire	0.065			
attack:fire	0.062*			
<i>Abies</i> :deficit	0.012			
richness:deficit	0			
attack	-0.121*			
MEDIATORS		attack	0.006	
Beetle Attack	DIRECT	deficit	0.086*	
		<i>Abies</i>	0.153*	
		richness	-0.183*	
		fire	-0.032	
		deficit: <i>Abies</i>	0.009	
		<i>Abies</i> :fire	0.019	
		richness:fire	-0.105*	
		richness:deficit	0.004	

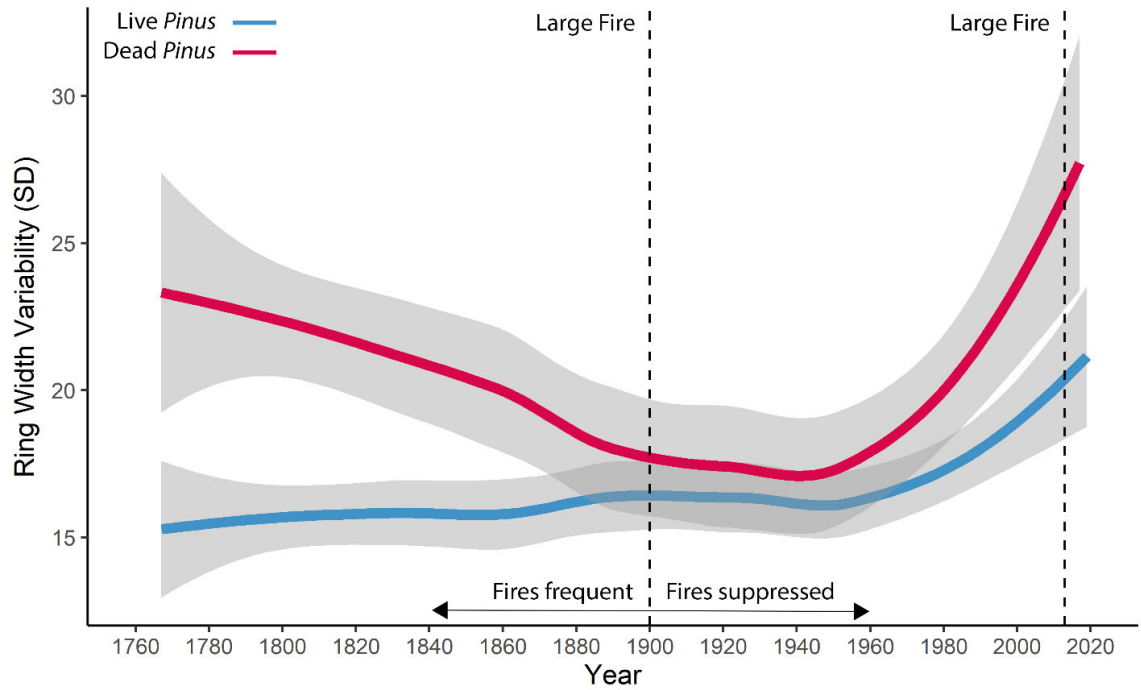


**Figure C.1.** Correlation between climate parameters and growth of live (A) or dead (B) trees, where values above zero indicate a positive relationship and below zero indicates a negative relationship. Variables represent mean total winter SWE  $\text{Nov}_p - \text{Apr}_c$ ; mean deficit  $\text{Jun}_c - \text{Jul}_c$ ; and mean annual PDSI. Dots indicate statistical significance.

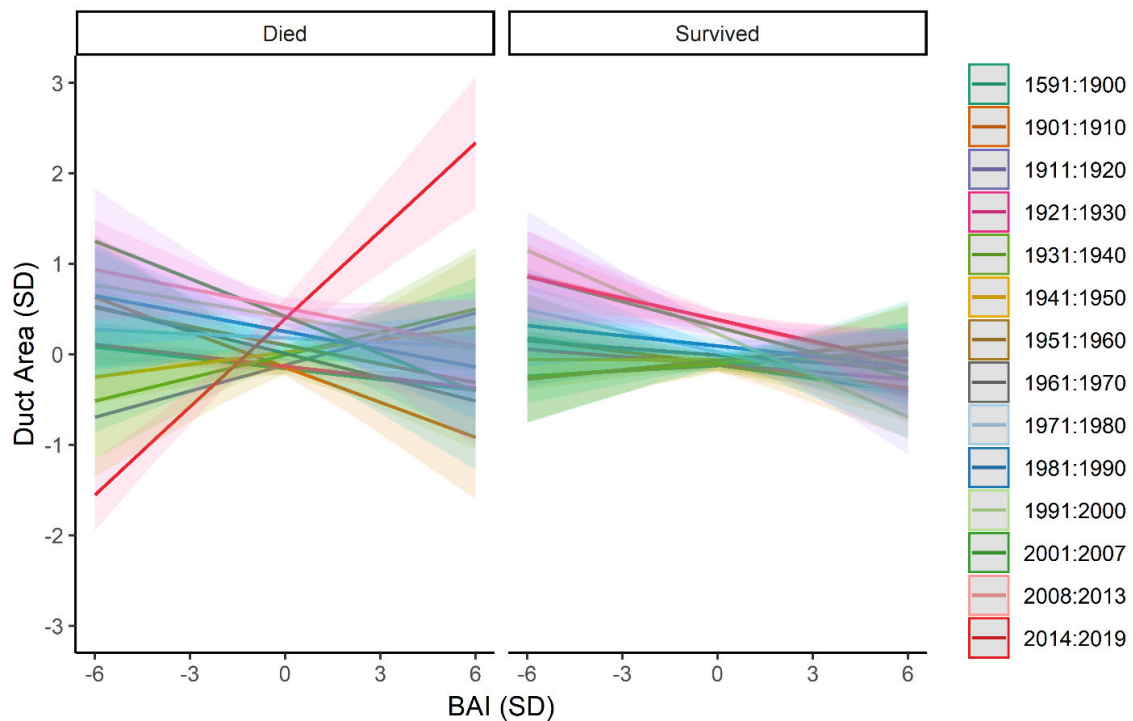


**Figure C.2.** Correlation between climate parameters and duct area of live (A) or dead (B) trees, where values above zero indicate a positive relationship and below zero indicates a negative relationship. Variables represent mean total winter SWE Nov<sub>p</sub> – Apr<sub>c</sub>; mean deficit Jun<sub>c</sub> – Jul<sub>c</sub>; and mean annual PDSI. Dots indicate statistical significance. Dead trees' duct area was more sensitive to climate, with generally higher duct area during drought (higher deficit, lower PDSI).

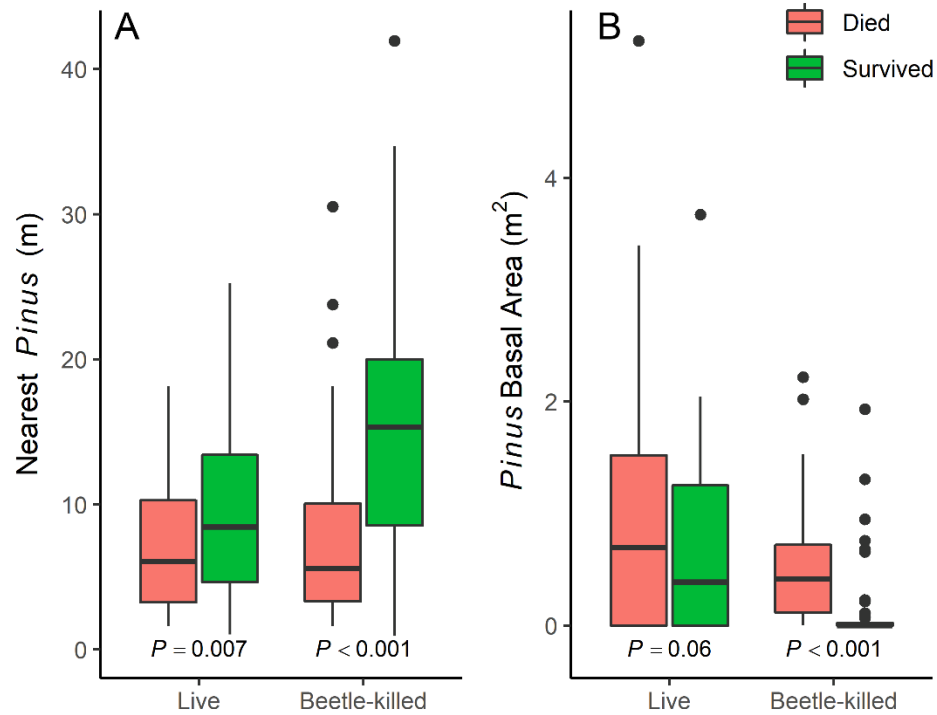




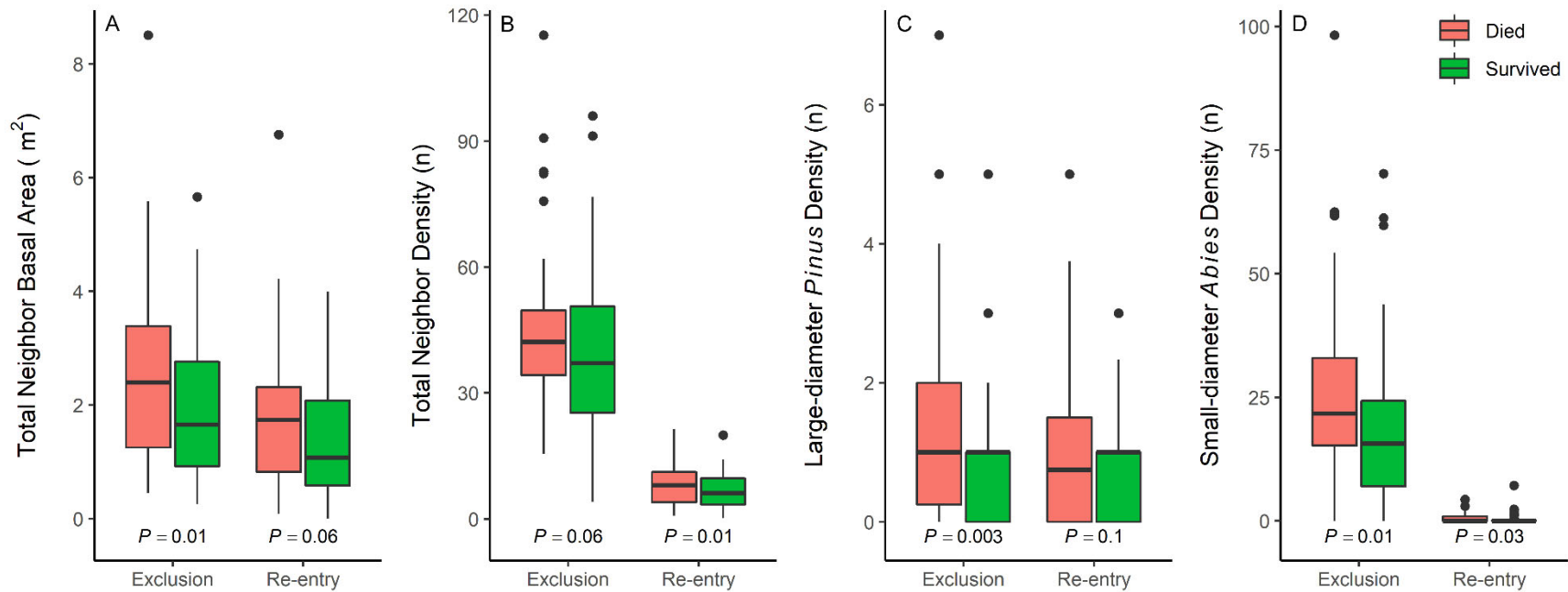
**Figure C.3.** Intraspecific variability of radial growth for live and dead trees. Dead trees differed more from each other than live trees differed from each other, especially during the fire-frequent historical period. BAI showed the same curves.



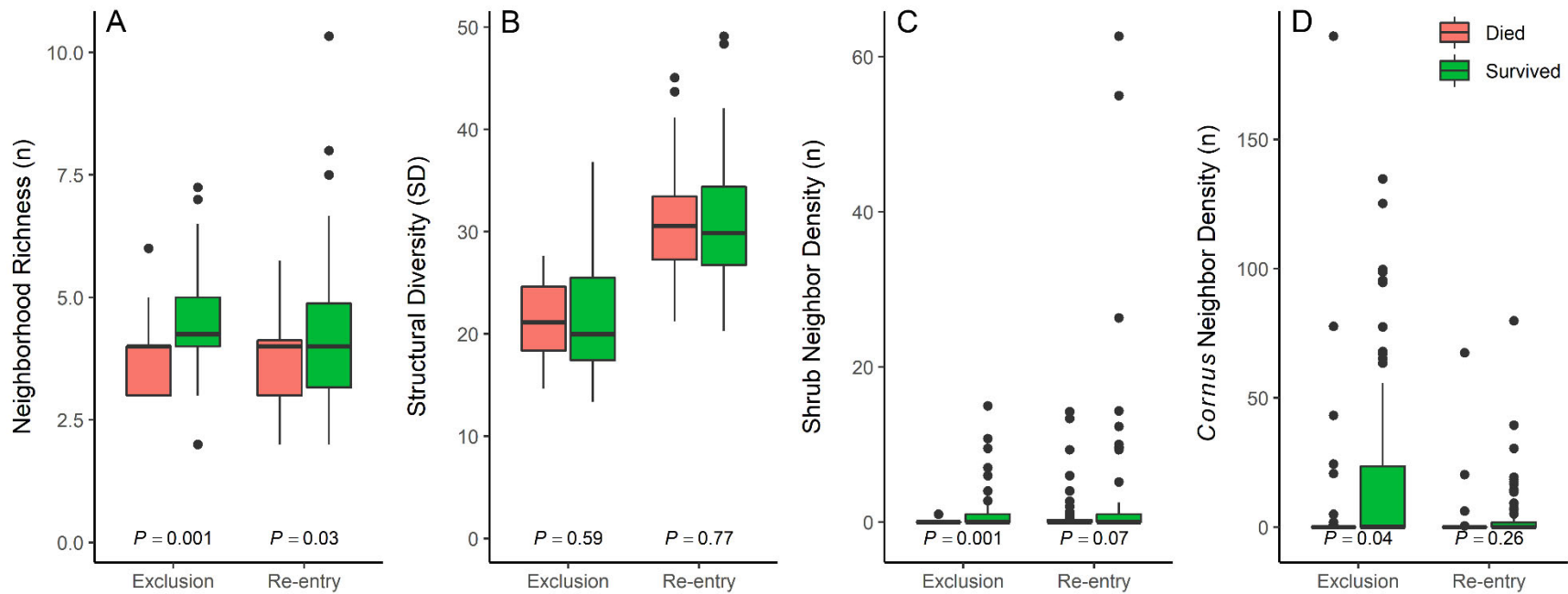
**Figure C.4.** Balance of growth and defense during subsets of the period of fire exclusion. At no time did growth-defense relationships become as extremely positive as those observed for beetle-susceptible trees following fire re-entry. Growth-defense models involving the interaction between time period, growth, and survival showed considerable noise (conditional and marginal  $R^2$  both 1.7%). Nonetheless, growth-period-survival interactions were highly significant predictors of duct area, showing that positive growth-defense relationships were only prevalent for susceptible trees during the post-fire period ( $P < 0.001$ ). Pre-fire models including drought also had low accuracy (conditional  $R^2 = 0.7\%$ ; marginal  $R^2 = 3.7\%$ ; not shown), and all G-D relationships were neutral. Post-fire models incorporating fire damage were the most accurate (conditional  $R^2 = 14.7\%$ ; marginal  $R^2 = 24.3\%$ ; not shown), but fire did not explain variability in growth-defense relationships between resistant and susceptible trees; in fact, susceptible trees with low fire damage showed even more extremely positive G-D relationships, while fire damage did not change resistant trees' G-D responses.



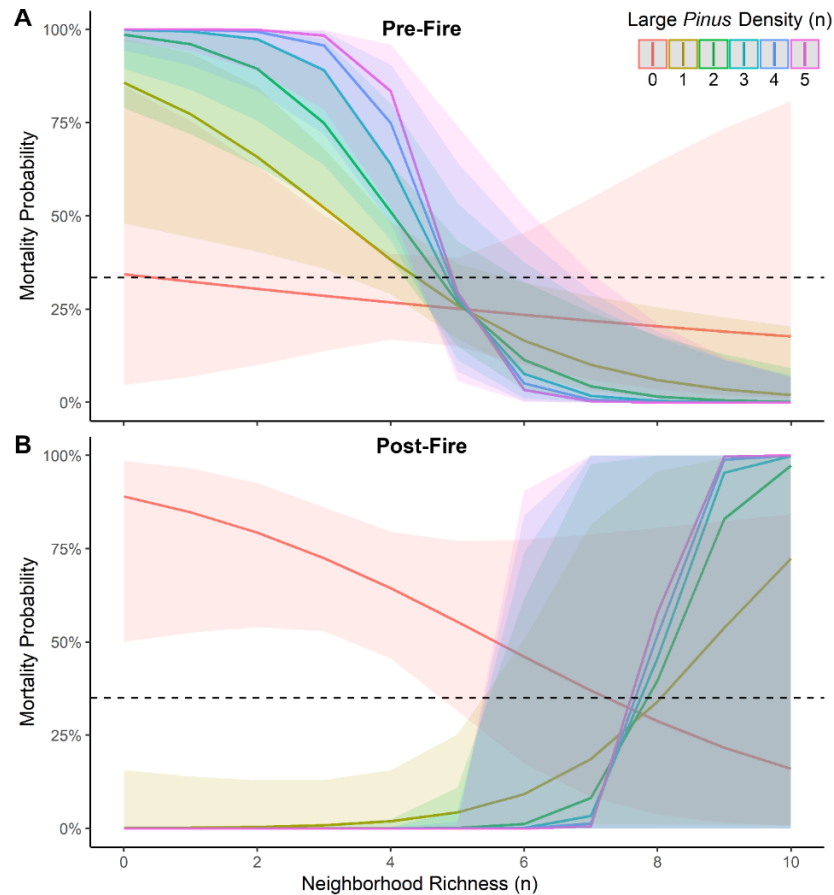
**Figure C.5.** Nearest distance to neighboring large-diameter live *Pinus* or bark beetle-killed *Pinus* (A) and total *Pinus* basal area within a 10-m radius (B) for trees that either died or survived beetle attack following fire re-entry in 2013. Surviving trees had further distances from both live and dead *Pinus*. Total *Pinus* basal area was similar for dead and surviving trees, but surviving trees had a smaller neighboring basal area of beetle-killed *Pinus* following fire. Basal area of beetle-kill within 10-m is a representation of the number of beetles emerging from those trees, as larger areas indicate more phloem available for successful beetle reproduction. Surviving trees were therefore exposed to smaller local populations of bark beetles emerging from killed trees.



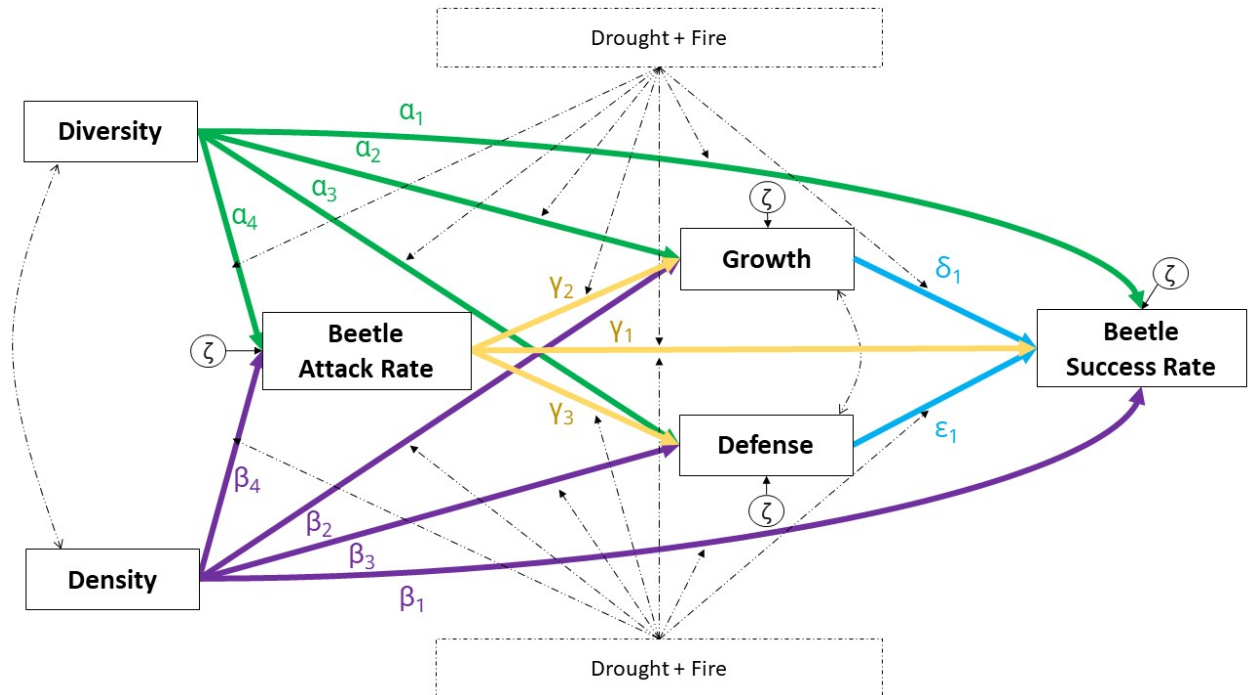
**Figure C.6.** Negative neighborhood characteristics within a 10-m radius of live and dead trees during the time periods: exclusion (no fires; 1900-2013), and re-entry (following first re-entry fire; 2014-2019). Trees that would eventually be killed by bark beetles following first re-entry fire had higher neighborhood basal area pre-fire (A), higher neighborhood density pre- and post-fire (B), higher large-diameter live *Pinus* density pre-fire (C), and higher small-diameter live *Abies* density pre- and post-fire (D) than those that survived. Total neighborhood metrics include all woody stems with DBH  $\geq 1$  cm. Large-diameter *Pinus* had DBH  $\geq 60$  cm, and small-diameter *Abies* had  $1 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$ . The 10-m radius was chosen through preliminary Random forests tests.



**Figure C.7.** Positive neighborhood characteristics within a 30-m radius of live and dead trees during the time periods: exclusion (no fires; 1900-2013), and re-entry (following first re-entry fire; 2014-2019). Trees that would eventually be killed by bark beetles following first re-entry fire had lower neighborhood richness pre- and post-fire (A), lower shrub neighborhood density pre-fire (B), and lower *Cornus* density pre-fire (C) than those that survived. The two groups did not differ in structural diversity (B; i.e., the standard deviation of all neighbors' DBH). Richness was the number of woody species, including both trees and shrubs.



**Figure C.8.** Interaction between large neighboring *Pinus* density within 10 m and neighborhood richness within 30 m in pre-fire (A) and post-fire (B) management-oriented models. Before fire re-entry, large neighboring conspecifics were associated with increased survival of the largest *Pinus* when high richness was present ( $\geq 5$  species). After fire re-entry, the opposite was true: large neighboring conspecifics were associated with increased survival only when low to moderate richness was present ( $\leq 7$  species). Horizontal dotted lines represent the classification threshold that optimized model sensitivity and specificity, above which trees were classified as dead. Before fire re-entry, large neighboring conspecifics were associated with increased survival of the largest *Pinus* when high richness was present ( $\geq 5$  species). After fire re-entry, large neighboring conspecifics were associated with increased survival only when low to moderate richness was present ( $\leq 7$  species). This opposing interaction catalyzed by fire likely represents the different effects of large conspecific neighbors and species richness pre- and post-fire. Richness pre-fire ranged from 2 to 8 species, perhaps indicating increased suppression of the harmful *Abies* neighbors. After fire, however, richness ranged from 2 to 13 species, likely representing an influx of strongly competitive fire-responding species that were not present prior to the fire. Meanwhile, large conspecific neighbors were likely strong competitors pre-fire, but not strong accumulators of bark beetles (low bark beetle activity pre-fire). In this case, increasing richness could offset competitive effects. Post-fire, large conspecifics became sources of insipient-epidemic level bark beetle activity. An explicit bark beetle term in the post-fire model accounted for this elevated accumulator effect.



**Figure C.9.** Multilevel moderated mediation structural equation model testing the mechanisms underpinning beetle attack/success and tree constitutive/induced defenses in a compound disturbance environment. Paths represent hypothesized causal relationships. Beetle success rate is measured as *Pinus* survival or mortality due to bark beetles. Beetle attack rate is approximated by total beetle-killed *Pinus* BA within a 10-m radius. Density is *Abies concolor* within 10-m radius, and diversity is species richness within a 30-m radius. Dashed lines connecting two factors indicate a covariance. Dashed lines connecting a factor to a path (i.e., drought and fire effects) indicate a moderation interaction. Drought and fire moderated paths independently from one another, though this is not depicted in the figure for aesthetic parsimony. Within-tree variability (level 1) was sampled by growth, defense, and drought over time; between-tree variability (level 2) was sampled by all other factors. Thus, all mediated (i.e., indirect) relationships are represented as cross-level interactions.

APPENDIX D  
SUPPLEMENTARY MATERIAL FOR CHAPTER V:  
SHARED FRIENDS COUNTERBALANCE SHARED ENEMIES  
IN OLD FORESTS

**SUPPLEMENTAL METHODS**

Pathology exam methodology was adapted and expanded from tree pathology protocols developed by the USGS (*sensu* Das et al. 2016) and the Pacific Northwest Permanent Sample Plot Program (*sensu* Lutz and Halpern 2006). Mortality data and categories are compatible with the categories used by the USGS and the Pacific Northwest Permanent Sample Plot networks (Appendix D: Section S1). During each annual census, we revisited every stem  $\geq 1$  cm DBH present in the three forest dynamics plots to assess survival or mortality. Upon approach to each tree, we conducted an initial, visual inspection of the crown and stem for evidence of possible mortality causes and predisposing stress factors, including: top dieback (often signifying drought stress or root fungi); flattened top (often signifying light competition from taller trees); mechanical damage (e.g., stem breakage, broken top, crushing, frost damage, uprooting, stripped bark or branches); fire damage (e.g., cat face, bole scorch, fire callus); fungal fruiting bodies or mycelia (identified to species; e.g., brown felt blight); cankers or galls (e.g., spruce gall adelgids); witch's brooms, mistletoe, or broom rust; bark sloughing (if in treetops, we inspected with binoculars to identify exposed beetle galleries, if present); animal damage or herbivory (e.g., woodpecker, elk, porcupine); leaf chlorosis, necrosis, or malformations (particularly on deciduous trees); dead leaf retention (particularly on conifers: presence of dead, reddened needles post-mortem indicate rapid death, often by



bark beetles, while no needles may indicate a slower death, often by fungal pathogens); pitch tubes; insect entry and exit holes or frass; and any other physical abnormalities or pertinent environmental context (e.g., growing on nurse log or in a stream). All observations from initial inspections were documented for both live and dead trees (Table D.3; also in field exam sheet found on Page 9 of Supporting Information for Furniss et al. 2020).

If no photosynthetic tissues were observed during the initial inspection (e.g., live leaves, active photosynthetic bark on some angiosperms), we declared mortality and initiated a detailed pathology exam. First, we removed a window of bark near breast height with a hatchet to examine sapwood and phloem condition for staining, rotten wood, mycelia, and beetle activity (bark beetles, engravers, ambrosia beetles, or wood borers). If entry/exit holes, frass, or pitch tubes were observed on the tree exterior, these sections were targeted for bark removal. If beetles were found, we identified them to species in the field or made collections for future identification; if only galleries were present, these were identified to bark beetle species based on the configuration of maternal and larval galleries (Fig. D.6). Second, we removed a window of bark at the base of the tree at or just below the soil surface to assess roots and the root collar for staining, rotten wood, mycelia, and other insect activity (e.g., carpenter ants). For example, the most common fungal pathogen, *Armillaria ostoyae* (Romagnesi) Herink (i.e. parasitic fungi attacking live cambium and phloem cells) was identified by presence of a thick, odiferous mycelial fan and/or rhizomorphs (Fig. D.7). Multiple windows were often removed from 0 to 2 meters above ground level in the search for evidence of multiple mortality factors. For dead trees that had recently experienced fire, removal of

bark along the entire tree root collar allowed assessment of the proportion of cambium killed by fire.

We noted the condition of the roots and stem (intact, partially ruptured, or fully disconnected) and measured the post-mortality dimensional properties of the tree (diameter, height, top diameter, percent of tree crown remaining, percent of tree height remaining, and any lean). We also noted the proportion of a fallen tree that was supported above the ground or resting directly on the ground. If the tree was uprooted or the stem broken, we dug into the exposed wood to look for saprophytic fungal activity (i.e. decay fungi attacking dead xylem cells; Fig. D.7). If rotten wood was present, the causal fungal agent was identified to species when possible based on rot characteristics (white vs. brown rot; stringy or spongy vs. cubical or crumbly; delamination or pitting), rot location (sapwood or heartwood; upper or lower stem; roots or root crown), other identifying characteristics (e.g., manganese deposits), and fruiting bodies when present. Whether the rot was the cause of breakage or invaded the wood post-mortem was determined *in-situ*. For example, the most common root rot, *Phellinus weirii* (Murr.) Gilb., was identified in uprooted trees with delaminated root sapwood that, when advanced, was stringy and whiteish in color without black manganese deposits.

Evidence provided by the initial inspection and the detailed pathology exam were consulted to determine mortality cause(s) and predisposing factors. Observations recorded in previous years were used to assist in final determinations. Trees often had more than one mortality cause (*sensu* Franklin et al. 1987), which were listed in order of estimated temporal importance (e.g., if *Armillaria* and bark beetles both present, *Armillaria* likely invaded first). Mortality factors – particularly when caused by biotic

agents – were considered distinct from predisposing factors (e.g., bole scorch; Table D.3). In the present study, we analyzed mortalities that involved at least one biotic agent, omitting those that died of mechanical crushing or direct fire damage alone (suppression by other trees was considered a biotic agent, here).

Because our protocols aim to minimize destructive sampling, there is likely some underreporting of certain agents – particularly root-feeding insects, saprophytic rot in snags (not uprooted or broken), or beetle activity in treetops that was not accompanied by sloughing bark and could therefore not be identified through binoculars (i.e. mortality caused by some *Ips* spp.). The mortality events analyzed here, however, showed pronounced evidence for at least one biotic mortality factor with high confidence (1% mortalities with undetected or unknown cause).

The annual sampling for mortality allows for correlation with climate events and also can resolve mortality agents that can also invade trees after death. As noted in Lutz (2015),

“For example, bark beetles (family Curculionidae, subfamily Scolytinae), an important disturbance agent in forests of western North America, both cause tree mortality and infest trees that have died from other causes. Although some species predominantly attack living trees (e.g. *Dendroctonus ponderosae* [Furniss and Carolin 1977]), some attack both living and newly dead trees (e.g., *Dendroctonus pseudotsugae* and *Scolytus ventralis* [Furniss and Carolin 1977]). The difference between a post-mortality bark beetle infestation and a bark beetle-caused mortality can be readily determined early in the season following mortality, but the timing of the creation of the beetle galleries will be obscured after two years. Similarly, common pathogenic fungi such as *Armillaria* spp. are facultative necrotrophs (Baumgartner et al. 2011). They colonize living tissue, but continue to spread following the death of the host.

With rates of spread from 0.7 to 1.3 m yr<sup>-1</sup> (Peet et al. 1996), an infection that is not severe enough to contribute materially to tree mortality could be misinterpreted as a factor associated with death if observed five years after tree death.”

## SUPPLEMENTAL DISCUSSION

### Dual Colonization

Plants able to form both AM and EM connections pose a unique challenge in research using mycorrhizal guilds as a proxy for underlying network connections. For example, we anticipated that the dual-hosting nature of *Populus tremuloides* Michaux (the primary dual-colonized species in our dataset; Cedar Breaks) may render different survival effects than EM-only species, and our sensitivity analyses confirmed that it was inappropriate to consider *Populus* EM or AM alone. Some studies have found what appear to be ontogenetic shifts, with AM more common in *Populus* seedlings and EM more common in mature adults (Malloch and Malloch 1981, Brundrett et al. 1990, Paul and Clark 1996). If ontogenetic shifts were occurring in Cedar Breaks, AM connections on *Populus* are unlikely to have been a prevailing dynamic in our dataset. Prior research has shown that the majority of *Populus* stems at Cedar Breaks belong to several clones rather than being a product of individual sexual reproduction events (Bishop et al. 2019). The genets and their ramets are quite old, and it is thus likely that most of the stems have transitioned to EM-dominance (Malloch and Malloch 1981). More recently, however, *Populus* has been shown to be simultaneously dual-colonized, with AM and EM stratified vertically in the soil profile and along moisture gradients (Lodge 1989, Neville et al. 2002). This form of connection may allow *Populus* to colonize both AM and EM

neighbors, potentially transferring resources between these two otherwise distinct networks. If this were instead the case in Cedar Breaks, our consideration of *Populus* as a separate dual-hosting guild would lead to a more conservative estimate of plant-soil feedbacks, as it is categorized a guild-disparate neighbor of AM and EM shrubs and trees alike. Though dual-hosting species present challenges that may be clarified through direct sampling of mycorrhizae, we addressed this limitation to the extent allowed by our dataset with the sensitivity analyses and conservative presentation of results.

#### AM vs. EM in Large Trees

Positive mycorrhizal effects were most evident for large EM trees. This finding supports prior study showing size-asymmetric facilitation (i.e. small trees clustered near large-diameter trees) among EM, but not AM, tree species (Johnson et al. 2018). AM trees tolerated high levels of guild-disparate crowding as long as richness remained low, while richness of guild-sharing neighbors maximized EM tree survival even at high crowding levels. As opposed to some forests where recruitment and mortality can be more balanced, particularly in tropical regions, that is not the case in our three mixed-conifer temperate forests. For example, *Thuja plicata* (WFDP AM species) has exceptionally low mortality, but is recruitment-limited; *Thuja* dynamics contribute substantially to our large-diameter AM tree sample. Consequently, it is important to note that low mortality of large-diameter AM trees, combined with lower frequency of AM trees as a whole, likely decrease our ability to detect mycorrhizal effects if they do exist. Likewise, detrimental effects of guild-disparate richness to AM survival (Fig. D.5) could simply reflect forest spatial patterns, as large, rare AM trees tend to be surrounded by guild-disparate heterospecifics (i.e. large-diameter Pinaceae) as a simple function of

frequency asymmetry.

### Phylogenetic Similarity

We cannot rule out the possibility that our analysis captured differences between guild-sharing and guild-disparate neighborhoods stemming from other phylogenetically conserved traits that are confounded with mycorrhizal guild (Kunstler et al. 2012, Lebrija-Trejos et al. 2014). However, more closely related individuals often experience stronger competition (Lebrija-Trejos et al. 2014, Chen et al. 2018), meaning we should expect that crowding by more phylogenetically similar species would reduce survival, not increase it. Regardless, functional similarity among more distantly related plants, not phylogenetic similarity, is a stronger driver of plant-plant interactions in these forests (Kunstler et al. 2012): the three western forests tested here do not show strong phylogenetic clustering, neither in terms of habitat specificity (Erickson et al. 2014, Furniss et al. 2017, Das et al. 2018) nor density dependence (Furniss et al. 2020, Wills et al. 2021). For example, the closely related *Abies bifolia* and *Pinus longaeva* (both EM) have less niche overlap than the more distantly related *Abies bifolia* and *Populus tremuloides* (EM and AM, respectively; Furniss et al. 2017). Conversely, the very phylogenetically dissimilar *Acer circinatum* and *Taxus brevifolia* are both AM and share a similar mesic understory niche. These factors support our interpretation that the simplest explanation for survival benefits shown here is through shared mycorrhizae rather than unmeasured traits of phylogenetic relatedness.

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## SUPPLEMENTAL TABLES AND FIGURES

**Table D.1.** All stems present in Wind River, WA (WFDP), Yosemite, CA (YFDP), and Cedar Breaks, UT (UFDP) were included in crowding calculations. Trees were defined as species with singular stems that do not rely on vegetative regeneration; shrubs were defined as multi-stemmed species and/or those capable of vegetative regeneration. Mycorrhizal guilds included arbuscular mycorrhizal (AM), ectomycorrhizal (EM), ericoid mycorrhizal (ErM), and species capable of forming both AM and EM (AM/EM). Trace basal area ( $t$ ) was  $< 0.1 \text{ m}^2$ . Mycorrhizal guild designated at the plant family level unless otherwise specified (where \* represents genus level; † represents species level). See Appendix D: Section S2 for guild citations.

Family	Genus	Species	Guild	Plot	Individuals (n)	Basal Area (m <sup>2</sup> )	Guild Citation
<b><u>Tree</u></b>							
Cupressaceae	<i>Calocedrus</i>	<i>decurrens</i>	AM	YFDP	1661	126.0	1
Cupressaceae	<i>Juniperus</i>	<i>scopulorum</i>	AM	UFDP	3	0.1	1
Cupressaceae	<i>Thuja</i>	<i>plicata</i>	AM	WFDP	238	130.4	1
Pinaceae	<i>Abies</i>	<i>amabilis</i>	EM	WFDP	5186	61.0	1,2
Pinaceae	<i>Abies</i>	<i>bifolia</i>	EM	UFDP	20384	195.6	1,2
Pinaceae	<i>Abies</i>	<i>concolor</i>	EM	YFDP, UFDP	25276	835.2	1,2
Pinaceae	<i>Abies</i>	<i>grandis</i>	EM	WFDP	74	8.5	1,2
Pinaceae	<i>Abies</i>	<i>magnifica</i>	EM	YFDP	9	0.7	1,2
Pinaceae	<i>Abies</i>	<i>procera</i>	EM	WFDP	16	6.7	1,2
Pinaceae	<i>Picea</i>	<i>engelmannii</i>	EM*	UFDP	1330	28.2	1,2
Pinaceae	<i>Picea</i>	<i>pungens</i>	EM*	UFDP	430	29.7	1,2
Pinaceae	<i>Pinus</i>	<i>edulis</i>	EM*	UFDP	8	$t$	1,2
Pinaceae	<i>Pinus</i>	<i>flexilis</i>	EM*	UFDP	1039	49.4	1,2
Pinaceae	<i>Pinus</i>	<i>lambertiana</i>	EM†	YFDP	4942	774.0	1,2
Pinaceae	<i>Pinus</i>	<i>longaeva</i>	EM*	UFDP	784	93.6	1,2
Pinaceae	<i>Pinus</i>	<i>monticola</i>	EM*	WFDP	8	3.9	1,2
Pinaceae	<i>Pinus</i>	<i>ponderosa</i>	EM†	YFDP, UFDP	3	0.4	1,2
Pinaceae	<i>Pseudotsuga</i>	<i>menziesii</i> ssp. <i>glauca</i>	EM†	UFDP	34	2.0	1,2
Pinaceae	<i>Pseudotsuga</i>	<i>menziesii</i> ssp. <i>menziesii</i>	EM†	YFDP, WFDP	626	$t$	1,2
Pinaceae	<i>Tsuga</i>	<i>heterophylla</i>	EM	WFDP	11212	965.2	1,2
Taxaceae	<i>Taxus</i>	<i>brevifolia</i>	AM*	WFDP	2183	46.3	3,4

Table D.1. Continued.

Family	Genus	Species	Guild	Plot	Individuals (n)	Basal Area (m <sup>2</sup> )	Guild Citation
<b><u>Shrub</u></b>							
Adoxaceae	<i>Sambucus</i>	<i>nigra</i> ssp. <i>caerulea</i>	AM*	YFDP	46	<i>t</i>	4,5
Adoxaceae	<i>Sambucus</i>	<i>racemosa</i>	AM*	UFDP	3	<i>t</i>	4,5
Betulaceae	<i>Alnus</i>	<i>rubra</i>	AM/EM <sup>†</sup>	WFDP	10	0.2	3,6,7
Betulaceae	<i>Corylus</i>	<i>cornuta</i> ssp. <i>californica</i>	EM*	YFDP, WFDP	1193	0.4	3,4
Cornaceae	<i>Cornus</i>	<i>nuttallii</i>	AM*	YFDP, WFDP	3340	8.5	3,4
Cornaceae	<i>Cornus</i>	<i>sericea</i>	AM*	YFDP	279	0.1	3,4
Cupressaceae	<i>Juniperus</i>	<i>communis</i>	AM	UFDP	187	<i>t</i>	1
Ericaceae	<i>Arcostaphylos</i>	<i>patula</i>	ErM*	YFDP	85	0.1	3
Ericaceae	<i>Gaultheria</i>	<i>shallon</i>	ErM*	WFDP	18	<i>t</i>	3,8
Ericaceae	<i>Menziesia</i>	<i>ferruginea</i>	ErM	WFDP	20	<i>t</i>	3
Ericaceae	<i>Rhododendron</i>	<i>macrophyllum</i>	ErM*	WFDP	543	0.3	3,4
Ericaceae	<i>Rhododendron</i>	<i>occidentale</i>	ErM*	YFDP	7	<i>t</i>	3,4
Ericaceae	<i>Vaccinium</i>	<i>ovalifolium</i>	ErM*	WFDP	101	<i>t</i>	3,4
Ericaceae	<i>Vaccinium</i>	<i>parvifolium</i>	ErM*	WFDP	1692	0.3	3,4
Fagaceae	<i>Chrysolepis</i>	<i>sempervirens</i>	EM*	YFDP	36	<i>t</i>	1,3
Fagaceae	<i>Quercus</i>	<i>kelloggii</i>	EM*	YFDP	2157	30.9	1,3
Grossulariaceae	<i>Ribes</i>	<i>cereum</i>	AM*	UFDP	90	<i>t</i>	4
Grossulariaceae	<i>Ribes</i>	<i>montigenum</i>	AM*	UFDP	1	<i>t</i>	4
Grossulariaceae	<i>Ribes</i>	<i>nevadense</i>	AM*	YFDP	1	<i>t</i>	4
Rhamnaceae	<i>Ceanothus</i>	<i>cordulatus</i>	AM*	YFDP	2	<i>t</i>	3,9
Rhamnaceae	<i>Ceanothus</i>	<i>integerrimus</i>	AM*	YFDP	15	<i>t</i>	3,9
Rhamnaceae	<i>Ceanothus</i>	<i>parvifolius</i>	AM*	YFDP	3	<i>t</i>	3,9
Rhamnaceae	<i>Frangula</i>	<i>californica</i>	AM*	YFDP	19	<i>t</i>	3,10
Rhamnaceae	<i>Frangula</i>	<i>purshiana</i>	AM*	WFDP	1	<i>t</i>	3,10

Table D.1. Continued.

Family	Genus	Species	Guild	Plot	Individuals (n)	Basal Area (m <sup>2</sup> )	Guild Citation
<b><u>Shrub</u></b>							
Rosaceae	<i>Amelanchier</i>	<i>alnifolia</i>	AM*	WFDP, UFDP	12	<i>t</i>	8,10-12
Rosaceae	<i>Cercocarpus</i>	<i>ledifolius</i>	AM/EM*	UFDP	9	<i>t</i>	2,3,12
Rosaceae	<i>Holodiscus</i>	<i>discolor</i>	AM*	WFDP	31	<i>t</i>	2,12
Rosaceae	<i>Oemleria</i>	<i>cerasiformis</i>	AM	WFDP	2	<i>t</i>	1,4
Rosaceae	<i>Prunus</i>	<i>emarginata</i>	AM*	YFDP	117	<i>t</i>	1,4,10
Rosaceae	<i>Rosa</i>	<i>gymnocarpa</i>	AM*	WFDP	1	<i>t</i>	1,4,10
Rosaceae	<i>Rubus</i>	<i>leucodermis</i>	AM*	WFDP	1	<i>t</i>	1,4,10
Rosaceae	<i>Rubus</i>	<i>spectabilis</i>	AM*	WFDP	5	<i>t</i>	1,4,10
Salicaceae	<i>Populus</i>	<i>tremuloides</i>	AM/EM†	UFDP	3143	101.6	4,8,13
Salicaceae	<i>Salix</i>	<i>scouleriana</i>	AM/EM*	YFDP	14	<i>t</i>	3,4
Sapindaceae	<i>Acer</i>	<i>circinatum</i>	AM*	WFDP	12465	16.7	1
Sapindaceae	<i>Acer</i>	<i>glabrum</i>	AM*	WFDP	1	<i>t</i>	1
<b>Total:</b>					<b>101,096</b>	<b>4059</b>	

**Table D.2.** Model validation results of Sensitivity Analysis 1 (area under curve, AUC; deviance information criterion, DIC). Models were built using factorial combinations of mycorrhizal guild designation, woody plant diameter, neighborhood radius, and density metric. Higher AUC and lower DIC indicate superior models.

Species	DBH	Radius	Guild Designations	Crowding		Density	
				AUC	DIC	AUC	DIC
All	Large	5	ErM + AM/EM + AM + EM	69.2%	3963.1	68.9%	3969.4
			ErM + AM + EM	69.3%	3961.9	68.9%	3968.5
			AM/EM + AM + EM	69.1%	3965.9	68.8%	3973.0
			AM + EM	69.2%	3964.6	68.8%	3972.2
		10	ErM + AM/EM + AM + EM	69.7%	3814.6	69.0%	3837.6
			ErM + AM + EM	69.7%	3817.2	69.0%	3837.2
			AM/EM + AM + EM	69.2%	3820.1	68.8%	3839.9
			AM + EM	69.1%	3821.1	68.9%	3837.7
		15	ErM + AM/EM + AM + EM	69.4%	3682.7	68.3%	3706.7
			ErM + AM + EM	69.2%	3687.8	68.4%	3708.7
			AM/EM + AM + EM	69.0%	3685.7	68.2%	3704.6
			AM + EM	69.0%	3687.9	68.2%	3705.1
	20	ErM + AM/EM + AM + EM	69.2%	3565.7	68.0%	3583.8	
		ErM + AM + EM	69.2%	3567.0	68.1%	3583.8	
		AM/EM + AM + EM	68.9%	3567.2	68.3%	3577.3	
		AM + EM	68.9%	3568.1	68.2%	3580.0	
	Small	5	ErM + AM/EM + AM + EM	80.2%	5282.0	79.4%	5319.3
			ErM + AM + EM	79.8%	5288.5	79.0%	5330.7
			AM/EM + AM + EM	80.4%	5278.8	79.7%	5313.3
			AM + EM	80.0%	5287.5	79.3%	5327.6
		10	ErM + AM/EM + AM + EM	79.5%	5024.1	78.4%	5064.9
			ErM + AM + EM	79.3%	5026.4	78.2%	5066.5
			AM/EM + AM + EM	79.6%	5026.3	78.6%	5064.8
			AM + EM	79.3%	5034.5	78.3%	5073.7
15		ErM + AM/EM + AM + EM	79.8%	4748.8	78.9%	4789.8	
		ErM + AM + EM	79.6%	4749.1	78.8%	4783.7	
		AM/EM + AM + EM	79.9%	4754.6	79.1%	4794.6	
		AM + EM	79.6%	4763.3	78.9%	4796.8	
20	ErM + AM/EM + AM + EM	80.2%	4502.5	79.3%	4547.6		
	ErM + AM + EM	79.9%	4509.9	79.2%	4543.5		
	AM/EM + AM + EM	80.3%	4504.0	79.5%	4550.0		
	AM + EM	80.0%	4519.7	79.2%	4554.0		
Tree	Large	5	ErM + AM/EM + AM + EM	72.3%	2542.7	72.1%	2544.5
			ErM + AM + EM	72.6%	2539.8	72.2%	2541.0
			AM/EM + AM + EM	72.3%	2542.8	72.1%	2544.5
			AM + EM	72.6%	2539.6	72.2%	2540.9
		10	ErM + AM/EM + AM + EM	72.2%	2436.4	72.3%	2444.5
			ErM + AM + EM	72.5%	2432.6	72.4%	2439.5
	15	10	AM/EM + AM + EM	72.2%	2436.4	72.3%	2444.8
			AM + EM	72.5%	2432.5	72.4%	2439.7
		15	ErM + AM/EM + AM + EM	72.3%	2356.8	72.2%	2362.1
			ErM + AM + EM	72.8%	2350.1	72.6%	2355.3
			AM/EM + AM + EM	72.3%	2357.0	72.2%	2362.2
			AM + EM	72.8%	2350.4	72.6%	2355.4
20	ErM + AM/EM + AM + EM	72.1%	2268.9	72.3%	2272.3		
	ErM + AM + EM	72.2%	2267.1	72.2%	2272.9		
	AM/EM + AM + EM	72.1%	2268.9	72.3%	2272.3		
	AM + EM	72.2%	2267.2	72.2%	2273.4		

Table D.2. Continued.

Species	DBH	Radius	Guild Designations	Crowding		Density		
				AUC	DIC	AUC	DIC	
Tree	Small	5	ErM + AM/EM + AM + EM	89.2%	2800.2	88.0%	2870.3	
			ErM + AM + EM	89.1%	2802.0	88.0%	2873.6	
			AM/EM + AM + EM	89.2%	2800.3	88.0%	2870.4	
			AM + EM	89.1%	2802.1	88.0%	2873.5	
		10	ErM + AM/EM + AM + EM	89.4%	2576.1	87.6%	2665.7	
			ErM + AM + EM	89.4%	2576.9	87.6%	2665.4	
			AM/EM + AM + EM	89.4%	2575.9	87.6%	2665.6	
			AM + EM	89.4%	2576.7	87.6%	2665.4	
		15	ErM + AM/EM + AM + EM	89.5%	2451.0	87.9%	2538.3	
			ErM + AM + EM	89.4%	2455.1	87.8%	2541.1	
			AM/EM + AM + EM	89.5%	2450.7	87.9%	2538.0	
			AM + EM	89.4%	2455.4	87.8%	2541.1	
	20	ErM + AM/EM + AM + EM	89.9%	2288.3	88.3%	2380.1		
		ErM + AM + EM	89.9%	2292.6	88.3%	2380.6		
		AM/EM + AM + EM	89.9%	2288.3	88.3%	2380.4		
		AM + EM	89.9%	2292.5	88.3%	2380.6		
	Shrub	Large	5	ErM + AM/EM + AM + EM	66.6%	1367.2	67.2%	1360.9
				ErM + AM + EM	66.4%	1367.3	67.1%	1361.7
				AM/EM + AM + EM	66.6%	1365.5	66.9%	1359.8
				AM + EM	66.6%	1365.1	67.0%	1360.5
			10	ErM + AM/EM + AM + EM	66.0%	1335.7	67.7%	1326.7
				ErM + AM + EM	65.9%	1337.4	67.1%	1330.7
				AM/EM + AM + EM	66.1%	1337.8	67.5%	1327.2
				AM + EM	65.9%	1338.2	67.3%	1330.6
15			ErM + AM/EM + AM + EM	66.6%	1281.0	67.7%	1274.5	
			ErM + AM + EM	66.1%	1283.6	67.5%	1276.2	
			AM/EM + AM + EM	66.0%	1284.2	67.3%	1275.6	
			AM + EM	65.8%	1285.4	67.2%	1279.2	
20		ErM + AM/EM + AM + EM	66.8%	1250.5	67.0%	1249.5		
		ErM + AM + EM	66.7%	1250.9	66.5%	1251.1		
		AM/EM + AM + EM	66.8%	1251.8	67.0%	1249.2		
		AM + EM	66.2%	1252.2	67.1%	1249.8		
Small		5	ErM + AM/EM + AM + EM	63.2%	2026.5	61.7%	2027.4	
			ErM + AM + EM	62.9%	2024.4	61.4%	2028.6	
			AM/EM + AM + EM	64.5%	2022.0	63.3%	2015.8	
			AM + EM	63.9%	2024.5	63.1%	2025.5	
		10	ErM + AM/EM + AM + EM	64.5%	1979.6	64.2%	1975.7	
			ErM + AM + EM	64.4%	1976.4	63.9%	1981.1	
			AM/EM + AM + EM	64.0%	1980.2	65.2%	1961.8	
			AM + EM	63.7%	1980.7	63.8%	1979.4	
	15	ErM + AM/EM + AM + EM	64.6%	1884.4	64.7%	1877.7		
		ErM + AM + EM	63.3%	1883.8	63.4%	1885.9		
		AM/EM + AM + EM	63.2%	1884.8	64.4%	1871.6		
		AM + EM	63.0%	1888.5	62.6%	1887.9		
20	ErM + AM/EM + AM + EM	64.5%	1821.1	65.8%	1806.2			
	ErM + AM + EM	63.5%	1821.2	64.2%	1819.9			
	AM/EM + AM + EM	63.8%	1824.2	65.5%	1802.6			
	AM + EM	63.4%	1830.0	64.1%	1824.8			

**Table D.3.** Biotic enemies and predisposing stressors recorded upon woody plant mortality. Pathology exams were performed for individuals that died on an annual basis, and multiple factors associated with mortality recorded. Predisposing factors were not considered the most proximate causes of death, but were recorded to provide further context for mortality. Fungal pathogens primarily attack live or active cells (cambium, phloem, active xylem); saprophytes attack inactive cells (dead cells, inactive xylem). Primary hosts were determined by sampled mortality events. For species-level mortality causes, see Fig. D.1. Asterix (\*) indicates an exotic enemy (mortality  $n = 1$ ).

Biotic Enemies	Primary Hosts
<u>Fungal Pathogens</u>	
<i>Armillaria ostoyae</i>	division generalist (gymnosperms + angiosperms)
<i>Cronartium ribicola</i> *	subsection specialist ( <i>Strobilus</i> pines)
<i>Cytospora chrysosperma</i>	species specialist ( <i>Populus tremuloides</i> )
<i>Grosmannia wagneri</i>	class generalist (gymnosperms)
<i>Encoelia pruinosa</i>	species specialist ( <i>Populus tremuloides</i> )
<i>Phellinus weirii</i>	class generalist (gymnosperms)
Blue stain fungi ( <i>Ceratocystis</i> spp., <i>Ophiostoma</i> spp.)	family generalist (Pinaceae)
Brown felt blight ( <i>Neopeckia coulteri</i> , <i>Herpotrichia juniperi</i> )	class generalist (gymnosperms)
Unidentified canker	species specialist ( <i>Acer circinatum</i> )
<u>Fungal Saprophytes</u>	
<i>Echinodontium tinctorium</i>	family generalist (Pinaceae)
<i>Fomitopsis pinicola</i>	class generalist (gymnosperms)
<i>Ganoderma applanatum</i>	division generalist (gymnosperms + angiosperms)
<i>Heterobasidion annosum</i>	class generalist (gymnosperms)
<i>Onnia tomentosa</i>	family generalist (Pinaceae)
<i>Phaeolus schweinitzii</i>	family generalist (Pinaceae)
<i>Peniophora polygonia</i>	species specialist ( <i>Populus tremuloides</i> )
<i>Phellinus pini</i>	family generalist (Pinaceae)
<i>Phellinus tremulae</i>	species specialist ( <i>Populus tremuloides</i> )

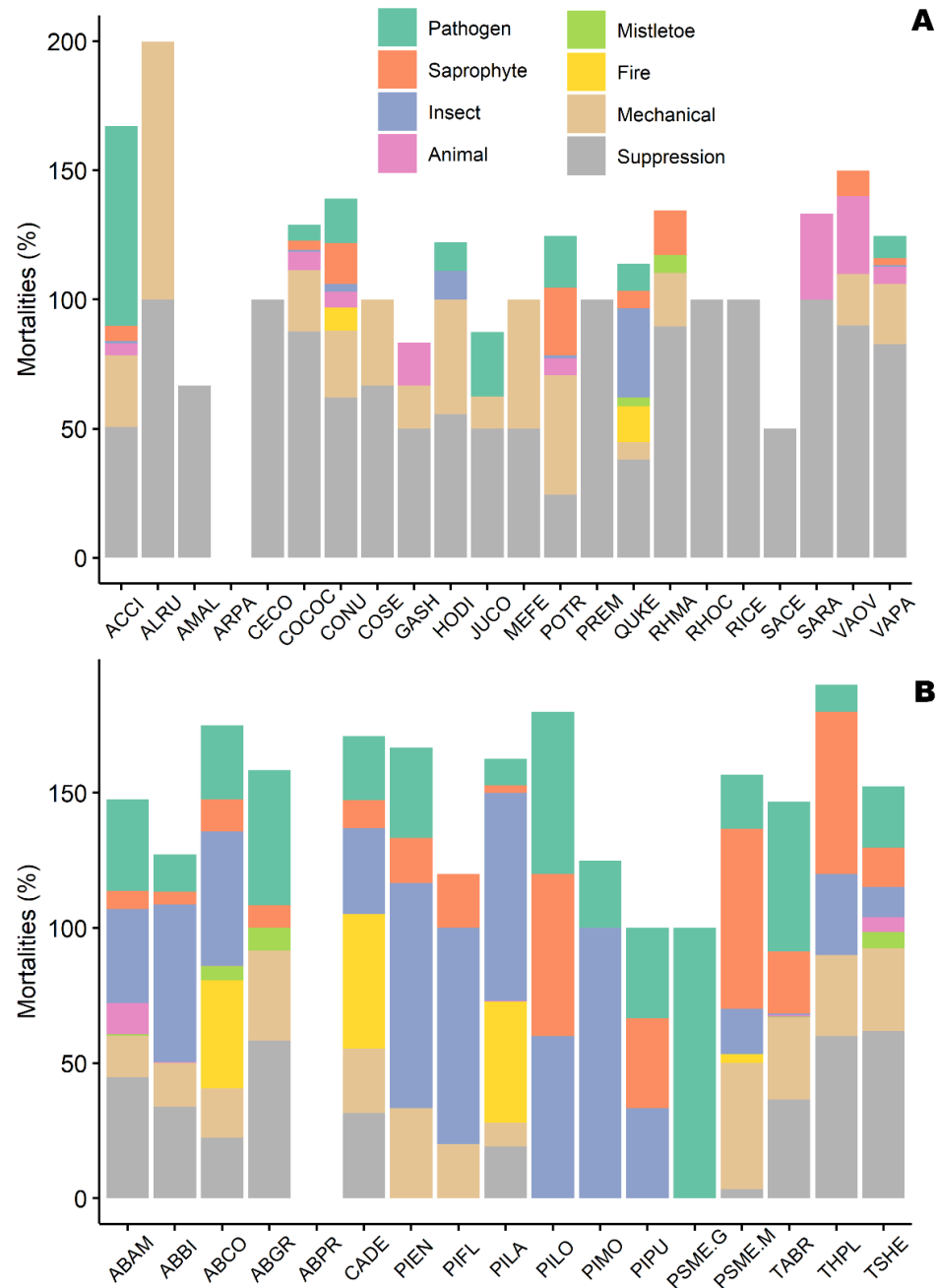
Table D.3. Continued.

Biotic Enemies	Primary Hosts
<u>Insects</u>	
<i>Dendroctonus brevicomis</i>	species specialist ( <i>Pinus ponderosa</i> )
<i>Dendroctonus ponderosae</i>	genus specialist ( <i>Pinus</i> spp.)
<i>Dendroctonus pseudotsugae</i>	species specialist ( <i>Pseudotsuga menziesii</i> )
<i>Dendroctonus rufipennis</i>	species specialist ( <i>Picea engelmannii</i> )
<i>Dendroctonus valens</i>	species*diameter specialist (large <i>Pinus lambertiana</i> )
<i>Dryocoetes confusus</i>	species specialist ( <i>Abies bifolia</i> )
<i>Ips paraconfusus</i>	species*diameter specialist (small <i>Pinus lambertiana</i> )
<i>Ips pini</i>	genus specialist ( <i>Pinus</i> spp.)
<i>Pityokteines</i> spp.	family generalist (Pinaceae)
<i>Phloeosinus</i> spp.	family generalist (Cupressaceae)
<i>Pseudopityophthorus pubipennis</i>	species specialist ( <i>Quercus kelloggii</i> )
<i>Scolytus subscaber</i>	genus*diameter specialist (small <i>Abies</i> spp.)
<i>Scolytus tsugae</i>	species specialist ( <i>Tsuga heterophylla</i> )
<i>Scolytus ventralis</i>	genus specialist ( <i>Abies</i> spp.)
Boring beetles (Buprestidae, Cerambicydae)	division generalist (gymnosperms + angiosperms)
Carpenter ants	class generalist (gymnosperms)
Termites	class generalist (gymnosperms)
<u>Animals</u>	
Deer	division generalist (gymnosperms + angiosperms)
Elk	division generalist (gymnosperms + angiosperms)
Sapsucker	division generalist (gymnosperms + angiosperms)
Woodpecker	division generalist (gymnosperms + angiosperms)

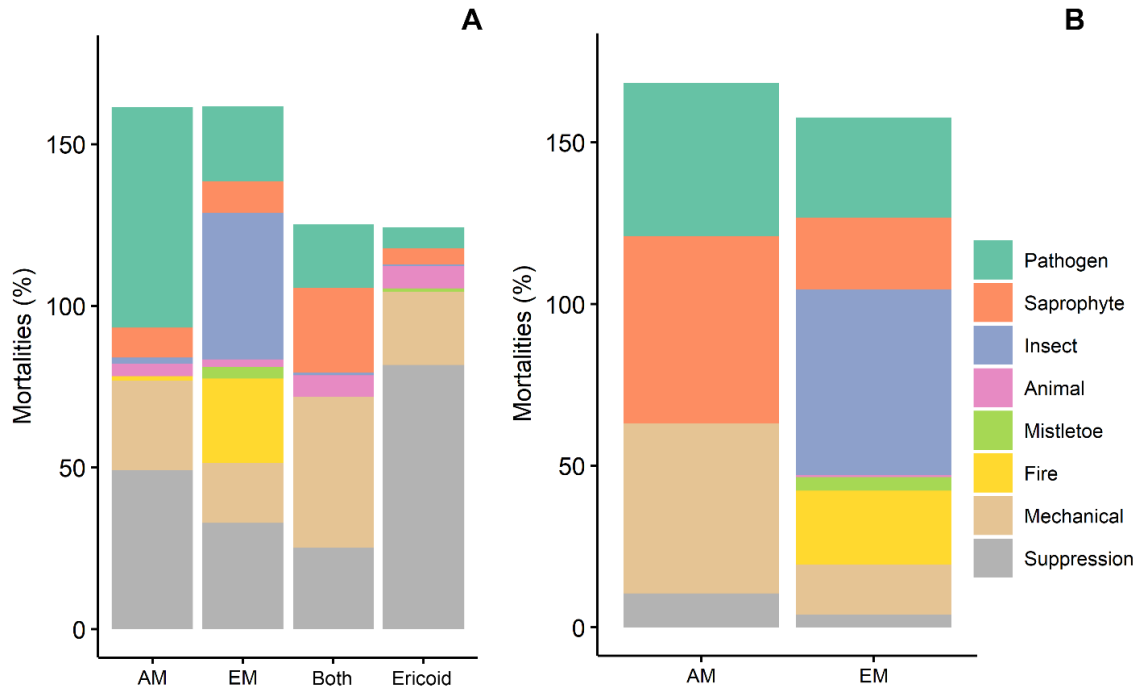
Table D.3. Continued.

Biotic Enemies	Primary Hosts
<u>Mistletoe</u> <i>Arceuthobium</i> spp. <i>Phoradendron</i> spp.	class generalist (gymnosperms) division generalist (gymnosperms + angiosperms)
Predisposing Stressors	
<u>Fire</u> Cambial heating Crown combustion Crown scorch Stem combustion Stem scorch	
<u>Mechanical</u> Crushing Windthrow Crown damage Stem breakage	
<u>Suppression</u> Flat crown Irregular or non-vertical growth	

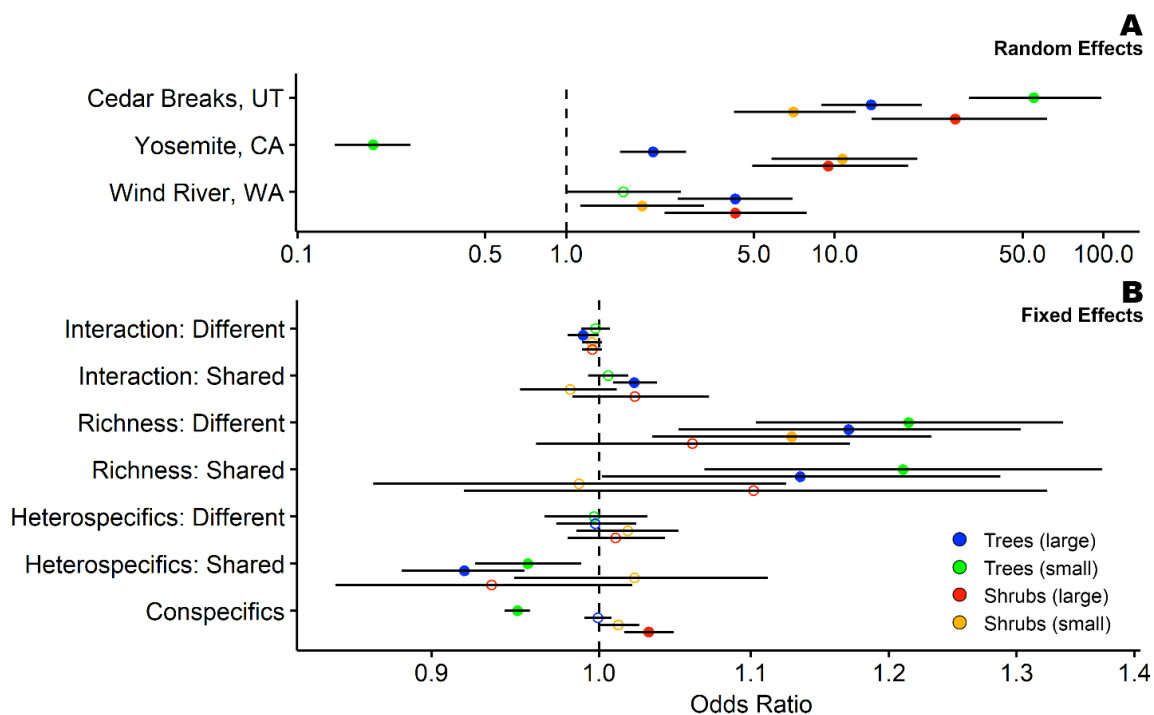




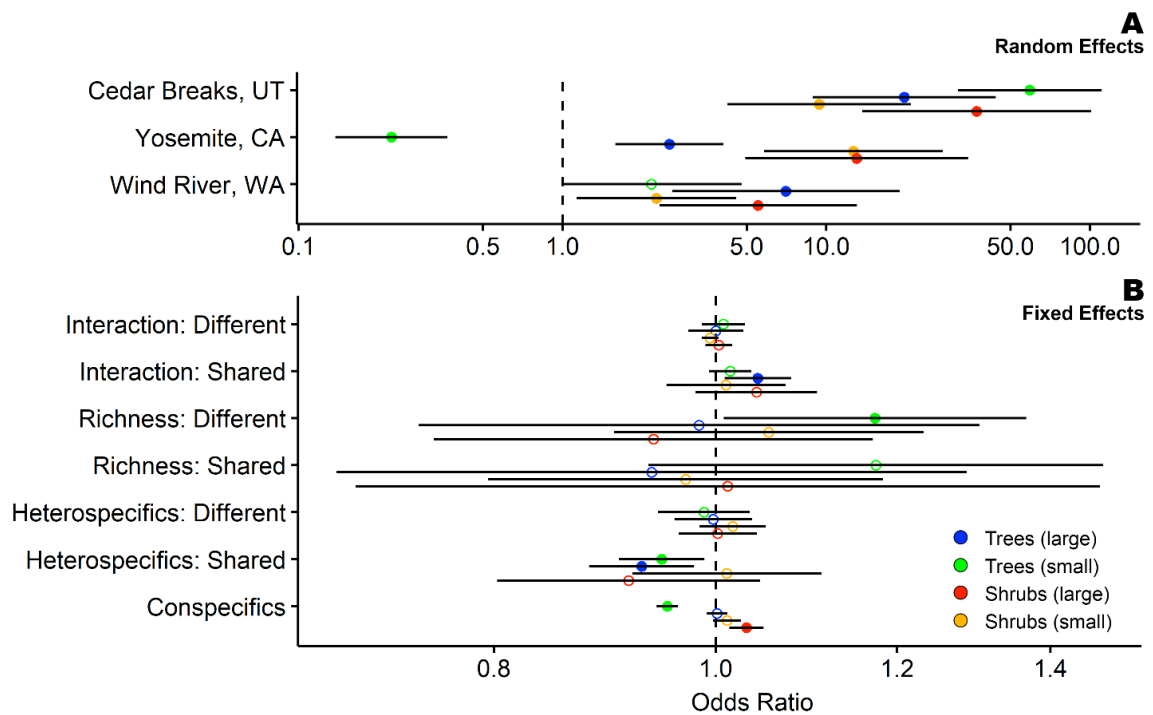
**Figure D.1.** Factors associated with mortality of all shrubs (A) and trees (B) across the three forest sites. Species names are four-letter codes *sensu* USDA nomenclature. Pathology exams were performed for newly dead individuals on an annual basis and multiple factors associated with mortality recorded (i.e. cumulative mortality > 100%; Table D.3). Predisposing factors were not considered the most proximate causes of death, but were recorded to provide further context for mortality. Species for which fire damage or crushing were the primary cause of mortality were omitted from analyses, so here, these processes represent predisposing factors only. *Abies procera* (ABPR) and *Arctostaphylos patula* (ARPA) mortality was rare and of unknown origin. For the mycorrhizal affiliations of each species, see Table D.1.



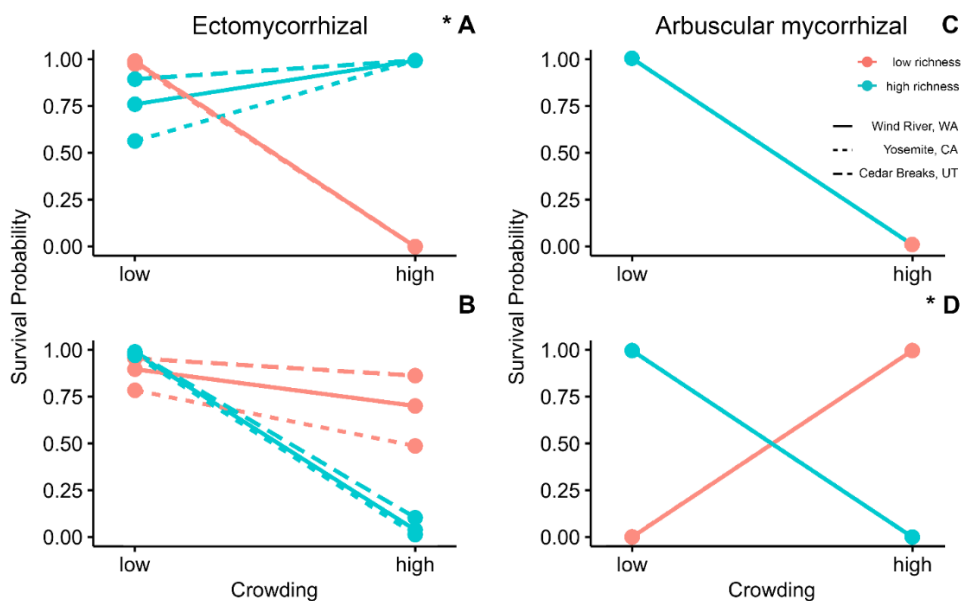
**Figure D.2.** Factors associated with mortality of all trees and shrubs (A) and of only large-diameter trees (B) categorized by mycorrhizal guild. Pathology exams were performed for newly dead individuals on an annual basis and multiple factors associated with mortality recorded (i.e. cumulative mortality > 100%; Table D.3). Predisposing factors were not considered the most proximate causes of death, but were recorded to provide further context for mortality. Species for which fire damage or crushing were the primary cause of mortality were omitted from analyses, so here, these processes represent predisposing factors only.



**Figure D.3.** Odds ratios for tree and shrub survival produced by final, chosen Bayesian hierarchical generalized linear models. Odds ratios  $>1$  indicate increased survival, and ratios  $<1$  indicate decreased survival. Small individuals were those with DBH  $\leq 10^{\text{th}}$  percentile per species, and large individuals had DBH  $\geq 90^{\text{th}}$  percentile per species. Points indicate the mean parameter estimate, and error bars capture the 95% credible intervals of each posterior distribution generated through a Gibbs sampler using Markov Chain Monte Carlo methods. Parameters have no detectable effect when 95% credible intervals overlap zero (hollow points).



**Figure D.4.** Sensitivity Analysis 2 of modeled odds ratios to neighborhood radius produced by Bayesian hierarchical generalized linear survival models. Neighborhood distances included 5-, 10-, 15-, and 20-m radii. Odds ratios  $>1$  indicate increased survival, and ratios  $<1$  indicate decreased survival. Small individuals were those with  $DBH \leq 10^{\text{th}}$  percentile per species, and large individuals had  $DBH \geq 90^{\text{th}}$  percentile per species. Points indicate the mean parameter estimate, and error bars capture the 95% credible intervals of each posterior distribution generated through a Gibbs sampler using Markov Chain Monte Carlo methods. Parameters have no detectable effect when 95% credible intervals overlap zero (hollow points). Mycorrhizal interactions (guild-sharing crowding and richness interactions) were detectable for large-diameter trees at all radii, as were conspecific effects for small trees and large shrubs (negative and positive, respectively).



**Figure D.5.** Interactions between heterospecific guild-sharing crowding and richness (A and C) and interactions between heterospecific guild-sharing crowding and richness (B and D) within a 20-m radius of ectomycorrhizal (A and B) or arbuscular mycorrhizal (C and D) large-diameter trees. Overlapping lines in C indicate no difference in results between study sites (dots, dashes, and lines overlap) nor richness levels (red and blue overlap); overlapping lines in A and D indicate no difference in results between study sites, but a present difference between high and low richness levels. Survival probabilities were assessed at the end of each study timeframe per plot (i.e. not annualized; WFDP: 2010–2020, YFDP: 2011–2020, UFDP: 2015–2020). Low heterospecific richness was the lowest observed number of different species within any large-diameter tree neighborhood (here,  $HSR_{\min} = 0$ ;  $HDR_{\min} = 0$ ), and vice versa for high richness ( $HSR_{\max} = 6$ ,  $HDR_{\max} = 10$ ). Heterospecific crowding was centered by diameter and species, so high and low categories reflect the *relative* effect of crowding. That is, low crowding was the lowest observed value within any large-diameter tree neighborhood, which after centering represented the lowest crowding that would be expected for any large-diameter tree species (here,  $HSC_{\min} = -37$ ;  $HDC_{\min} = -31$ ), and vice versa for high crowding ( $HSC_{\max} = 117$ ,  $HDC_{\max} = 105$ ). We held all other parameters at mean observed values (0 for all after centering) so only the values for the parameters of interest were permuted to create interaction slopes; this included using mean HDC/HDR when assessing the effect of guild-sharing interactions, and vice versa when assessing guild-disparate interactions. Survival probabilities were calculated using these parameter values and the mean of posterior distributions for all coefficients in either EM- or AM-specific large-diameter tree models following Eq. 2. The positive interactions between guild-sharing crowding and richness observed for large-diameter trees (AM and EM combined; Fig. 5.2) appears to be driven by ectomycorrhizal species responses (A), while negative interactions between guild-disparate crowding and richness are driven by arbuscular mycorrhizal species (D). Asterisk (\*) indicates a significant interaction, i.e. 95% credible intervals for parameter estimates do not include zero.



**Figure D.6.** Examples of beetle galleries identified during pathology exams: *Scolytus ventralis* on *Abies concolor* in YFDP (A), *Dendroctonus pseudotsugae* on *Pseudotsuga menziesii* ssp. *menziesii* in WFDP (B), *Ips paraconfusus* on *Pinus lambertiana* in YFDP (C), *Dryocoetes confusus* on *Abies bifolia* in UFDP (D), *Pityokteines minutus* on *Abies bifolia* in UFDP (often forming a disease complex with *Armillaria ostoyae*; E). Windows of bark were removed near 1.4 m height (B) to uncover galleries and/or live beetles. Calipers were used to distinguish between galleries of similar shapes but distinct sizes (D, E). Photo credits: Sara Germain (A, C–E), Tucker Furniss (B).



**Figure D.7.** Examples of fungal mortality agents identified during pathology exams: *Encoelia pruinosa* on exterior stem of *Populus tremuloides* in UFDP (A), *Armillaria ostoyae* on root collar under bark of *Abies concolor* in YFDP (B), *Phellinus pini* on exposed sapwood and heartwood of fallen *Pseudotsuga menziesii* ssp. *menziesii* in WFDP (C). Photo credits: Sara Germain (A–C).

## SECTION S1: PATHOLOGY EXAM DATA SHEETS

## Mortality Survey

Mortality Data

**DBH** (cm), one decimal place. If unmeasurable, estimate DBH in comments.

**Root condition**

- 1 = Root-soil interface intact
- 2 = Root-soil interface damaged but stem still freestanding
- 3 = uprooted, stem no longer free standing.

**Stem condition**

- 1 = Main stem intact
- 2 = Main stem pinned or ruptured (e.g., crushed)
- 3 = Main stem snapped (no longer connected)

**Take snag height reading with laser**

**Snag top diameter** (cm). If main stem is fully intact, record 0 cm.

**% Crown:** Estimate percent of crown still intact. Do not enter values <100% for sparse crowns or gradual dieback.

**% Tree:** Estimate percent of the entire main stem length that is standing unbroken.

**Leaner Angle:** If tree is still rooted and is leaning, estimate the angle of lean in degrees from vertical (see diagram). Use this category for trees that are standing with crown and for trees that are crushed but still rooted.

**Down:** Entering information here indicates that part or all of the dead tree is down. Use this category only if the % tree standing is less than 100% and only when the tree position code is 2 or 3. A tree that is crushed but still rooted is not considered to be down. Consider the down part of the stem only. The % on ground and % supported must equal 100%.

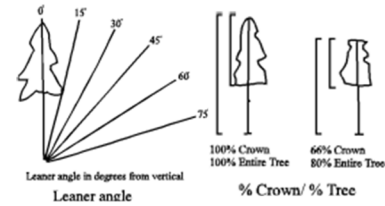
**% on Ground:** Estimate the percent of the down stem portion that is in direct contact with the ground.

**% Supported:** Estimate the percent of the down stem portion that is supported above ground.

**Special cases:** If data can't be recorded, leave cell blank and note reason in comments. For example, if the top portion of the tree is broken off and can't be found, record data about the standing portion of the tree under STANDING and leave both columns of DOWN blank. Broken tops hung up in the canopy are considered down but supported. If tree cannot be found, look again, then comment "Not found" and list CC=38. Fill out the Fallen/CWD data sheet for newly fallen tree parts  $\geq 10$  cm in diameter at base.

**Knock nail** completely into tree to ensure tag is secured.

**Comments:** Record details regarding the condition codes and FADs

**Tree Condition Codes****Crown**

- 01 Dead needles or leaves present
- 02 Earlier loss of crown portion
- 03 Foliage Damage
- 04 Spike top/ top dieback
- 05 Crown flat topped
- 06 Mistletoe plants observed (use binoculars)
- 07 Witches brooms

**Bole/Branches/Roots**

- 13 Rotten wood
- 14 Mycelia/ rhizomorphs/ fungal fruiting body (non-conk)
- 15 Rot at break
- 16 Pitch tube on bole
- 17 Beetle galleries
- 18 Exit/entrance holes
- 19 Conks (indicate type and position)
- 20 Swelling
- 21 Canker
- 22 Evidence of scale (black bark)
- 23 Tree is hollow
- 24 Pitching
- 25 Pitch sheets
- 26 Oozing wounds
- 27 Bark sloughing
- 28 Scar on bole (note cause, location, extent)
- 29 Girdling (note cause)
- 30 Woodpecker/ Sapsucker activity (note extent)
- 31 Snow/ ice damage

**Other**

- 32 Uprooted or partially ruptured but foliage is still live.
- 35 Sprouting at base (if sprout is from same stem, use 37)
- 36 Tree dead several years (note reasoning, estimate years)
- 37 Tree dead above breast height, live below (if sprouting at base, use 35)
- 38 Tree not found

**Factors Associated with Death (list in order of importance)**

40 Unknown

**Biotic**

- 50 Suppression
- 51 Animal damage (specify animal if possible)
  - 51.1 Herbivory (specify)      51.3 Cat scratch
  - 51.2 Elk scrape
- 52 Mistletoe

**Disease**

- 61 White pine blister rust
- 62 Rot (specify accordingly, if possible)
  - 62.1 Armillaria ostoyae      62.6 Echinodontium tinctorium
  - 62.2 Phellinus weirii      62.7 Phellinus hartigi
  - 62.3 Heterobasidium annosum      62.8 Phellinus pini
  - 62.4 Phaeolus schweinitzii      62.9 Onnia tomentosa
  - 62.5 Fomitopsis pinicola
- 63 Canker
- 64 Other (specify)
  - 64.1 Brown felt blight/Snow fungus
  - 64.2 Black/Brown stain (Leptographium)
  - 64.3 Blue stain (Ceratocystis, Ophiostoma)

65 Unknown

**Insect**

- 71 Bark (specify accordingly, if possible)
  - 71.1 Dendroctonus brevicomis      71.8 Pityokteimes spp.
  - 71.2 Dendroctonus ponderosae      71.9 Phloeosinus spp.
  - 71.3 Dendroctonus pseudotsugae      71.11 Scolytus subscaber
  - 71.4 Dendroctonus rufipennis      71.12 Scolytus tsugae
  - 71.5 Dendroctonus valens      71.13 Scolytus ventralis
  - 71.6 Dryocoetes contusus      71.14 Pseudopityophthorus pubipennis
  - 71.7 Ips spp.

72 Defoliating (specify if possible)

73 Other (specify)

**Physical— Note**

- 80 Uprooted by falling tree or tree parts (note originating tree)
  - 81 Uprooted (note cause)
  - 82 Broken stem by falling tree or tree parts (entire or partial crown loss)
  - 83 Broken stem (entire or partial crown loss) (note cause)
  - 84 Crown damage (stripped, broken branches, etc.)
  - 85 Crushed by falling tree or tree parts (note originating tree)
  - 86 Crushed (note cause)
  - 87 Lightning
  - 88 Other (note cause)
  - 89 Tree located, physically removed from plot, i.e. landslide.
- Fire**
- 91 Crown scorch (killed by fire scorch, not consumption)
  - 92 Crown combustion (note extent of consumption)
  - 93 Bole/stem scorch
  - 94 Bole/stem combustion
  - 95 Cambial heating
  - 96 Burned through at base (for small trees, due to litter & duff consumption around base)
  - 97 Other (describe)
  - 98 Fire, mechanical (fire burned base, but tree died because of structural failure. The tree would have survived if it didn't fall over)
  - 99 Complete consumption (<25% of stem remaining, or tag found on ground)





## SECTION S2: TABLE D.1 REFERENCES

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## APPENDIX E

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## CURRICULUM VITAE

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PROFESSIONAL PREPARATION

## EDUCATION

<i>Institution</i>	<i>Degree</i>	<i>Program</i>	<i>Year</i>	<i>GPA</i>
Utah State University	<u>PhD</u>	Ecology "Hidden mechanisms of climate impacts in western forests: integrating theory and observation for climate adaptation" Defense Date: May 3, 2022 Committee Chair: Jim Lutz	2022	3.85
Utah State University	<u>B.S.</u>	Conservation and Restoration Ecology, <i>Cum Laude</i> <u>Minors</u> : Statistics, Soil Science <u>Research</u> : Two studies in Utah and Laikipia, Kenya	2016 2014-15	3.75

## WORKSHOPS

2019	North American Dendroecological Fieldweek. A.L. Mickelson Field Station, Cody, WY, USA. July 20–29, 2019.
2019	The Smithsonian Forest Global Earth Observatory Analytical Workshop. Nanyang Technological University, Singapore. June 22–July 6, 2019.

GRADUATE PROGRAM

## RESEARCH

2016- 2022	<b>Doctoral fellow and research assistant.</b> Utah State University, Logan, UT, USA. I trained undergraduate field technicians as a field crew lead, managed undergraduate laboratory technicians, and mentored undergraduate and graduate researchers in dendroecological techniques, statistics, and grant writing.
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## TEACHING

2019	<b>Instructor.</b> <i>WILD 3820: Forest Plants: Identification, Biology, and Function.</i> Required hybrid course. I instructed lectures and labs, developed new materials and class activities, managed the course herbarium, and mentored an undergraduate teaching fellow. Utah State University.
2018–2021	<b>Co-instructor.</b> <i>NSF-GRFP workshop series.</i> Elective course. I co-developed this annual series with the USU Science Writing Center to teach scientific writing. I mentored undergraduate and graduate students as they assembled grant applications. Utah State University.
2015–2019	<b>Teaching associate.</b> <i>WILD 4570: Forest Ecology of the Sierra Nevada and White Mountains.</i> I organized field logistics and safety, and taught mensuration, plant species identification, and pathology exam methods. I also developed the WILD 3820 herbarium. Collaborative course between Utah State University, University of Montana, and Washington State University.
2018	<b>Co-instructor.</b> Earthwatch Expeditions. Wind River Forest Dynamics Plot, WA.
2015	<b>Co-instructor.</b> Botanical specimen workshop. Mpala Research Center, Kenya.

## SERVICE

- 2019-2021 **Co-chair.** Ecology Center Seminar Series Committee. Utah State University.  
 2020 **Co-organizer.** Ecological Society of America organized oral session: Enhancing our ecological understanding of the new fire normal with large datasets, novel methods, and new perspectives. Salt Lake City, UT.
- 2019 **Graduate liaison.** Greenhouse Gas Reduction Committee, Education Subcommittee. Utah State University.
- 2016–2021 **Canine search specialist.** Other positions: mentorship program coordinator. Utah Task Force 1: FEMA Urban Search and Rescue national incident response team.
- 2013–2021 **Search and rescue field operative.** Other positions: testing officer, information technology officer. Utah Search Dogs: non-profit search and rescue team.

PUBLICATIONS

Google Scholar statistics (as of 2022/July/18)

Citations: 333

h-index: 5

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- [9] **Germain, S. J.**, and J. A. Lutz. 2022. Climate warming may weaken stabilizing mechanisms in old forests. *Ecological Monographs*, 92(2):e1508. <https://doi.org/10.1002/ecm.1508>
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- [3] Lutz, J. A., T. J. Furniss, D. J. Johnson, S. J. Davies, D. Allen, A. Alonso, K. Anderson-Teixeira, A. Andrade, J. Baltzer, K. M. L. Becker, E. M. Blomdahl, N. A. Bourg, S. Bunyavejchewin, D. F. R. P. Burslem, C. A. Cansler, K. Cao, M. Cao, D. Cárdenas, L-W. Chang, K-J Chao, W-C. Chao, J-M. Chiang, C. Chu, G. B. Chuyong, K. Clay, R. Condit, S. Cordell, H. S. Dattaraja, A. Duque, D. Escobar, C. E. N. Ewango, G. A. Fisher, C. Fletcher, J. A. Freund, C. Giardina, **S. J. Germain**, G. S. Gilbert, Z. Hao, T. Hart, B. C. H. Hau, F. He, A. Hector, R. W. Howe, C-F. Hsieh, Y-H. Hu, S. P. Hubbell, F. M. Inman-Narahari, A. Itoh, D. Janík, A. R. Kassim, D. Kenfack, L. Korte, K. Král, A. J. Larson, Y-D. Li, Y. Lin, S. Liu, S. Lum, K. Ma, J-R. Makana, Y. Malhi, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. Mi, M. Morecroft, P. M. Musili, J. A. Myers, V. Novotny, A. de Oliveira, P. Ong, D. A. Orwig, R. Osterag, G. G. Parker, R. Patankar, R. P. Phillips, G. Reynolds, L. Sack, G-Z. M. Song, S-H. Su, R. Sukumar, I-F. Sun, H. S. Suresh, M. E. Swanson, S. Tan, D. W. Thomas, J. Thompson, M. Uriarte, R. Valencia, A. Vicentini, T. Vrška, et

al. 2018. Global importance of large-diameter trees. *Global Ecology and Biogeography* 27(7): 849-864. <http://dx.doi.org/10.1111/geb.12747>

- [2] **Germain, S. J.**, R. K. Mann, T. A. Monaco, and K. E. Veblen. 2018. Short-term regeneration dynamics of Wyoming big sagebrush at two sites in northern Utah. *Western North American Naturalist* 78(1): 7-16. <http://dx.doi.org/10.3398/064.078.0103>
- [1] Lutz, J. A., T. J. Furniss, **S. J. Germain**, K. M. L. Becker, E. M. Blomdahl, S. M. A. Jeronimo, C. A. Cansler, J. A. Freund, M. E. Swanson, and A. J. Larson. 2017. Shrub communities, spatial patterns, and shrub-mediated tree mortality following reintroduced fire in Yosemite National Park, California, USA. *Fire Ecology* 13(1): 104-126. <http://dx.doi.org/10.4996/fireecology.1301104>

#### INVITED PUBLICATIONS

- [1] **Germain, S. J.**, and J. A. Lutz. 2021. Shared friends counterbalance shared enemies in old forests. International Mycorrhiza Society Quarterly Newsletter.

#### NON-REFEREED PUBLICATIONS

- [1] Lutz, J. A., A. J. Larson, K. M. L. Becker, T. J. Furniss, E. M. Blomdahl, **S. J. Germain**, and M. E. Swanson. 2016. Post Rim Fire assessment of fuel consumption and mortality in the Yosemite Forest Dynamics Plot. Final Report to the National Park Service.

#### PRESENTATIONS

##### INVITED

- [5] **Germain, S. J.** and J. A. Lutz. Hidden mechanisms of climate impacts in western forests. Cary Institute of Ecosystem Studies. Millbrook, NY. June 8, 2022.
- [4] **Germain, S. J.** and J. A. Lutz. Hidden mechanisms of climate impacts in western forests. University of Wyoming. Laramie, Wyoming. June 1, 2022.
- [3] **Germain, S. J.** and J. A. Lutz. Canary in the old growth: Yew survival limited by extreme drought. Intermountain Society of American Foresters annual meeting [webcasted via Zoom]. April 23, 2021.
- [2] **Germain, S. J.** and J. A. Lutz. Parsing density dependence to better predict climate change impacts in forests. CTFS-ForestGEO Analytical Workshop. Nanyang Technological University, Singapore. July 3, 2019.
- [1] **Germain, S. J.** and J. A. Lutz. Climate warming may hinder coexistence among forest trees. Wind River Forest Dynamics Plot NSF Symposium. Carson, Washington. June 10, 2019.

##### CONTRIBUTED

- [12] Bhandari, S., S. A. Collins-Key, C. L. Dems, **S. J. Germain**, A. L. Kaiser, W. C. Wittenbraker, M. F. Bekker, and G. von Arx. Investigating anatomical features of whitebark pine (*Pinus albicaulis*) to explain growth and mortality trends in the Greater Yellowstone Ecosystem, Wyoming, USA. North American Dendroecological Fieldweek. Cody, WY. July 28, 2019.
- [11] **Germain, S. J.** and J. A. Lutz. Attenuation of associational resistance in a compound-disturbance landscape. Department of Wildland Resources Graduate Symposium, Utah State University. Logan, Utah. April 12, 2019.
- [10] **Germain, S. J.** and J. A. Lutz. Time-varying covariates and the Cox proportional hazards assumption using tree mortality as a working example. Biostatistics Graduate Symposium, Utah State University. Logan, Utah. April 23, 2018.
- [9] **Germain, S. J.** and J. A. Lutz. Climate modifies competitive interactions in a late-seral Douglas-fir forest. Student Research Symposium, Utah State University. Logan, Utah. April 12, 2018.
- [8] **Germain, S. J.** and J. A. Lutz. Climatic water deficit alters background mortality of a late-successional tree species in old-growth Douglas-fir forests. Department of Wildland Resources Graduate Research Symposium, Utah State University. Logan, Utah. April 14, 2017.
- [7] **Germain, S. J.** and J. A. Lutz. Tree death and forest change in old-growth Douglas-fir forests. Intermountain Society of American Foresters annual meeting. Logan, Utah. March 31, 2017.
- [6] **Germain, S. J.** and K. E. Veblen. Plant functional traits respond as multivariate suites to herbivory in a Kenyan savannah. Multivariate Statistics poster session, Utah State University. Logan, Utah.

May 6, 2016.

- [5] **Germain, S. J.** and K. E. Veblen. Responses of plant functional traits to grazing in a Kenyan savannah. Student Research Symposium, Utah State University. Logan, Utah. April 14, 2016.
- [4] **Germain, S. J.** and K. E. Veblen. Responses of plant functional traits to grazing in a Kenyan savannah. Categorical Statistics poster session, Utah State University. Logan, Utah. December 10, 2015.
- [3] **Germain, S. J.** and K. E. Veblen. Sagebrush steppe community response to low-rate tebuthiuron treatment: implications for rangeland and wildlife management. Student Research Symposium, Utah State University. *First place oral presentation award*. Logan, Utah. April 9, 2015.
- [2] **Germain, S. J.** and K. E. Veblen. Sagebrush steppe community response to low-rate tebuthiuron treatment: implications for rangeland and wildlife management. Society for Range Management Utah Chapter annual meeting. Logan, Utah. November 7, 2014.
- [1] **Germain, S. J.** and K. E. Veblen. Effects of tebuthiuron on Wyoming big sagebrush seedling emergence: a case study in northern Utah. Undergraduate Research Symposium poster session, Utah State University. Logan, Utah. October 24, 2014.

#### ACCESSIONED DATASETS

- [5] **Germain, S. J.** and J. A. Lutz. Yosemite Forest Dynamics Plot Living Trees - PILA - ITRDB CA728. NOAA National Centers for Environmental Information. <https://www.ncdc.noaa.gov/paleo/study/33853>
- [4] **Germain, S. J.** and J. A. Lutz. Yosemite Forest Dynamics Plot Dead Trees - PILA - ITRDB CA727. NOAA National Centers for Environmental Information. <https://www.ncdc.noaa.gov/paleo/study/33852>
- [3] Macriss, N., T. J. Furniss, S. M. A. Jeronimo, E. L. Crowley, O. W. Germain, **S. J. Germain**, V. R. Kane, A. J. Larson, and J. A. Lutz. 2019. Data for tree mortality calibration of satellite and LiDAR-derived fire severity estimates. Utah State University Dataset 63. <https://doi.org/10.26078/jsz1-3980>
- [2] Lutz, J. A., J. A. Freund, A. J. Larson, M. E. Swanson, T. J. Furniss, K. M. L. Becker, E. M. Blomdahl, C. A. Cansler, **S. J. Germain**, and S. M. A. Jeronimo. 2017. Data for allometric equations of *Chrysolepis sempervirens*, *Cornus sericea*, *Corylus cornuta* ssp. *californica*, and *Leucothoe davisiae*. Utah State University Dataset 72. <https://doi.org/10.15142/T3WK55>
- [1] Lutz, J. A., T. J. Furniss, **S. J. Germain**, K. M. L. Becker, E. M. Blomdahl, S. M. A. Jeronimo, C. A. Cansler, J. A. Freund, M. E. Swanson, and A. J. Larson. 2017. Shrub consumption and immediate community change by reintroduced fire in Yosemite National Park, California, USA; Supplemental Information. Utah State University. <http://doi.org/10.15142/T3HP4D>

#### OUTREACH

- [7] Utah Public Radio: Undisciplined, 11/4/2021. Underground allies by Shoshannah Buxbaum. Also on podcast. <https://www.upr.org/post/undisciplined-underground-allies#stream/0>
- [6] Utah State Today, 8/23/2021. Hidden allies aid survival of the West's largest trees. Text by Lael Gilbert. Video by Taylor Emerson. Eureka Alert. <https://www.usu.edu/today/story/hidden-allies-aid-survival-of-the-wests-largest-trees>
- [5] Smithsonian ForestGEO News Blog, 7/6/2021. Census Update from the Field: Wind River Edition. <https://forestgeo.si.edu/blog/census-update-field-wind-river-edition?fbclid=IwAR1MC7lxzN31yGGApBpFRKreeX4Dg1K4FqEeVi3IoV7HyTGzPfvYDYS6Cl8>
- [4] Columbia Insight, 10/22/2020. The secret power of old-growth. By Marina Richie. <https://columbiainsight.org/the-secret-power-of-old-growth/>
- [3] BBC News, 6/12/2019. Tracking the lives of some of the oldest and tallest trees in the world. Filmed and edited by Colleen Hagerty. BBC Radio by Peter Bowes. BBC Facebook . Peter Bowes' blog . Picked up by Utah State Today. <https://www.bbc.com/news/av/world-us-canada-48564750>
- [2] University of Montana, 5/10/2018. Study: Largest 1 Percent of Trees Make Up Half of Mature Forest Biomass Worldwide. By Anne James. <https://k96fm.com/study-largest-1-percent-of-trees-make-up-half-of-mature-forest-biomass-worldwide/>
- [1] EurekaAlert, 5/8/2018. Inequality is normal: Dominance of the big trees. By Traci Hillyard. <https://www.eurekaalert.org/news-releases/801733>

**SYNERGISTIC ACTIVITIES**

2016–present **Investigator.** Wind River Forest Dynamics Plot, Smithsonian ForestGEO network.  
 2021–present **Investigator.** Cedar Breaks Forest Dynamics Plot, Smithsonian ForestGEO network.  
 2021–present **Investigator.** Yosemite Forest Dynamics Plot, Smithsonian ForestGEO network.

**AFFILIATIONS**

2016–present Xi Sigma Pi honor society, Lambda Chapter  
 2016–present Society of American Foresters  
 2016–present Ecological Society of America  
 2019–present American Association for the Advancement of Science

**AWARDS**

<i>Source</i>	<i>Timespan</i>	<i>Quantity</i>
Ecology Center, Utah State University	2021-2022	\$5 000
Ecology Center, Utah State University	2019-2020	\$4 984
Quinney Doctoral Fellowship, Utah State University	2018-2022	\$40 000
Graduate Research Fellowship Program, National Science Foundation	2016-2021	\$138 000
Research Experiences for Undergraduates (Veblen, PI), NSF	2015-2016	\$9 398
Undergraduate Research and Creative Opportunities, Utah State University	2014	\$2 000
Paul M. and Neva Dunn Scholarship, Utah State University	2014	\$800
USU Inaugural Scholarship, Utah State University	2013-2014	\$2 000
	<b>Totals</b>	2013-2022 \$202 182

**RELATED QUALIFICATIONS**

**CERTIFICATIONS:** Desert Mountain Medicine: wilderness first responder, wilderness anaphylaxis training, CPR, AED; Federal Emergency Management Agency: canine search specialist, canine disaster Type I live search; Federal Emergency Management Agency: hazardous materials operations, bloodborne pathogens awareness; National Association for Search and Rescue: canine avalanche search, search and rescue technician level II.

**SOFTWARE PROFICIENCIES:** MySQL, Microsoft Excel, SAS, R, Coorecorder, CDendro, ImageJ, ArcMap, Garmin Basecamp, Adobe Dreamweaver, Overleaf, RMarkdown, Zotero Reference Manager, Zoom, Slack

**TECHNICAL SKILLS:** Emergency medicine and rescue in a wilderness setting, Dendroecological techniques (tree core collection and processing; measurement and assessment of tree anatomical features, detrending, cross-dating); Herbarium management (botanical specimen collection, pressing, mounting, and tending); Plant identification at multiple life stages (seed, seedling, immature, mature, dormant, dead); Taxonomic keys (Flora of North America, Jepson Manual, Hitchcock & Cronquist, Pojar & MacKinnon); Plant tissue processing (biomass, leaf scanning, specific leaf area, resin duct area); Plant rearing and tending in a greenhouse; Forest stand analysis (prism, height and diameter measurements); Forest pathology surveys (beetle and fungi identification, stress symptoms and causes); Vegetation sampling (line-point intercept, belt transect, Daubenmire frame, nested quadrats); Soil sampling (structure, horizons, taxonomic designations, pH, texture, chemical reactivity); Site characterization (rock fragment class densities, slope, aspect, landform); Surveying (Topcon DS105 Total Station, HiPer V GNSS GPS); Navigation (map and compass, GPS); Labor (auger, post-hole digger, post driver, hatchet, saw, drill, hammer, etc.)