THE LOCAL NEIGHBORHOOD INTERACTIONS SHAPING TREE COMMUNITIES THROUGH ECOLOGICAL DISTURBANCE AND ENVIRONMENTAL CHANGE

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THE LOCAL NEIGHBORHOOD INTERACTIONS SHAPING TREE COMMUNITIES THROUGH ECOLOGICAL DISTURBANCE AND ENVIRONMENTAL CHANGE

by

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ABSTRACT

THE LOCAL NEIGHBORHOOD INTERACTIONS SHAPING TREE COMMUNITIES THROUGH ECOLOGICAL DISTURBANCE AND ENVIRONMENTAL CHANGE

Cole J. Doolittle, B.Sc.

Marquette University, 2025

My dissertation consists of four chapters focused on understanding the factors maintaining local species diversity, addressing a central goal of ecology increasingly critical for preserving ecosystem services and human well-being in the face of climate change. Specifically, I investigate how local neighborhoods – that is, the spatial arrangement, density, and identity of nearby competitors – contribute to patterns of growth and survival along gradients of ecological disturbance and environmental change using forest tree communities as a study system.

In my first chapter, I develop a conceptual framework that synthesizes why we may expect local neighborhood interactions to weaken under ecological disturbances that primarily affect competitive densities or nutrient availability. This framework provides a foundation for understanding how disturbance-altered neighborhood interactions may influence forest recovery trajectories and community assembly.

For my second and third chapters, I focus on examining neighborhood interactions of two dominant conifer species in Pacific Northwest: *P. menziesii* (Douglas-fir) and *T. heterophylla* (Western hemlock) across life-stage and environmental condition. First, I examine how wildfires influence local neighborhood interactions between seedlings and surviving adults, revealing how wildfire disrupts neighborhood interactions that are otherwise thought to stabilize local populations in undisturbed ecosystems. Then, I use dendrochronological techniques to analyze how neighborhood interactions influence 60 years of climate-growth relationships in large, established adult trees. I demonstrate that interannual climate variability alters the strength and direction of neighborhood interactions, with species-specific responses to temperature and precipitation that may shift competitive dynamics under future climate scenarios.

Finally, my fourth chapter investigates an important underlying driver of neighborhood interactions: the soil microbiome. I demonstrate that pathogenic fungi are more associated with tree community composition at low elevations, which have stronger stabilizing neighborhood interactions, whereas ectomycorrhizal fungi are more associated with tree community composition at high elevations, which have weaker stabilizing neighborhood interactions.

Collectively, this dissertation advances our understanding of how stressors associated with environmental change and ecological disturbance alter the local interactions thought to contribute to maintaining diverse communities, with implications for predicting forest community responses to climate change and climate-altered disturbance regimes.

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INTRODUCTION

Ecology, the study of interactions among organisms and their environment, represents a cornerstone of contemporary biological understanding with applications in resource management, conservation, and global sustainability. While the roots of ecology can be traced back to the early naturalists and philosophers (Egerton, 2001), its modern study has developed into a robust scientific discipline with specialized subfields examining certain aspects of ecological phenomena. One important subdivision is community ecology, a primary goal of which is to integrate the factors, relationships, and processes that govern species diversity into a synthetic understanding of life's variety on Earth (Elton, 1927). Community ecology investigates how species interactions including competition, predation, parasitism, mutualism, and commensalism shape community properties including diversity and stability within their abiotic context.

Several theoretical paradigms have advanced our understanding of the maintenance of species diversity over the past century. Early ecologists focused predominantly on abiotic factors and deterministic succession (Clements, 1916; Cowles, 1899; Egler, 1954), which gradually led to the incorporation of abiotic preferences, niche differentiation, and competitive exclusion (Hardin, 1960; Hutchinson, 1957; Tilman, 1982), stochastic and emergent properties (Hubbell, 2001; Levin, 1992), and metacommunity dynamics (Leibold et al., 2004). Broadly, the breadth of ecological principles developed over the last century to explain ecological communities can be organized into 4 categories, each echoed in evolutionary biology: speciation, dispersal, drift, and selection (Vellend, 2010). Speciation and dispersal represent the creation and dispersal of species by which ecological community diversity increases. Drift refers to stochastic changes in species abundance resulting from random demographic processes. Lastly, selection encompasses deterministic differences in fitness among species that arise from environmental factors and species interactions. This conceptual framework provides an elegant lens for organizing the factors influencing community diversity in recognition that both deterministic and stochastic processes structure ecological systems across scales.

Within this broader context, my dissertation focuses on selection processes operating at the local neighborhood scale, where differences in the effects of conspecific neighbors (same-species) relative to heterospecific neighbors (different-species) mediate individual performance and population growth (Broekman et al., 2019; Chesson, 2000; LaManna et al., 2024; Wright, 2002). First formalized as the Janzen-Connell hypothesis in the early 1970s, the idea that conspecific neighbors are a detriment to individual growth, survival, and reproductive rates (performance) was primarily driven by observations that natural enemies aggregate around their preferred hosts (Janzen, 1970; Connell, 1971). Since that time, ecologists have expanded this hypothesis to incorporate other forms of neighborhood interactions differing between conspecifics and heterospecifics including direct intraspecific competition (e.g., Adler et al., 2018), relatively host-specific mutualists (e.g., Bachelot et al., 2015; Delavaux et al., 2023; Kandlikar et al., 2019; Liang et al., 2015), and drivers across spatial and temporal scales (e.g., Swenson et al., 2023).

Collectively, this broad group of factors contributing to ecological selection at local scales is referred to as local conspecific density dependence (CDD; Hülsmann et al., 2021; LaManna et al., 2024). In the Plant Kingdom, local CDD is most often negative, meaning that individual performance is disadvantaged in conspecific neighborhoods relative to heterospecific neighborhoods (Bagchi et al., 2014; Comita et al., 2014). All else being equal, negative local CDD (also known as CNDD) should stabilize local populations by disadvantaging dense conspecific neighborhoods and contributing to a rare species advantage (Chesson, 2000; Connell et al., 1984; LaManna et al., 2016; Smith, 2022; Wright, 2002). Alternatively, while less frequently observed, positive local CDD (also known as reverse Janzen-Connell effects; Zahra et al., 2021) should destabilize local populations by advantaging conspecific aggregation and causing competitive exclusion (Bachelot et al., 2015; Chesson, 2000; Delavaux et al., 2023). In this dissertation, I refer to local CDD as stabilizing or destabilizing to refer to the prediction that local-scale differences between conspecific and heterospecific neighborhood effects scale up to cause community stabilization or destabilization, and not as an explicit prediction of coexistence (Hülsmann et al., 2024; LaManna et al., 2024).

Empirically, the magnitude and even direction of local CDD is increasingly attributed to abiotic factors, generally becoming less stabilizing (less negative) as environmental conditions become more stressful, such as with increasing drought-stress or declining nutrient availability (Johnson et al., 2017; LaManna et al., 2016; Lebrija-Trejos et al., 2023; Liu & He, 2021; Milici et al., 2025; Song et al., 2018; Uriarte et al., 2018). Still, our understanding of how local CDD is altered by changing environmental conditions remains largely restricted to early life-stage plants and lacks a central framework for examining its underlying drivers. Moreover, our understanding of local CDD along environmental gradients is largely derived from relatively mild abiotic changes, and the applicability of these findings to ecological communities experiencing dramatic abiotic changes, such as ecological disturbances, remains uncertain. These limitations represent a fundamental gap in knowledge critical to understanding ecological communities that are increasingly subjected to changing environmental conditions under climate change.

My dissertation investigates how local CDD measured in individual growth and survival responds to broad environmental gradients and ecological disturbances in forest systems. Specifically, I employ complementary empirical approaches to assessing local CDD across life-stage in the temperate rainforests of the Pacific Northwest with the goal of understanding how changing regimes of climate and ecological disturbance are affecting these important neighborhood interactions. My methodological toolkit includes a theoretical synthesis, an observational study of seedling demography, dendrochronological analyses, and characterizing tree-associated fungal communities. This multifaceted approach allows me to investigate local CDD across different spatial scales, life stages, and environmental contexts.

In Chapter 1, I develop a conceptual framework synthesizing how ecological disturbances may influence the strength and direction of local CDD. I categorize disturbances based on their primary effects on forest structure—distinguishing between those that primarily affect resource availability (interference disturbances), competitive densities (destruction disturbances), or both simultaneously (combined disturbances). For each category, I predict how disturbances might alter the underlying mechanisms generating local CDD and discuss implications for forest recovery and community assembly. This theoretical contribution provides a foundation for predicting disturbance effects on stabilizing neighborhood interactions.

Chapter 2 presents an empirical investigation of how wildfire affects local CDD in tree seedlings. By comparing seedling mortality between burned and unburned forests experiencing varying degrees of heat stress, I demonstrate that wildfire fundamentally disrupts the stabilizing density feedbacks that otherwise promote diversity in undisturbed forests. My findings reveal that under the combined stressors of fire and extreme heat, local CDD in seedling survival becomes neutral, not contributing to patterns of individual performance. These results have important implications for understanding post-disturbance forest recovery in a warming climate.

In Chapter 3, I focus on large adult trees, using dendrochronological techniques to analyze how neighborhood interactions alter climate-growth patterns in two dominant conifer species that represent the majority of aboveground biomass in the Pacific Northwest. Across an elevation gradient, I demonstrate that local neighborhoods are important modifiers of tree growth under abnormal climate conditions. Specifically, I find that local CDD in Douglas-fir (*Pseudotsuga menziesii*) growth becomes increasingly destabilizing in cooler years, while Western hemlock (*Tsuga heterophylla*) exhibits stronger stabilizing local CDD in wetter years. These species-specific responses to climate fluctuations reveal an underappreciated temporal dimension of neighborhood interactions that will become increasingly important to predicting the future of forest systems under climate change.

Finally, Chapter 4 investigates a key underlying mechanism driving patterns of local CDD across environmental gradients: shifts in the composition and spatial aggregation of soil fungal communities. By pairing soil microbiome analyses with forest inventory data, I test the "Stress Gradient Feedback Hypothesis," which posits that relatively host-specific antagonistic interactions (e.g., with pathogenic fungi) are more abundant and important in benign environments, while relatively host-specific mutualistic interactions (e.g., with mycorrhizal fungi) become increasingly important under stressful conditions. My results demonstrate that site-to-site differences in tree community composition are more strongly associated with differences in pathogenic fungal communities at lower elevations, but more strongly associated with ectomycorrhizal fungal communities at higher elevations, thereby providing a mechanistic explanation for changing patterns of local CDD across environmental stress gradients.

Collectively, this research advances ecological theory by integrating concepts from community ecology, disturbance ecology, and microbial ecology to better understand the factors thought to contribute to species diversity in changing environments. My findings have important implications for predicting how forest communities will respond to increasing disturbance frequency and severity under climate change and contribute to addressing the primary goals of community ecology.

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Chapter 1 | Local stabilizing density effects in the context of ecological disturbance and community assembly

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Abstract

The maintenance of species diversity in ecological communities has many promising explanations, including certain types of local biotic interactions that generate differential effects on the performance of conspecific and heterospecific individuals. To date, most studies of these local biotic interactions have focused on relatively stable systems, such as mature forests or undisturbed grasslands. However, many ecosystems are far from a stable state, especially under accelerating global climate change. Here, we present a synthesis of local differences between conspecific and heterospecific interactions following disturbances – and how disturbances may alter the strength and scaling of these effects to population growth and species diversity. First, we clarify terminology and categorize disturbances based on their primary mode of impact on species interactions. Second, we leverage existing literature to develop a framework for understanding of how disturbances may alter the strength and role of local biotic interactions in regenerating communities. Third, we use prominent examples of disturbance: drought, windthrow, and wildfire, to highlight remaining gaps in knowledge. Finally, we discuss implications for future populations and communities in unstable states. We emphasize the need for empirical studies to further integrate disturbance and local conspecific density effects within broader ecological models of community assembly and functioning

1. Introduction

Ecosystems that generate global cultural and economic wellbeing are increasingly threatened by anthropogenic climate change and climate-related changes to natural patterns of ecological disturbance. Today, ecologists are concerned that unpredictable patterns and severity of disturbance events will erode key ecosystem services and diversity in future ecological systems (Lindenmayer *et al.* 2019, Seidl *et al.* 2017, Swanson *et al.* 2011). In part, this concern reflects uncertainty about how disturbance events alter the underlying processes generating and maintaining species diversity in regenerating ecosystems (Seidl & Turner 2022). To address this uncertainty, the need exists for synthesis of literature on ecological disturbance and the processes that affect species diversity. Here, we synthesize recent advances on interactions between ecological disturbances and one such process that can affect species diversity: local density-dependent species interactions.

Ecologists have a longstanding interest in determining relationships between ecological disturbances and species diversity (Clements 1916, King 1685, Turner 2010), which has often manifested in identifying the "winners and losers" of abiotic change based on functional traits and life-history strategies (Keith *et al.* 2007, McKinney & Lockwood 1999, Noble & Slatyer 1980, *see* Tabarelli *et al.* 2012). The "winner and losers" paradigm suggests that disturbances alter species composition and diversity by changing the availability and heterogeneity of both resources and competitors, which either stochastically (i.e., random dispersal, priority effects; Egler 1954, Horn 1975) or deterministically (i.e., succession trajectories, CSR theory; Fox 1982, Grime 1977, Peet & Christensen 1987) promote assemblages of species with disturbance-adapted strategies (*reviewed by* Pulsford *et al.* 2016). However, disturbances may also alter the occurrence and outcome of density-dependent mutualistic, antagonistic, and resource interactions - a nuance that has rarely been integrated with the "winners and losers" paradigm (Anderson 2018, Gasith & Resh 1999, Post 2013). Given evidence for the prevalence of density-dependent interactions (Comita *et al.* 2014, Song *et al.* 2021) and their potential to affect local species diversity (Bagchi *et al.* 2014, Brown *et al.* 2020, LaManna *et al.* 2017, LaManna *et al.* 2022, Mitchell *et al.* 2006), incorporating density-dependent interactions into frameworks of community regeneration and recovery following disturbance presents a key opportunity to bridge the gap between community and disturbance ecology.

One important conceptual area examining how density-dependent interactions influence species diversity is the study of local conspecific density dependence (CDD). Local CDD is defined as the relative influence of local conspecific densities on individual performance (i.e. growth, survival, reproductive rates) arising primarily from intraspecific competition and interactions with shared antagonists and/or mutualists (LaManna *et al.* 2024). To distinguish from single-species concepts of density-dependent population regulation, we adopt the term local "stabilizing" CDD to describe local density-dependent effects that may stabilize population growth and influence species diversity in the context of a multi-species community. For example, population growth may be stabilized by local CDD that generates a negative relationship between conspecific densities and individual performance relative to heterospecific densities (i.e., stronger negative effect of conspecifics than heterospecifics; Hülsmann *et al.* 2024). Alternatively, local CDD can also destabilize population growth under certain conditions where the relationship between conspecific densities and individual performance is positive relative to heterospecific densities (i.e., stronger negative effect of heterospecifics than conspecifics; Hülsmann *et al.* 2024). Local stabilizing CDD is hypothesized to promote or stabilize local species diversity under certain conditions (Broekman *et al.* 2019, LaManna *et al.* 2017, Wright 2002), while local destabilizing

CDD is hypothesized to destabilize or erode local species diversity under certain conditions (Delavaux *et al.* 2023, Zahra *et al.* 2021). Hereafter, we use the term "stabilizing CDD" to refer to local conspecific density effects on individual performance that could scale to affect population growth and species diversity under certain conditions, regardless of whether the net effect is stabilizing or destabilizing. When discussing directional predictions for local CDD in the context of ecological disturbance (e.g., becoming more or less stabilizing), we explicitly state the direction of change.

Ecological disturbances, which disrupt local abiotic properties and/or the density of organisms, likely alter the role of stabilizing CDD in affecting individual performance and shaping local species diversity. However, the strength, directionality, and effects of stabilizing CDD in disturbed environments remains critically unexplored (Comita & Stump 2020, LaManna *et al.* 2024). In part, this knowledge gap persists due to a lack of underlying predictions for understanding how the drivers of local stabilizing CDD may be altered in disturbed environments. Moreover, studies integrating local stabilizing CDD and disturbance are hampered by: 1) complex interactions between the underlying drivers of local stabilizing CDD; 2) variability of disturbance effects due to system-specific resilience and susceptibility to rapid change; and 3) context-dependent factors affecting the outcome of interactions between individuals including phylogenetic relatedness, resource requirements, and functional traits.

Here, we begin to bridge the gap between disturbance ecology and the study of local stabilizing CDD using tree communities as a focal study system. First, we review recent observational and experimental studies of stabilizing CDD along abiotic gradients. Next, we develop a conceptual framework for exploring how disturbances might impact the local drivers of stabilizing CDD and how differences between conspecific and heterospecific effects may scale up to affect community assembly and diversity. Finally, we present critical gaps in knowledge and future directions for ecologists interested in integrating density-dependent interactions into frameworks of recovery and succession following disturbance.

2. Evaluating the Drivers of Local Stabilizing CDD in a Changing World

Over half a century has passed since Janzen (1970) and Connell (1971) first hypothesized that species diversity may be maintained by local, density-dependent interactions between relatively host-specific natural enemies (i.e., pathogens, herbivores, etc.) and their hosts. Since that time, ecologists have expanded this hypothesis to incorporate direct intraspecific competition (e.g., Adler *et al.* 2018), relatively host-specific mutualists (e.g., Bachelot *et al.* 2015, Delavaux *et al.* 2023, Kandlikar *et al.* 2019), and drivers that generate stabilizing CDD across spatial and temporal scales (e.g., Swenson *et al.* 2023). Today, there is broad support for the ability of disproportionately strong or weak conspecific interactions within a local neighborhood context to mediate performance, particularly among early life-stage plants (Comita *et al.* 2014; Hülsmann *et al.* 2021; Song *et al.* 2021). Debate continues to surround the ability of these local interactions to scale up and generate stabilizing CDD in population growth rates at the community and regional scales, a requirement for local interactions to affect species diversity (Chesson 2012, Hubbell 2001, Hülsmann *et al.* 2021, Hülsmann *et al.* 2024, LaManna *et al.* 2021, LaManna *et al.* 2024). However, theory and simulation studies suggest that under certain scenarios stabilizing CDD within local neighborhoods should contribute to community composition, diversity, and function (Chesson 2000, Levi *et al.* 2019, Smith 2022).

To distinguish between the types of local interactions capable of generating stabilizing CDD in individual performance, we place each driver into one of three categories: apparent, allelopathic, and resource interactions (Box 1-1, Figure 1-1). Each driver is hypothesized to generate either a negative (stabilizing) or positive (destabilizing) effect on conspecific relative to heterospecific performance. We highlight that each driver must be relatively host-specific, meaning it causes disproportionate effects on the performance of conspecific individuals relative to heterospecific individuals. For these purposes, host-specificity does not necessarily represent host-adaptation or preference (Bever *et al.* 2002). Additionally, functional or relative host-specificity, as opposed to absolute host-specificity, is sufficient to generate differential effects across hosts and therefore contribute to local stabilizing CDD (Spear & Broders 2021).

Ecologists are increasingly interested in how abiotic gradients affect the relative importance and strength of drivers that generate local stabilizing CDD (Comita & Stump 2020, LaManna *et al.* 2024). In general, local CDD appears to become more stabilizing in areas with low light, high soil moisture, and aseasonal climates (Table 1-1; Augspurger & Kelly 1984, Brown *et al.* 2021, LaManna *et al.* 2016, Lebrija-Trejos *et al.* 2023, Lin *et al.* 2012, Milici *et al.* 2020, Song *et al.* 2018). On broader spatial scales, local stabilizing CDD also appears to weaken with increasing elevation and latitude (Fibich *et al.* 2021, Hülsmann *et al.* 2024, LaManna *et al.* 2017, LaManna *et al.* 2021, LaManna *et al.* 2022). Together, these studies indicate that local CDD may vary predictably along abiotic gradients, suggesting common mechanisms contributing to patterns of plant performance.

Assigning mechanism to correlations between local stabilizing CDD and abiotic gradients is challenging. For example, abundant shade, humidity, and resources may generate stronger local stabilizing CDD by increasing host-specific antagonist loads (Inman-Narahari *et al.* 2016, Kobe & Vriesendorp 2011), or by altering spatial heterogeneity of resources (Johnson *et al.* 2017). Similarly, gradients of local stabilizing CDD may result from increased relatively host-specific facilitation under abiotic stress, such as interactions between plants and mycorrhizal fungi (Delavaux *et al.* 2023, Fajardo & McIntire 2011, Maestre *et al.* 2009). Finally, gradients of local stabilizing CDD may result from stress-mediated allelopathic or resource interactions, although these possibilities remain less explored (Devaney *et al.* 2018, Record *et al.* 2016). Given increasing uncertainty over the future of abiotic conditions and stressors (Seidl & Turner 2022), understanding the mechanisms underlying central ecological processes such as local stabilizing CDD will be important for predicting the effects of future disturbance patterns under climate change.

3. Categorizing Disturbances by Primary Effects on Forest Structure

Ecological disturbances have long been understood to influence community structure and dynamics across spatial and temporal scales (Cooper 1926, Pickett & White 1985, White 1979). However, developing inclusive definitions of disturbance that integrate a variety of causes, scales, and consequences for community structure and diversity remains a prominent challenge. Over the past century, the term "disturbance" has often been used to generally describe an event that disrupts any ecological level, environmental component, or the organizational status of organisms (Pickett 1989). Alternatively, disturbance can be defined as external events that influence ecosystem processes such as energy cycling, biomass accumulation, and hydrological patterns (Sousa *et al.* 1984, Swanson *et al.* 2011). More recently, explicit definitions of disturbances based on their spatial scale and/or level of ecological organization they affect have been proposed (i.e., local vs. regional disturbances; Battisti *et al.* 2016, Levin 2000). We acknowledge that clearly defining disturbance is central to understanding disturbance effects on local stabilizing CDD. Towards that goal, we present generalizable categories of ecological disturbance tailored to exploring their potential impacts on the interactions that generate local stabilizing CDD in forest ecosystems.

The function and structure of forest ecosystems are defined by the spatial composition and age distribution of trees (Ammer 2019). It is no surprise, therefore, that ecological disturbances in forests are often defined by their primary mode of influence on trees – either directly causing tree mortality or indirectly altering compositions through rapid changes to resources, habitats, and/or competitive environments. Forests experience a wide spectrum of naturally occurring disturbance events, including drought, windthrow, wildfire, and insect outbreaks, among others. Here, we group these individual disturbance types into three categories based on their primary mode of influence on trees: interference, destruction, and combined disturbances (Box 1-2). Interference disturbances, such as nutrient depletion, initially impact the availability of resources such as nutrients, light, and space while leaving competitive densities relatively un-disturbed in the short-term. Destruction disturbances, such as windthrow, initially impact tree abundance, density, and/or health while leaving resource availability relatively un-disturbed in the short-term. Finally, combined disturbances, such as wildfires, have initial impacts on both aboveground tree structures and resource environments in the short term.

While the initial effects of interference, destruction, and combined disturbances differ, each triggers a complex recovery timeline with cascading consequences for both the availability of nutrients and competitive densities. Here, we focus explicitly on predicting local stabilizing CDD through initial and late recovery phases following disturbance. We define initial recovery as the period immediately following disturbance, characterized by rapid changes in community composition and ecosystem processes as organisms respond to altered abiotic conditions. Late recovery is defined as the subsequent period when community composition begins to stabilize, characterized by slower rates of change and increasing functional redundancy (Chang & Turner 2019). We acknowledge two important caveats to this approach. First, not all disturbances fall cleanly into any one category (Box 1-2). Second, recovery phases are complex, and our predictions may need future refinement to account for system-specific successional trajectories. We highlight that most literature on local CDD along abiotic gradients focuses on one component of abiotic change (Table 1-1), and therefore categorizing disturbances by their initial abiotic effects represents a natural first step towards a more inclusive understanding of disturbance-CDD dynamics.

4. How Disturbances May Affect Local CDD in Individuals, Populations, and Communities

4.1: Primary Effects of Disturbance on Apparent, Allelopathic, and Resource Interactions

The primary mechanism by which disturbances might alter local stabilizing CDD is by strengthening or weakening the effects from its underlying drivers. Apparent, resource, and allelopathic interactions (Box 1-1, Figure 1-1**)** may all be altered by disturbance, which may increase or decrease the difference between local conspecific and heterospecific effects on performance depending on the primary effects of disturbance (Figure 1-2A). For example, combustion from wildfires reduces the abundance and colonization rates of many tree-associated mycorrhizal fungi (DeVan *et al.* 2023, Dove & Hart 2017). Reduced facilitation from mycorrhizal fungi following wildfire may cause stronger local stabilizing CDD because relatively host-specific benefits from mycorrhizal fungi should otherwise counteract stabilizing effects from shared pathogens. Alternatively, if wildfire were to disproportionately reduce the abundance of host-specific pathogens relative to host-specific mutualists, then wildfire may weaken local stabilizing CDD, even to the point of generating local destabilizing CDD (Hewitt *et al.* 2023). Understanding how the underlying drivers of local stabilizing CDD respond to different categories of disturbance across time is key to estimating the relative differences between conspecific and heterospecific effects on individual performance.

A central challenge with generalizing the primary effects of disturbance on local interactions is that species do not monolithically respond to disturbance. Instead, individual performance in disturbed environments differs on life-history, stress tolerance, and functional trait axes (Lavorel *et al.* 1997), which together alter the apparent, allelopathic, and resource interactions generating local stabilizing CDD in recovering communities (Brown *et al.* 2020, Pu *et al.* 2020, Zhang *et al.* 2021). For example, fast growing tree species benefit from increased light (Seidl *et al.* 2014) but are often more susceptible to natural enemies due to reduced investment in physical and chemical defenses compared to slow-growing tree species (McCarthy-Neumann & Kobe 2008, Zhu *et al.* 2018, Zang *et al.* 2021). The strength of apparent, allelopathic, and resource interactions of fast-growing and slow-growing tree species may therefore vary with life-history strategies and functional traits through community assembly and recovery.

4.2: Primary Effects of Disturbance on Local Stabilizing CDD in Populations and Communities

While not central to our synthesis, we highlight that disturbances may also alter the effect of local stabilizing CDD at the population and community scales by altering fitness hierarchies, selecting for closely-related species, and limiting conspecific densities (Fig 2B-C). Such factors at higher levels of ecological organization likely influence the extent to which local stabilizing CDD scales up to impact populations and communities, and we highlight Scale Transition Theory as a potentially useful framework for understanding the scaling of local CDD effects (Chesson 2012). Given that disturbances occur along variable spatial and temporal scales, creating complex feedbacks between individual-level processes and population-level outcomes, these factors are important considerations for future studies.

Local stabilizing CDD is thought to stabilize populations that otherwise would not coexist due to intrinsic fitness differences, disadvantaging performance of otherwise dominant species and maintaining local diversity (Adler *et al.* 2007, Chesson 2000). As disturbances alter the availability of space and resources (nutrients, light, space, etc.), they likely confer competitive advantages to species with disturbance-adapted traits - thereby generating novel fitness hierarchies in multi-species communities (Figure 1-2B, Loehle 2000**)**. The performance of disturbance-adapted species may be released from otherwise strong local stabilizing CDD if disturbances accentuate intrinsic fitness differences.

Additionally, disturbed environments favor species that share similar adaptations – potentially increasing phylogenetic relatedness among recovering communities (Burns & Strauss 2011). Increased relatedness may affect the degree to which heterospecific apparent, allelopathic, and resource interactions influence conspecifics, and vice versa. For example, many tree-associated taxa (i.e., herbivores, mycorrhizal fungi, etc.) are clade or genera-specific (Novotny *et al.* 2002, Gilbert & Webb 2007), which can lead to stabilizing density effects at higher taxonomic levels (e.g., con-mycorrhizal density dependence; Averill *et al.* 2022, Delavaux *et al.* 2023, Zhu *et al.* 2015). Generally, we expect that increased relatedness could strengthen local stabilizing CDD by intensifying competitive interactions among related species – unless functional traits are uncorrelated with phylogeny (Bunker & Carson 2005, Mayfield & Levine 2010, Kraft *et al.* 2015).

Finally, disturbance-altered local stabilizing CDD may have limited effects on community dynamics due to lower local densities following disturbances (Figure 1-2C, Kobe & Vriessendorp 2011). For example, strong local stabilizing CDD may fail to influence populations or communities if disturbed conditions limit conspecific densities or interactions. Limited conspecific densities may have long-term consequences for community assembly driven by declines in relative host-specificity among interactions. Altered fitness hierarchies, phylogenetic relatedness, and limited conspecific densities are important considerations for examining local CDD at the population and community scales – but fall outside the scope of our synthesis which is primarily focused on the underlying interactions generating local stabilizing CDD in individual performance.

5. Disturbance Severity and Biological Legacies

The effects of disturbance on ecological communities depends on the severity as well as the spatial and temporal regime of disturbance (Figure 1-3, Turner 2010). Disturbances range from spatially and temporally discrete (e.g., wildfire, hurricanes) to spatially and temporally ambiguous, often overlapping in time and space (e.g., nutrient deposition, extreme heat events, drought; Graham *et al.* 2021, Reyer *et al.* 2015). These spatial and temporal disturbance regimes likely have long-term consequences for local conspecific and heterospecific densities as well as fitness hierarchies defining the effects of local CDD on community structure (Comita & Stump 2020). Generally, we predict that high frequencies or severities of disturbance are expected to limit conspecific densities and select for stress-tolerant species that generate less stabilizing conspecific density effects, thereby reducing the overall effect of local CDD on community assembly (Fig 3A-B, Vasquez & Simberloff 2002). Still, severity and frequency are not sufficient to explain variations of local CDD along abiotic gradients, as the category of disturbance (i.e., interference, destruction, combined) plays a significant role in determining community dynamics through recovery (Box 1-2).

Recovery and successional trajectories are frequently mediated by persisting abiotic properties, species compositions, and disturbance refugia – a phenomenon known as biological legacies or legacy effects (Bowd *et al.* 2021, Cuddington 2011, Jacquet & Altermatt 2020). Biological legacies are a primary pathway by which local stabilizing CDD may persist following disturbance. For example, root structures of damaged or dead trees may provide important refugia for host-associated natural enemies and mutualists (Mayer *et al.* 2022), which remain able to influence performance among neighboring conspecific individuals (Magee *et al.* 2024). Similarly, legacies of resource and allelopathic interactions may persist through disturbance and alter the recovery of both conspecific and heterospecific individuals. Thus, legacy effects are an important consideration for predicting local stabilizing CDD through initial and late recovery.

In the following sections we discuss the implications of the three disturbance categories, interference, destruction, and combined, for local stabilizing CDD (Figure 1-4). In each disturbance category we 1) synthesize studies of local CDD along observational or experimental abiotic gradients, 2) predict the generalizable effects of disturbance on local stabilizing CDD, and 3) present a prominent disturbance example to explore CDD-disturbance relationships in more detail. In each example we further specify the implications of local stabilizing CDD through initial and late recovery – highlighting gaps in knowledge and generating predictions where possible.

6. Effects of Interference Disturbance on Local Stabilizing CDD

Interference disturbances, which primarily alter abiotic conditions without immediately impacting tree species composition, are common and expected to increase in frequency and intensity over the next century (Box 1-2, Cook *et al.* 2018, Seidl *et al.* 2017). Initially, interference alters the availability and spatial heterogeneity of key limiting resources, such as water, nutrients, and light. Classic examples of interference include organic matter depletion (Federer *et al.* 1989), nitrogen deposition (Janssens *et al.* 2010), extreme rain events (Margrove *et al.* 2015), and drought. Given that many mechanisms driving local stabilizing CDD are directly related to resource availability or are impacted by resource-related stress, we emphasize that interference may have strong cascading effects on local stabilizing CDD in forest systems. To synthesize and highlight knowledge gaps, we focus on the primary effects and implications for recovery of a prominent natural interference disturbance: drought.

6.1. Initial Effects of Drought on Local Stabilizing CDD

The initial mechanism by which drought alters local interactions is by reducing water availability, which likely affects the negative apparent interactions driving local stabilizing CDD. Moisture is a central requirement for the germination and dispersal of many pathogenic host-associated taxa (fungi, bacteria, oomycetes, etc.), and reduced moisture is associated with reduced pathogen loads and pathogen spread between conspecifics (Milici *et al.* 2020, Boczoń *et al.* 2021). However, pathogenic host-associated taxa and herbivores also induce mortality at higher rates in drought-stressed adult trees compared to controls (Anderegg *et al.* 2015, Bell *et al.* 2020, Caldeira 2019, Gely *et al.* 2020, Oliva *et al.* 2014). To date, most relevant studies of local stabilizing CDD have focused on small observational or experimental reductions in precipitation, finding that local stabilizing CDD weakens, even to the point of becoming destabilizing, with decreasing precipitation (Figure 1-4A; Bachelot *et al.* 2020, Jiang *et al.* 2024, Lebrija-Trejos *et al.* 2023, Milici *et al.* 2025, Ramage *et al.* 2023, Song *et al.* 2020, Song *et al.* 2024, Uriarte *et al.* 2018). There remain uncertainties over the degree to which this trend is generalizable across functional traits and life histories, and how drought severity and recovery timelines impact local stabilizing CDD (Bachelot *et al.* 2015, Milici *et al.* 2020).

Key to understanding drought effects on local stabilizing CDD is the relative impact of reduced water availability on the abundance of host-specific natural enemies relative to generalists. Certain tree-associated pathogenic microorganisms are more protected from drought, including endophytic pathogens which colonize intercellular apoplastic spaces. Other pathogenic microorganisms, such as externally attached epiphytic pathogens, are likely more drought sensitive (Sohrabi *et al.* 2023). Little is known of the relative host-specificity of epiphytic and endophytic pathogens associated with tree roots (Barrett & Heil 2012), and our understanding is complicated by microorganisms that switch from pathogenic to mutualistic, and endophytic to epiphytic, over life stages (Redman *et al.* 2001).

General support for weakened local stabilizing CDD, or even local destabilizing CDD, under drought conditions may be caused by increasing effects of mutualistic interactions paired with declines in pathogen spread between conspecifics (Milici *et al.* 2020). For example, mycorrhizal fungi and leaf endophytes both confer drought tolerance by providing physical protections against water loss and pathogen infection as well as upregulating exchange of mineral ions and water (Augé *et al.* 2015, Püschel *et al.* 2021). Strong destabilizing apparent interactions with mutualists may therefore contribute to weaker local stabilizing CDD immediately following drought (Figure 1-4A, Bachelot *et al.* 2015, de Vries *et al.* 2023). Additionally, relative differences in host-specificity among mycorrhizal fungal types and leaf endophytes, along with functional trait variety in tree hosts, may underly species-specificity in initial drought effects on local stabilizing CDD (Lebrija-Trejos *et al.* 2023, Liu & He 2022, Ramage *et al.* 2023, Song *et al.* 2021, Uriarte *et al.* 2018).

For example, the contribution of mycorrhizal fungi to local stabilizing CDD under drought likely varies between dominant eco-physiological types: ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM; de Vries *et al.* 2023). AM fungi form arbuscules within root cell walls and therefore are thought to be more drought resistant than EcM fungi, which form sheaths around root structures and between root cells (Osonubi *et al.* 1991, Wu & Zou 2017, Kilpeläinen *et al.* 2017). AM fungi are also thought to be less relatively host-specific than EcM fungi therefore contribute less to local stabilizing CDD (Laliberté *et al.* 2015). Local stabilizing CDD may be disproportionately weakened in EcM trees relative to AM trees under drought, although the degree to which mycorrhizal type alters drought tolerance and recovery timelines remains uncertain.

Along with apparent interactions, the ratio of intraspecific to interspecific competition under drought appears to vary, likely contributing to local destabilizing CDD in some cases (Gazol & Camarero 2016, Lin *et al.* 2012), and local stabilizing CDD in others (O'Brien *et al.* 2017, Jourdan *et al.* 2020). These context dependencies are likely a product of novel fitness hierarchies under drought (Castagneri *et al.* 2022, Hommel *et al.* 2016). For example, species with disturbance-adapted traits may experience stronger stabilizing effects as spatially aggregated conspecifics compete for increasingly limited water and mobile soil nutrients. Future studies should consider interactions between intraspecific competition, functional traits, and the implications of reduced plant defenses under drought conditions as factors affecting the strength and directionality of local stabilizing CDD.

6.2. Effects of Drought on Local Stabilizing CDD through Late Recovery

As forest communities recover from drought, increased adult mortality rates open forests canopies and reduce microclimatic buffering – increasing sub-canopy temperatures and incident radiation levels (Hanson & Weltzin 2000). Increased temperatures may be particularly relevant for early ontogenetic stages such as seedlings, where local stabilizing CDD effects on performance are generally strongest (Comita *et al.* 2014, Song *et al.* 2021). Among seedlings, there appears to be no generalizable effects of warming on local stabilizing CDD (Table 1-1, Bachelot *et al.* 2020, Germain & Lutz 2022, Liu & He 2021, Song *et al.* 2018). Disparity among prior studies may point to nonlinear functional responses to drought depending on the intensity of warming. For example, Bachelot *et al.* (2020) find evidence for increased survival for conspecific seedlings under strong warming (4°C) while Liu & He (2021) find decreased survival for conspecific seedlings under weaker warming conditions (1.2 ± 0.5°C). There also appears to be a role for functional traits

(Song *et al.* 2021) and tolerance among host-associated taxa (Liu & He 2022) in mediating warming effects on local CDD.

Beyond warming effects, the relative strength of apparent, allelopathic, and resource interactions through late recovery remains largely underexplored. Uriarte *et al.* (2018) found evidence for stabilizing local CDD in dry tropical sites, but not for wet tropical sites under drought conditions, which may indicate that short- and long-term drought have different implications for community assembly. Reduced plant defenses under drought may persist through late recovery (Xu *et al.* 2010), increasing the stabilizing effect of antagonists. Reduced defenses may also contribute to increased stabilizing apparent interactions through the proliferation of secondary antagonists that specifically target weak, stressed trees (Jactel *et al.* 2012). However, decreased defenses may not always translate to stronger stabilizing effects, such as when reduced production of negative allelopathic compounds weakens local stabilizing CDD in regenerating seedlings (Hasanuzzaman *et al.* 2013). Moreover, the implications of weakened tree defenses and additional secondary antagonists for local stabilizing CDD may or may not be additive and may vary between leaf and root structures where drought severity and recovery timelines also vary (Milici *et al.* 2020, de Vries *et al.* 2023). We highlight interactions between reduced defenses, reduced allelopathy, and increased virulence of primary and secondary antagonists as important considerations for future studies assessing local stabilizing CDD under drought.

6.3. Predictions and Gaps for Local Stabilizing CDD and Interference Disturbances

Interference disturbances are thought to have wide ranging implications on the underlying apparent, allelopathic, and resource interactions driving local stabilizing CDD. We predict that local CDD becomes generally destabilizing following interference and returns to stabilizing as recovery progresses (Figure 1-4A). There are several important limitations to our predictions. First, most studies of local CDD under interference rely on short-term variations or seasonal differences of precipitation, nutrients, and temperature and disproportionately examine seedling mortality in tropical systems (Table 1-1). Interference effects may be limited among seedlings when nearby canopy adults buffer against macroclimatic extremes (de Frenne *et al.* 2021), an effect which may only erode under severe interference (Davis *et al.* 2019). Studies of interference under buffered canopies may miss critical interactions with light availability, warming, and seedling performance that only emerge when disturbance is severe or prolonged. Second, recovery from interference involves factors that may not be present following short-term interference, including secondary antagonists and compound disturbance events (e.g., insect outbreaks following wildfire; Gely *et al.* 2020, Littell *et al.* 2016). Additionally, functional trait and life history variety among individuals in local communities is likely to modulate the effects of interference on local stabilizing CDD, although this has received relatively little attention in the literature. We emphasize the need for observational and experimental studies of population dynamics under severe and long-term interference to increase our confidence in predicting future community responses to drought and other interference disturbances.

7. Effects of Destruction Disturbance on Local Stabilizing CDD

Destruction disturbances primarily alter plant competitive densities, compositions, and condition, while having limited initial effects on nutrient and chemical properties (Box 1-2). Destruction disturbances are highly variable in spatial scale, ranging from local windfall events or pathogen infections that create patches of downed trees to landscape-scale destructive disturbances such as hurricanes or massive pathogen outbreaks. Destructions disturbances are often associated with biological legacies in the form of remnant trees, residual organisms (e.g., microbes, herbivores), propagules, and abiotic conditions (e.g., allelopathy, spatial resource patterns) influenced by previous plant compositions (Johnstone *et al.* 2016). To date, the degree to which destruction and biological legacies interact to influence local stabilizing CDD remains largely unstudied. Chan *et al.* (2023) simulate that local stabilizing CDD may be relatively unaffected by destruction disturbance if legacies of conspecific density are strong. Magee *et al.* (2024) corroborate this prediction, finding that local stabilizing CDD among adult trees remains strong, and even becomes more stabilizing, when individual mortality events are considered. Still, others find that biological legacies may erode quickly after destruction disturbances – or even flip from stabilizing to destabilizing (Figure 1-4B, Brown *et al.* 2021, Esch & Kobe 2021). To synthesize and highlight knowledge gaps, we focus on how local stabilizing CDD responds both in initial and late recovery from a prominent destruction disturbance: windthrow.

7.1. Initial Effects of Windthrow on Local Stabilizing CDD

Windthrow generates canopy gaps and structural heterogeneity, reducing host availability and indirectly altering resource environments (Ulanova 2000). To date, few studies have focused explicitly on local stabilizing CDD in gaps despite their ubiquity and potential to affect forest structure (*but see* Brown *et al.* 2021, Wulantuya *et al.* 2020). For species with root functional traits conferring resistance to wind-damage, such as deep root systems or roots that spread laterally into regions of dense soil (Dupuy *et al.* 2005, Ray & Nicoll 1998), windthrow may increase the ratio of intraspecific resource competition relative to interspecific competition. Shared functional traits and life history strategies among wind-resistant trees may translate to increased intraspecific competition for limiting resources – although these effects may be muted by an overall release from competitive interactions.

We predict that windthrow effects on local stabilizing CDD through initial recovery largely depend on the spatial patterns and scale of disturbance. Small windthrow events, where atmospheric and light conditions remain relatively unchanged, likely maintain stronger biological legacies (Sicoe *et al.* 2023). In contrast, larger events may create edge-like conditions where local stabilizing CDD is typically weaker (Krishnadas *et al.* 2018). Patch connectivity further influences these dynamics – larger and more connected patches maintain more diverse communities of host-specific organisms (Johnsone *et al.* 2016), while the arrangement of fallen trees can create corridors or barriers affecting organism movement between patches (Franklin *et al.* 2000). In areas with numerous canopy gaps, Brown *et al.* (2021) found that local CDD varied from stabilizing to neutral to destabilizing among sapling species – potentially pointing to the importance of functional traits in determining disturbances responses. Wulantuya *et al.* (2020) found similar functional variety, with shade-tolerant trees experiencing more stabilizing local CDD in gaps relative to shade intolerant species. We expect small-scale windthrow disturbances to have limited initial effects on the apparent and allelopathic interactions contributing to local CDD. Allelopathic compounds likely persist in relatively unaltered soils, particularly where fallen trees create dense patches of woody debris. Similarly, apparent drivers of local stabilizing CDD, such as microbial communities and herbivores, likely persist in undisturbed soils and gap refugia (Seidl *et al.* 2014).

7.2. Effects of Windthrow on Local Stabilizing CDD through Late Recovery

The persistence of biological legacies of local stabilizing CDD through recovery likely depends on system-specific decomposition and nutrient cycling rates (Johnstone *et al.* 2016, Ke & Levine 2021). For example, microbial compositions appear to quickly to match pre-disturbance compositions in some systems (Mayer *et al.* 2022), and follow priority effects towards alternative stable states in others (Jacquet & Altermatt 2020, Miller *et al.* 2021). Rapid turnover may contribute to findings that legacies of local stabilizing CDD in seedling mortality erodes rapidly following destruction (Esch & Kobe 2021). However, legacies of local stabilizing CDD may persist longer in adults, particularly after small-scale individual mortality events (Magee *et al.* 2024). Since successional stages are correlated with distinct microbial compositions (Liang *et al.* 2022), future studies of local stabilizing CDD following destruction disturbance should consider life and successional stages, microbial priority effects, and system-specific turnover rates.

Late recovery following windthrow disturbance is characterized by increased light availability and radiation and decreased moisture and microclimatic buffering (Mitchell 2013), which likely reduces the abundance and spread of natural enemies – and may amplify the effects of mutualists on individual performance (Wulantuya *et al.* 2020). Locally dry and hot conditions, coupled with mechanical damage, likely increases the susceptibility of trees to secondary antagonists (Bouget & Duelli 2004), which could strengthen local stabilizing CDD. Ultimately, we expect that correlated changes to abiotic conditions and apparent interactions will have significant implications for remnant tree health and local stabilizing CDD through recovery.

During long trajectories of recovery, repeated windthrow events can promote structural complexity, which may have emergent effects on local stabilizing CDD at both individual and community scales. Windthrow-generated structural heterogeneity can persist for extended periods (Ulanova 2000, Marra *et al.* 2014), creating diverse microhabitats that promote local diversity and could contribute to stronger local stabilizing CDD. However, repeated windthrow events may also limit conspecific densities and reduce the effects of local CDD on community dynamics (Kobe & Vriesendorp 2011). We emphasize that structural heterogeneity, biological legacies, and microclimatic conditions generated by windthrow are all important factors to consider when assessing local stabilizing CDD in destruction-disturbed forests.

7.3. Predictions and Gaps for Local Stabilizing CDD and Destruction Disturbances

Destruction disturbances present interesting opportunities for studying how biological legacies and spatially heterogenous disturbance patterns affect local stabilizing CDD. We predict that local CDD may initially remain strongly stabilizing following destruction disturbances, especially if injured trees enhance the stabilizing effect of antagonists and intraspecific competition (Figure 1-4B). As recovery progresses, we predict that strong legacies of local CDD may slowly weaken as abiotic conditions become less favorable to tree-associated microbiomes and new spatial patterns of tree hosts emerge. Several important knowledge gaps remain. First, the relative importance of biological legacies versus remnant-tree populations in maintaining local stabilizing CDD following destruction is poorly understood. Second, the spatial scale at which destruction affects local stabilizing CDD requires further study, particularly how the size and distribution of gaps influences apparent interactions (Brown *et al.* 2021). Finally, the interaction between destruction and other disturbances (e.g., insect outbreaks triggered by damaged trees) may have complex effects on local stabilizing CDD that warrant investigation. To address these gaps, we highlight the need for long-term studies and experimental manipulations of the interactions between gap size, biological legacies, and local stabilizing CDD following destruction disturbance.

8. Effects of Combined Disturbance on Local Stabilizing CDD

Combined disturbances are defined as ecological disturbances with initial effects on abiotic conditions as well as plant densities, compositions, and/or mean plant condition (Box 1-2). In forests, combined disturbances alter the physical structure and composition of trees, soil properties, and the nutrient-cycling processes that define community structure and function (Huston 2014). Many combined disturbance events, such as wildfires, are increasing in frequency, extent, and intensity with climate change (Ellis *et al.* 2022). To date, little is known about how combined disturbances interact with local stabilizing CDD. The prevailing paradigm is that combined disturbances decrease the relative importance of biotic interactions relative to functional traits and abiotic conditions (Hollingsworth *et al.* 2013). In the following section, we highlight how this paradigm may be useful – and yet insufficient – to explain conspecific density effects in combined disturbance settings using a prominent example: wildfire.

8.1. Initial Effects of Wildfire on Local Stabilizing CDD

Wildfires initially induce tree mortality through combustion and lethal tissue temperatures, reducing conspecific densities and surging nutrient availability, particularly in the form of pyrogenic carbon (Bodi *et al.* 2014). Reduced conspecific densities, altered nutrient availability, and mortality among organisms generating stabilizing or destabilizing apparent interactions appears to generally neutralize local stabilizing CDD (HDD = CDD; Figure 1-4C; Senior *et al.* 2018, Warneke *et al.* 2023). Influxes of pyrogenic carbon associated with wildfires can also neutralize allelopathic compounds (Zackrisson *et al.* 1996), potential reducing the stabilizing effect of negative allelopathy on local CDD. However, species-specific susceptibility to wildfire and the conditions created by the post-fire environment challenge generalizations (Furniss *et al.* 2022, Tamjidi & Lutz 2020). For example, wildfire likely reduces stabilizing resource interactions by increasing resource availability, which may advantage performance of fire-adapted species (such as those with functional advantages to survival in high-light, low moisture environments) over fire-susceptible species (Andreu *et al.* 2001, Burkle *et al.* 2015, Spasojevic *et al.* 2016). However, relative intraspecific competition among fire-adapted species, and increased phylogenetic relatedness in the post-fire environment, may intensify local stabilizing CDD through initial recovery.

Along with altered abiotic conditions and spatial patterns of nutrient availability, wildfires also have primary effects on belowground microbial communities of natural enemies and mutualists that drive apparent interactions between conspecific individuals. Increased nutrient availability and decreased allelopathic chemical concentrations following wildfire generally result in saprotroph-dominated fungal communities (Hewitt *et al.* 2023, Rodriguez-Ramos *et al.* 2021). Much remains uncertain surrounding the effects of wildfire on soil microbial communities that influence plant performance, including the degree to which wildfires impact host-specific antagonists relative to generalist antagonists and whether dead, remnant wood (e.g. debris and standing snags) provide refugia for host-specific antagonists (Senior *et al.* 2018. Warneke *et al.* 2023). Among mutualists, ectomycorrhizal fungi are thought to be disproportionately susceptible to wildfire-induced mortality due to external root sheathing (Dove & Hart 2017, Mizraei *et al.* 2023). Therefore, ectomycorrhizal trees may experience more stabilizing local CDD than pre-fire conditions – although these effects would be muted in community assembly if coupled with dramatic reductions in conspecific densities (Figure 1-3B, 1-4C).

8.2. Effects of Wildfire on Local Stabilizing CDD through Late Recovery

Limited studies indicate that the effects of conspecific adult density on community assembly through recovery are species- and context-specific (Furniss *et al.* 2020, Larson & Franklin 2005). Context-specificity may arise due to system-specific soil compositional changes, such as erosion, compaction, and changing nutrient abundances along with biological legacies (Bowd *et al.* 2021). Additionally, wildfire-produced charcoal from different tree species can have unique structural and chemical traits (Pluchon *et al.* 2015) that may have consequences for spatial relationships between conspecific densities and nutrient availability through recovery. Moreover, context-specific nutrient availability likely mediates novel spatial patterns of host-specific antagonists and mutualists (Hewitt *et al.* 2023, Pulido-Chavez *et al.* 2021) in ways that may alter local stabilizing CDD (Furniss *et al.* 2022).

We predict that some species-specificity in local stabilizing CDD through long-term recovery from wildfire arises from emergent effects of phylogenetic relatedness and shared tree-associated taxa. For example, ectomycorrhizal fungi are more likely to disperse, establish, and thrive in burned areas relative to other tree-associated fungi that lack the ability to decompose organic matter (Day *et al.* 2020). If post-fire communities are closely phylogenetically-related and associate with ectomycorrhizal fungi, then local stabilizing CDD may be weak or destabilizing through recovery. To date, studies of microbial function and compositional changes following wildfire indicate a wide spectrum of resiliency among functions of the microbiome (e.g., nutrient cycling), and long-lasting priority effects on microbial community structure (Hewitt *et al.* 2023, Pérez-Valera *et al.* 2020). We emphasize that understanding changes to the tree-associated microbiome through late recovery is essential to estimating the strength and role of local stabilizing CDD.

8.3. Predictions and Gaps for Local Stabilizing CDD and Combined Disturbances

Combined disturbances present unique challenges for understanding local stabilizing CDD due to their simultaneous effects on conspecific densities and abiotic conditions. We predict that local stabilizing CDD is initially neutralized following most combined disturbances, which reduce conspecific densities and remove biological legacies (Furniss *et al.* 2022, Tamjidi & Lutz 2020, Senior *et al.* 2018, Warneke *et al.* 2023). Through late recovery, the strength and direction of local stabilizing CDD likely depends on interactions between pyrogenic carbon, disturbance refugia, and the success of antagonists relative to mutualists in colonizing disturbed sites (Furniss *et al.* 2020, Larson & Franklin 2005). Several critical knowledge gaps remain. First, the relative host-specificity of early-colonizing microbes following combined disturbances, and their effects on remnant tree hosts, requires further study (Nelson *et al.* 2022). Second, the degree to which novel nutrient compositions alter apparent and allelopathic interactions through initial and later recovery remains poorly understood. Finally, the severity and spatial heterogeneity of combined disturbance may create complex mosaics of local stabilizing CDD with unpredictable or emergent effects at population and community scales. We emphasize that research should focus on long-term studies across gradients of severity and incorporate the effects of refugia and successional trajectories on local stabilizing CDD.

9. Special Considerations for CDD-Disturbance Dynamics

9.1. Biological Invasion

A related conservation concern associated with ecological disturbances is the establishment and proliferation of naturalized taxa. Ecological disturbances open niche space and alter fitness hierarchies, priming disturbed areas for invasion (Hobbs & Huenneke 1992, Lembrechts *et al.* 2016). This is reflected in the life-histories and functional traits of many prominent naturalized plants, which thrive in high-light, low-nutrient disturbed environments. The potential effects of invasion on local stabilizing CDD have received relatively more attention in the literature than the drivers of ecological disturbance discussed here (*see* Klironomos 2002, Mitchell *et al.* 2006, Reinhart & Callaway 2006, Sullivan *et al.* 2017, Taylor & Hasting 2005). Much like interference disturbances, biological invasions alter interactions between trees and their surrounding environment. Invading taxa are often released from natural enemies, negative resource interactions, and negative allelopathic interactions, and therefore are expected to exhibit destabilizing CDD (enemy-release hypothesis; Williamson 1996, Williams & Levine 2018). However, enemy release likely correlates with mutualist release, a potential limit to local diversity

(Delavaux *et al.* 2024). Future studies of the enemy-release hypothesis in the context of local stabilizing CDD could shed light on the degree to which invasion success is mediated by the underlying drivers of local CDD and the role of functional similarity or phylogenetic relatedness in driving invasion patterns.

9.2. Temporal Variation and Climate Change: A Split Perspective

We know little about how novel disturbance regimes under climate change may affect the strength and role of local stabilizing CDD. Warming and novel disturbance regimes are likely to increase average physiological stress and phenological mismatches (Keeler *et al.* 2021), potentially weakening the underlying drivers of local stabilizing CDD and generating cascading negative impacts on species diversity, productivity, and carbon storage (Broekman *et al.* 2019, Germain & Lutz 2022). Additionally, increasing interannual climate variability may weaken local stabilizing CDD by exposing individuals to novel and extreme abiotic conditions (Germain & Lutz 2020). However, there remains the possibility that warming and altered climatic regimes may benefit pathogens driving local stabilizing CDD (Delgado-Baquerizo *et al.* 2020, Pugnaire *et al.* 2019), as well as the possibility that species with similar functional traits (i.e., “winners” of climate change) may contribute to communities where intraspecific competition is disproportionately strong (de Bello *et al.* 2021). Predictions of forest composition and diversity under future climate scenarios should consider how stabilizing factors like local CDD may mediate community responses to a rapidly changing world.

10. Conclusions

Understanding how ecological disturbances influence the organisms that interact to generate local stabilizing CDD is critical to understanding individual performance, population growth, and local diversity across spatial and temporal scales. Our synthesis reveals that different categories of disturbance—interference, destruction, and combined—have distinct implications for the underlying drivers of local stabilizing CDD and their ability to influence community assembly. While interference disturbances weaken local stabilizing CDD and even generate destabilizing CDD, destruction disturbances may maintain stronger biological legacies of local stabilizing CDD, and combined disturbances often neutralize local stabilizing CDD entirely. Moving forward, empirical studies that integrate local stabilizing CDD within broader ecological frameworks of disturbance and recovery will be essential for predicting community responses to novel disturbance regimes. Particular attention should be paid to species-specific responses, spatial heterogeneity of disturbance effects, and the persistence of biological legacies through recovery - all of which may fundamentally alter how local biotic interactions contribute to maintaining species diversity in an era of accelerating global change.

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Boxes, Figures and Tables

Box 1-1: Defining the Drivers Causing Local Conspecific Density Dependence (CDD) to be stronger than Local Heterospecific Density Dependence (HDD)

Hülsmann *et al.* (2021) categorize the mechanisms capable of generating local stabilizing CDD (also negative CDD; CNDD) into three separate groups: 1) host-specific enemies, 2) abiotic niche differentiation, and 3) autotoxicity. Here, we additionally integrate the drivers capable of generating destabilizing CDD including host-specific mutualists, strong interspecific competition, and allelopathy (Figure 1-1). We generalize these new categories to 1) apparent interactions, 2) resource interactions, and 3) allelopathic interactions. Importantly, stabilizing and destabilizing CDD are defined in relation to heterospecific densities, or the measurement of conspecific effects after accounting for the effects of heterospecifics (Hülsmann *et al.* 2024, LaManna *et al.* 2024).

Apparent Interactions

Local CDD in trees is most often stabilizing and largely thought to be generated by negative apparent interactions with host-specific taxa in the phyllosphere and rhizosphere; including herbivores, root and leaf-associated fungi, and other microscopic organisms (apparent competition; Bagchi *et al.* 2010, Bachelot *et al.* 2020, Chen *et al.* 2019, Desprez-Loustau *et al.* 2006, Holt 1977, Liu *et al.* 2022, Mangan. *et al.* 2010, Packer & Clay 2000, Song *et al.* 2018).

However, local CDD can also be destabilizing, driven by positive apparent interactions with mycorrhizal fungi and mutualistic foliar endophytes (apparent facilitation*;* Bachelot *et al.* 2015, Delavaux *et al.* 2023, Pu *et al.* 2022, Zahra *et al.* 2021). Together, antagonistic and mutualistic apparent interactions contribute to the net stabilizing or destabilizing effects of local CDD (Bever *et al.* 1997, Jiang *et al.* 2020)

Resource Interactions

Local stabilizing CDD in trees can also be generated by strong intraspecific relative to interspecific competition. For example, many tree species exploit resources or habitat spaces in a manner that reduces the survival and growth of other nearby conspecific individuals, thereby generating local stabilizing CDD (Comita *et al.* 2014, Johnson *et al.* 2017). Resource interactions often contribute to local stabilizing CDD at both individual (Umaña *et al.* 2018) and population scales (Wiegand *et al.* 2021). While less common, resource interactions can also generate local destabilizing CDD through stronger interspecific competition than intraspecific competition, which advantages demographic rates of clustered conspecifics relative to those near heterospecific individuals (e.g., resource facilitation such as hydraulic lift of limiting resources; Armas *et al.* 2010).

Allelopathic* Interactions

Less frequently invoked as a driver of local CDD are allelopathic compounds produced by trees. These compounds can generate locally stabilizing or destabilizing CDD by disproportionately impacting the growth and survival of conspecific individuals relative to heterospecific individuals (Mazzoleni *et al.* 2015, Hierro & Callaway 2021, Yuan & van Kleunen 2022). Allelopathic interactions are thought to be most often stabilizing, such as chemical production that inhibits conspecific relative to heterospecific demographic rates. However, allelopathic interactions can also be destabilizing when allelopathy benefits conspecific demographic rates relative to heterospecifics (e.g., pathogen suppression).

*****In 1937, Molisch first presented the term allelopathy with the publication of *The influence of one plant on another: allelopathy* (Molisch 1937 [2001]). Although our modern use of *pathy* often exclusively refers to harmful, negative effects, Molisch's original definition sought to incorporate both positive and negative chemical interactions among plants. Here, we use the original meaning of Molisch's term *allelopathy*, and distinguish directionality with "positive", "negative", or "neutral" (*as described by* Hierro & Callaway 2021).

Box 1-2: Defining Categories of Ecological Disturbance for Understanding Disturbance Effects on CDD

In 1985, Edward Rykiel proposed four categories for ecological disturbances: interference, destruction, decomposition, and suppression (Rykiel 1985). Here, we adapt these categories to delineate how different disturbances may have differing effects on the underling apparent, allelopathic, and resource interactions generating local stabilizing CDD in forests.

Interference

- **Rykiel 1985 Definition:** Matter/energy/information exchange processes are inhibited.
- **Working Definition:** An *event* or *agent* that primarily alters nutrient availability or chemical properties in the system while leaving plant competitive densities and compositions relatively intact.
- **Examples:** In trees this category of disturbance most often influences soil nutrient, water, and light availability. Prominent examples of interference include drought, nutrient depletion, and

nutrient decomposition – all of which primarily act by altering the availability and compositional heterogeneity of resources.

Destruction

- **Rykiel 1985 Definition:** Existing biomass is reduced in quantity (*see also* Grime 1979).
- **Working Definition:** An *event* or *agent* that dramatically alters plant competitive densities and compositions, or lowers mean plant health, while leaving nutrient and chemical properties largely intact.
- **Examples:** Prominent examples of plant disturbances include logging, windthrow (treefall), and epidemics caused by disease or herbivory – all of which primarily act by altering aboveground tree structures.

Combined (Discomposition)

- **Rykiel 1985 Definition:** Particular populations are selectively eliminated, reduced, added, or expanded.
- **Working Definition:** An *event* or *agent* that comprehensively alters plant composition, nutrient availability, and mean plant health.
- **Examples:** Prominent examples of combined disturbances include wildfire and geologic disturbances that initiate primary succession. These disturbances act by altering nutrients, habitat availability, and pre-disturbance tree composition.

While useful for understanding locally mediated biotic interactions, we acknowledge that many ecological disturbances do not cleanly fall into interference or destruction disturbance categories. Many disturbances, including windthrow and drought, have secondary implications for both nutrient availability and aboveground tree structures. We emphasize that categories are based on their primary mode of impact on forests – which has consequences for community assembly, successional trajectories, and the net effect of disturbance on local biotic interactions through recovery.

Table 1-1: Empirical Studies of Local CDD Along Abiotic Gradients (Selected Publications)

Paper	**System**	**Life Stage**	**Study Type**	**Interactions Between Environmental Variable and Conspecific Density Effects (M = mortality, G = growth)**
Light				
Augspurger & Kelly 1984	Tropical Forest	Seedlings	Obs.	Weakens local stabilizing CDD (M)
Holík *et al.* 2021	Temperate Forest	Seedlings	Obs.	Weakens local stabilizing CDD (M)
Inman-Nahari *et al.* 2016	Tropical Forest	Seedlings	Obs.	Weakens local stabilizing CDD (M)
Kobe & Vriesendorp 2011	Tropical Forest	Seedlings	Obs.	Weakens local stabilizing CDD (M)
McCarthy-Neumann & Ibanez 2013	Tropical Forest	Seedlings	Exp.	Weakens local stabilizing CDD (M)
Record *et al.* 2016	Tropical Forest	Seedlings	Obs.	Weakens local stabilizing CDD (M)

Brown *et al.* 2021	Temperate Forest	Saplings (2-12.7-cm DBH)	Obs.	Weakens local stabilizing CDD (G)
Song *et al.* 2021	Tropical Forest	Seedlings	Obs.	Weakens local stabilizing CDD (G)
Soil Nutrients				
Brown *et al.* 2021	Temperate Forest	Saplings (2-12.7-cm DBH)	Obs.	Weakens local stabilizing CDD (G)
LaManna *et al.* 2016	Temperate Forest	Seedlings & Saplings (<10-cm DBH)	Obs.	Strengthens local stabilizing CDD (M)
Record *et al.* 2016	Tropical Forest	Seedlings	Obs.	Weakens local stabilizing CDD (M)
Zhang *et al.* 2021	Tropical Forest	Adults (≥1-cm DBH)	Obs.	Strengthens local stabilizing CDD (M)
Moisture/Precipitation				
Bachelot *et al.* 2020	Tropical Forest	Seedlings	Obs.	No distinct effect on local stabilizing CDD (G & M)
Lebrija-Trejos *et al.* 2023	Tropical Forest	Seedlings	Exp.	Strengthens local stabilizing CDD (M)
Lin *et al.* 2012	Tropical Forest	Seedlings	Obs.	No distinct effect on local stabilizing CDD (G & M)
Milici *et al.* 2025	Tropical Forest	Seedlings	Exp.	Strengthens local stabilizing CDD (G & M)
O'Brien *et al.* 2017	Tropical Forest	Seedlings	Exp.	Strengthens local stabilizing CDD (G)
Song *et al.* 2020	Tropical Forest	Seedlings	Obs.	Strengthens local stabilizing CDD (M)
Song *et al.* 2024	Tropical Forest	Seedlings	Obs.	Strengthens local stabilizing CDD (M)
Uriarte *et al.* 2018	Tropical Forest	Seedlings	Obs.	Strengthens local stabilizing CDD (M)
Temperature/Warming				
Bachelot *et al.* 2020	Tropical Forest	Seedlings	Exp.	Weakens local stabilizing CDD in M but strengthens local stabilizing CDD in G
Germain & Lutz 2022	Temperate Forest	Adults (≥ 1-cm DBH)	Obs.	Weakens local stabilizing CDD (M)
Liu & He 2021	Temperate Forest	Seedlings	Exp.	Strengthens local stabilizing CDD (M)
Liu & He 2022	Tropical Forest	Seedlings	Exp.	Weakens local stabilizing CDD (M) for one of two focal species
Song *et al.* 2018	Tropical Forest	Seedlings	Obs.	Strengthens local stabilizing CDD (M)
Elevation				
Fibich *et al.* 2021	Temperate Forest	Saplings (<15-cm DBH)	Obs.	Weakens local stabilizing CDD (M)

LaManna *et al.* 2022	Temperate Forest	Adults (≥ 5-cm DBH)	Obs.	Weakens local stabilizing CDD (M), particularly for 5 to 15-cm DBH class)
Xu & Yu 2014	Subtropical Forest	Seedlings	Obs.	Weakens local stabilizing CDD (M)

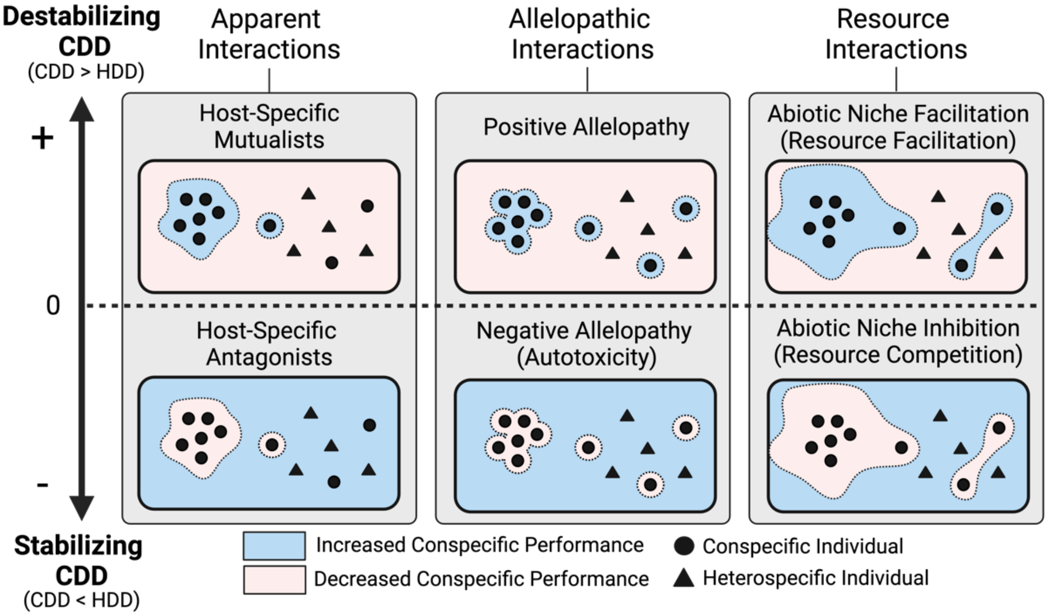


Figure 1-1: Contribution of apparent, allelopathic, and resource interactions to stabilizing or destabilizing local CDD. The drivers of local CDD can be divided into three categories: apparent, allelopathic, and resource interactions. Each of these interaction types may have positive (destabilizing) density effects on conspecific performance (circles, blue areas) or negative (stabilizing) density effects on conspecific performance (circles, pink areas). The net strength of stabilizing or destabilizing CDD, therefore, corresponds to the net strength and directionality of each interaction category. Importantly, local CDD is measured in reference to heterospecific densities. Heterospecific neighbors are represented as triangles. While the functional result of all drivers of local CDD remains constant (i.e, suppression or bolstering of local conspecific performance) the spatial patterns of these effects may vary with category. For instance, in forests trees draw down resources from their surrounding areas – often extending beyond root area via mycorrhizal networks. Allelopathic interactions, however, are almost always restricted to canopy crown area. This figure illustrates the similarities between apparent, allelopathic, and resource interactions, as well as how they may differ in spatial effects and contribution to net local CDD. For examples of each, refer to Box 1. Created in BioRender. Doolittle, C. (2025) https://BioRender.com/3x24can

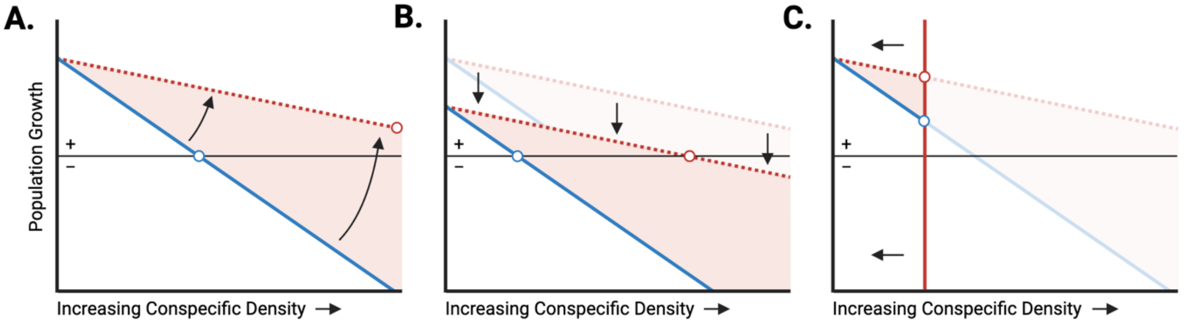


Figure 1-2: Effects of disturbance on local stabilizing CDD. Local stabilizing CDD, arising from relatively host-specific interactions (Figure 1-1), is depicted here as the slope of the relationship between local population growth rate and local conspecific density (blue line). While not always negative (CDD < HDD), local stabilizing CDD is often hypothesized to maintain species diversity by maintaining species abundances at equilibrium where sloped growth-density lines cross zero. We acknowledge that these slopes may be positive (CDD < HDD) but simplify to negative effects here for brevity. Disturbances may affect the relationship between conspecific density and population growth (A) by altering the relatively host-specific interactions generating local stabilizing CDD. These may be small perturbations, or large to the point where population growth is no longer limited by density (no equilibrium abundance, red-dotted line). Disturbance-altered local CDD may be further affected by novel intrinsic fitness differences (B). Novel patterns of resource availability (light, space, nutrients, etc.) confer advantages to disturbance-adapted species and disadvantages for disturbance-sensitive species along functional trait and life history axes. Depicted is an average decline in fitness (population growth when conspecific density = 0, which decreases equilibrium abundance). Finally, repeat disturbance events or dramatic abiotic changes may reduce the effects of disturbance-altered local CDD on community dynamics by limiting conspecific densities (C; solid red line). Even if local stabilizing CDD is strong, severely limited conspecific densities would reduce the effects of local CDD on recovery. Here, we focus on the effects of disturbance on the underlying drivers of local CDD (A), but acknowledge that disturbances may alter the intercept and population growth equilibriums while not interfering with the underlying relationship between conspecific density and population growth (B-C). Created in BioRender. Doolittle, C. (2025) https://BioRender.com/zyo3735

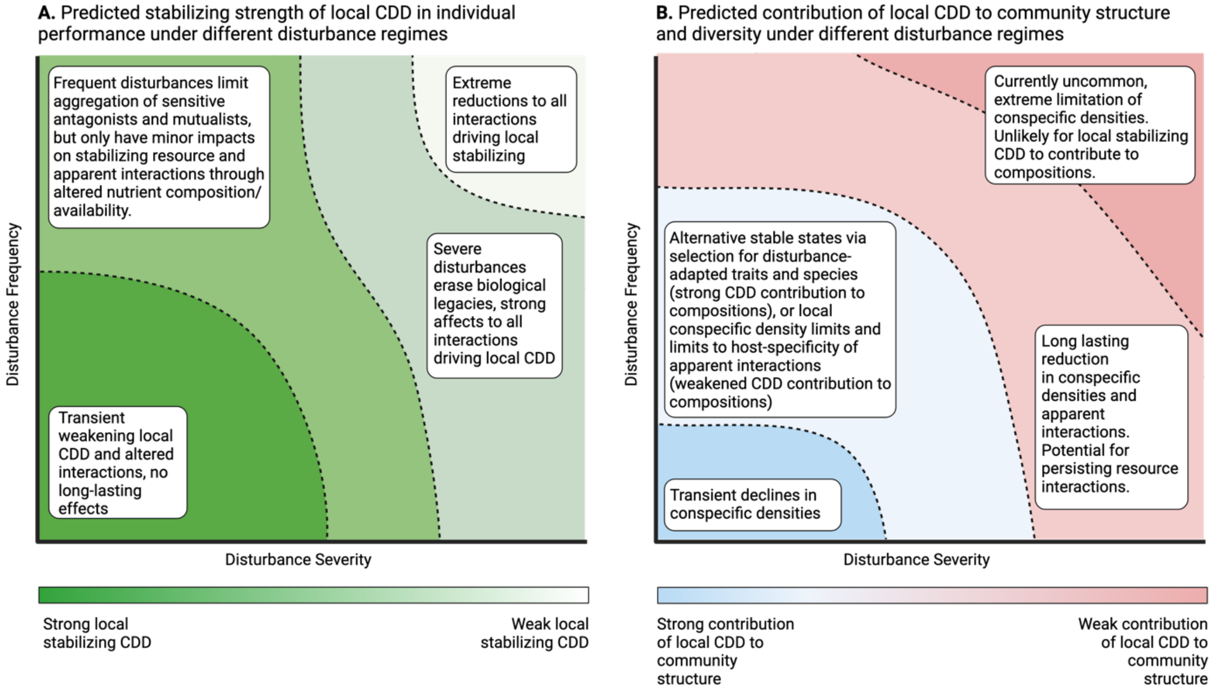
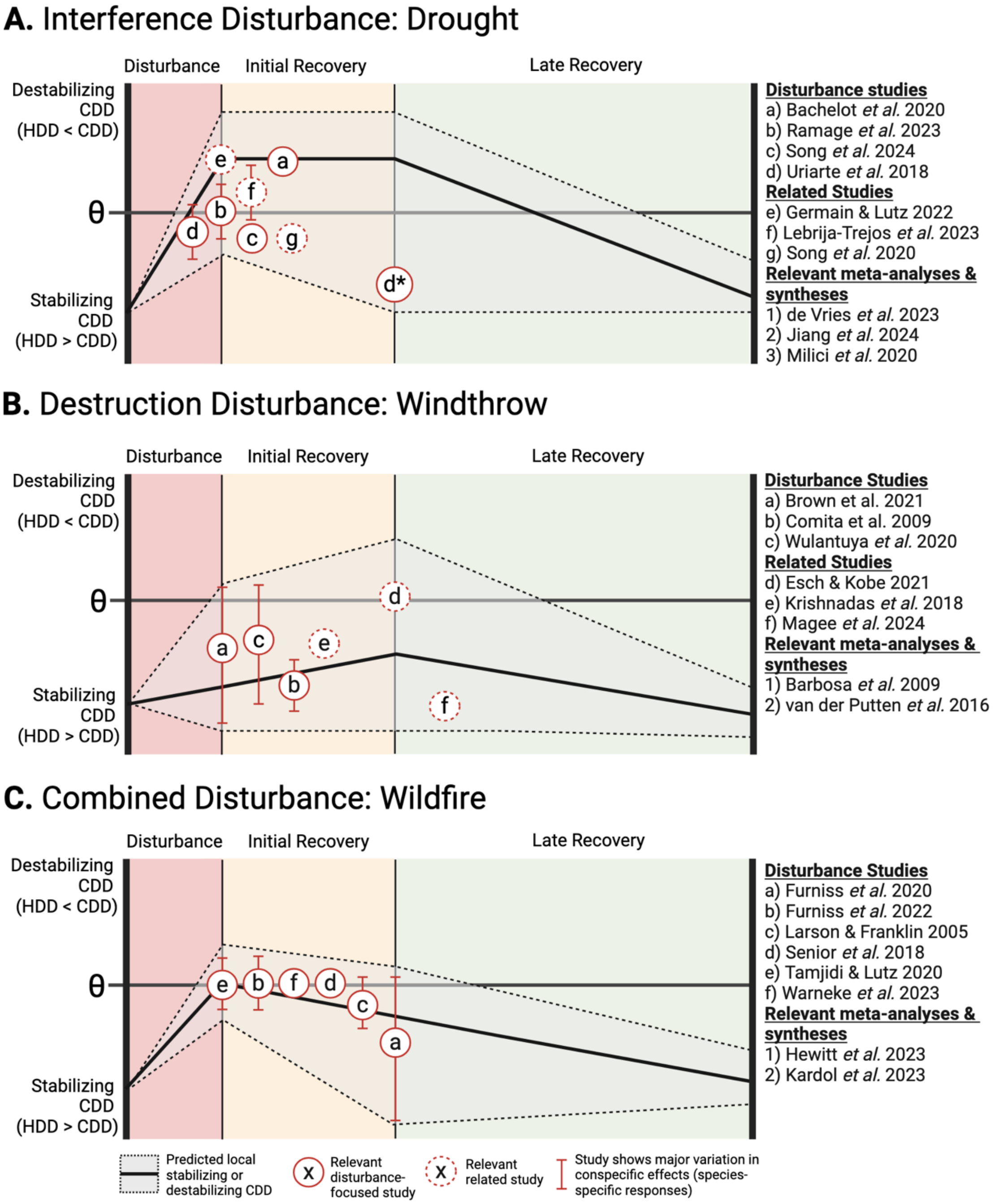


Figure 1-3: Heatmaps of predicted impacts of disturbance regimes on the relative stabilizing strength of local CDD, as well as the contribution of local CDD to patterns of community assembly. Disturbance regimes, defined as patterns of disturbance severity and frequency, are expected to generally reduce the stabilizing effect of local CDD in individual performance as well as the contribution of local CDD to community structure and assembly (A). We predict that local stabilizing CDD will generally decrease in strength (become less stabilizing, green to white) with increasing disturbance severity and frequency. Along with disturbance effects on the stabilizing strength of local CDD, we predict that increases to disturbance frequency and severity decrease the potential for local CDD to affect community structure and assembly (B). In red regions, we predict that local CDD is unlikely to overcome novel fitness hierarchies and/or local conspecific density limits. Created in BioRender. Doolittle, C. (2025) https://BioRender.com/b969tv3



A. Interference Disturbance: Drought

B. Destruction Disturbance: Windthrow

C. Combined Disturbance: Wildfire

Figure 1-4: Predicted primary effects of (A) interference, (B) destruction, and (C) combined disturbances on local stabilizing CDD, and implications through short and long-term recovery. Disturbances have category-specific effects on the underlying drivers of local stabilizing CDD: apparent, allelopathic, and resource interactions, which may lead to category-specific strength and directionality of local stabilizing CDD through various stages of recovery. For each disturbance category, the black line represents our predictions for the relative strength and directionality of local CDD through disturbance and recovery. Grey shaded areas correspond to our relative confidence in predicted effects and highlight areas where more study is warranted. To formulate these predictions (and confidence intervals) we rely on selected studies of disturbance and environmental change across plant-soil feedback, conspecific density dependence, and frequency dependence literature. Letters correspond to specific studies on the right of each panel and are offset from one another for visual clarity – not to indicate relative differences in study timeline. When few empirical studies were available, we relied on related studies of conspecific density effects across changing environmental conditions to generate our predictions. These relevant non-disturbance studies are outlined in a dashed-line circle instead of a solid-line circle. If the selected study found evidence for both positive and negative (destabilizing and stabilizing) effects, we included a red confidence interval to highlight uncertainty. Uriarte et al. (2018) find weakened conspecific density effects in dry years (Panel A, study D) and enhanced conspecific density effects at dry sites (Panel A, study D*). Additionally, our predictions were informed by several meta-analyses and syntheses which we include on the right side of each panel. We acknowledge that in certain systems local CDD begins as destabilizing but opt to begin our predictions at the most common observation: strong stabilizing CDD (CDD < HDD). Created in BioRender. Doolittle, C. (2025) https://BioRender.com/6iw6u8y

Chapter 2 | Wildfire and Extreme Heat Disrupt Stabilizing Conspecific Feedbacks

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Abstract

The frequency of both wildfires and extreme heat events is increasing with climate change, yet their combined effects on the composition and diversity of recovering forest ecosystems remains unclear. One way that disturbances may influence forest recovery is by altering neighborhood interactions between trees and relatively host-specific natural enemies and mutualists, which can contribute to the maintenance of local diversity by differentially affecting individual performance in conspecific relative to heterospecific neighborhoods. We investigated how wildfire and extreme heat influence such conspecific feedback by monitoring seedling mortality following a mixed-severity fire in the old-growth conifer forests of the Pacific Northwest. Because wildfires are known to reduce abundances of relatively host-specific natural enemies and mutualisms, we hypothesized that wildfire results in more equivalent performance in conspecific and heterospecific neighborhoods, thus neutralizing conspecific feedback. We tested this hypothesis using data on Douglas-fir (*Pseudotsuga menziesii*) and Western hemlock (*Tsuga heterophylla*) seedling mortality from 80 burned 1-m^2 plots across a burn-severity gradient. We found that wildfire neutralized conspecific feedback in seedling survival regardless of the extent of heat exposure whereas conspecific feedback in seedling survival responded strongly to heat exposure in nearby unburned forest. These findings suggest that wildfire disrupts key

neighborhood interactions between trees and their natural enemies and mutualists that are thought to generate conspecific feedback and thereby contribute to forest structure. Increased mortality in burned areas was higher for shade-tolerant *T. heterophylla* relative to shade-intolerant *P. menziesii*. As climate change increases the co-occurrence of wildfire and heat extremes, the reduced contribution of neighborhood interactions to forest structure may erode tree species diversity and accelerate shifts toward fire-adapted species, with consequences for ecosystem resilience to future disturbance events.

Introduction

Ecologists have a longstanding interest in determining relationships between ecological disturbances and species diversity, which has grown increasingly critical to understanding the potential impacts of climate change on the structure and function of ecosystems (Clements, 1916; King, 1685; Lindenmayer et al., 2019; Turner, 2010). Disturbances are often thought to alter local diversity by influencing local abiotic conditions – effectively selecting “winners and losers” along functional traits and life-history strategies axes (Keith et al., 2007; McKinney & Lockwood, 1999; Noble & Slatyer, 1980; Tabarelli et al., 2012). However, the template upon which the structure, function, and diversity of post-disturbance communities is defined is not purely abiotic. Disturbances also alter the spatial arrangement, density, and identity of local competitors and other associates like natural enemies and mutualists, generating novel neighborhoods which may have cascading consequences for the function, diversity, and structure of subsequent communities (Doolittle & LaManna, 2025; Gasith & Resh, 1999; Post, 2013; van der Putten et al., 2013). Here, we use patterns of seedling regeneration following wildfire to assess the role of neighborhood interactions on the recovery of an old-growth forest community.

Neighborhood interactions are thought to contribute to the composition and diversity of local communities when conspecific neighborhoods have stronger or weaker effects on individual performance relative to heterospecific neighborhoods, a phenomenon known as local conspecific density dependence (local CDD; Smith 2022, Broekman et al. 2019, LaManna et al. 2024). Among early-life stage plants, local CDD is most often negative, meaning that seedlings in conspecific neighborhoods are disadvantaged (e.g., lower growth, higher mortality) relative to seedlings in heterospecific neighborhoods. This relationship between conspecific density and individual performance is thought to contribute to contribute to a rare-species advantage and stabilize populations under certain conditions (Broekman et al., 2019; Smith, 2022). Negative local CDD (also known as CNDD) has many potential causes, including strong intraspecific competition and relatively host-specific natural enemies that accumulate in conspecific neighborhoods (Comita et al., 2014; Janzen, 1970; Connell, 1971). While less prevalent, local CDD can also be positive, which has the potential to destabilize populations by advantaging conspecific aggregation and competitive exclusion due to mechanisms including strong interspecific competition and the accumulation of relatively host-specific mutualists in conspecific neighborhoods (Chesson, 2000; Delavaux et al., 2023; Jiang et al., 2021; Liang et al., 2021). Here we refer to local CDD as ‘stabilizing’ or ‘destabilizing’ to refer to local conspecific density effects on individual performance that have the theoretical potential to affect population growth and species diversity under certain conditions (Broekman et al., 2019; Delavaux et al., 2023; LaManna et al., 2024; Wright, 2002; Zahra et al., 2021), and not as an explicit prediction of coexistence.

Wildfire is an important disturbance that can restructure ecological communities, creating a complex mosaic of novel abiotic conditions and surviving competitors influential on subsequent patterns of recovery (Andrus et al., 2022; Bowd et al., 2021). Typically, fire effects in forest communities are viewed through the lens of direct relationships between fire and plants (i.e., fire tolerance) and how fire modifies competitive relationships between plants. Yet, many factors contributing to individual plant performance, including local CDD, are driven by fire-prone apparent interactions between plants and host-associated enemies and mutualists (Hewitt et al., 2023; Kardol et al., 2023). Accumulating evidence highlights the susceptibility of apparent interactions and local CDD to changing environmental conditions (Brown et al., 2021; LaManna et al., 2022; Liu & He, 2021, 2022; Song et al., 2018; Uriarte et al., 2018). A natural extension to this literature is to investigate the role that ecological disturbances, which dramatically and comprehensively changes environmental conditions, alter the contribution of local CDD to subsequent patterns of recovery (Doolittle & LaManna, 2025).

One primary way that wildfire may alter local CDD is by altering the contribution of microbial natural enemies and mutualists to individual performance. For instance, fire often causes widespread mortality among ectomycorrhizal fungi (Cairney & Bastias, 2007; Taudière et al., 2017), eliminating mutualists that would otherwise facilitate resource acquisition and pathogen defense among aggregated conspecifics (DeVan et al., 2023; Kardol et al., 2023). Along with ectomycorrhizal fungi, wildfires can reduce the abundance of microbial natural enemies, potentially reducing their contribution to local stabilizing CDD through early regeneration. (Nelson et al., 2022; Rodriguez-Ramos et al., 2021). Recent evidence from unburned forests indicate that ectomycorrhizal fungi and other relatively host-specific mutualists become increasingly influential to structuring plant communities in stressful environments, contributing to less stabilizing, or even destabilizing, local CDD under stress by bolstering growth and survival of nearby conspecifics (LaManna et al. *in prep*, Doolittle et al. *in prep*). However, since wildfires reduce abundances of the microbial natural enemies and mutualisms largely generating local CDD, we may expect neutral local CDD and poor performance in post-fire environments regardless of environmental stress (Doolittle & LaManna, 2025). In other words, we predict that differences in seedling performance between conspecific and heterospecific neighborhoods evident in unburned forests are neutralized in recently burned forests and decoupled from environmental stress.

Climate change is not only expected to increase the frequency and range of wildfire disturbances (Halofsky et al., 2020) but also the frequency and intensity of extreme heat events (McKinnon & Simpson, 2022). To the extent that these disturbances overlap, they may have unexpected and extreme effects on seedling performance with cascading consequences for the stability and functioning of future forest systems (Andrus et al., 2022; Furniss et al., 2020; A. L. Smith et al., 2014). Recent evidence suggests that local CDD is affected by temperature. Relatively small increases in temperature appear to benefit natural enemies (herbivores, fungal pathogens, etc.; Delgado-Baquerizo et al., 2020) and strengthen local stabilizing CDD (LaManna et al., 2022; Liu & He, 2021, Doolittle et al. *in prep*). However, extreme increases in temperature have been associated with less stabilizing local CDD (Bachelot et al., 2020; Germain & Lutz, 2022), potentially related to physiological thresholds for plants and/or associated natural enemies.

In our study system, a recent study in unburned forests found that local CDD in seedlings becomes less stabilizing with increasing abiotic stress (nutrient limitation) along an elevation gradient (LaManna et al. *in prep*). However, this study also found that local CDD flips from stabilizing (less than zero) to destabilizing (greater than zero) at low elevations under increased exposure to extreme heat (LaManna et al. *in prep*). Extreme heat events (temperatures above 38° C) are through to cause local CDD to become more destabilizing because these temperatures are beyond thermal physiological limits of seedlings (Marias et al., 2017), increasing the value to plants of interactions with relatively host-specific mutualists such as mycorrhizae or foliar mutualists that might help the plant maintain critical functions in extreme heat (Beniwal et al., 2010; Lau et al., 2017). When combined with fire disturbance, we expect extreme heat events to have less of an impact on local CDD due to greatly reduced natural enemies and mutualists in the post-fire environment. In other words, we expect that fire erodes the relationship between local CDD and extreme heat events by reducing performance differences between seedlings in conspecific and heterospecific neighborhoods. Over longer periods of succession, understanding these interactive disturbance events becomes important to predicting recovery trajectories and the composition of early- to mid-seral forests (Anyomi et al., 2022; Tepley et al., 2014; Turner et al., 1998).

We aimed to gain a mechanistic understanding of how extreme heat and wildfire interact with neighborhood-scale biotic interactions to influence forest recovery from wildfire. We conducted an observational study of early post-fire seedling mortality following a large mixed-severity fire and across multiple extreme heat events in the central Cascade Range of Oregon, USA. Seasonal rainforests in the Pacific Northwest, such as those in the central Cascade Mountain range, are characterized by old-growth forests where patterns of local CDD are well documented (LaManna et al. 2022, LaManna et al. *in prep*). Our study focused on two dominant conifer species that account for the majority of basal area in forests of the Pacific northwest of North America: *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (Western hemlock). We paired seedling demography surveys with post-fire forest inventory datasets to disentangle the relative importance of neighborhood effects and climatic extremes on seedling survival in the post-fire environment. We predicted that stabilizing and destabilizing local CDD observed in nearby unburned forests (LaManna et al. *in prep*) would instead be neutralized in burned forests (i.e., neither stabilizing or destabilizing, indicating roughly equivalent mortality rates between seedlings growing under conspecific and heterospecific adult trees). Additionally, we predicted that local CDD would not vary under extreme heat due to the loss of natural enemies and mutualists in the post-fire environment. Our prediction differs from findings in unburned forests, where local CDD trends from stabilizing to destabilizing under extreme heat (LaManna et al. *in prep*). Understanding these mechanisms is crucial for predicting forest recovery patterns in an era where climate change is simultaneously altering fire regimes and increasing the frequency of extreme heat events across historically fire-infrequent forest ecosystems.

Methods

Site description

This study took place at the Andrews Experimental Forest LTER near Blue River, Oregon. The tree communities at the Andrews LTER are characteristic of old-growth Pacific Northwest temperate rainforests, home to some of the tallest trees and largest above-ground biomass in forests globally. Canopies of these temperate rainforests are dominated by Douglas-fir (*Pseudotsuga menziesii*), Western red-cedar (*Thuja plicata*), Western hemlock (*Tsuga heterophylla*), and a variety of *Abies* species including Silver fir (*Abies amabilis*) and Noble fir (*Abies procera*). Many other broadleaf and conifer species are common in mid-canopy and understory canopy layers, including Big-leaf maple (*Acer macrophyllum*) and Pacific dogwood (*Cornus nuttallii*). At lower elevations, where our study took place, moderate temperatures and higher moisture provide a long growing season for evergreen plant species, even through mild conditions in winter (Waring & Franklin 1979).

Establishing burned understory demography plots

In 2020, the lower watersheds of the Andrews Forest experienced a mixed-severity wildfire as part of the Holiday Farm Fire, one of the largest wildfires in Oregon's history and part of the historic Labor Day Fires (Reilly et al., 2022). To monitor the abiotic and biotic factors determining seedling survival following this fire, we established 80 1-m^2 understory demography plots in June and July of 2021 across a fire severity gradient within the old-growth Andrews Forest watersheds affected by the Holiday Farm Fire (WS02, WS09). We selected these specific watersheds because they contained long-term forest inventory plots (either 18-m diameter circles or 25-m^2 squares) with available pre- and post-fire measurements as part of the Permanent Sample Plot (PSP) Program jointly run by Oregon State University and the USDA Forest Service Northwest Station (Franklin et al., 2024).

We placed two 1-m^2 demography plots within each PSP plot stratified under different focal adults and across fire severity. To minimize edge effects and ensure spatial independence, each demography plot was positioned at least 5-meters from the inventory plot boundary and at least 10-meters from other demography plots. Since we were specifically interested in measuring pairwise feedbacks between conspecifics and heterospecifics, we placed each plot within 3-meters (mean = 1.83-m) of the base of a living adult focal tree (> 15-cm DBH, mean = 56.2-cm; Figure S2-2). Our focal trees were one of two species, *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (Western hemlock). In the lower watersheds of the Andrews, canopies are often dominated by *P. menziesii,* which limited our ability to place understory demography plots under dominant *T. heterophylla* adults. Our 80 plots were distributed between our focal species with 50 understory demography plots under *P. menziesii* adults and 30 understory demography plots under *T. heterophylla* adults. In addition to being placed under living adults of our focal species, plots were also stratified along a fire severity gradient measured as percent basal area mortality of adult trees > 5-cm DBH in each PSP plot, surveyed in the summer (June – July) of 2021. Since we were interested in the effect of nearby living adults on seedling mortality, our range of fire severity was constrained (0.1% - 75% basal area mortality; Figure S2-3). When possible, within the constraints of plot size and focal tree availability, plot location and azimuth to focal tree was randomized.

Comparison to unburned understory demography plots

Our 80 1-m^2 understory demography plots were designed explicitly to match to those established in 2019 by LaManna et al. (*in prep*). Namely, seedling plots in both datasets were located within three meters of a focal adult and co-located with long-term forest inventory plots. Since LaManna et al. (*in prep*) utilize more focal species than available within our burned plots, we extracted seedling demography data for only low-elevation understory plots associated with either *P. menziesii* or *T. heterophylla* adults (55 total plots, 26 plots paired with *P. menziesii*, 29 plots paired with *T. heterophylla*). This unburned seedling demography dataset used here to compare mortality between burned and unburned forest incorporated 922 total seedling observations; 76 *P. menziesii* seedlings under *P. menziesii* adults, 400 *T. heterophylla* seedlings under *T. heterophylla* adults, 83 *P. menziesii* seedlings under *T. heterophylla* adults, and 433 *T. heterophylla* seedlings under *P. menziesii* adults. Seedling mortality rates were estimated the same way for unburned and burned datasets (see analysis section below).

Surveying burned understory demography plots

We surveyed each understory demography plot annually during the summer growing season (June to October) from 2021 through 2024. Surveys were conducted by trained field technicians who received standardized training to ensure consistency in data collection protocols. For woody plants, we individually tagged each stem to track growth and mortality over time, measured height, and documented any visible injuries or diseases. We additionally measured plot-level abiotic characteristics including light availability using a handheld mirror densiometer (Spherical Crown Densiometer, Concave Model C, Forestry Suppliers, Jackson, MS), plot char cover, and any notable site conditions that might influence vegetation dynamics. We observed 1207 seedlings in burned understory plots across 3 intervals from 2021 to 2024 (330 *P. menziesii* seedlings and 887 *T. heterophylla* seedlings; Table S2-2).

At the beginning of our study (2021), all focal adults were living. However, by the end of our study (2024), 5 adults in the highest severity sites had experienced delayed mortality common to the post-fire environment (2 *P. menziesii*, 3 *T. heterophylla* adults; Brown et al., 2013). We accounted for delayed mortality by comparing our analysis to a secondary analysis excluding adults that experienced mortality, which had no impact on our inferences (Figure S2-4).

Measuring the occurrence and intensity of extreme heat events

Since our hypotheses of seedling performance were centered on the combined influence of neighborhood interactions and extreme heat events, we calculated the number of degree-hours that each seedling experienced above 38°C through each survey interval (Figure S2-1). 38° C was chosen *a priori* based on prior studies that indicate that key physiological processes involved with nutrient acquisition and photosynthesis in seedlings break down at temperatures exceeding 38° C (Marias et al., 2017). We included a categorical fixed effect in our models where each seedling experienced different levels of extreme heat being either ‘low’ degree-hours of extreme heat (less than 3 DH), ‘moderate’ degree-hours of extreme heat (3-10 DH) or ‘high’ degree-hours of extreme heat (greater than 10 DH; Table S2-1; Figure S2-3).

Bayesian hierarchical models

To evaluate the contribution of local neighborhoods and extreme heat events to annual seedling mortality in burned forest plots, we developed hierarchical Bayesian generalized additive mixed models (GAMMs). Our Bayesian GAMM approach is similar in design and execution to the approach used in LaManna et al. (*in prep*). This approach generates posterior distributions (as opposed to point estimates) which were advantageous for the propagation of error through pairwise feedback calculation steps (addition and subtraction of posteriors). We used Bayesian GAMMs instead of generalized linear mixed models (GLMMs) because we hypothesized that responses to fire severity, seedling height, and seedling density may be non-linear across predictor ranges and between focal species (Hülsmann et al., 2024). All analyses were conducted in R, version R 4.2.1 (R Core Team, 2021) using the 'tidyverse' packages (Wickham & RStudio, 2023) for preparation and visualization along with 'brms' (Bürkner et al., 2024) and 'tidybayes' (Kay, 2024) for hypothesis testing.

We fit a series of flexible models to burned forest plots with a response variable for binary seedling mortality (hazard), where one indicated death and zero indicated survival across a single interval of annual surveys following a Bernoulli error distribution modeled through a logit link function. For each model, we began with a maximal random effect structure to fully account for spatial hierarchy and allow flexibility of hazard estimates across surveys. We selected the optimal random effect structure for each model using Leave-One-Out (LOO) cross-validation, EPLD scores, and LOO information criterion along with posterior predictive checks (Table S2-3; Barr et al., 2013). We tested the contribution of random intercepts for seedling survey interval, cohort, year of initial measurement, species, and neighborhood effects, as well as four spatial hierarchical levels which include individual understory demography plots, PSP quadrat or plot (within which two understory plots are located), reference stand (within which a set of PSP quadrats are located), and watershed (two levels referring to the different slopes that plots were located on; see Table S2-1). We additionally tested for two-way, three-way, and four-way interactions between species, watershed, neighborhood effects, and year to capture any potential spatial or temporal divergences in effects through our study period.

We included smooth functions to model the continuous contribution of seedling height, conspecific and total seedling density, and basal area mortality to seedling hazard (Pedersen et al., 2019). We compared two approaches to letting each of these continuous predictors vary by species. First, we fit models with global thin-plane regression splines and species-specific factor-smooth interactions, which constrains the slope of response similarly between species. Next, we fit models with no global effect and separate thin-plane regression splines for each species, which allows complete independence in response of each species to the predictor. Using cross-validation we determined the second option, where separate thin-plane regression splines are fit to each species, to be a better fit to our data. Seedling height, conspecific and total seedling density, and basal area mortality smooth terms used 15 basis functions (k) to allow for complex non-linear relationships.

Estimating pairwise feedbacks and watershed-level estimates

To estimate relative differences between seedling mortality in conspecific and heterospecific adult neighborhoods, we quantified species-level and neighborhood-level mortality for our focal species and compared them using pairwise feedbacks (Bever, 2003; Bever et al., 1997). Since our estimates are in terms of seedling mortality (as opposed to its inverse, survival), pairwise feedbacks I_s were calculated as:

$$I_{s_{h,w,i,c}} = A_{H_{h,w,i,c}} - A_{C_{h,w,i,c}} - B_{C_{h,w,i,c}} + B_{H_{h,w,i,c}}$$

where $A_{C_{h,w,i,c}}$ and $B_{C_{h,w,i,c}}$ represent the posterior distribution of mortality risk of *T. heterophylla* and *P. menziesii* under a conspecific adult for a given heat level h, watershed w, interval i, and cohort c, and $A_{H_{h,w,i,c}}$ and $B_{H_{h,w,i,c}}$ represent the posterior distribution of mortality risk of *T. heterophylla* and *P. menziesii* under a heterospecific adult in each parameter combination. We determined that fire severity (basal area mortality) had an insignificant effect on estimates and opted to average across the observed fire severity combinations (Figure S2-5).

To have robust estimates of conspecific feedback in each condition, we estimated pairwise feedback I_s as computed posterior draws from the expected value of the posterior predictive distribution nested within each level of extreme heat, watershed, interval, and cohort. Therefore, we only calculated feedbacks for only parameter combinations for which we observed seedlings in each of $A_{C_{h,w,i,c}}$, $B_{C_{h,w,i,c}}$, $A_{H_{h,w,i,c}}$, and $B_{H_{h,w,i,c}}$. In the case of low heat (less than 3 degree-hours), we were unable to calculate posterior draws from the expected value of the posterior predictive distribution for $A_{H_{h,w,i,c}}$ given data limitations (Table S2-1) and instead used our model to simulate the posterior predictive distribution for a new level for this one case. We caution that the estimate for $A_{H_{h,w,i,c}}$ in low heat was not derived from seedlings observed in that exact parameter combination, but instead predicted from model fit borrowing information from A_H under different combinations of *h, w, i,* and c. For all resulting posterior distributions for $I_{s_{s,w,i,c}}$ we then averaged across intervals and cohorts to get a watershed-level mean feedback posterior.

We then used Bayesian bootstrapping (Rubin, 1981) to make inferences on the posterior distributions of species-level and neighborhood-level mortality and feedback posteriors across watersheds. Our application of the Bayesian bootstrap accounts for the fact that the watersheds used in this study were a subsample of the broader population of forest watersheds affected by wildfire. We weighted each watershed by its area and iterated over randomly determined Dirichlet weights at each posterior sample to achieve a mean posterior across watersheds. We tested our hypotheses relating to the impact of wildfire on mortality and local CDD by comparing our posteriors to those of LaManna et al. *in prep* (which used identical methods and analytical approaches). To aid in interpretation, we denote contrasts for which the 95% credible interval did not overlap 0 as significant.

Results

Drivers of Seedling Mortality

Our analysis revealed that wildfire increased average mortality rates (Figure 2-1A), largely driven by increases to *T. heterophylla* mortality across heat levels: low (mean difference = 0.409, 95% CI [0.146, 0.648]), mid (mean difference = 0.280, 95% CI [0.117, 0.498]), and high (mean difference = 0.258, 95% CI [0.112, 0.473]). *P. menziesii* seedling mortality rates increased less dramatically, only significantly higher across intervals with high levels of extreme heat (> 10 degree-hours; Fig 1B). Species contrasts within heat levels indicate that in burned plots, *T. heterophylla* experienced significantly higher mortality than *P. menziesii* at both low (mean difference = 0.143, 95% CI [0.020, 0.305]) and moderate levels of extreme heat (mean difference = 0.115, 95% CI [0.009, 0.241]), while no significant species-level differences were observed under high levels of extreme heat (Table S2-4). Of all factors examined between unburned and burned models, burn condition (i.e., burned or unburned) had the strongest overall effect (average effect size = 0.316), followed by extreme heat events (0.184) and species identity (0.129). Pairwise contrasts for all species-level contrasts are presented in Table S2-4.

Pairwise Feedbacks

Mortality under conspecifics and heterospecifics was consistently higher in burned plots relative to unburned plots (Fig 2 A, B). As in LaManna et al. (*in prep*), we find that heterospecifics mortality significantly increases between low and moderate levels of extreme heat. Pairwise feedbacks between our focal species trended towards negative in unburned demography plots at low levels of extreme heat (mean = -0.14; 95% CI [-0.38, 0.10]) and positive in unburned demography plots at high levels of extreme heat (mean = 0.159, 95% CI [0.390,-0.0658]). Burned feedbacks, however, did not vary with level of extreme heat. Still, burned feedbacks were marginally less than unburned feedbacks high levels of extreme heat (difference mean = -0.19, 90% CI [-0.38 – 0.002]). Pairwise contrasts for all feedback estimates are available in Table S2-5.

Discussion

Our findings provide evidence that wildfires neutralize local CDD and the effects of extreme heat on patterns of seedling mortality. We find that mortality in burned plots is consistently higher than unburned plots under both conspecific and heterospecific adults across levels of extreme heat (Figure 2), contributing to broadly neutral conspecific feedbacks between our focal species (Figure 2-2C). This result contrasts with the findings of LaManna et al. (*in prep*), where pairwise feedbacks between *P. menziesii* and *T. heterophylla* become increasingly positive (destabilizing) with increasing levels of extreme heat exposure. Finally, we find general increases to average mortality across our species, most prominently reflected in *T. heterophylla* at low and moderate heat levels, highlighting the importance of integrating life-history into frameworks of recovery (Fig 1A, B). Our findings add to a small but growing body of literature finding neutral feedbacks in burned forests (Senior et al., 2018; Warneke et al., 2023), and pointing to extreme heat events as mediators of conspecific feedback (Bachelot et al., 2020; Germain & Lutz, 2022). Together, our findings highlight the importance of considering the combined effects of multiple stressors when considering the maintenance of species diversity in disturbed forests.

Wildfire neutralizes differences between seedling mortality in environments dominated by conspecific and heterospecific adult trees in our system with important implications for forest composition and recovery. We caution that our interpretation of pairwise feedbacks in burned plots experiencing low levels of extreme heat is based on a relatively small sample size (Table S2-1). However, we also highlight that our findings are consistent other studies have found similar patterns in systems with frequent fire return intervals (Senior et al., 2018; Warneke et al., 2023). Importantly, our study is the first to our knowledge to demonstrate neutral pairwise feedbacks in fire-disturbed old-growth Pacific Northwestern rainforests where return intervals for high-severity fire are measured in centuries (Reilly et al., 2017). The consistency of our findings with literature from other forest systems suggest a generalizable mechanism by which wildfires reduce the contribution of conspecific feedback and neighborhood interactions to community assembly through early recovery.

The erosion of pairwise feedbacks in burned forests likely reflects fire-induced changes to soil microbial communities that mediate local neighborhood interactions. Fire can dramatically alter soil biota through direct heat mortality and changes to soil physicochemical properties (DeVan et al., 2023; Nelson et al., 2022). In the Pacific Northwest, the majority of dominant conifer species associate with ectomycorrhizal fungal networks which are sensitive to fire due to their position in organic soil and litter layers (Cairney & Bastias, 2007; Taudière et al., 2017). Moreover, loss of soil to combustion predisposes the early post-fire environment to erosion and overland flows (Nave et al., 2022; Wondzell & King, 2003) that likely further reduce communities of tree-associated microbes. When establishing our study, we noticed exposed roots due to soil and litter loss even in areas with low basal area mortality. With reduced fungal networks, ectomycorrhizal-associated trees including *P. menziesii* and *T. heterophylla* are likely less capable of tolerating drought-like conditions (Kilpeläinen et al., 2017; Lehto & Zwiazek, 2011). Simultaneously, wildfires impact populations and diversity of host-specific soil pathogens that normally contribute to negative feedbacks (Nelson et al., 2022; Rodriguez-Ramos et al., 2021). We found that pairwise feedbacks did not vary with fire severity (Figure S2-5), suggesting that even low mixed-severity wildfires in our system are reducing soil microbiota and altering neighborhood effects. The sensitivity of pairwise feedbacks to even low-severity fire suggests that more frequent and extensive fires predicted for the Pacific Northwest under climate change (Halofsky et al., 2020) could reduce the contribution of neighborhood effects to patterns of local diversity.

We find neutral feedbacks across survey intervals regardless of heat level in contrast to LaManna et al. (*in prep*) who find negative feedbacks in years with less extreme heat, and positive feedbacks with more extreme heat in unburned forests (Figure 2-1). This contrast suggests that wildfire disrupts the mechanisms by which extreme heat interacts with local CDD. In unburned forests, findings of stabilizing feedback switching to destabilizing in extreme heat were associated with much larger increases in seedling mortality in neighborhoods dominated by heterospecific relative to conspecific adults (Figure 2-1B; LaManna et al. *in prep*). These findings in unburned forests suggest that physiological stress caused by extreme heat increases the need for seedlings to rely on partnerships with mutualists to survive those extreme conditions (LaManna et al. *in prep*; David et al., 2020; Usman et al., 2021; Doolittle et al. *in prep*). In burned forests, however, significant reductions in abundances of ectomycorrhizal communities likely limit the extent to which those mutualists can benefit seedlings by ameliorating heat stress. Additionally, post-fire changes to soil structure, organic matter content, and nutrient availability may override or mask the effects of extreme heat on seedling performance (Nolan et al., 2021). The resulting neutral conspecific feedback we observe in burned forests across heat levels suggest that wildfire creates a simplified competitive environment where abiotic filtering and direct physiological stress become more important determinants of seedling survival than specialized or relatively specialized apparent interactions, at least during initial post-disturbance recovery phases.

Early-successional burned forests are productive, diverse ecosystems influential on the composition of later successional stages (Swanson et al., 2011; Tepley et al., 2014). Our findings suggest that early-successional burned forests may benefit from the decoupling of local CDD from environmental stressors. In unburned forests, local CDD becomes increasingly destabilizing under stressful environmental conditions, which is thought to erode local diversity (Fibich et al., 2021; LaManna et al., 2022; Liu & He, 2021, 2022; Uriarte et al., 2018). Given that the post-fire environment can be physiologically stressful even for disturbance-adapted species, the neutral local CDD we observe may paradoxically support broader regeneration by preventing the competitive exclusion that would otherwise occur via destabilizing CDD. However, it is worth noting that stabilizing CDD would be optimal for maintaining diversity in the post-fire environment – which LaManna et al. (*in prep*) find is most prevalent in unburned forests under low heat stress. If local CDD became destabilizing in burned areas under heat stress, post-fire succession might favor only the most stress-tolerant species through positive feedback, potentially leading to more homogeneous early seral communities dominated by disturbance specialists. We caution that our inference is based on early recovery, the long-term dynamics of which are likely to vary from their initial state. Nevertheless, the disruption of local CDD by fire may be an important pathway by which fire promotes diversity in early-successional forests, though its persistent effects through later successional stages require additional study.

Differing mortality rates between our focal species provides important insights into how wildfire and extreme heat may jointly reshape forest composition under future climate scenarios. *T. heterophylla,* a shade-tolerant species, experienced higher mortality in burned plots compared to *P. menziesii*, a relatively shade-intolerant species, with the difference being most pronounced across intervals with low to moderate levels of extreme heat (Figure 2-2). We hypothesize that these differences reflect differences in thermotolerance between our focal species. with *P. menziesii* exhibiting greater physiological resilience to heat stress (Marias et al., 2017; Still et al., 2023). For both species, wildfire and extreme heat have non-additive effects on seedling mortality when occurring simultaneously (Figure 2-1), which supports the hypothesis that initial stressors make individuals less responsive to additional stressors (Stevens-Rumann & Morgan, 2019). Increasing frequencies and intensities of wildfire and extreme heat, therefore, may advantage *P. menziesii* in both burned and unburned Pacific Northwestern forests, following the trend of widespread structural shifts in western North American forests towards fire- and drought-adapted species (Hagmann et al., 2021).

Conclusions

Our study demonstrates that wildfires and extreme heat events have similar but distinct effects on the contribution of neighborhood interactions to patterns of seedling mortality. We find support for species-specific differences in mortality following wildfire and heat stress, which neutralized pairwise feedback following wildfire. As wildfire frequency and extreme heat events increase across the globe, these altered neighborhood interactions may accelerate compositional shifts beginning at the regeneration stage, potentially leading to simplified forest communities dominated by disturbance-adapted species like *P. menziesii*. The consequences extend beyond simple changes in species abundance to potentially affect fundamental ecosystem processes, diversity, and resilience to future disturbances. By revealing how combined stressors disrupt the fine-scale neighborhood interactions that are thought to structure forest communities, our findings highlight the need to incorporate species interactions into predictions of forest response to climate change. Understanding these dynamics will be critical for developing management strategies that maintain diverse, functioning forest ecosystems in an era of unprecedented environmental change.

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Figures and Tables

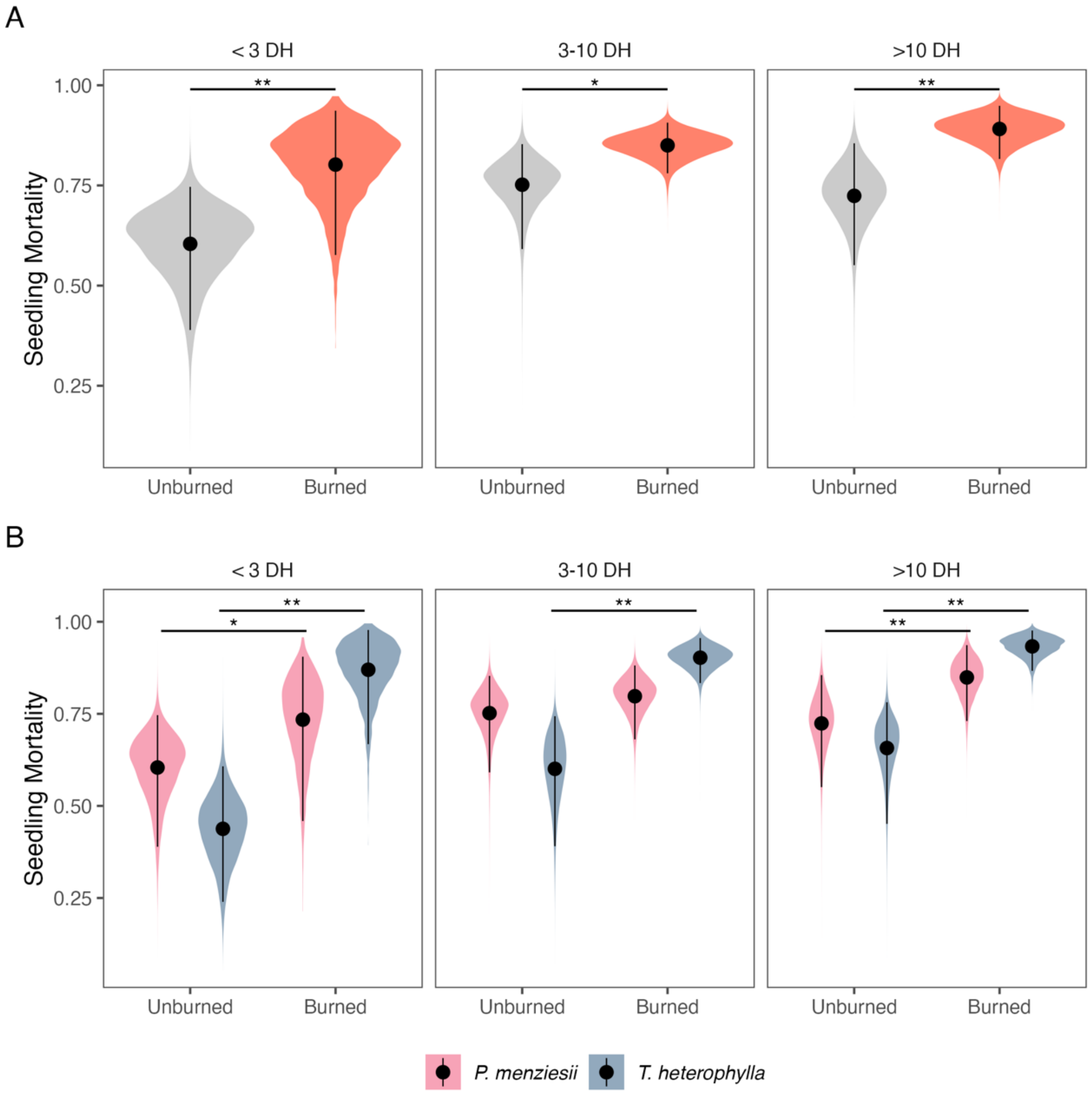

Figure 2-1: Average and species-specific mortality rates in unburned and burned understory plots across intervals with differing intensities of extreme heat events. Seedling mortality posteriors for each species in each category were estimated from hierarchical Bayesian GAMM fits conditioned on all population-level random effects. Results are split into average mortality rates across both focal species (A), and species level mortality rates (B) stratified along categorical levels of extreme heat measured as degree-hours (DH), reflecting the relative intensity of extreme heat over each survey interval. Black dots represent medians and lines represent 95% credible intervals. Pink depicts average seedling mortality posterior distribution of P. menziesii under both conspecific and heterospecific adults. Blue depicts average seedling mortality posterior distribution of T.

heterophylla under both conspecific and heterospecific adults. Since posteriors for unburned and burned mortality are derived from separate models, we assigned significance to contrasts for which the difference between the burned and unburned posteriors excluded 0 in either the 90% (*) or 95% (**) credible interval. Here, we only visualize the significance of contrasts between unburned results from LaManna et al. (in prep) and our analysis. For pairwise comparisons within burn category (i.e., burned or unburned) see Table S2-4.

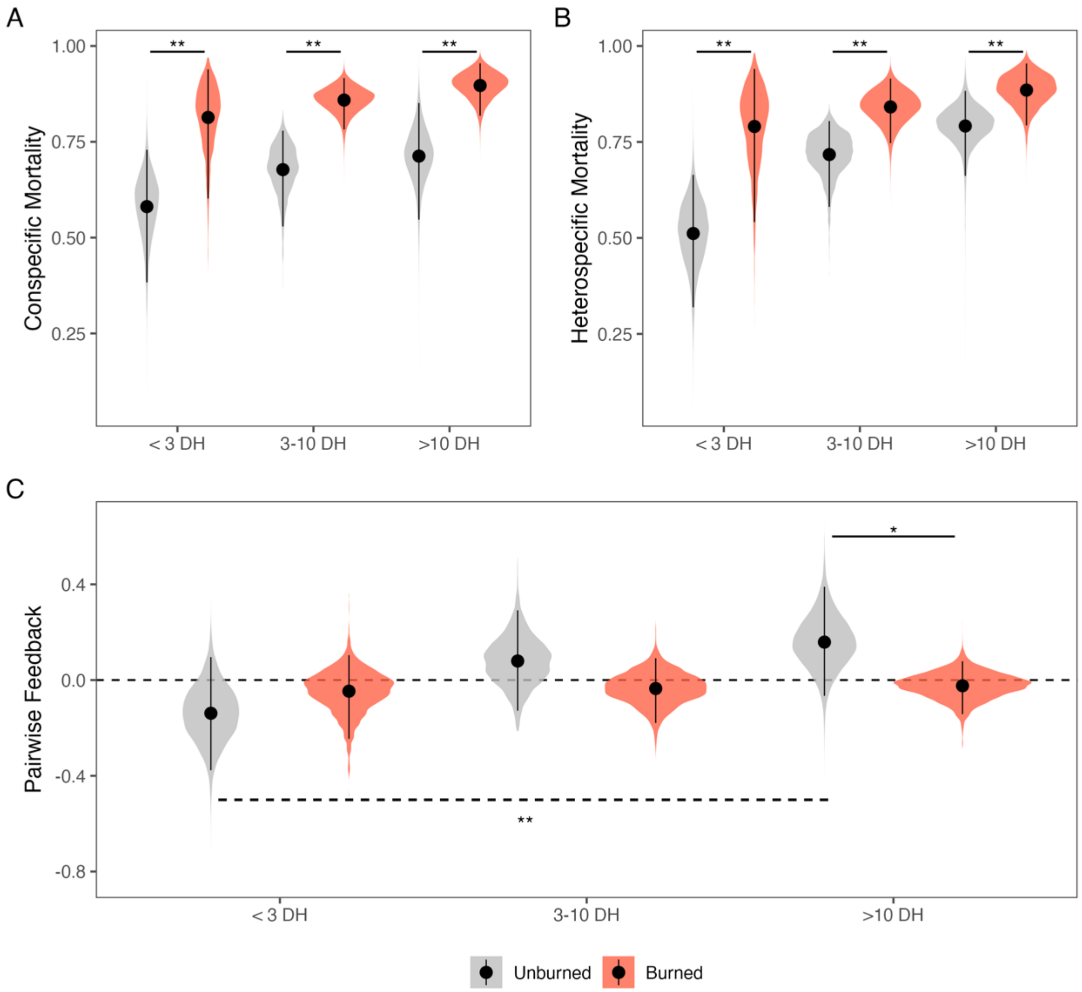

Figure 2-2: Conspecific mortality rates, heterospecific mortality rates, and pairwise feedback in unburned and burned understory plots across intervals with differing intensities of extreme heat events. We find generally higher average mortality rates for focal species in burned plots under conspecific and heterospecifics (A, B). Whereas LaManna et al. (in prep) find that pairwise feedback increases with increasing levels of extreme heat, we find generally neutral pairwise feedback across heat levels (C). Black dots indicate medians, and black lines depict 95% credible interval of estimates. Colored shapes depict posterior distributions of unburned (blue) and burned (red) model estimates. Results are split by degree-hours (DH), reflecting the relative intensity of extreme heat over each survey interval. Since posteriors for unburned and burned mortality are derived from separate models, we assigned significance to contrasts for which the difference between the burned and unburned posteriors excluded zero in 95% credible interval (Table S2-4).

(A) Average conspecific mortality across unburned and burned plots under differing intensities of extreme heat events. (B) Average heterospecific mortality across unburned and burned plots under differing intensities of extreme heat events. (C) Pairwise feedbacks where values less than zero indicate that individual performance (survival) is higher in heterospecific environments relative to conspecific environments. Pairwise feedbacks greater than zero indicate that individual performance is higher in conspecific environments relative to heterospecific environments. Here, we only visualize the significance of contrasts between unburned results from LaManna et al. (in prep) and our analysis. For pairwise comparisons within burn category (i.e., burned or unburned) see Table S2-5.

Supplemental Tables and Figures

Table S2-1: Distribution of extreme heat levels across survey intervals in burned plots. Over the 3 seedling intervals between 2021 and 2024 burned understory demography plots experienced multiple extreme heat events. Since 38ºC is a critical threshold for seedling physiology, we calculated degree hours (DH) above 38ºC using Andrews Forest primary meteorological station (PRIMET) aspirated air temperature data at a resolution of 15 minutes (Figure S2-1). We split DH into 3 categories (less than 3 DH, 3 – 10 DH, and greater than 10 DH).

	Survey Interval		
	2021-2022	2022-2023	2023-2024
High (> 10 DH)	405	0	0
Mid (3 – 10 DH)	427	139	214
Low (<3 DH)	0	0	22

Table S2-2: Burned seedling observations by watershed and adult species. We fit our models with a total of 1207 observations (seedling intervals). These observations were split between 5 locations in the lower watersheds of the Andrews Experimental Forest and across two focal species (PSME = P. menziesii, TSHE = T. heterophylla). We omitted RS08 from subsequent analyses given that only 1 TSHE seedling was observed across our study period.

	PSME	**TSHE**	***Location Totals***
WS09 - Upper	148	147	295
WS09 – RS08	31	1	32
WS09 - RS01	126	55	181
WS02 - Upper	21	443	464
WS02 – RS15	4	231	235
Species Totals	330	877	***Grand Total:* 1207**

Table S2-3: Bayesian Model Selection LOOIC. We ran a series of Bayesian GAMMs with different model structures to identify the model best fit to our data. We began with a maximal random effect structure including year-varying effects of extreme heat (Ex. H.), separate smoothing parameters for conspecific and total seedling density, different smoothing parameters for height by species, multiple hierarchical spatial levels representing the spatial arrangement of our plots, and two different link functions common to discrete survival analyses (cloglog, logit). Model results are sorted by LOOIC. While the cloglog-link model had the best LOOIC score we considered this to be an overfit due to the number of Pareto-K values greater than 0.7, which represents potentially overly influential data points. We selected the model in bold due to the combination of low LOOIC (within 2 LOOIC of next highest model) and superior number of problematic Pareto-K values (5 compared to 17).

Seedling Density Params	**Smooth Function**	**Ex. Heat Levels**	**Year-varying Ex. H.**	**Hierarchical Spatial Levels**	**Link Function**	**LOOIC**	**LOO SE**	**Problematic Pareto-K values**
Con + Total	Global + FS	3	Yes	4	cloglog	718.22	40.4	197
Con + Total	Global + FS	3	Yes	4	logit	725.58	41.01	17
Con + Total	**Separate TP**	**3**	**Yes**	**4**	**logit**	**727.56**	**42.72**	**5**
Con	Global + FS	3	Yes	4	logit	727.91	42.19	13
Con + Total	Global + FS	2	Yes	4	logit	730.2	41.61	5
Total	Global + FS	2	Yes	4	logit	770.1	40.43	0
Total	Separate TP	2	Yes	3	logit	770.3	41.33	8
Total	Separate TP	2	Yes	4	logit	770.38	41.22	5
Total	Global	2	Yes	4	logit	772.38	40.89	1
Total	Separate TP	2	Yes	2	logit	773.76	41.32	7
Total	Separate TP	2	Yes	2	logit	774.1	41.2	8
Con + Total	Global + FS	2	No	4	logit	776	41.25	2
Total	Global	2	Yes	2	logit	780.32	40.76	1
Total	Global	2	Yes	3	logit	780.71	40.75	1
Con + Total	Separate TP	2	Yes	3	logit	780.83	41.98	6
Total	Global	3	Yes	3	logit	783.89	40.82	2
Con + Total	Global + FS	3	No	3	logit	789.23	40.3	0
Con	Global + FS	3	Yes	4	logit	805.16	39.99	0
Con	Global	2	No	4	logit	806.97	41.18	2
Con + Total	Global + FS	2	No	4	logit	807.83	40.45	0
Con	Global + FS	2	No	4	logit	809.01	40.26	0

Table S2-4: Species-level pairwise contrasts. This table presents pairwise contrasts between levels of extreme heat (Low, Mid, High), burn status (Burned, Unburned), and species (PSME = P. menziesii, TSHE = T. heterophylla). Mean differences are shown with 95% confidence intervals.

Contrasts for which the 95% credible interval does not overlap zero are bolded an annotated (**) along with comparisons for which the 90% credible interval does not overlap zero (*).

Heat Level Comp.		Burn Status Comp.		Species Comp.		Mean diff	Lower CI	Upper CI
Lo	Mid	Burned	Burned	PSME	PSME	-0.0635	-0.323	0.113
Lo	High	Burned	Burned	PSME	PSME	-0.115	-0.389	0.0806
Lo	Lo	Burned	Unburned	PSME	PSME	0.132	-0.194	0.416
Lo	Mid	Burned	Unburned	PSME	PSME	-0.016	-0.321	0.225
Lo	High	Burned	Unburned	PSME	PSME	0.0118	-0.297	0.267
Lo	Lo	Burned	Burned	PSME	TSHE	**-0.135****	**-0.307**	**-0.0171**
Lo	Mid	Burned	Burned	PSME	TSHE	**-0.168***	**-0.452**	**0.023**
Lo	High	Burned	Burned	PSME	TSHE	**-0.199****	**-0.483**	**-0.00682**
Lo	Lo	Burned	Unburned	PSME	TSHE	**0.298***	**-0.0217**	**0.57**
Lo	Mid	Burned	Unburned	PSME	TSHE	0.135	-0.183	0.414
Lo	High	Burned	Unburned	PSME	TSHE	0.0787	-0.23	0.354
Mid	High	Burned	Burned	PSME	PSME	-0.0511	-0.165	0.0621
Mid	Lo	Burned	Unburned	PSME	PSME	**0.194****	**0.00597**	**0.425**
Mid	Mid	Burned	Unburned	PSME	PSME	0.0464	-0.112	0.226
Mid	High	Burned	Unburned	PSME	PSME	0.0742	-0.099	0.267
Mid	Lo	Burned	Burned	PSME	TSHE	-0.072	-0.23	0.134
Mid	Mid	Burned	Burned	PSME	TSHE	**-0.105****	**-0.226**	**-0.0072**
Mid	High	Burned	Burned	PSME	TSHE	**-0.135****	**-0.263**	**-0.0304**
Mid	Lo	Burned	Unburned	PSME	TSHE	**0.36****	**0.154**	**0.578**
Mid	Mid	Burned	Unburned	PSME	TSHE	**0.198****	**0.0109**	**0.423**
Mid	High	Burned	Unburned	PSME	TSHE	0.141	-0.0336	0.363
High	Lo	Burned	Unburned	PSME	PSME	**0.244****	**0.0524**	**0.479**
High	Mid	Burned	Unburned	PSME	PSME	0.0968	-0.0611	0.281
High	High	Burned	Unburned	PSME	PSME	0.125	-0.0517	0.32
High	Lo	Burned	Burned	PSME	TSHE	-0.0208	-0.188	0.197
High	Mid	Burned	Burned	PSME	TSHE	-0.0536	-0.187	0.0615
High	High	Burned	Burned	PSME	TSHE	**-0.0843***	**-0.195**	**0.00374**
High	Lo	Burned	Unburned	PSME	TSHE	**0.411****	**0.202**	**0.634**
High	Mid	Burned	Unburned	PSME	TSHE	**0.248****	**0.0579**	**0.48**
High	High	Burned	Unburned	PSME	TSHE	**0.191****	**0.0148**	**0.417**
Lo	Mid	Unburned	Unburned	PSME	PSME	**-0.148****	**-0.308**	**-0.0151**
Lo	High	Unburned	Unburned	PSME	PSME	-0.12	-0.29	0.028
Lo	Lo	Unburned	Burned	PSME	TSHE	**-0.266****	**-0.521**	**-0.0205**
Lo	Mid	Unburned	Burned	PSME	TSHE	**-0.298****	**-0.522**	**-0.139**
Lo	High	Unburned	Burned	PSME	TSHE	**-0.329****	**-0.552**	**-0.169**

Lo	Lo	Unburned	Unburned	PSME	TSHE	**0.166***	**-0.0063**	**0.328**
Lo	Mid	Unburned	Unburned	PSME	TSHE	0.00353	-0.185	0.19
Lo	High	Unburned	Unburned	PSME	TSHE	-0.0529	-0.226	0.111
Mid	High	Unburned	Unburned	PSME	PSME	0.0278	-0.114	0.17
Mid	Lo	Unburned	Burned	PSME	TSHE	-0.119	-0.322	0.112
Mid	Mid	Unburned	Burned	PSME	TSHE	**-0.151****	**-0.318**	**-0.0266**
Mid	High	Unburned	Burned	PSME	TSHE	**-0.181****	**-0.347**	**-0.0595**
Mid	Lo	Unburned	Unburned	PSME	TSHE	**0.314****	**0.143**	**0.484**
Mid	Mid	Unburned	Unburned	PSME	TSHE	**0.151***	**-0.00567**	**0.335**
Mid	High	Unburned	Unburned	PSME	TSHE	0.0947	-0.0582	0.265
High	Lo	Unburned	Burned	PSME	TSHE	-0.147	-0.361	0.0899
High	Mid	Unburned	Burned	PSME	TSHE	**-0.178****	**-0.359**	**-0.0314**
High	High	Unburned	Burned	PSME	TSHE	**-0.209****	**-0.387**	**-0.0627**
High	Lo	Unburned	Unburned	PSME	TSHE	**0.286****	**0.11**	**0.46**
High	Mid	Unburned	Unburned	PSME	TSHE	0.123	-0.0514	0.317
High	High	Unburned	Unburned	PSME	TSHE	0.0669	-0.0916	0.239
Lo	Mid	Burned	Burned	TSHE	TSHE	-0.0327	-0.23	0.0859
Lo	High	Burned	Burned	TSHE	TSHE	-0.0635	-0.27	0.0601
Lo	Lo	Burned	Unburned	TSHE	TSHE	**0.433****	**0.178**	**0.67**
Lo	Mid	Burned	Unburned	TSHE	TSHE	**0.27****	**0.029**	**0.515**
Lo	High	Burned	Unburned	TSHE	TSHE	**0.214***	**-0.0232**	**0.454**
Mid	High	Burned	Burned	TSHE	TSHE	-0.0307	-0.101	0.0355
Mid	Lo	Burned	Unburned	TSHE	TSHE	**0.465****	**0.279**	**0.671**
Mid	Mid	Burned	Unburned	TSHE	TSHE	**0.302****	**0.139**	**0.52**
Mid	High	Burned	Unburned	TSHE	TSHE	**0.245****	**0.103**	**0.459**
High	Lo	Burned	Unburned	TSHE	TSHE	**0.495****	**0.31**	**0.702**
High	Mid	Burned	Unburned	TSHE	TSHE	**0.332****	**0.171**	**0.552**
High	High	Burned	Unburned	TSHE	TSHE	**0.276****	**0.134**	**0.49**
Lo	Mid	Unburned	Unburned	TSHE	TSHE	**-0.163***	**-0.327**	**0.00324**
Lo	High	Unburned	Unburned	TSHE	TSHE	**-0.219****	**-0.362**	**-0.0712**
Mid	High	Unburned	Unburned	TSHE	TSHE	-0.0564	-0.223	0.11

Table S2-5: Pairwise contrasts of feedback estimates. This table presents pairwise contrasts between levels of extreme heat (Low, Mid, High), and burn status (Burned, Unburned). Mean differences are shown with 95% confidence intervals. Contrasts are considered significant when the credible interval does not include zero. Contrasts for which the 95% credible interval does not overlap zero are bolded an annotated (**) along with comparisons for which the 90% credible interval does not overlap zero (*). Here, no contrasts fell outside the 95% credible interval, but the high unburned feedback was marginally different than the low unburned feedback and the high burned feedback (outside 90% credible interval).

Heat Level Comp.		**Burn Status Comp.**		**Mean Diff**	**Lower CI**	**Upper CI**
Lo	Mid	Burned	Burned	-0.0112	-0.123	0.0622
Lo	High	Burned	Burned	-0.0228	-0.162	0.0595
Lo	Lo	Burned	Unburned	0.0929	-0.209	0.374
Lo	Mid	Burned	Unburned	-0.125	-0.419	0.126
Lo	High	Burned	Unburned	-0.204	-0.499	0.0716
Mid	High	Burned	Burned	-0.0116	-0.0724	0.0331
Mid	Lo	Burned	Unburned	0.104	-0.166	0.374
Mid	Mid	Burned	Unburned	-0.114	-0.364	0.121
Mid	High	Burned	Unburned	-0.193	-0.459	0.0656
High	Lo	Burned	Unburned	0.116	-0.142	0.377
High	Mid	Burned	Unburned	-0.103	-0.344	0.122
High	High	Burned	Unburned	**-0.182***	**-0.437**	**0.0635**
Lo	Mid	Unburned	Unburned	-0.218	-0.525	0.0698
Lo	High	Unburned	Unburned	**-0.297***	**-0.617**	**0.0126**
Mid	High	Unburned	Unburned	-0.0789	-0.37	0.223

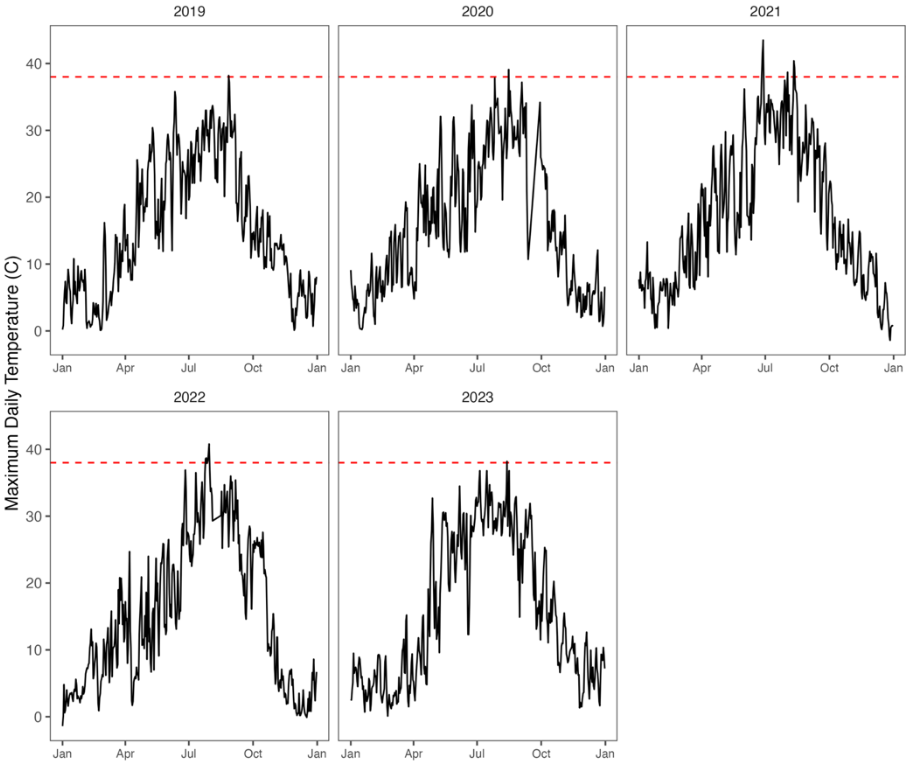

Figure S2-1: Maximum daily temperature (°C) in years from 2019-2023 measured from the primary meterological station (PRIMET) at Andrews Forest. Since 38° C is a critical threshold for seedling physiology (Marias et al, 2017), we calculated degree hours above 38° C using aspirated air temperature data at a resolution of 15 minutes (Daly & McKee 2019). Seasonal maximums occur in the summer (June – September) months in the Pacific Northwest. We highlight that the largest extreme heat event occurred in late June 2021, but other years included in our study also crossed our temperature threshold.

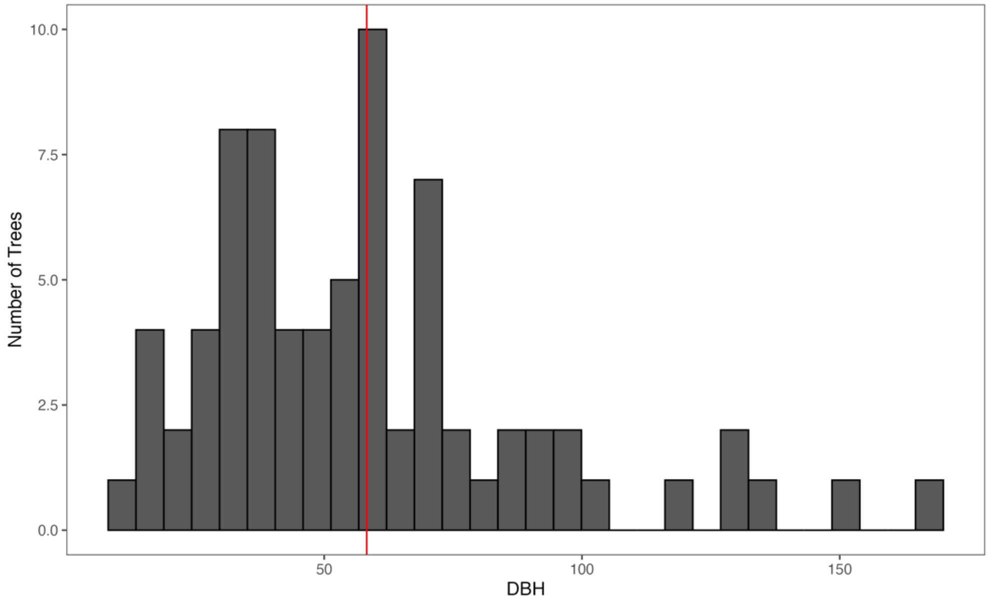

Figure S2-2: Distribution of focal adult DBH. The diameter of each focal adult was measured at breast height in centimeters (height of measurement: 1.37-m, DBH) which was incorporated as a fixed effect in our Bayesian GAMMs. We preferentially selected larger adults when available based on knowledge of their outsized contribution to structuring local environments (Lutz et al. 2018). Mean DBH is depicted as a solid red line (mean = 58.2 cm).

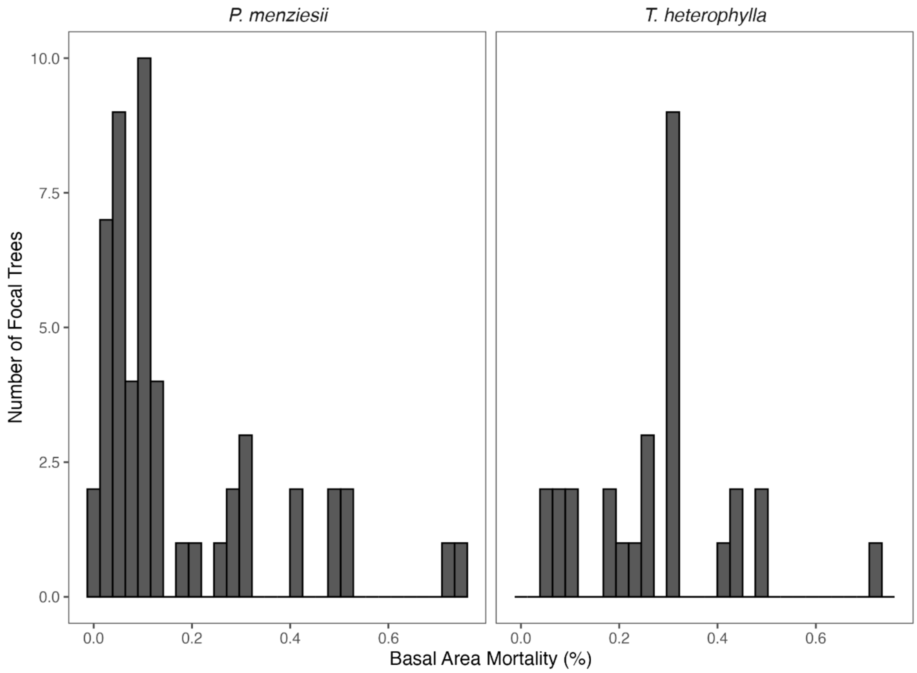

Figure S2-3*:* Distribution of adult focal trees across focal species and basal area mortality. Basal area mortality measured as the fraction of total neighborhood tree basal area (> 5-cm DBH) that experienced fire-induced mortality. Since we chose to avoid the potentially confounding effect of including adults that experienced mortality, our study was constrained to living adults and is disproportionately distributed towards the lower bounds of basal area mortality. Basal area mortality was estimated within each PSP plot, being either an 18-m diameter circle or a 25-m^2 square.

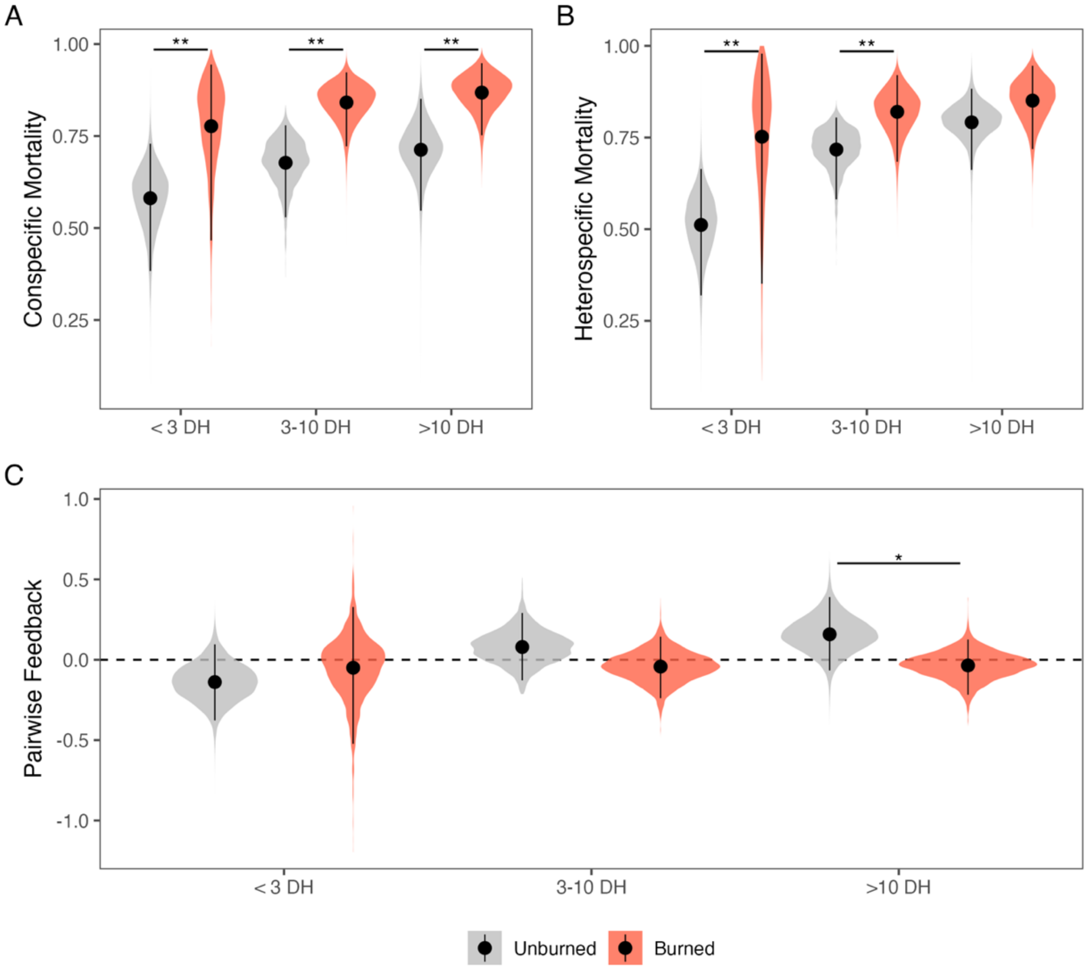

Figure S2-4: Mortality and feedback estimates excluding dead focal adults. Over the course of our study 5 adult trees died, 2 P. menziesii adults and 3 T. heterophylla adults. Here we present identical analyses to those in the main manuscript with these 5 individuals removed. This reduced our seedling sample size from 1207 observations to 1117 observations. While loss of these adults reduces the confidence of our conspecific and heterospecific mortality estimates at low levels of extreme heat (< 3 DH), inference remains the same. Black dots indicate medians, and black lines depict 95% credible interval of estimates. Colored shapes depict posterior distributions of unburned (blue) and burned (red) model estimates. Results are split by degree-hours (DH), reflecting the relative intensity of extreme heat over each survey interval. Since posteriors for unburned and burned mortality are derived from separate models, we assigned significance to contrasts for which the difference between the burned and unburned posteriors excluded zero in 95% credible interval (Table S2-2). (A) Average conspecific mortality across unburned and burned plots under differing intensities of extreme heat events. (B) Average heterospecific mortality across unburned and burned plots under differing intensities of extreme heat events. (C) Pairwise feedbacks where values less than zero indicate that individual performance (survival) is higher in heterospecific environments relative to conspecific environments. Pairwise feedbacks greater than zero indicate that individual performance is higher in conspecific environments relative to heterospecific environments.

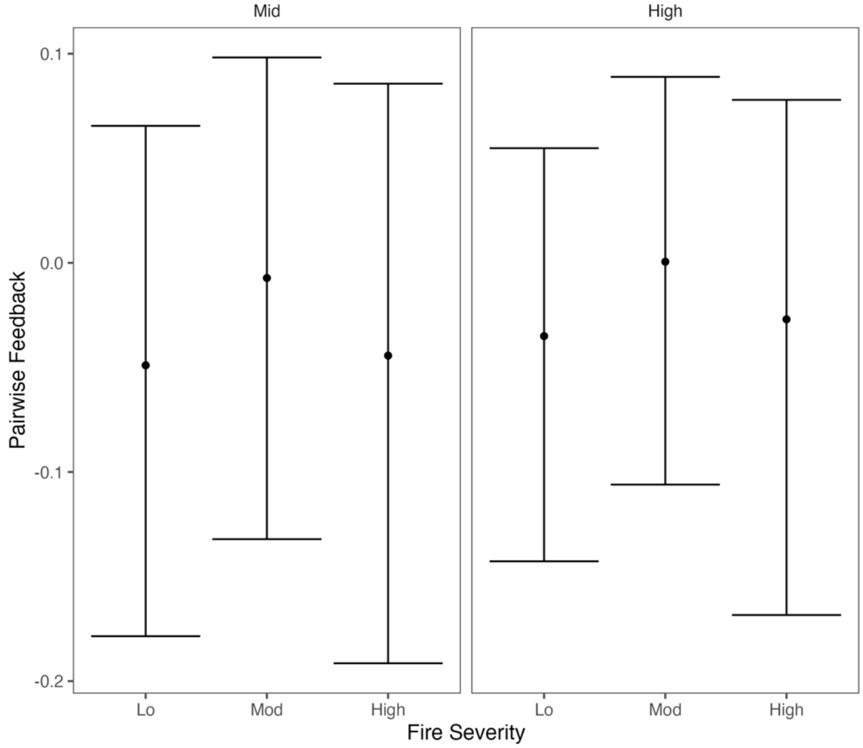

Figure S2-5: Pairwise feedbacks across heat levels as estimated at distinct fire severity quantiles. Fire severity was estimated using the percentage of basal area mortality within the PSP long-term forest inventory plot that each understory demography plot was co-located with. We predicted feedbacks (see methods) at three different basal area mortality levels corresponding to fire severity (Lo = 0.25, Mod = 0.5, High = 0.75). Panels represent categories of extreme heat, separated into "Mid" (3-10 degree hours) and "High" (> 10 degree hours). Here we exclude the "Low" degree hour category presented in the main manuscript due to the challenges associated with extrapolating our relatively small sample size to increasingly fine-scale predictors (see methods). Dots represent median of the feedback posterior, and error bars represent the 95% credible interval. Fire severity as measured by basal area mortality was not a significant factor and averaged across for our final analyses.

Chapter 3 | Adult tree growth responses to climate are altered by neighborhood composition and density

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Abstract

Neighborhood interactions, arising from the spatial arrangement, density, and identity of nearby competitors, are increasingly thought to contribute to the maintenance of species diversity across taxa and scale. Recent evidence indicates that the local effects of neighborhood interactions may be exacerbated or ameliorated in response to changing climates, with cascading implications for the diversity and stability of future ecosystems. In forests, the study of climate-altered neighborhood interactions has primarily focused on seedlings, despite adult trees disproportionately contributing to carbon storage and nutrient cycling. Interactions between neighboring adult trees may respond differently than seedlings to changing climatic conditions due to increased canopy exposure and increased physiological reserves. Here, we investigated how climate alters the neighborhood interactions thought to contribute to local diversity in two conifer species that dominate the old-growth temperate rainforests of the Pacific Northwest: *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (Western hemlock). Combining dendrochronological data from 1960 to 2019 with forest inventory measurements across an elevational gradient in Oregon's Cascade Range, we assessed how changing patterns of temperature, precipitation, and vapor pressure deficit interact with conspecific neighborhood density to affect annual basal area growth. Growth patterns in both species exhibited interactions

between climate and conspecific neighborhood density. For *P. menziesii*, conspecific neighborhood interactions became increasingly destabilizing (positive) in cooler years. For *T. heterophylla*, conspecific neighborhood density effects became increasingly stabilizing (negative) in wetter years. Differing sensitivities to climate variables between these two conifer species potentially reflects differences of life history strategies and canopy position. Pairwise feedback between focal species became significantly positive in cooler years, indicating that temperature fluctuations temporarily alter competitive hierarchies to advantage growth in conspecific neighborhoods relative to heterospecific neighborhoods. Our findings demonstrate that interannual climate variability can alter the outcome of neighborhood interactions among established adults, with implications for forest dynamics and community structure under changing climate regimes. These results highlight the importance of considering both climate and neighborhood context when predicting forest responses to climate change, particularly for carbon-rich old-growth forests dominated by long-lived species.

Introduction

Uncovering the factors that sustain diverse ecosystems across different spatial and temporal scales is a central goal of ecology (Brown, 1984; Holdridge, 1967). This goal is critically important because species diversity is an essential component of ecosystem health and a strong predictor of the ecological services provided to humans (Cardinale et al., 2012; Chen et al., 2023). Over the last 50 years, ecologists have grown increasingly interested in how local interactions between neighboring individuals contribute to patterns of species diversity – finding strong associations between neighborhood interactions and species diversity at local, regional and global scales (Delavaux et al., 2023; Hülsmann et al., 2024; Johnson et al., 2012; LaManna et al., 2017, 2022). More recently, interest has shifted towards understanding how local neighborhood interactions confer resiliency to, or exacerbate the effects of, changing climates (*e.g.* (Bell et al., 2020; De Frenne et al., 2021; Grossiord, 2020; Luo et al., 2024). Despite these advances, our understanding of how climate variables alter neighborhood interactions and subsequent patterns of local species diversity remains reliant on short-term studies that disproportionately focus on early life stage plants. Here, we investigate the degree to which climate alters neighborhood interactions in large, established adult trees to improve our understanding of the impacts of climate on the ecological processes defining local productivity and diversity.

A useful framework for understanding how neighborhood interactions might influence species diversity under changing climates is local conspecific density dependence (CDD). Originating with the Janzen-Connell hypothesis, local CDD describes density-dependent patterns of individual growth, survival, and reproduction (e.g., individual performance) arising in multi-species communities from differences in the effects of local interactions between conspecific (same-species) and heterospecific (different-species) individuals (Chesson, 2000; Comita et al., 2014; Hülsmann et al., 2024; Janzen, 1970; Connell, 1971; LaManna et al., 2024). Local CDD is thought to stabilize community structure and diversity when conspecific effects are disproportionately negative relative to heterospecific effects (Broekman et al., 2019; Wright, 2002). Such differences can be caused by, for example, strong intraspecific competition or interactions with relatively host-specific natural enemies (Adler et al., 2018; Song et al., 2021). Alternatively, local CDD is thought to erode local diversity when conspecific effects are disproportionately positive relative to heterospecific effects, which could be caused by weak intraspecific competition or interactions with relatively host-specific mutualists (Delavaux et al., 2023; Ke & Wan, 2020; Zahra et al., 2021). We emphasize that references to "stabilizing" or "destabilizing" local CDD refer to the potential for local conspecific density effects to affect community diversity and composition and is not an explicit prediction of coexistence. Hereafter, we use the term "local CDD" to refer to local stabilizing or destabilizing CDD (i.e., relative differences in conspecific and heterospecific density effects).

Widespread evidence supports the hypothesis that the strength and directionality of local CDD (i.e., stabilizing or destabilizing) varies with environmental conditions, including seasonal and regional climate patterns (Comita et al., 2014; Milici et al., 2020, Doolittle & LaManna 2025). To date, empirical studies have focused on early-life stage plants, finding that local CDD generally becomes more stabilizing in humid, warm, aseasonal climates (*e.g.* Bachelot et al., 2015, 2020; Brown et al., 2021; Lebrija-Trejos et al., 2023; Liu & He, 2021; Milici et al., 2025; Song et al., 2018; Uriarte et al., 2018). In adults, local CDD is predicted to be generally weaker since established adults are more resilient to externalities including antagonisms and short-term climate stressors (Comita et al., 2007; Pu & Jin, 2018; Zhu et al., 2015). Nevertheless, assessing neighborhood interactions in adult trees is a critical step in understanding the factors that structure and maintain local diversity, as the total effect of these interactions throughout the lifespan of an individual ultimately determines fitness. Moreover, large adults disproportionately contribute to carbon storage and nutrient cycling rates (Lutz et al., 2018), and long-term temporal shifts in local CDD with climate could reveal community-level vulnerabilities to climate change that remain undetected in seedling focused studies. In forests dominated by long-lived species, accurately representing forest dynamics requires understanding how large, established trees respond to their local climatic and neighborhood context.

Dendrochronology and studies of tree rings provide a long-term record of annual growth increments for temperate tree species that is invaluable for understanding the lives of adult trees and their contribution to forest dynamics (Amoroso et al., 2017; Fritts & Swetnam, 1989). These natural archives aggregate the effects of interannual climate variations and the outcomes of density-dependent species interactions, which can be disentangled to examine the effects of climate variability from other ecological processes (Fritts, 2012). By associating tree-rings with climate variables and indices of neighborhood contexts, we can reveal how climate sensitivity varies with tree size and neighborhood, providing important insights into the mechanisms underlying forest responses to climate change. Furthermore, dendrochronological approaches enable high-resolution reconstruction of historical growth patterns and their relationship to climate variables across multiple decades, offering a temporal perspective that is difficult to achieve through other methods such as forest inventories.

Here, we combine dendrochronological approaches with long-term forest inventory data to examine how neighborhood context influences climate sensitivity in two dominant conifer species that account for the majority of basal area in forests of the Pacific northwest of North America: *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (Western hemlock). First, we compare 60 years of tree growth along an elevational gradient in Oregon's central Cascade Range to examine historical patterns of growth for each focal species. Then, we test the hypothesis that warmer and dryer years weaken local CDD in growth of large diameter trees. A growing body of literature indicates that local competitive environments can ameliorate or intensify the sensitivity of tree growth to climate (Buechling et al., 2017; Ford et al., 2017; Kunstler et al., 2011; Zhang et al., 2015). Since the effects of competition and host-associated natural enemies and mutualists vary between conspecific and heterospecific individuals, we hypothesized that conspecific neighborhoods would have disproportionately strong effects on climate-growth sensitivity than heterospecific neighborhoods. Specifically, we predicted that local CDD would become more destabilizing (i.e., more positive effect of conspecific neighborhoods) under climatic conditions that increase physiological stress (i.e., abnormally warm, dry years); which has found recent support in seedling-focused studies (Bachelot et al., 2020; Milici et al., 2025; Song et al., 2018; Uriarte et al., 2018, LaManna et al. *in prep*). By assessing the interactions between climate and local neighborhoods, we improve our understanding of how climate-altered species interactions contribute to functioning and diversity in current and future forest communities.

Methods

Data sources and preparation

We analyzed tree-ring data collected in two summer seasons (2003 and 2022) from the Andrews Experimental Forest in Blue River, Oregon. The Andrews is situated on an old-growth temperate rainforest elevational gradient (410-meters to 1590-meters), where temperature (range = 7.4°C to 10.3°C) and precipitation (range = 2,040 mm/yr to 2,354 mm/yr; Wang et al., 2016) vary. At lower elevations, moderate temperatures and high moisture provide a long growing season for evergreen plant species, even during favorable conditions in winter (Waring & Franklin, 1979). At higher elevations, a short pulse of water from snowmelt in spring/early summer, a dry summer and freezing temperatures throughout the wet season shorten the growing season. Pacific Northwestern temperate rainforests are home to some of the tallest trees and largest above-ground biomass in forests globally. Canopies of the Andrews Forest are dominated by Douglas-fir (*Pseudotsuga menziesii*), Western red-cedar (*Thuja plicata*), Western hemlock (*Tsuga heterophylla*), and a variety of *Abies* species including Silver fir (*Abies amabilis*) and Noble fir (*Abies procera*). Many other broadleaf and conifer species are common, including Big-leaf maple (*Acer macrophyllum*) and Pacific dogwood (*Cornus nuttallii*).

We utilized 612 tree cores collected from 306 adult trees within the long-term forest inventory plots at Andrews Forest (Figure 3-1, Table 3-1). Cores for 171 trees were collected sampled from 4 forest inventory plots in 2003 for previous studies (Harmon & Woolley, 2013) and downloaded from the Andrews Forest Data Portal in August 2023. To supplement these cores, we collected cores from an additional 135 trees in June and July of 2022 from 2 additional forest inventory plots and 1 forest inventory plot overlapping with the 2003 core dataset. All cores were cross-dated and measured by the original researchers using standard dendrochronological practices (Stokes & Smiley, 1996).

To remove sources of error, we excluded cores for which we detected technical or sampling errors (e.g., broken cores, unreconcilable dating errors). Additionally, we excluded cores for which we detected abnormal growth patterns relating to sudden competitive release (gap creation), mechanical damage, cores for which tree diameter at breast height (DBH) at time of latest measurement was less than 30-cm, or other external factors that may mask growth-sensitivity to climate (Anderson-Teixeira et al., 2022). We defined the threshold for core removal to be growth for which absolute growth across 3 consecutive years exceeding 1 standard deviation in core growth. In total, we included 498 cores from 249 trees distributed across 6 forest stands (Table 3-1). Examples of the core selection process can be found in Figure S3-1. Distribution of selected adult tree DBH can be found in Figure S3-2. Data preparation and validation were all performed in R 4.2.1 (R Core Team 2022) using the dplR (Bunn et al. 2024) and tidyverse packages (Wickham et al. 2019).

Converting ring-width to basal area increments

We utilized basal area increments (BAI) in lieu of ring-width (RW) measurements as BAI provides a more biologically meaningful representation of tree growth compared to raw RW and directly relates to carbon storage. BAI accounts for the geometric constraint that requires a tree to produce more wood to maintain the same ring width as it gets larger. This approach has been widely adopted in dendrochronological studies examining tree growth responses to environmental changes and forest dynamics (Biondi & Qeadan, 2008; Duchesne et al., 2019). To calculate BAI, we first reconstructed yearly DBH from RW based on the most-recent forest inventory survey before the sampling of each core. When forest inventory surveys occurred in years preceding core sampling, we removed RW of years after the forest inventory survey. To reconstruct yearly DBH, we first applied allometric equations for each of our two focal species to estimate bark thickness and subtracted this from the forest inventory survey DBH (Table S3-1; Miles & Smith, 2009). We then sequentially removed twice the ring widths to reconstruct DBH, accounting for changing bark thickness. Reconstructed DBH values were then transformed into BAI using the following equation, where t is the current year, and t-1 is the previous year:

$$\mathrm{BAI}_t = \pi\left(\frac{DBH_t}{2}\right)^2 - \pi\left(\frac{DBH_{t-1}}{2}\right)^2$$

BAI values included in downstream models were first transformed using the natural logarithm, which addressed heteroscedasticity and approximated a normal distribution of residuals (Wykoff, 1990). We note that recent debate has emphasized the value of applying square-root transformations to BAI to improve estimation of growth in small trees (Zell, 2018). We opted to use the traditional natural logarithm transformation since our analysis is restricted to large trees greater than 30-cm DBH.

Estimating neighborhood density

To estimate neighborhood density, we calculated indices of conspecific density and total density for each tree. Trees that are larger and nearer are expected to have greater competitive influence (Canham et al., 2004). Therefore, we used a size-dependent and distance-weighted formula to calculate the local neighborhood density index (LDI) within a 10-meter radius of each focal individual (*as in* LaManna et al., 2022; Magee et al., 2024).

$$LDI_i = \left(\sum_{j=1}^{n} \frac{DBH_j^a}{distance_{ij}^b} \right)^d$$

Where $j = 1, 2, \ldots, n_i$ neighboring trees within a specified radius; DBH_j is the DBH of the *jth* neighbor; $distance_{ij}$ is the distance from the *ith* tree to the *jth* neighbor; and a, b, and d are nonlinear scaling coefficients fit from the data (Canham et al., 2006; Uriarte et al., 2004). Based on previous work at this site, we used a neighborhood radius of 10-m (LaManna et al., 2022). Instead of omitting focal stems that were near the plot boundary, we opted to apply an edge correction factor to account for any portion of the 10-m neighborhood radius falling outside of the forest inventory survey area. These corrections were applied to 56 out of 249 trees (mean correction factor = 1.22, SD = 0.08).

We limited neighborhoods of 10-meter radii to adult trees greater than or equal to 15-cm DBH. In Pacific Northwestern old-growth forests, individual trees of our focal species can take 40 to 80 years to reach the 15-cm DBH class (Ruth, 1964). Therefore, by limiting our neighborhoods to 15-cm DBH, we account for the growth of neighbors over time and remove trees that were unlikely to contribute to neighborhood dynamics dating back to 1960. We validated our approach against duplicate analyses with more restrictive cutoff dates (Figure S3-5).

To evaluate the functional form of the relationship between neighborhoods and annual growth, we conducted a grid search on *a, b*, and *d* as suggested by Smith (2022) and performed by

LaManna et al. (2022) and Magee et al. (2024). Our grid search used linear mixed effect models in the nlme package (Pinheiro et al., 2025) with the following formula:

$$log(BAI) = \beta_0 + \beta_1 DBH + \beta_2 LDI_{con} + \beta_3 LDI_{total} + u_i + v_{ij} + \epsilon_{ijt}$$

Where LDI_{con} is the conspecific local density index, LDI_{total} is the total local density index, u is the random effect for forest stand i, v is the tree-level random effect of individual j in stand i, and ϵ_{ijt} follows a continuous t time autoregressive process CAR(1) within each i,j combination (Pinheiro & Bates, 2000). We used the same $a, b,$ and d coefficients for both conspecific and total density neighborhoods. Importantly, we scaled and mean-centered each conspecific and total LDI together to retain the relationship between conspecific density and total density. We included the continuous time autoregressive correlation structure to account for the biological artifact that rings closer in time are typically more strongly correlated than those taken further apart, which could otherwise lead to biased parameter estimates and incorrect inference. Our grid search models selected a = 0, b = 1, and d = 1 for *T. heterophylla* (Western hemlock; TSHE) and a = 0, b = 1.4, and d = 2 for *P. menziesii* (Douglas-fir; PSME; Figure S3-3).

Climate data sources & preparation

To integrate climate into our downstream analyses we downloaded monthly climate data from 1960 – 2019 obtained from the satellite-derived PRISM 4km grid dataset (PRISM Climate Group, Oregon State University) and validated against local high-resolution climate records (Daly et al. 2019). We focused on monthly mean temperature (Tmean), total precipitation (PPT), and monthly maximum monthly vapor pressure deficit (VPD). VPD is a key driver of tree physiological stress that combines the effects of temperature and atmospheric moisture demand, making it a more mechanistic predictor of tree growth than temperature or precipitation alone (Williams et al., 2010). We included temperature and precipitation as alternatives to account for the possibility that neighborhood density effects may be altered by climate variables affecting the underlying antagonists and mutualists driving local CDD – which may be more responsive to temperature or precipitation at the forest floor relative to atmospheric VPD.

To select time periods for which tree BAI growth was most associated with climate, we adapted a climate-window approach similar to the 'slidingwin' function from the climwin package (Anderson-Teixeira et al., 2022; van de Pol & Bailey, 2020). We ran separate, parallel climate-growth models for each combination of species and climate variable using the nlme package. We fixed effects for tree size (DBH) and linear and quadratic terms for climate with random intercepts for individual trees and a continuous autoregressive term to account for temporal autocorrelation. These models were iteratively fit to different monthly period means ranging from 2 – 8 months in length. We selected the model for each climate variable for which log-likelihood was the highest. This climate-window approach yielded 3 new climate window variables included in downstream analyses ($VPD_{climwin,}$ $Tmean_{climwin,}$ and $PPT_{climwin}$). We considered this data-driven to be more robust than arbitrary window selection (i.e., average spring or summer conditions), but present the alternative with identical seasonal windows across species and elevation in Figure S3-4.

Along with PRISM climate data, we tested the inclusion of meteorological data from the Andrews Forest which demonstrate that low-elevation valleys generally have higher mean-spring temperatures and lower mean-summer temperatures than higher elevation ridgelines (Frey et al., 2016). These cold air drainages represent climate variability that is not well captured at the 4km grid PRISM scale. Our full models included a principal component axis ($PC_{spatial}$) orthogonal built from mean spring temperature, mean summer temperature, and orthogonal to elevation. In other words, we tested the inclusion of a variable derived from local temperature sensors to account for site-specific variations from macroclimatic temperature trends resulting from local topography.

Estimating long-term growth patterns

To assess long-term growth trends at the forest plot level, we fit species-level general additive models (GAMs) using the 'mgcv' package (Wood, 2025). We modeled natural log-transformed BAI with predictor for the global effect of year using a thin-plane regression spline, plot-level thin-plane regression splines for individual plots, and a tree-level random spline (akin to a random intercept in linear model framework; Pedersen et al., 2019). GAMs were selected for this analysis to capture non-linear relationships between tree growth and time without imposing rigid assumptions about the shape of these relationships.

Bayesian hierarchical models and hypothesis testing

Our analytical pipeline for assessing growth-climate sensitivity is generally similar to that of Anderson-Teixeira et al. (2022), where analyses consisted of two main steps: 1) identifying the primary climate drivers (i.e., variables and seasonal windows over which they are most influential on tree growth) and 2) combining climate variables, BAI, and local density indices into a multivariate hypothesis testing model (Fig 1). Our approach differs in the estimation of neighborhood density and interactions of density effects with climate factors, as well as the implementation of Bayesian hierarchical models as opposed to a frequentist modeling approach.

To test for the interactive effects of climate and density on growth, we fit separate Bayesian generalized linear mixed models (GLMMs) with autoregressive processes for each tree to account for temporal autocorrelation using the brms package (Bürkner et al., 2024). We selected Bayesian GLMMs over GAMs for hypothesis testing of climate-density interactions because we anticipated a high degree of correlated error between estimates and had *a priori* assumptions that the interactions between climate and competition should approximate a quadratic function (Anderson-Teixeira et al., 2022; Ford et al., 2017; Williams et al., 2010). Functionally, this approach is like other mixed-modeling approaches but differs in the use of posterior distributions for downstream analyses and the specification of an autocorrelation structure within the error term. For each species, we fit separate models to explore linear fixed effects between each of our temporal climate variables ($VPD_{climwin}$, $Tmean_{climwin}$, and $PPT_{climwin}$) and log-transformed BAI and elevation, $PC_{spatial}$, LDI_{con}, and LDI_{total}. We included linear and quadratic fixed effects for DBH and temporal climate, and interactions between linear and quadratic combinations of LDI_{con} and LDI_{total} with both $PC_{spatial}$ and temporal climate. We opted to use the brms default uninformative priors. Through initial model testing we determined that our dataset deviated from normality and best approximated a Student's t distribution, meaning that our dataset of tree BAI growth exhibited more outliers than expected by a normal distribution. Each Bayesian GLMM model accounted for the spatial non-independence of data and repeated measurements through random intercepts for forest plot and individual trees, along with a first-order autoregressive correlation structure.

We systematically compared models with different combinations of predictor variables and their interactions, as well as different combinations of random effects that allowed the effects of conspecific and total density to vary with forest stand while maintaining the autoregressive correlation structure to determine the best model structure. Since our hypothesis explicitly focuses on the interaction between climate and density, we forced all model comparisons to include the selected climate variable and the linear interaction between the selected climate variable and both LDI_{con} and LDI_{total}. For each species, we ranked candidate models according to their Leave-One-Out cross validation score (LOO) and considered models with increases in expected log predictive density (ELPD) exceeding twice the ELPD standard deviation to be supported by our data. Final model selection based on our constrained model selection approach accounts for variables necessary to test our hypotheses and the biological interpretability of parameter estimates. Posterior predictive checks and residual plots were used to check model fits using the DHARMa (Hartig, 2022) and brms (Bürkner et al., 2024) packages (Fig S9-S14).

Quantifying local conspecific density dependence

To quantify how a change in conspecific density affects annual growth, we calculated relative and absolute average marginal effects (AMEs) of adding one conspecific adult (15-cm DBH, minimum size included in our forest inventory datasets) 1-meter from the focal tree assuming an otherwise heterospecific local neighborhood. Relative and absolute AMEs were calculated with the following equations:

$$\text{rAME} = \frac{(P_{i,LDI_{con+1}} - P_{i,LDI_{con=0}})}{P_{i,LDI_{con=0}}}$$

$$\text{aAME} = P_{i,LDI_{con+1}} - P_{i,LDI_{con=0}}$$

Where $P_{i,LDI_{con=0}}$ represents the model-predicted growth for an individual *i* assuming an entirely heterospecific neighborhood where conspecific density is zero, and $P_{i,LDI_{con=0}}$ represents the model-predicted growth when a 15-cm DBH conspecific adult is added 1-meter from the focal tree. For both rAME and aAME, model predictions were derived while leaving all other confounders (i.e., DBH, total density, etc.) at their observed values. The relative AME (rAME) can be interpreted as relative change in growth (%) caused by the increase in conspecific density (Hülsmann et al., 2024). Here, we focus our results and discussion on CDD as estimated by rAME because we consider relative changes in growth to be more ecologically relevant than absolute changes. As an alternative to estimating rAME as a standardized increase in conspecific density from an otherwise entirely heterospecific neighborhood, we additionally estimated rAME as a standardized addition observed conspecific densities. This alternative rAME, along with results for aAME, are presented in Figure S3-6 and Figure S3-7, respectively.

Estimating pairwise feedback between focal species

To understand the community implications of climate-mediated density effects, we quantified pairwise feedback strength between our focal species. While conspecific density effects describe how individuals respond to neighbors of their own species, pairwise feedback provides insight into the reciprocal effects that two species have on each other's performance, which can indicate whether their interaction tends to promote coexistence or competitive exclusion (Bever, 2003; Bever et al., 1997). This approach is particularly relevant in forest ecosystems where trees modify their local environment through allelopathy and associations with microbial communities, creating legacy effects that influence subsequent performance (Bennett et al., 2017).

We quantified pairwise feedback strength (I_s) between our focal species following the approach outlined in Bever et al. (1997). Pairwise feedback was calculated as:

$$I_s = A_{LDI_{con+1}} - B_{LDI_{con=0}} - A_{LDI_{con=0}} + B_{LDI_{con+1}}$$

where $A_{LDI_{con+1}}$ and $B_{LDI_{con+1}}$ represent the growth of *T. heterophylla* and *P. menziesii* in neighborhoods where one 15-cm DBH conspecific tree has been added and one 15-cm DBH heterospecific tree has been removed, and $A_{LDI_{con=0}}$ and $B_{LDI_{con=0}}$ represent their growth in entirely heterospecific neighborhoods. Positive I_s values indicate that species perform better in conspecific soil (positive feedback), while negative values indicate improved performance in heterospecific soil (negative feedback). We calculated I_s at 5 evenly spaced quantiles (10% to 90%) for each climate variable and considered those for which 95% of the posterior distribution fell above or below zero to be significant.

Results

Growth trends for focal species

The GAM fit to long-term growth patterns of *P. menziesii* revealed a significant overall temporal trend (Figure 3-2, Table S3-2, F = 7.939, $p < 0.001$), indicating substantial year-to-year variation in growth across all stands. Additionally, all stand-specific smooth terms were highly significant ($p < 0.001$), demonstrating that each stand exhibited unique growth trajectories over time. In particular, stands RS02, RS31, and RS22 (which are low, mid, and high elevation, respectively; Table 3-1) showed the strongest deviations from the overall temporal pattern (F = 9.67, 11.445, and 10.795).

For *T. heterophylla*, the GAM fit to long-term growth patterns revealed no overall temporal trend (Figure 3-2, Table S3-3, F = 0.990, p = 0.486), but strong stand-specific trends. Stand-specific temporal patterns were significant for all stands, with stand RS22 showing the strongest effect (F = 68.540, $p < 0.001$), followed by RS34 (F = 39.524, $p < 0.001$). The remaining stands (RS02, RS31) showed significant but less pronounced effects ($p < 0.05$).

The random effects term for individual trees was highly significant in both models ($p < 0.001$). *P. menziesii* exhibited relatively consistent growth trajectories across stands until approximately 1990, after which the stands diverged considerably. In contrast, *T. heterophylla* showed greater stand-level differentiation throughout the entire sample period, with stand RS22 demonstrating particularly distinctive growth patterns characterized by higher growth rates – especially in recent decades.

Climate-growth sensitivity of *T. heterophylla* (Western hemlock)

Across all *T. heterophylla* climate-growth sensitivity models, DBH consistently showed a positive relationship with basal area increment (BAI; Figure 3-3; Table S3-4; β = 0.64, 95% CI [0.55, 0.73]), with a significant negative quadratic component (β = -0.14, 95% CI [-0.18, -0.10]), indicating that growth increases with diameter but at a diminishing rate in larger trees. Climate variables displayed distinct patterns of influence on growth**.** Temperature had no significant linear effect (β = 0.00, 95% CI [-0.01, 0.01]) or quadratic effect (β = -0.00, 95% CI [-0.01, 0.01]). Vapor pressure deficit (VPD) exhibited a weak negative linear relationship (β = -0.01, 95% CI [-0.02, -0.00]) with a more pronounced negative quadratic response (β = -0.01, 95% CI [-0.02, -0.01]), indicating reduced growth under both very high and very low VPD conditions. Precipitation was a significant positive linear influence (β = 0.03, 95% CI [0.02, 0.04]) with a negative quadratic relationship (β = -0.02, 95% CI [-0.02, -0.01]), suggesting optimal growth at moderate to high precipitation levels with slight declines under extreme precipitation.

Neighborhood density estimates were insignificant for *T. heterophylla*, and interactions between neighborhood density estimates were also insignificant with the exception of a negative interaction between conspecific density and the quadratic precipitation term (Fig 4B, β = -0.02, 95% CI [-0.03, -0.00]), and an interaction between total density and VPD (Fig 3; β = -0.01, 95% CI [-0.02, -0.00]). Substantial tree-level and stand-level variation was detected across models. Temporal autocorrelation in growth was consistently strong (φ = 0.84, 95% CI [0.82, 0.87]), indicating high year-to-year consistency in individual tree growth patterns. The Student's t distribution shape parameters (ν = 7.56, 95% CI [6.20, 9.33]) suggested moderate deviations from normality in residual errors. All models demonstrated good convergence with $\hat{R}$ values of 1.00 and adequate effective sample sizes for parameter estimation.

Climate-growth sensitivity of *P. menziesii* (Douglas-fir)

Like *T. heterophylla*, *P. menziesii* showed strong positive relationships between DBH and growth (Figure 3-3; Table S3-4; β = 0.53, 95% CI [0.37, 0.67]), and a significant negative quadratic term (β = -0.13, 95% CI [-0.23, -0.03]), indicating growth increases with size but plateaus in larger individuals. Climate variables exhibited distinct effects on Douglas-fir growth**.** VPD was a significant negative linear influence (β = -0.04, 95% CI [-0.04, -0.03]) with no significant quadratic component (β = 0.00, 95% CI [-0.00, 0.01]), suggesting that growth consistently decreases with atmospheric dryness. Temperature showed no significant linear effect (β = 0.01, 95% CI [-0.01, 0.03]) but displayed a significant positive quadratic relationship (β = 0.03, 95% CI [0.02, 0.04]), indicating potentially increased growth at both low and high temperature extremes. Precipitation exhibited a positive linear effect (β = 0.02, 95% CI [0.01, 0.02]) with no significant quadratic component (β = -0.00, 95% CI [-0.01, 0.00]), suggesting generally improved growth with increasing precipitation.

Neighborhood density effects varied across models. Total neighborhood density showed a consistently negative influence approaching significance (β = -0.11, 95% CI [-0.21, 0.01]). Conspecific neighborhood density demonstrated no significant direct effect (β = 0.03, 95% CI [-0.12, 0.20]) but showed complex interactions with climate variables. Notably, there were significant interactions between conspecific density and temperature, with negative linear (β = -0.06, 95% CI [-0.08, -0.04]) and positive quadratic (β = 0.02, 95% CI [0.01, 0.03]) interactions (Figure 3-4B). For VPD, there was a significant negative linear interaction with conspecific density (β = -0.03, 95% CI [-0.04, -0.02]). Precipitation models showed significant positive linear interactions with conspecific density (β = 0.03, 95% CI [0.03, 0.04]) and negative quadratic interactions (β = -0.01, 95% CI [-0.01, -0.00]). Substantial variation in growth was observed at both tree and stand levels. Growth patterns showed high temporal autocorrelation within individual trees ($\varphi = 0.78$, 95% CI [0.76, 0.80]). Student's t distribution shape parameters ($\nu = 9.34$, 95% CI [7.59, 11.67]) indicated moderate departures from normality in residual errors. All models demonstrated good convergence with $\hat{R}$ values of 1.00 and adequate effective sample sizes for parameter estimation.

Pairwise Feedback (I_s)

Pairwise feedbacks as estimated through I_S between *T. heterophylla* and *P. menziesii*, were neutral for both precipitation and VPD (Figure 3-4C). I_S became significantly positive only at extreme low temperatures (10% temperature quantile, 97.7% of posterior distribution above zero) but was otherwise neutral across the rest of the temperature range. Changes to pairwise feedbacks were largely driven by changes to BAI growth in relatively conspecific neighborhoods compared to heterospecific neighborhoods across focal species (Figure S3-8).

Discussion

Our results reveal that climate alters conspecific neighborhood density effects on the growth patterns of large, established trees with important implications for forest dynamics under climate change. Two key findings emerge. First, local CDD becomes more destabilizing in cooler years for *P. menziesii*, and more stabilizing in wetter years for *T. heterophylla* (Figure 3-4B). Second, pairwise feedback between these dominant conifer species becomes positive in cool years, suggesting that climate fluctuations can temporarily alter neighborhood interactions to advantage each species in relatively conspecific neighborhoods (Figure 3-4C). A growing body of literature indicates that climatic extremes are likely to affect neighborhood interactions and local CDD (Crawford et al., 2019; Pugnaire et al., 2019). Our findings expand upon recent seedling-based studies by demonstrating that local CDD in adult trees can similarly become more stabilizing in wetter (e.g. Milici et al., 2025; O'Brien et al., 2017; Song et al., 2020) and hotter (e.g. Liu & He, 2021, 2022; Song et al., 2018) years, with important species-level differences highlighting the complex ways that interannual climatic variability influences old-growth forest dynamics.

A key finding is that local CDD is associated with different climate variables, and in different directions, for each of our focal species (Figure 3-4B). For *P. menziesii,* local CDD becomes increasingly destabilizing (positive) in cooler years, indicating that colder temperatures advantage *P. menziesii* growth in conspecific neighborhoods relative to heterospecific neighborhoods (Figure 3-4B; 2.9% - 54.8% increase as estimated using rAME, see Figure S3-6 for aAME estimates). In contrast to *P. menziesii*, local CDD in *T. heterophylla* growth became increasingly stabilizing in wetter years despite not varying with temperature. Wet years translated to a 0.3% - 15.6% decrease in *T. heterophylla* BAI growth in conspecific neighborhoods relative to heterospecific neighborhoods (Figure 3-4B; estimated using rAME, for Figure S3-7 for aAME estimates). Extending beyond local CDD to pairwise feedbacks between these two dominant conifer species, we find that conspecific environments are preferred for both *P. menziesii and T. heterophylla* in cool years (positive feedback) but no changes to feedback strength with precipitation (Fig 4C). Our findings highlight that both precipitation and temperature alter the effects of local neighborhoods with consequences for growth rates and subsequent carbon storage under changing climates.

Differences in climate-mediated shifts in local CDD between our focal species may arise from several non-exclusive mechanisms, including differences in life-history strategies, forest structure, and microbial interactions. *P. menziesii*, a relatively drought-tolerant species, may be more sensitive to colder conditions compared to the shade-tolerant *T. heterophylla*, which occurs at higher latitudes than *P. menziesii* and may possess more robust physiological mechanisms conferring cold resilience (Lassoie et al., 1985). The heightened sensitivity of *P. menziesii* to interannual variations in summer temperature may also result from greater exposure to temperature and other atmospheric extremes relative to the shorter, old-growth specialist *T. heterophylla*, aligning with previous work demonstrating that canopy trees are more responsive to climatic fluctuations (Bennett et al., 2015; Rollinson et al., 2021). Our results complement other recent studies that find life-history and forest structure introduce important variation in the sensitivity of neighborhood effects to climate (Kobe & Vriesendorp, 2011; Liu & He, 2022; Luo et al., 2024; Ramage et al., 2023).

Along with life-history and forest structure, microbial interactions, which contribute to local CDD when relatively host-specific, may underly our main finding that neighborhood effects are sensitive to interannual variations in climate. For example, ectomycorrhizal networks that facilitate resource sharing among trees may amplify conspecific advantages in cooler years by buffering against climatic stress when decomposition rates are slower (Castaño et al., 2017; Steidinger et al., 2019). In warm years, when nutrients are more readily accessible, ectomycorrhizal networks may become less important to patterns of large adult tree growth. Conversely, wetter years are associated with increased abundance and virulence of root- and leaf-associated pathogens (Delgado-Baquerizo et al., 2020; Milici et al., 2020), which may contribute to our finding of stronger stabilizing CDD in *T. heterophylla* growth in wet years.

We highlight the stress gradient feedback hypothesis as a useful framework for understanding our results, which posits that increasing environmental stress should increase the benefits of relatively host-specific mutualisms relative to antagonisms (Doolittle et al. *in prep*). Under this framework, trees in stressful environments should receive amplified benefits from proximity to conspecifics that share mutualists, potentially shifting the balance from competition to facilitation along stress gradients (David et al., 2020). Integrating the stress gradient feedback hypothesis with life-history differences, we hypothesize that canopy-exposed, shade-intolerant *P. menziesii* experiences increased physiological stress in cool years relative to dry years – which can be reduced in relatively conspecific environments by amplified benefits from ectomycorrhizal networks. Similarly, *T. heterophylla*, being less canopy-exposed and more shade tolerant, may experience more physiological stress in dry years relative to wet years, which can be reduced by resource sharing among conspecifics through ectomycorrhizal networks.

Among the remaining questions limiting our understanding of neighborhood interactions is the degree to which thresholds exist at climatic extremes. While our study detected gradual shifts in local CDD with temperature and precipitation, ecosystems often exhibit non-linear responses when critical climate thresholds are exceeded (Franklin et al., 2016). The existence of such a threshold at climatic extremes may manifest as abrupt changes in the strength or direction of local CDD, and explain why studies like ours and Liu & He (2021) find that local CDD is negatively correlated with temperature (more stabilizing with mild warming), while others find that extreme warming erodes stabilizing neighborhood effects (Bachelot et al., 2020; Germain & Lutz, 2022).

We find that tree growth is responsive to different climatic variables across different seasonal periods of growth. For both focal species, growth is most correlated with early summer VPD at lower elevations and late summer VPD at higher elevations (Figure 3-4A). Similar trends are present for precipitation in both species and temperature in *T. heterophylla*. Notably, selected climate windows do not always align with elevation – which may be indicative of temperature inversions caused by cool-air drainages (i.e., higher mean-spring temperatures and lower mean-summer temperatures in valleys relative to ridgelines; Frey et al., 2016). While tree growth is not uniformly responsive to seasonality, we find that both focal species are responsive to interannual differences in macroclimate.

Overall, tree growth was most strongly predicted by tree size and highest for the largest trees at higher elevation sites. This pattern was particularly evident at the highest elevation site (RS22) where annual growth for both *P. menziesii* and *T. heterophylla* has dramatically increased in recent decades (Figure 3-2). While recent increases to growth rates at higher elevations could be reflective of reduced thermal constraints and extended growing seasons (Lenoir et al. 2008), we expect that increased growth at RS22 is likely driven by recent declines in populations of mid-seral, climate-sensitive species (e.g., *Abies procera; Franklin et al. 2024*). Regardless of the mechanism, recent changes to local conditions appear to be advantageous to growth rates of both *P. menziesii* and *T. heterophylla* at the highest end of our elevational gradient.

We highlight that our pairwise feedback result finding a demographic advantage for both focal species in conspecific environments in cool years is restricted to established adult trees, which typically experience weaker density-dependent effects than earlier life stages (Pu & Jin, 2018; Zhu et al., 2015). Adult trees have more extensive root systems, greater carbon reserves, and enhanced resistance to pathogens compared to earlier life stages. Notably, our reliance on a static neighborhood measurement constrained our analysis to a maximum of 60 years of growth, which represents a relatively short window in the lifespan of these long-lived tree species. We accounted for this limitation by limiting our neighborhoods to trees ≥15-cm DBH, which were likely present throughout our study period given the growth rates of our focal species (Ruth, 1964). Nevertheless, future studies incorporating more frequent and detailed neighborhood measurements would provide additional insights into temporal neighborhood dynamics.

Our focus on large established adults likely also explains why we find generally neutral local CDD under most climate scenarios while studies of earlier life stages disproportionately reveal negative stabilizing local CDD (Comita et al., 2014; Hülsmann et al., 2024; Song et al., 2021). The spatial patterns of large adult trees are the product of environmental and biotic constraints on growth and survival in earlier life stages. As climate change alters both the mean and variability of temperature regimes, these periodic disruptions to established competitive hierarchies could have cascading consequences for forest community composition and carbon dynamics. Understanding these stage-specific responses to climate-neighborhood interactions will be critical for forecasting forest resilience in an era of rapid environmental change, particularly in old-growth systems where large trees contribute disproportionately to ecosystem function and carbon storage.

Conclusions

Our results demonstrate that interannual climate variation can have important effects on growth patterns of large trees, weakening stabilizing conspecific density effects for *P. menziesii* in cool years and strengthening conspecific density effects for *T. heterophylla* in wet years. As climate change increases the frequency and intensity of extreme fluctuations in climate, these altered neighborhood dynamics may play an increasingly important role in reshaping growth patterns of large, established adults – with cascading consequences for carbon storage, ecosystem functioning, and local diversity. Future research should focus on integrating these local-scale, climate-mediated biotic interactions into models predicting forest responses to climate change, which have traditionally emphasized direct physiological responses to climate while overlooking the important role of neighborhood interactions.

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Tables & Figures

Table 3-1: Distribution of Sites and Tree Sampling. We utilized 612 cores from 306 trees collected either specifically for this study or in 2003 by Harmon & Woolley (2013). We omitted cores with broken wood, obvious dating errors, abnormal growth patterns, and cores for which the previous forest inventory survey recorded a diameter at breast height (DBH) less than 30-cm. Final core dataset included 249 trees distributed across 6 long-term forest inventory plots across 800-meters of elevation at the H.J. Andrews Experimental Forest LTER in Blue River, Oregon.

Forest Stand	**Elevation (m)**	**Trees Cored (2003)**		**Trees Cored (2022)**		**Site Totals**
		P. menziesii	*T. heterophylla*	*P. menziesii*	*T. heterophylla*	
RS07	490	0	18	0	0	18
RS01	510	67	0	0	0	67
RS02	580	0	0	13	20	33
RS34	820	7	22	0	0	29
RS31	900	0	0	23	16	39
RS22	1290	10	16	19	18	63
	Totals:	**84**	**56**	**55**	**54**	**249**

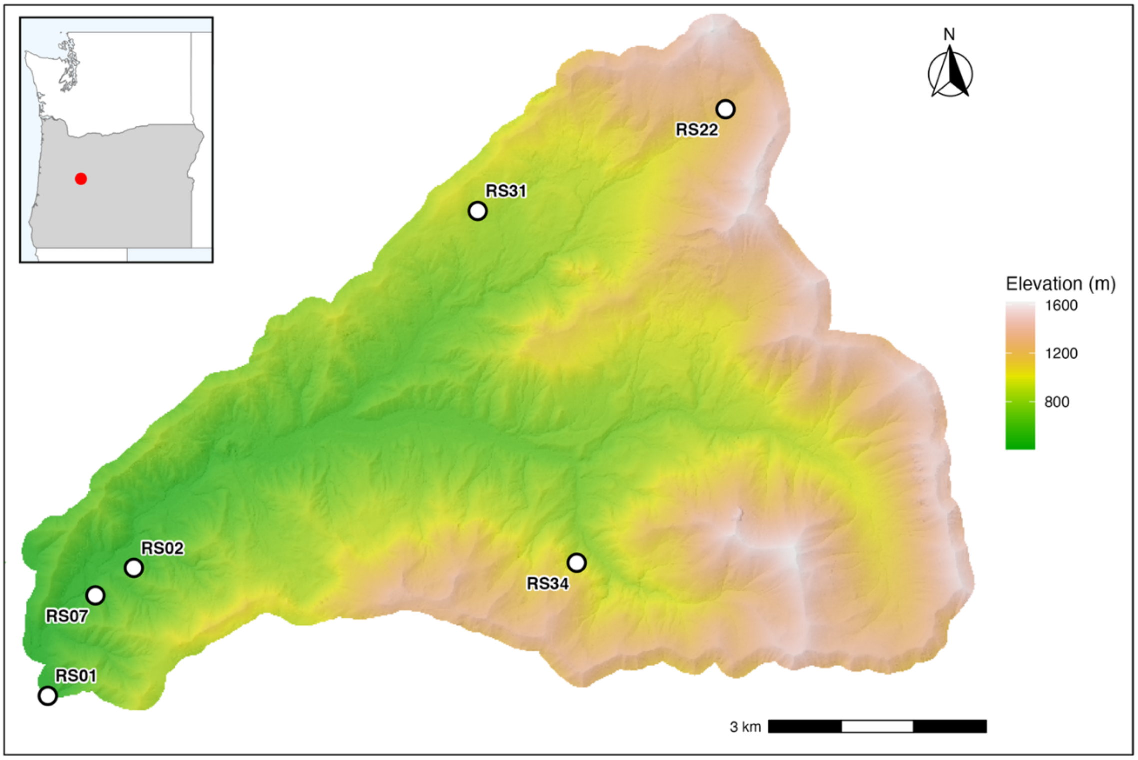

Figure 3-1: Location of sampled reference stands within Andrews Forest in the central Cascade Range of Oregon, USA. Located in the central Cascade Range of Oregon, the H.J. Andrews Experimental Forest (Andrews Forest) is a long-term ecological research station (LTER) situated on forests, streams, and meadows that indigenous peoples have been in relationship for thousands of years. In the Kalapuya Treaty of 1855 (aka Treaty of Dayton, Willamette Valley Treaty), the Kalapuya were forced to cede this land to the US Government. This overview map of the Andrews Forest depicts the location of tree core sampling along an 800-meter elevational gradient, where light colors refer to high elevation and green, dark colors refer to low elevation (Table 1). Cores were taken from long-term forest inventory measurement plots (or "reference stands"; RS) dating back to the 1970s.

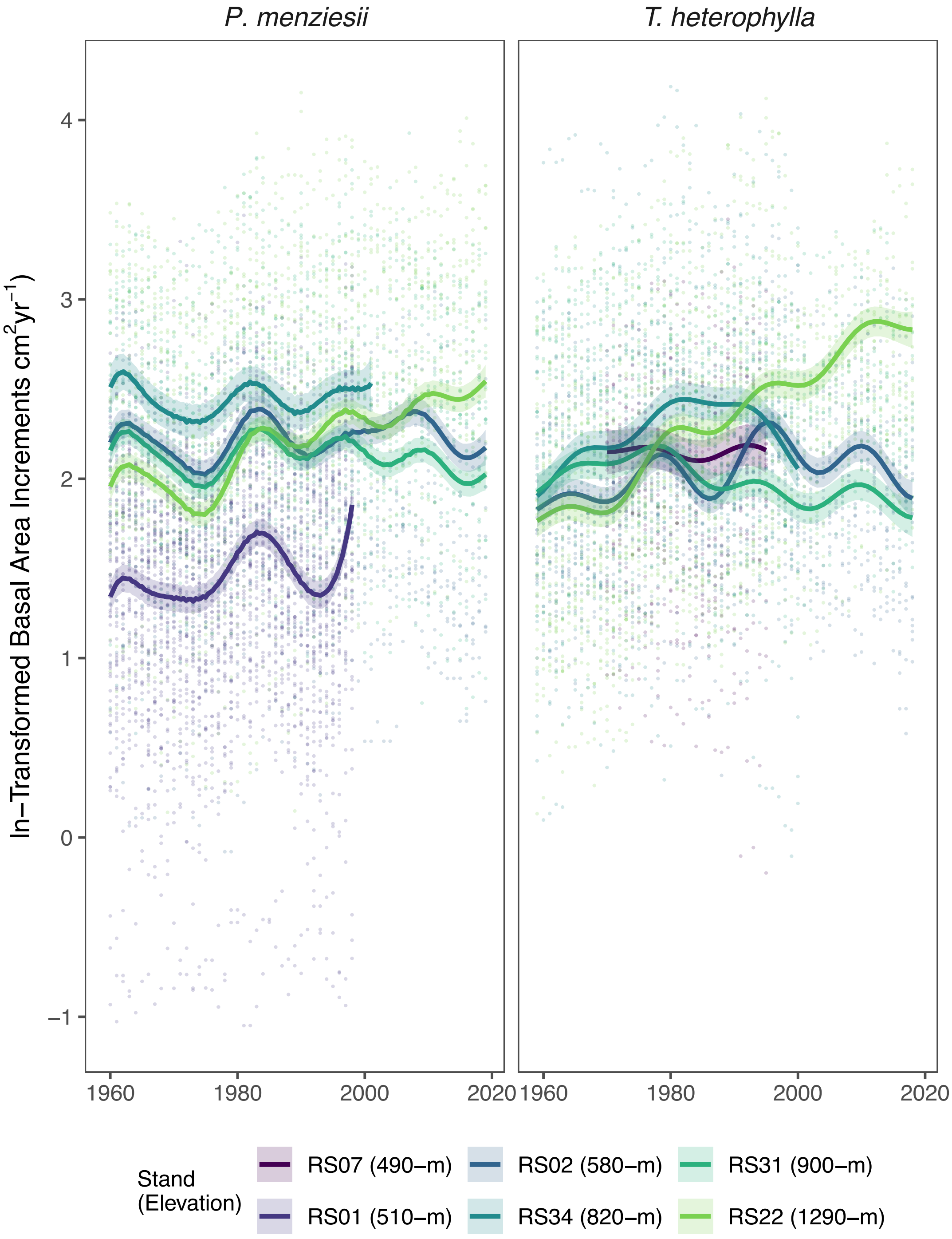

Figure 3-2: Growth patterns for *T. heterophylla* and *P. menziesii* from 1960 to 2019. Basal area increments (BAI) were modeled (natural log-transformed) in a GAM framework with global and stand-level time effects and random smoothing effects for individual trees (Table S3-2, S3-3). Here, plots are sorted by elevation and growth trends for each species are visualized over time ranges for which tree-ring records exist. Plots exhibited similar relationships to time, with notably low growth for RS01 in *P.menziesii* and notably high growth for both species in RS22. Dots represent individual tree growth and are colored to match stand scale.

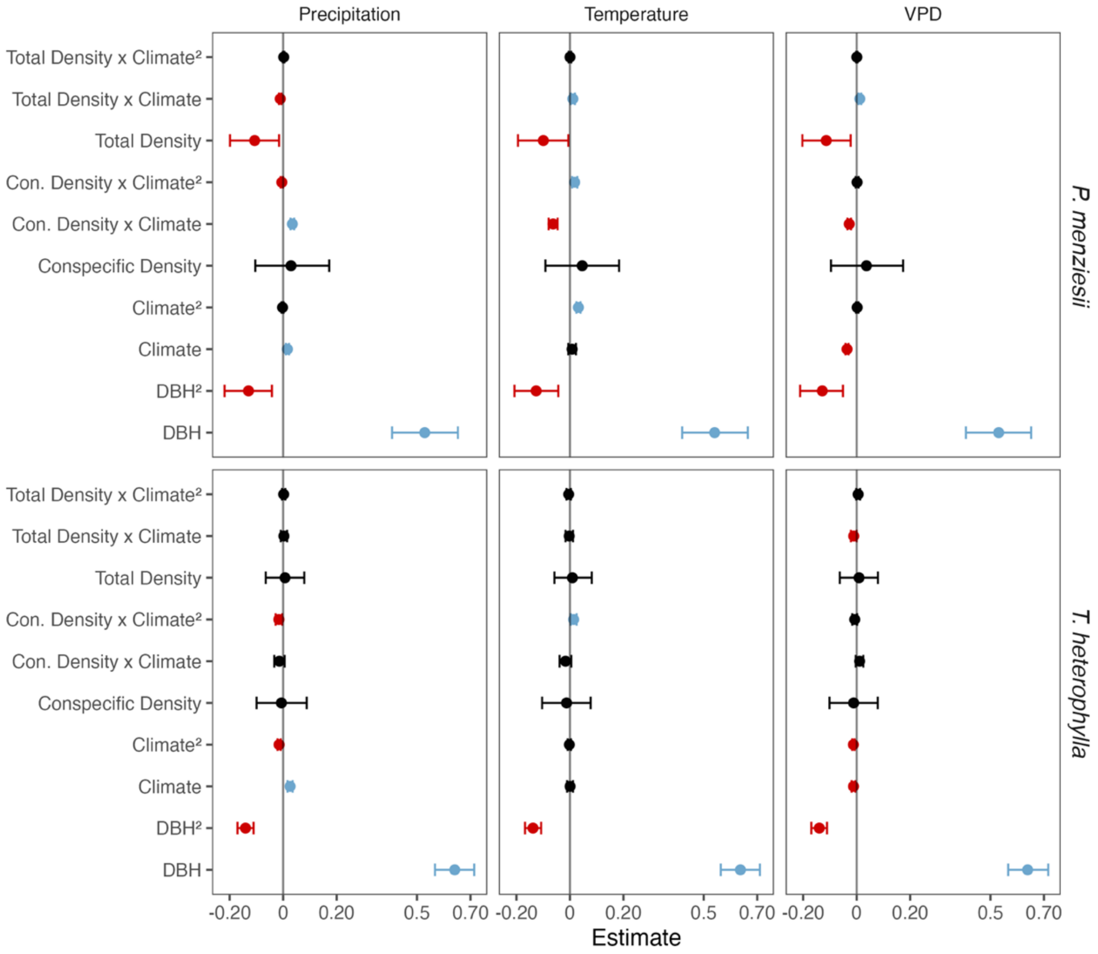

Figure 3-3: Parameter estimates for density, climate, and size effects on tree growth across species and climate variables. Separate Bayesian GLMMs were used for each combination of species and climate variable to account for differences in climate window selections (Figure 3-4A). Estimates for which the 90% credible interval overlap zero are considered insignificant and colored black. Positive estimates indicate a positive effect on BAI (blue). Negative estimates indicate a negative effect on BAI growth (red). Note that both linear and quadratic terms are presented and are significant for DBH and many climate variables. For instance, a negative quadratic term indicates a saturating or parabolic shape for positive linear effects, and an inverse saturating or parabolic shape for negative linear effects. Growth was generally most associated with tree DBH, with density and climate varying in estimation with species and variable, respectively.

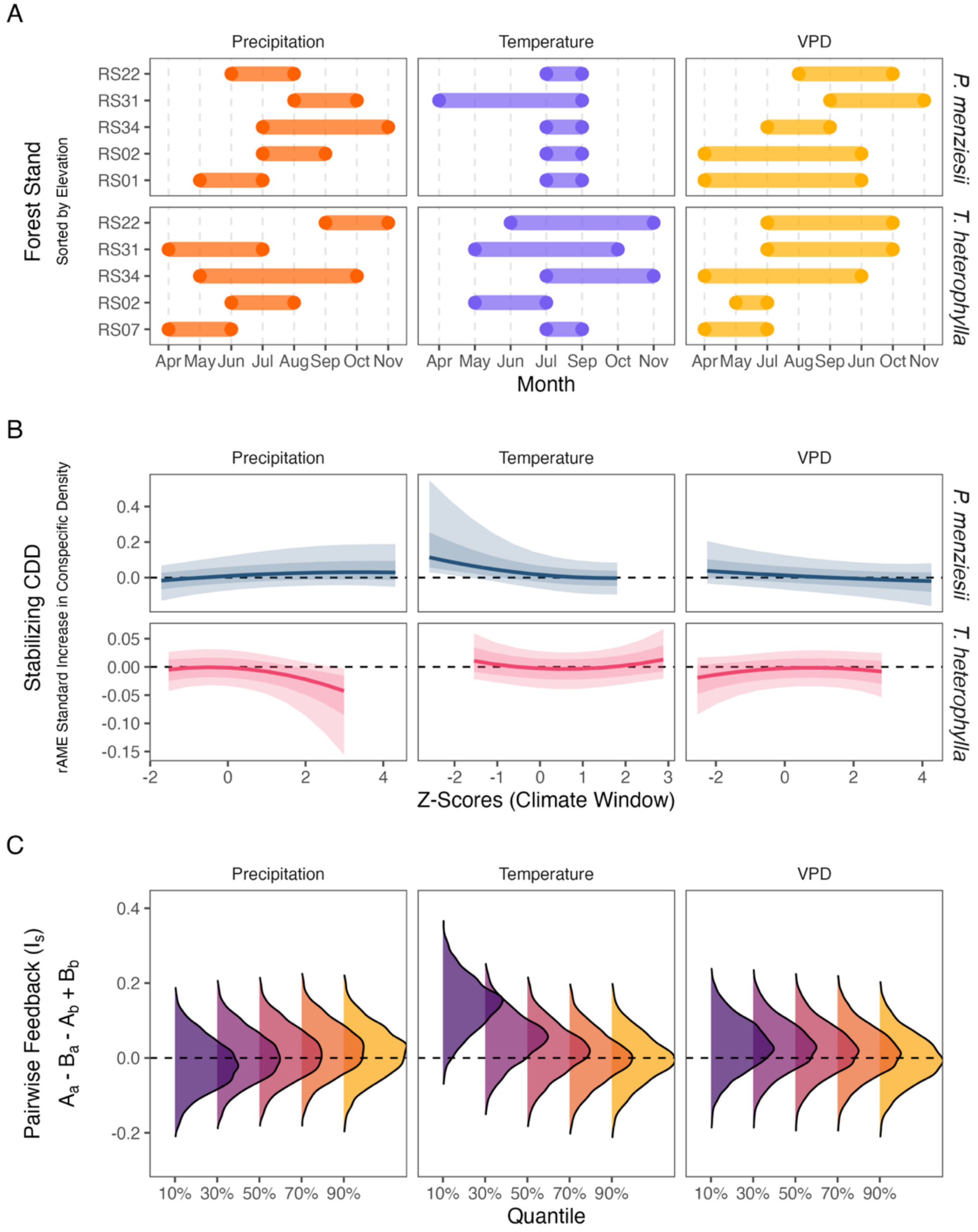

Figure 3-4: Analysis of local CDD and Pairwise Feedback (I_s) across climate variables. We selected climate windows (A) by modeling BAI with linear and quadratic climate variables across different climate windows corresponding to months between April and November. Each model accounted for temporal autocorrelation and tree size. Here, we visualize the best-fit window as selected by log-likelihood. In other words, Panel A depicts the seasonal period for which tree growth of each species is most associated with each climate variable. Each selected climate window was then used in hierarchical Bayesian GLMMs of individual tree growth. We estimated stabilizing CDD (B) as the relative average marginal effect (rAME) of adding a single 15-cm

conspecific adult 1-meter from the base of the focal tree to an otherwise entirely heterospecific neighborhood. Positive rAME estimates indicate relatively increased performance (% change) in conspecific neighborhoods relative to heterospecific neighborhoods (destabilizing local CDD). Negative rAME estimates indicate relatively decreased performance (% change) in conspecific neighborhoods relative to heterospecific neighborhoods (stabilizing local CDD). We related rAME estimates for our focal species by estimating pairwise feedbacks I_s (C) from the posterior distributions of each combination of focal species and conspecific or heterospecific neighborhood across 5 quantiles (10% to 90%). Positive values indicate destabilizing feedback where each species growth is highest in conspecific neighborhoods, and negative values indicate stabilizing feedbacks where each species growth is highest in heterospecific neighborhoods.

Supplemental Tables and Figures

Table S3-1: Allometric Equations for Bark Thickness. We accounted for the biological reality that bark thickness scales with tree size to improve the reliability of our basal area increment calculations. We calculated bark thickness (BT) as a linear function of tree size for each species using standardized equations.

Species	Allometric Equation for Bark Thickness (BT, cm)	Citation
P. menziesii	$BT = 0.04 + 0.09 * DBH$	Miles & Smith 2009
T. heterophylla	$BT = 0.40 + 0.17 * DBH$	Miles & Smith 2009

Table S3-2: Results of the generalized additive model (GAM) for *Pseudotsuga menziesii* (Douglas-fir) growth. The model includes a global smooth term for time and its factor interactions with each stand included in our study (Table 3-1) as well as a random smooth effect for individual trees (TAG). EDF represents estimated degrees of freedom, Ref.df is the reference degrees of freedom, F-value indicates the significance of each term, and p-values are shown with significance levels (*** indicates $p < 0.001$). Our model finds high degree of variation in growth among individual trees and significant global- and stand-level patterns emerging across our elevation gradient.

Term	EDF	Ref.df	F-value	p-value	Significance
s(time)	9.000	9	7.829	< 0.001	***
s(time): RS01	3.774	8	5.538	< 0.001	***
s(time): RS02	8.000	8	9.763	< 0.001	***
s(time): RS22	8.000	8	10.563	< 0.001	***
s(time): RS31	8.000	8	11.209	< 0.001	***
s(time): RS34	6.922	8	5.801	< 0.001	***
s(TAG)	135.808	138	358.909	< 0.001	***

Table S3-3: Results of the generalized additive model (GAM) for *Tsuga heterophylla* (Western hemlock) growth**.** The model includes a global smooth term for time and its factor interactions with each stand included in our study (Table 3-1) as well as a random smooth effect for individual trees (TAG). EDF represents estimated degrees of freedom, Ref.df is the reference degrees of freedom, F-value indicates the significance of each term, and p-values are shown with significance levels (*indicates $p < 0.05$, *** indicates $p < 0.001$). Our model finds high degree of variation in growth among individual trees and significant stand-level patterns emerging across our elevation gradient. Stand-level patterns are dissimilar from one another as distinguished by the insignificant global smooth for time.

Term	EDF	Ref.df	F-value	p-value	Significance
s(time)	7.469	7.964	0.990	0.486	
s(time): RS02	7.464	8.000	9.117	0.024	*
s(time): RS07	0.000	8.000	0.000	0.025	*
s(time): RS22	7.361	8.000	68.540	< 0.001	***
s(time): RS31	6.130	8.000	8.007	0.019	*
s(time): RS34	5.152	8.000	39.524	< 0.001	***
s(TAG)	109.356	110.000	179.869	< 0.001	***

Table S3-4: Parameter estimates for Bayesian hierarchical GLMMs estimating contribution of tree size, neighborhood variables, and climate variables to tree growth. Estimates are presented along with 95% credible intervals for each species (PSME = *P. menziesii*, TSHE = *T. heterophylla*).

Species	Climate Model	Parameter	Estimate	95% CI
PSME	VPD	Intercept	1.996	[1.473, 2.503]
PSME	VPD	DBH	0.531	[0.384, 0.675]
PSME	VPD	DBH^2	-0.128	[-0.232, -0.034]
PSME	VPD	VPD	-0.036	[-0.043, -0.029]
PSME	VPD	VPD^2	0.002	[-0.003, 0.007]
PSME	VPD	Con. Density	0.037	[-0.121, 0.201]
PSME	VPD	Total. Denisty	-0.114	[-0.219, -0.007]
PSME	VPD	Con:VPD	-0.028	[-0.036, -0.02]
PSME	VPD	Total:VPD	0.012	[0.006, 0.018]
PSME	VPD	$Con:VPD^2$	0.001	[-0.005, 0.008]

Species	Climate Model	Parameter	Estimate	95% CI
PSME	VPD	Total:VPD^2	0.001	[-0.002, 0.004]
PSME	Temperature	Intercept	1.972	[1.41, 2.493]
PSME	Temperature	DBH	0.541	[0.399, 0.689]
PSME	Temperature	DBH^2	-0.126	[-0.229, -0.028]
PSME	Temperature	Temperature	0.008	[-0.009, 0.025]
PSME	Temperature	Temperature^2	0.032	[0.023, 0.041]
PSME	Temperature	Con. Density	0.046	[-0.118, 0.208]
PSME	Temperature	Total Density	-0.099	[-0.215, 0.011]
PSME	Temperature	Con:Temp	-0.063	[-0.083, -0.043]
PSME	Temperature	Total:Temp	0.011	[0.002, 0.02]
PSME	Temperature	Con:Temp^2	0.018	[0.006, 0.03]
PSME	Temperature	All:Temp^2	0.000	[-0.005, 0.006]
PSME	Precipitation	Intercept	1.993	[1.468, 2.505]
PSME	Precipitation	DBH	0.529	[0.383, 0.679]
PSME	Precipitation	DBH^2	-0.129	[-0.235, -0.027]
PSME	Precipitation	Precipitation	0.016	[0.009, 0.023]
PSME	Precipitation	Precipitation^2	-0.002	[-0.007, 0.002]
PSME	Precipitation	Con. Density	0.029	[-0.133, 0.196]
PSME	Precipitation	Total Density	-0.107	[-0.216, -0.002]
PSME	Precipitation	Con:Precip	0.034	[0.026, 0.042]
PSME	Precipitation	Total:Precip	-0.011	[-0.016, -0.006]
PSME	Precipitation	Con:Precip^2	-0.005	[-0.01, 0]
PSME	Precipitation	Total:Precip^2	0.002	[-0.001, 0.005]
TSHE	VPD	Intercept	2.181	[2.031, 2.323]
TSHE	VPD	DBH	0.639	[0.551, 0.73]
TSHE	VPD	DBH^2	-0.140	[-0.176, -0.104]
TSHE	VPD	VPD	-0.012	[-0.02, -0.003]
TSHE	VPD	VPD^2	-0.012	[-0.017, -0.007]

Species	**Climate Model**	**Parameter**	**Estimate**	**95% CI**
TSHE	VPD	Con. Density	-0.011	[-0.119, 0.099]
TSHE	VPD	Total Density	0.009	[-0.077, 0.092]
TSHE	VPD	Con:VPD	0.011	[-0.006, 0.028]
TSHE	VPD	Total:VPD	-0.011	[-0.023, 0.002]
TSHE	VPD	Con:VPD^2	-0.007	[-0.018, 0.003]
TSHE	VPD	Total:VPD^2	0.005	[-0.003, 0.014]
TSHE	Temperature	Intercept	2.180	[1.997, 2.363]
TSHE	Temperature	DBH	0.637	[0.55, 0.725]
TSHE	Temperature	DBH^2	-0.138	[-0.174, -0.101]
TSHE	Temperature	Temperature	0.001	[-0.013, 0.014]
TSHE	Temperature	Temperature^2	-0.002	[-0.009, 0.005]
TSHE	Temperature	Con. Density	-0.013	[-0.121, 0.096]
TSHE	Temperature	Total Density	0.009	[-0.071, 0.094]
TSHE	Temperature	Con:Temp	-0.016	[-0.042, 0.009]
TSHE	Temperature	All:Temp	-0.003	[-0.019, 0.014]
TSHE	Temperature	Con:Temp^2	0.014	[0.001, 0.028]
TSHE	Temperature	All:Temp^2	-0.005	[-0.014, 0.005]
TSHE	Precipitation	Intercept	2.178	[2.035, 2.317]
TSHE	Precipitation	DBH	0.641	[0.554, 0.727]
TSHE	Precipitation	DBH^2	-0.141	[-0.176, -0.104]
TSHE	Precipitation	Precipitation	0.026	[0.014, 0.037]
TSHE	Precipitation	Precipitation^2	-0.015	[-0.022, -0.008]
TSHE	Precipitation	Con. Density	-0.007	[-0.114, 0.107]
TSHE	Precipitation	Total Density	0.007	[-0.076, 0.096]
TSHE	Precipitation	Con:Precip	-0.014	[-0.036, 0.009]
TSHE	Precipitation	All:Precip	0.003	[-0.011, 0.017]
TSHE	Precipitation	Con:PPT^2	-0.016	[-0.03, -0.001]
TSHE	Precipitation	All:PPT^2	0.002	[-0.006, 0.009]

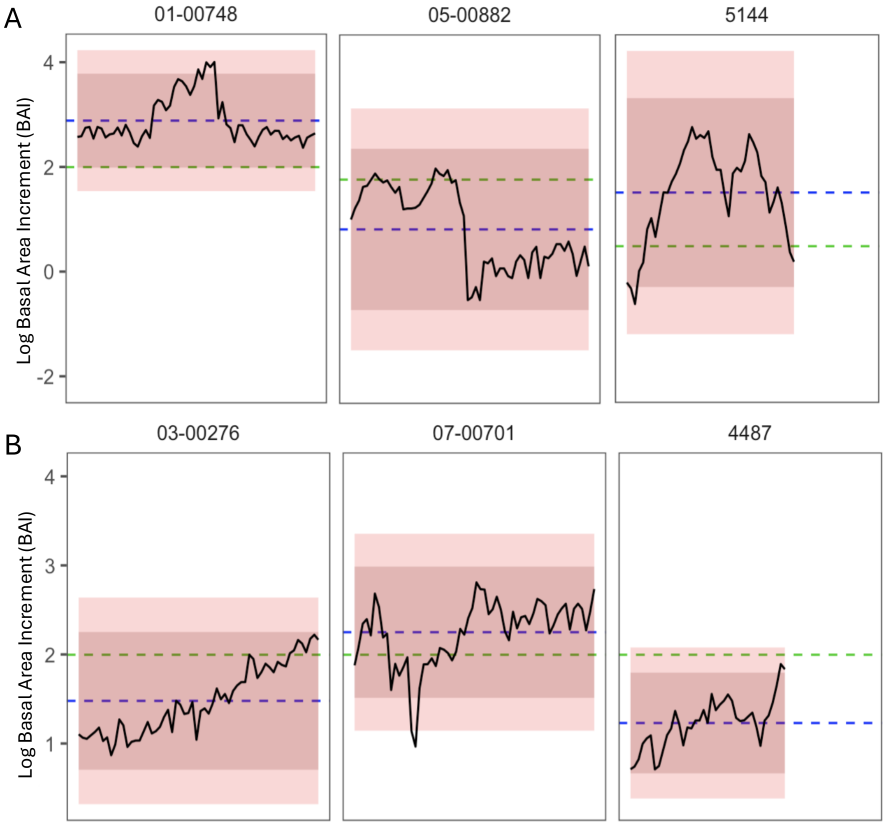

Figure S3-1: Example of Core Selection. (A) depicts core time series from 3 different trees that were excluded in the core selection process due to 3 consecutive years that sum to greater than 1 standard deviation in growth representative of external factors (damage, competitive release, etc.). (B) depicts core time series from 3 different trees that were retained in the core selection process. Dark red band indicates 2 standard deviations from core mean (blue dashed line). Light red band indicates 3 standard deviations from core mean (blue dashed line). Mean growth of all cores is depicted with a green dashed line. Cores were flagged as potentially problematic using standardized criteria and reviewed by hand. We note that our selection procedure is flexible enough to include dramatic growth changes in short time periods, which could be indicative of climate sensitivity to extreme events (Panel B; Tree 07-00701), and yet robust enough to identify trees for which competitive release or suppression has altered growth trajectories (Panel A).

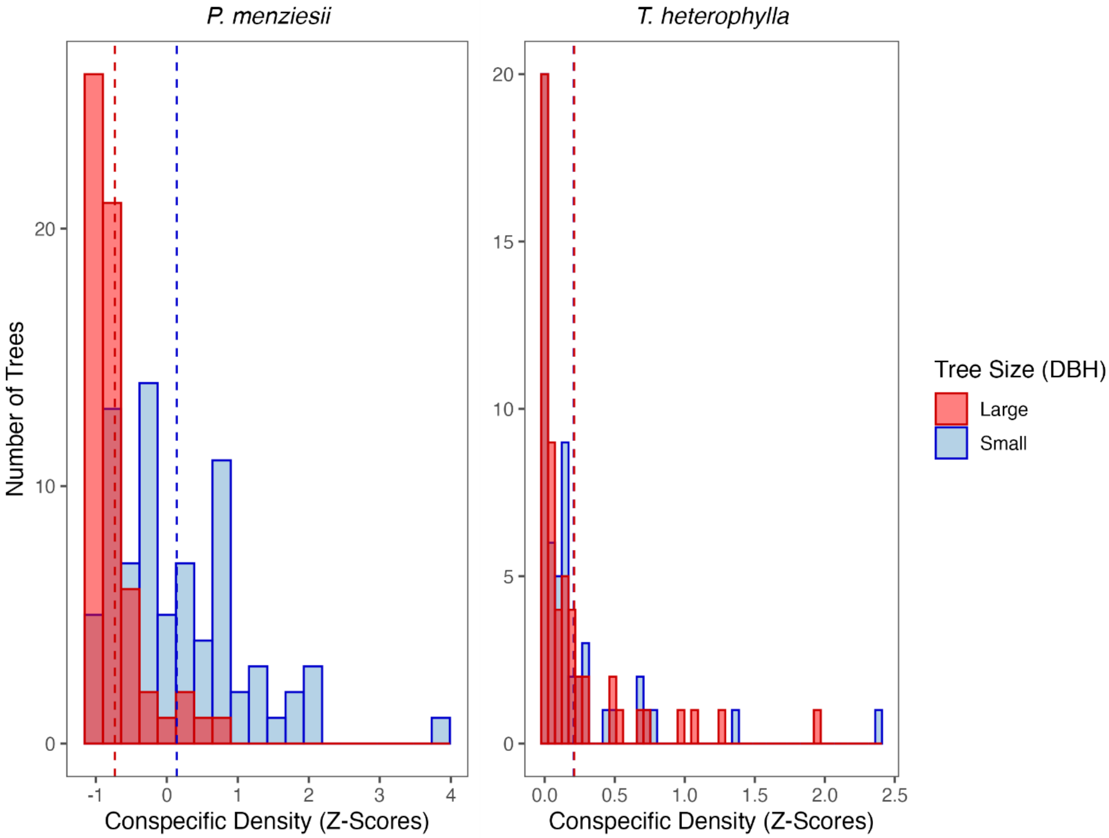

Figure S3-2: Observed distribution of conspecific densities across species and size classes. To ensure that our dataset captured relatively smaller and larger trees under similar conspecific densities we divided trees into two categories based on DBH at time of latest forest inventory survey (red = above mean DBH, blue = below mean DBH). Histogram depicts distribution of unique trees across a range of conspecific densities (Z-scores) which were calculated in combination with total densities. Dotted vertical line depict group means, which are nearly identical for *T. heterophylla* but differ substantially from *P. menziesii*. Conspecific densities are standardized Z-Scores selected from the grid-search models (Figure S3-3).

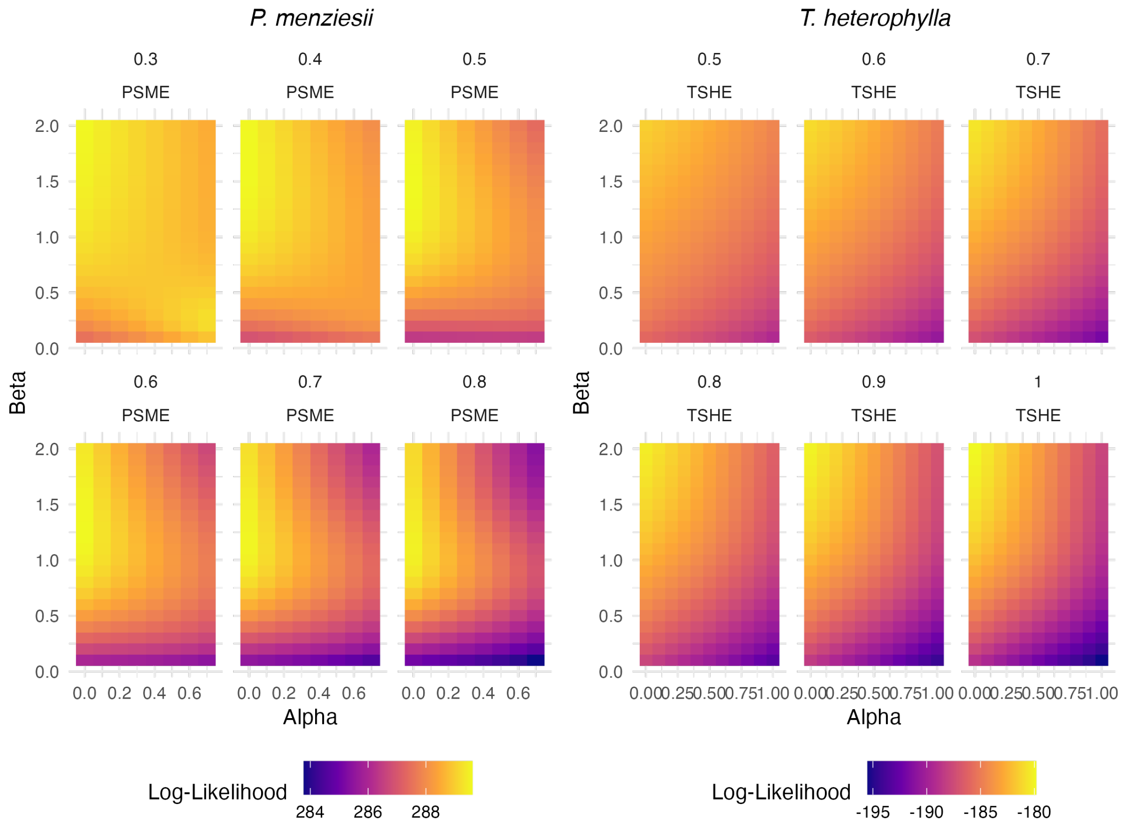

Figure S3-3: Effect on model fit by shifting alpha, beta, and D in conspecific and total LDI calculation. Linear mixed effect models with temporal autoregressive processes were iteratively tested with different combinations of alpha, beta, and D to account for the size- and distance-dependent nature of neighborhood effects. Models were compared and selected using log-likelihood. Heatmaps visualize a, b, and D around each optimal model with light colors equating to high log-likelihood values (better fits) and dark colors equating to low log-likelihood values (worse fits). This grid search selected a = 0, b = 1, and d = 1 for *T. heterophylla* and a = 0, b = 1.4, and d = 2 for *P. menziesii*.

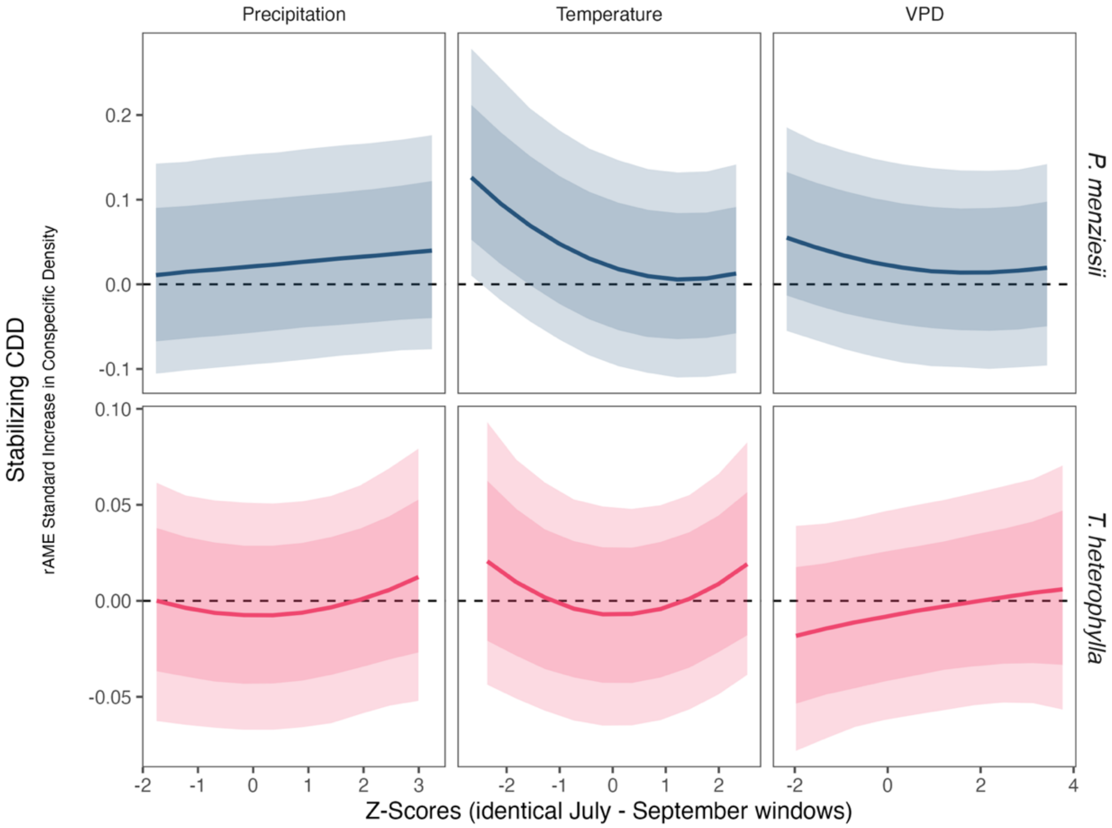

Figure S3-4: Local CDD estimated across identical seasonal windows. As an alternative to allowing climate windows to vary in length and season across sites (see Figure 3-4), we estimated stabilizing CDD in identical July through September climate windows for each climate variable (precipitation, temperature, and VPD). Local stabilizing CDD is measured as the relative average marginal effect (rAME) of adding a single 15-cm conspecific adult 1-meter from the base of the focal tree to an otherwise entirely heterospecific neighborhood (see methods). Calculating across identical windows does not change our inference for *P. menziesii* but does remove the relationship between CDD and precipitation for *T. heterophylla*. We consider this analysis to be less informative to our dataset since trees are distributed across an elevational gradient and likely exhibit variability in seasonal associations (as seen in Figure 3-4A).

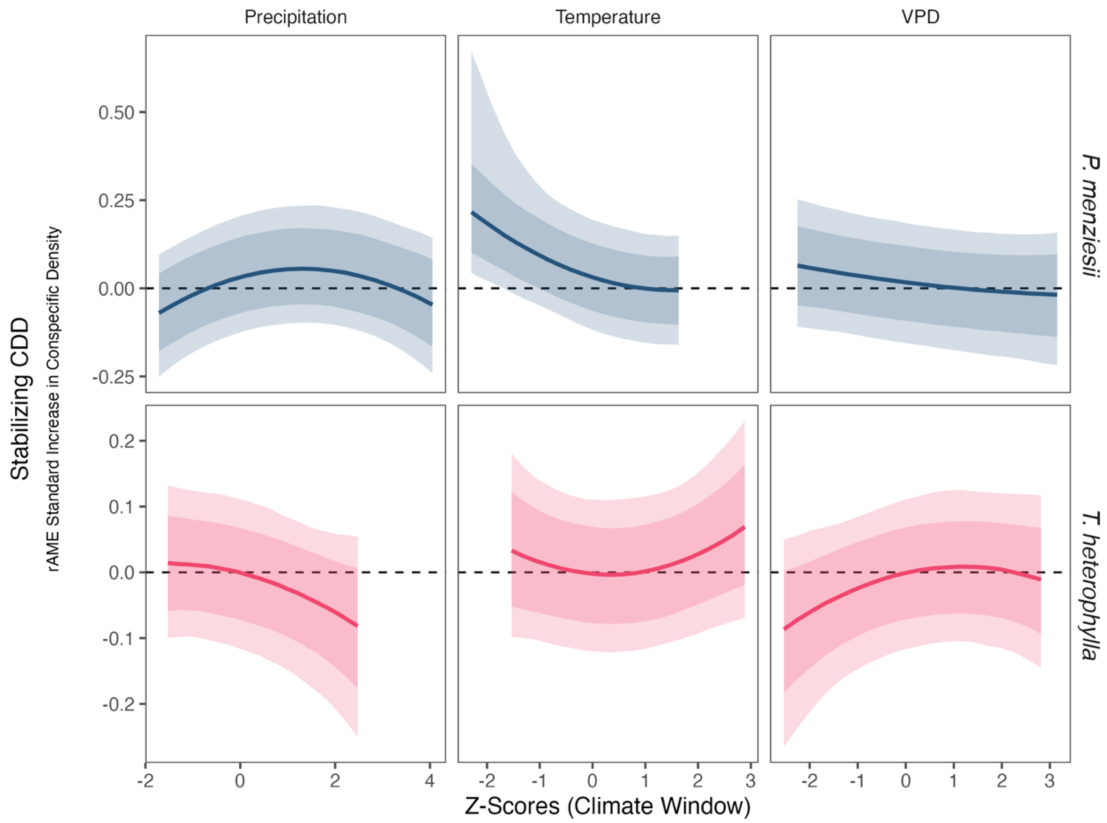

Figure S3-5: Local CDD estimated across short timespan (1980-2019). To validate including all dendrochronological data dating back to 1960, we ran a separate analysis with a cutoff date of 1980, measuring stabilizing CDD using rAME of adding a single 15-cm conspecific adult 1-meter from the base of the focal tree to an otherwise entirely heterospecific neighborhood (see Fig 4 and methods). Restricting our dataset did not change our inference for *P. menziesii* but did remove the wettest years experienced by *T. heterophylla* and thus made the otherwise significant relationship between precipitation and CDD insignificant. Given the slow growth rates of adult trees in old-growth forests in our system (Ruth, 1964) we considered including data back to 1960 to be appropriate and advantageous given the restricted precipitation range for *T. heterophylla* with more restrictive cutoffs.

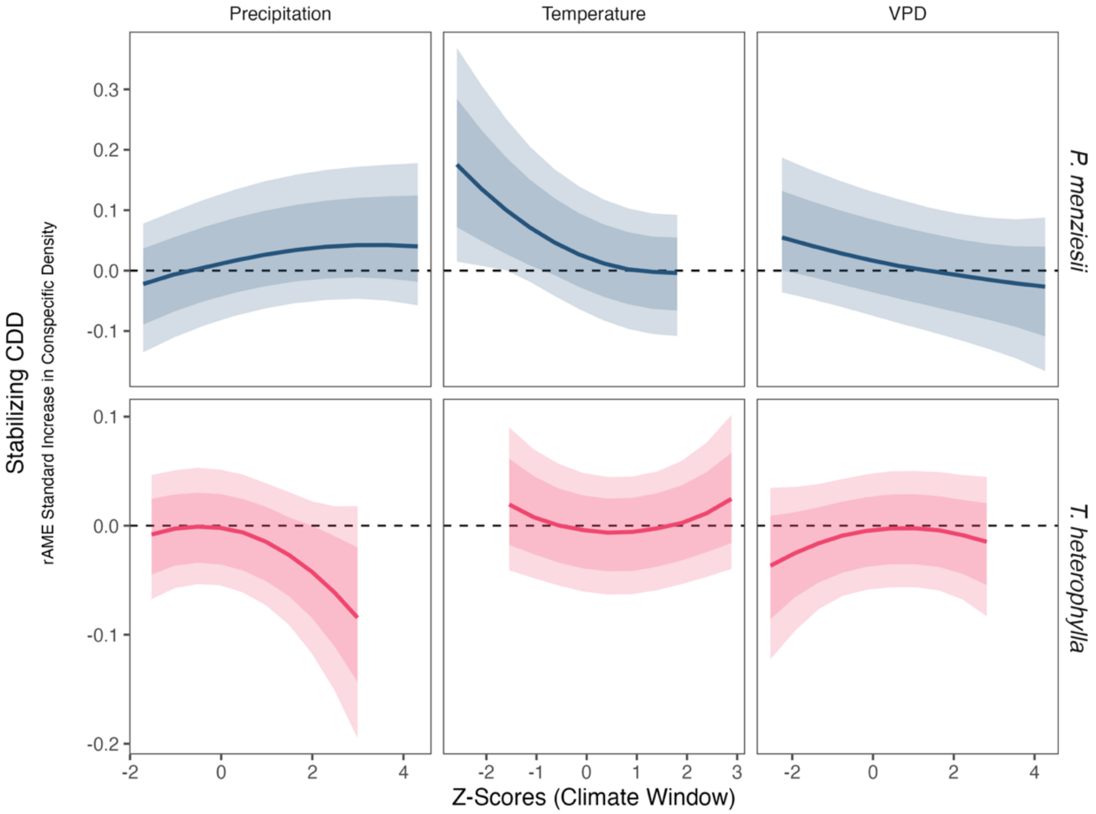

Figure S3-6: Local CDD estimated as a standardized addition to observed conspecific densities as opposed to a heterospecific neighborhood. An alternative estimation of local CDD adds a standardized conspecific adult to the observed conspecific neighborhood (Hülsmann et al., 2024), as opposed to our main approach of adding a standardized conspecific adult to an otherwise heterospecific neighborhood. To account for any non-linearities in conspecific responses, we validated our approach against this alternative rAME estimation of local CDD and found no significant deviations from our inference. This indicates that across ranges from entirely heterospecific neighborhoods to observed neighborhood compositions conspecifics have a similar effect on individual growth.

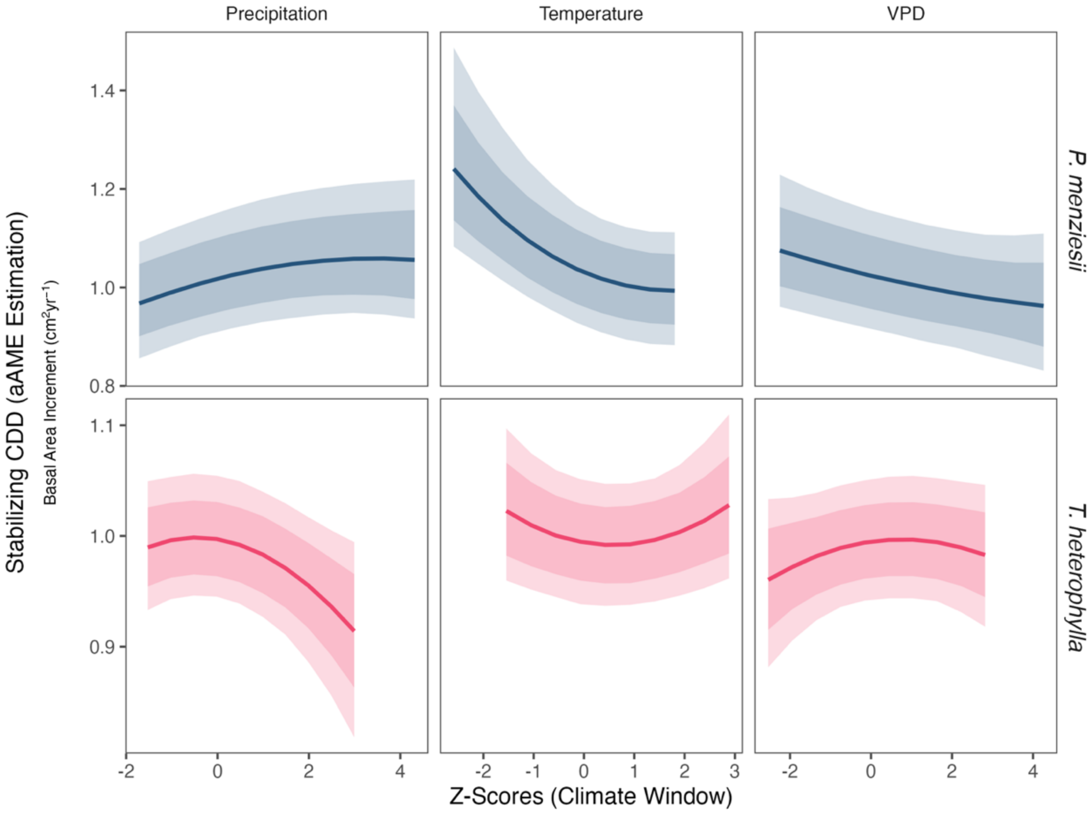

Figure S3-7: Local CDD estimated as absolute change (aAME) from a adding a standardized conspecific adult to an otherwise heterospecific neighborhood. While we generally consider relative changes in growth to be more informative than absolute changes in growth, we present here the absolute average marginal effects (aAME) calculated by subtracting growth in a relatively conspecific neighborhood from an otherwise entirely heterospecific neighborhood (see methods). Results are presented on the scale of basal area increments in cm^2yr^{-1}.

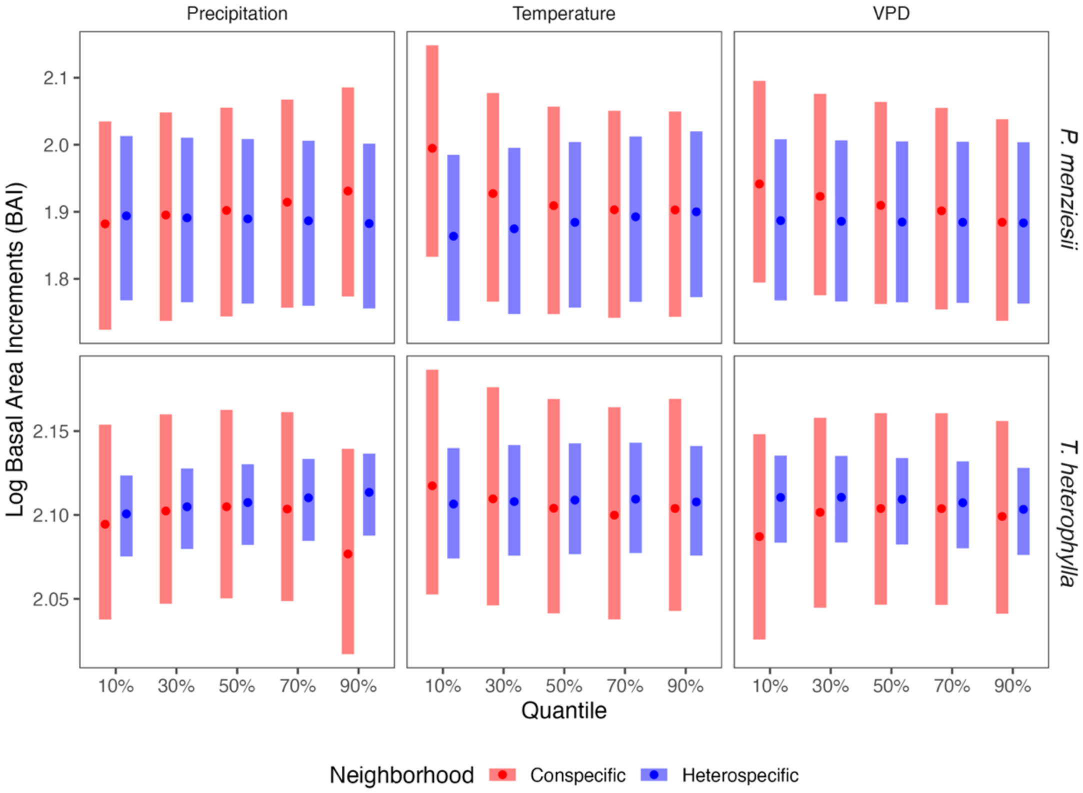

Figure S3-8: Model estimated basal area increments across climate quantiles in standardized heterospecific and conspecific neighborhoods. While pairwise feedbacks (I_s) provide important context for the community-level implications of local conspecific density effects, we also sought to understand whether positive feedbacks in cool years were driven by changes in P. menziesii growth or T. heterophylla growth. Here, predicted growth in relatively conspecific neighborhoods (standardized conspecific addition as in rAME estimation, see methods) is depicted in red, and growth in heterospecific neighborhoods is depicted in blue. Dots indicate posterior medians, and tails indicate 95% credible intervals. We note that in the case of precipitation for *T. heterophylla* and temperature for *P. menziesii* growth is changing most in conspecific environments relative to heterospecific environments.

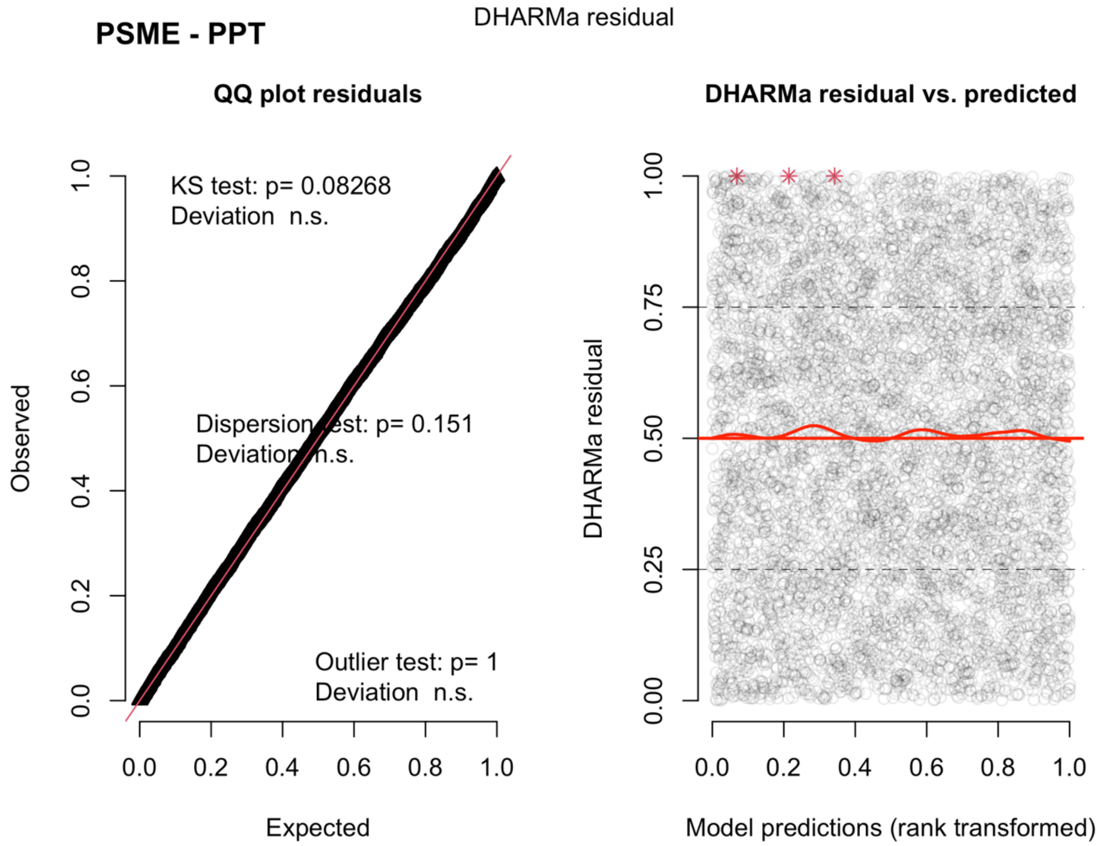

Figure S3-9: QQ and residual plots from DHARMa output for *P. menziesii* precipitation model. The left panel displays a QQ plot comparing observed versus expected residuals, with statistical tests indicating no significant deviations from normality (KS test p=0.08268, Dispersion test p=0.151, Outlier test p=1). The right panel shows DHARMa residuals plotted against model predictions (rank transformed), with residuals scattered around 0.5 (red line) across the prediction range, suggesting the model assumptions are adequately met with no apparent patterns of heteroscedasticity or bias in the residuals.

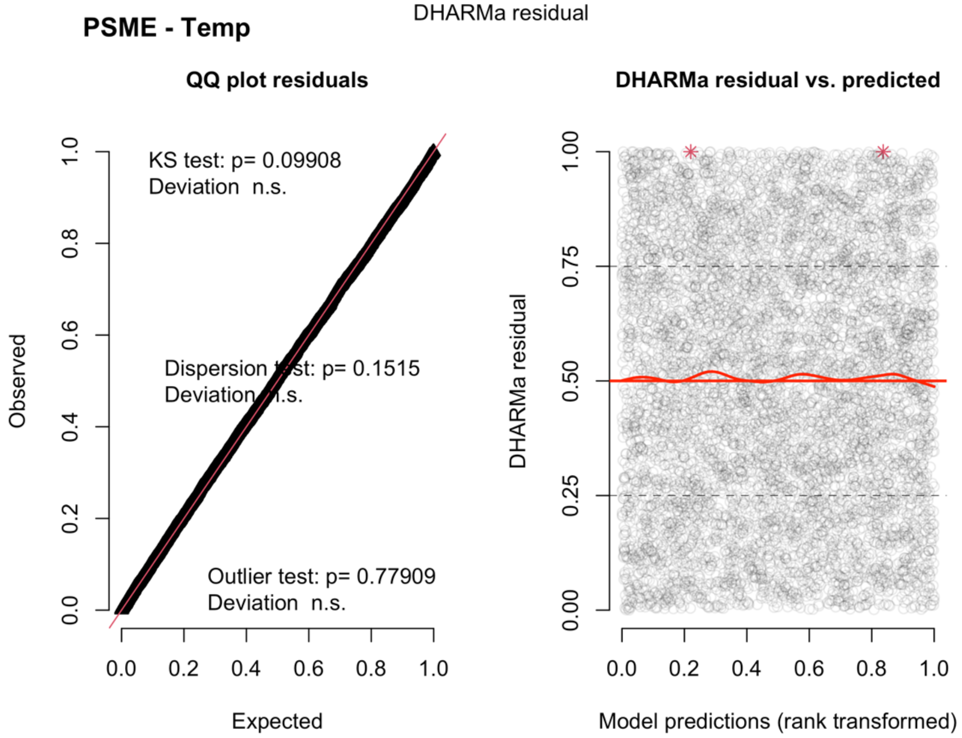

Figure S3-10: QQ and residual plots from DHARMa output for *P. menziesii* temperature model**.** The left panel displays a QQ plot comparing observed versus expected residuals, with statistical tests indicating no significant deviations from normality (KS test p=0.09908 Dispersion test p=0.151, Outlier test p=1). The right panel shows DHARMa residuals plotted against model predictions (rank transformed), with residuals scattered around 0.5 (red line) across the prediction range, suggesting the model assumptions are adequately met with no apparent patterns of heteroscedasticity or bias in the residuals.

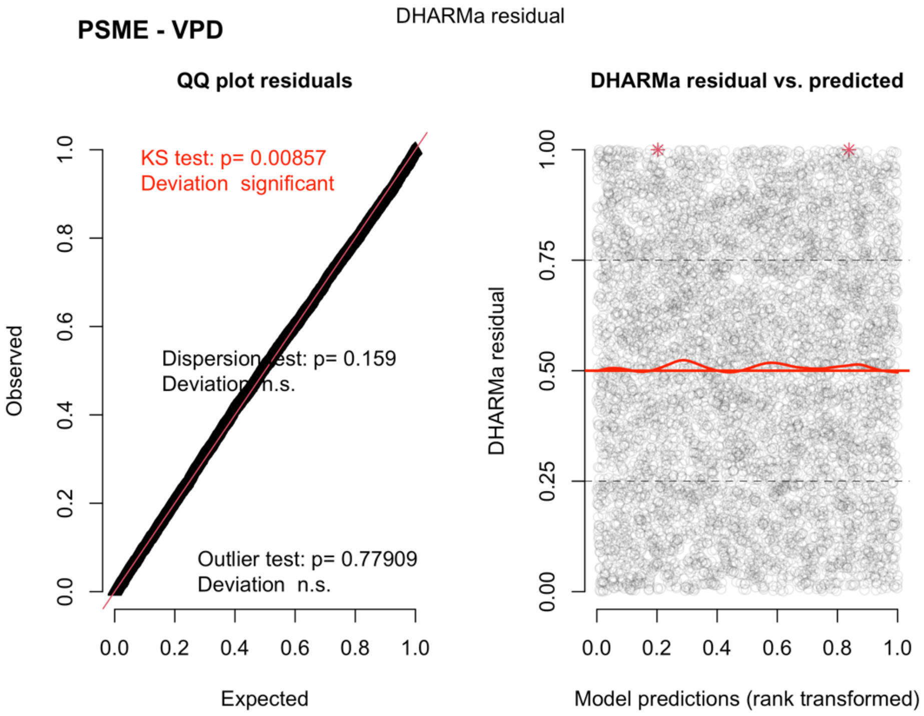

Figure S3-11: QQ and residual plots from DHARMa output for *P. menziesii* VPD model. The left panel displays a QQ plot comparing observed versus expected residuals, with statistical tests indicating no significant deviations from normality (KS test p=0.0.00857 Dispersion test p=0.159, Outlier test p=0.779). While the KS test was significant, KS tests are sensitive to large sample sizes and we did not consider this to suggest model misspecification. The right panel shows DHARMa residuals plotted against model predictions (rank transformed), with residuals scattered around 0.5 (red line) across the prediction range, suggesting the model assumptions are adequately met with no apparent patterns of heteroscedasticity or bias in the residuals.

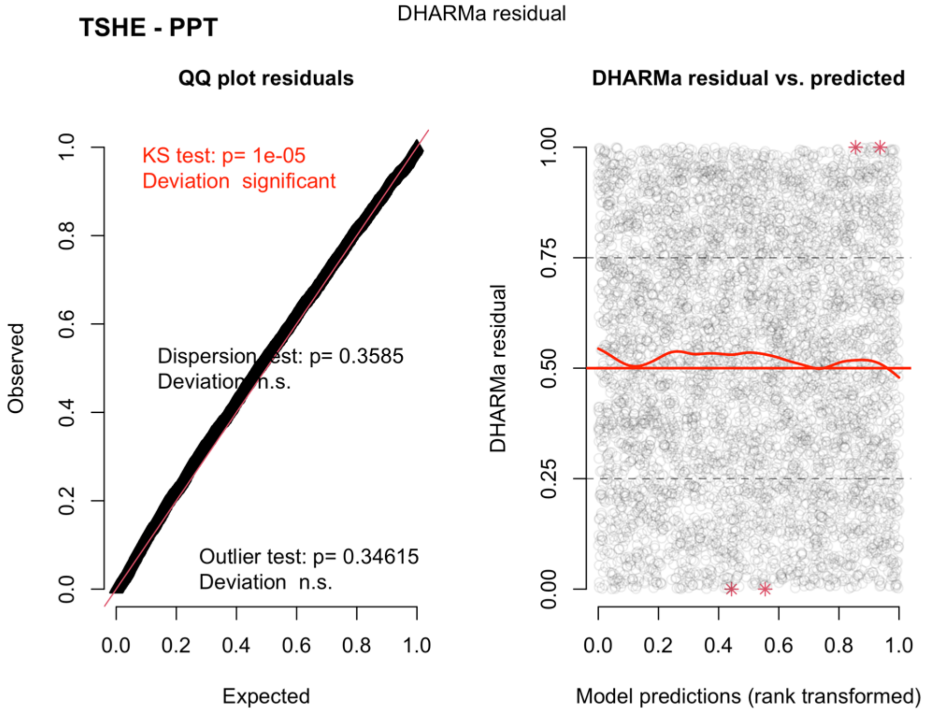

Figure S3-12: QQ and residual plots from DHARMa output for *T. heterophylla* precipitation model. The left panel displays a QQ plot comparing observed versus expected residuals, with statistical tests indicating no significant deviations from normality (KS test p=.00001, Dispersion test p=0.385, Outlier test p=0.346). While the KS test was significant, KS tests are sensitive to large sample sizes and we did not consider this to suggest model misspecification. The right panel shows DHARMa residuals plotted against model predictions (rank transformed), with residuals scattered around 0.5 (red line) across the prediction range, suggesting the model assumptions are adequately met with no apparent patterns of heteroscedasticity or bias in the residuals.

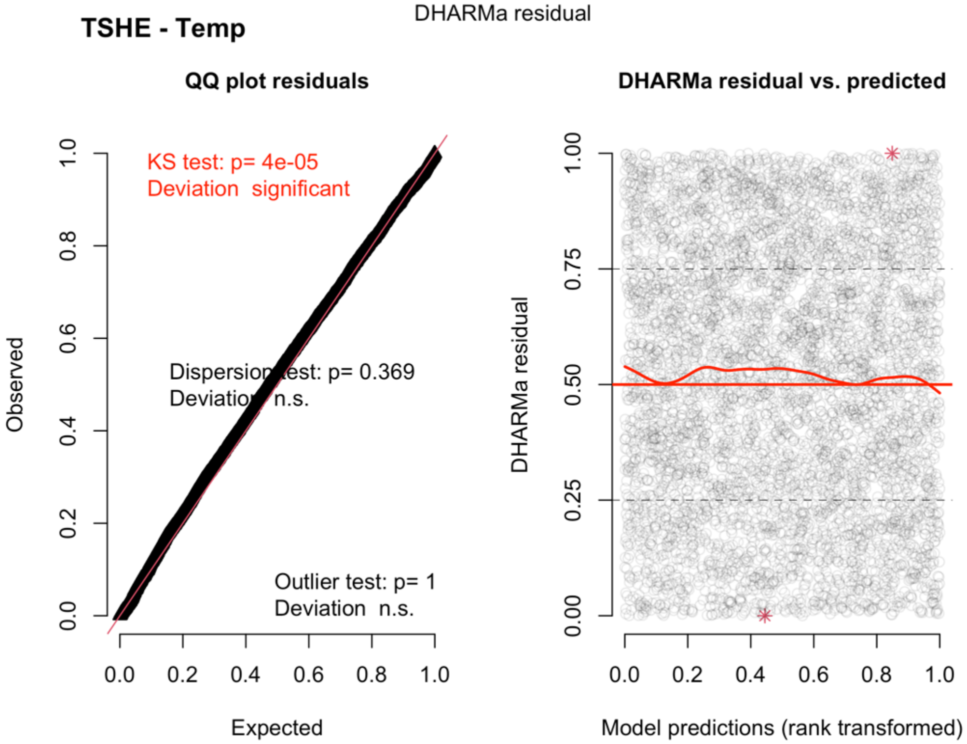

Figure S3-13: QQ and residual plots from DHARMa output for *T. heterophylla* temperature model. The left panel displays a QQ plot comparing observed versus expected residuals, with statistical tests indicating no significant deviations from normality (KS test p=.00004, Dispersion test p=0.369, Outlier test p=1). While the KS test was significant, KS tests are sensitive to large sample sizes and we did not consider this to suggest model misspecification. The right panel shows DHARMa residuals plotted against model predictions (rank transformed), with residuals scattered around 0.5 (red line) across the prediction range, suggesting the model assumptions are adequately met with no apparent patterns of heteroscedasticity or bias in the residuals.

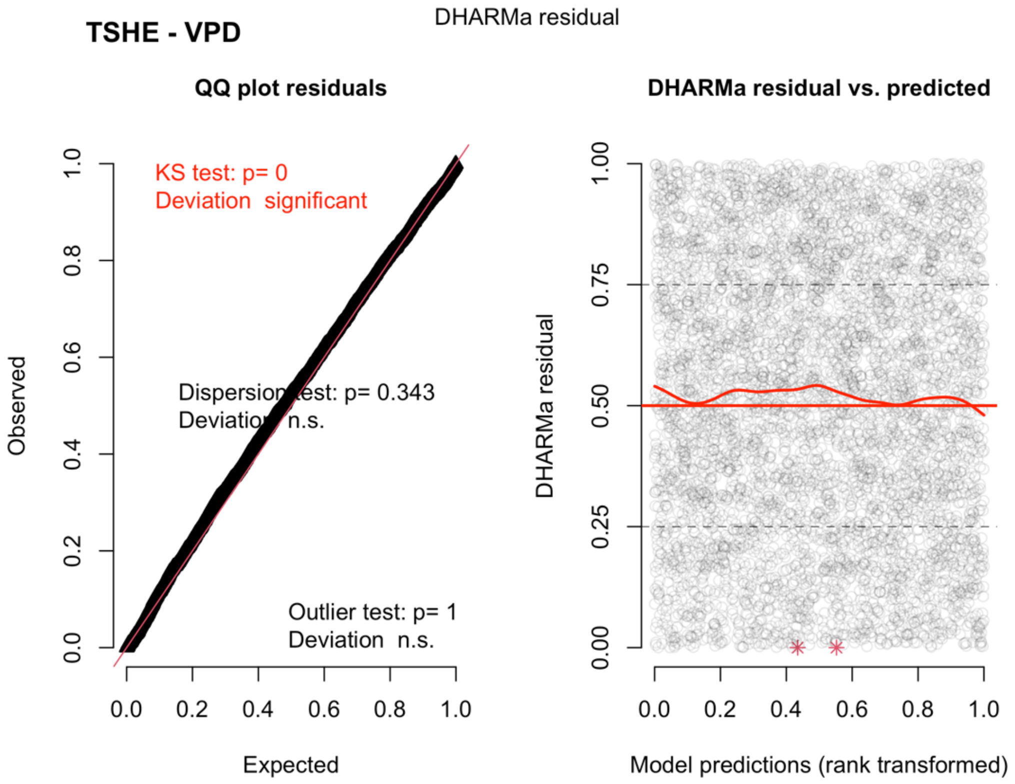

Figure S3-14: QQ and residual plots from DHARMa output for *T. heterophylla* VPD model. The left panel displays a QQ plot comparing observed versus expected residuals, with statistical tests indicating no significant deviations from normality (KS test p=0, Dispersion test p=0.343, Outlier test p=1). While the KS test was significant, KS tests are sensitive to large sample sizes and we did not consider this to suggest model misspecification. The right panel shows DHARMa residuals plotted against model predictions (rank transformed), with residuals scattered around 0.5 (red line) across the prediction range, suggesting the model assumptions are adequately met with no apparent patterns of heteroscedasticity or bias in the residuals.

Chapter 4 | The Stress Gradient Feedback Hypothesis: Plant communities increasingly associate with mycorrhizal fungi under stress

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Abstract

Understanding how environmental stress alters the strength of local plant interactions is key to explaining diversity in current and future plant communities. Along gradients of increasing environmental stress, traditional theory posits that plants experience stronger facilitative interactions and weaker antagonistic interactions. However, it remains unclear whether this pattern holds for the relative host-specificity of plant-microbe interactions along stress gradients. Understanding the dynamics between stress and host-specificity is particularly important for plant interactions with pathogenic and mycorrhizal fungi, which can drive opposing density-dependent processes that shape plant community compositions. We posit that increases in abiotic environmental stress are associated with greater abundances of relatively host-specific facilitative interactions, as plants rely on more specialized mutualists to acquire resources needed to cope with abiotic environmental stressors. We tested this prediction along an abiotic stress gradient in the central Cascade Range of Oregon, USA, using overlapping datasets of large high-resolution forest inventory plots, soil chemistry, and amplicon sequencing. Consistent with predictions derived from the SGFH, in low-elevation forest stands with benign abiotic conditions and abundant nutrients, within-plot site-to-site differences in local tree community composition were more associated with site-to-site differences in pathogenic fungal composition than site-to-site

differences in ectomycorrhizal fungal composition. However, in forests at high elevations with nutrient limitation and harsher microclimates, within-plot site-to-site differences in local tree community composition were more associated with differences in ectomycorrhizal fungal composition than site-to-site differences in pathogenic fungal composition. Additionally, we find that the within-plot spatial aggregation of ectomycorrhizal fungi increases across plots with increasing abiotic stress. These findings, while observational early tests of the SGFH, nonetheless suggest that mutualists become more closely associated with their host-tree species as abiotic stress increases. Interactions between fungal and tree communities likely play an important role in shaping forest composition along environmental stress gradients.

Introduction

Understanding the contribution of abiotic and biotic factors to species diversity remains a central goal of ecology (Brown, 1984). At local scales, plant species diversity is most often attributed to a mix of species-specific abiotic preferences for resources (e.g., nutrients, space; Grime, 1977; Tilman et al., 1982) and the outcomes of interactions between individuals (e.g., facilitation, antagonism; (Chesson, 2000). Interactions between abiotic preferences and species interactions form the foundation for the Stress Gradient Hypothesis (SGH), which posits that the ratio of facilitative to antagonistic species interactions increases with abiotic stress (Figure 4-1A; Bertness & Callaway, 1994; Maestre et al., 2009). In recent years, the SGH has been expanded and applied to cross-kingdom interactions between trees and root- and leaf-associated fungi which reciprocally mediate plant growth, survival, and reproductive rates (individual performance; (Allsup et al., 2023; David et al., 2020; Fadiji et al., 2023). However, predictions for species composition and diversity under the SGH often do not address whether plant-fungal interactions are relatively general (fungal species interacting broadly with approximately even strength across many plant species) or relatively specialized (fungal species interacting strongly with relatively few plant species, even if they have weaker interactions with many plant species). Since host-specific plant-fungal interactions are thought to have strikingly different implications for plant communities than general interactions (Bever, 2003; Broekman et al., 2019; LaManna et al., 2024), it is important to consider how relative host-specificity of these interactions is influenced by differences in abiotic stress.

Relatively host-specific plant-fungal interactions (as defined above) are hypothesized to contribute to plant species diversity by generating differing density-dependent effects on conspecific individuals relative to heterospecific individuals, a phenomenon known as locally stabilizing or destabilizing conspecific density dependence (hereafter abbreviated as 'local stabilizing CDD' as in (Hülsmann et al., 2024; LaManna et al., 2024). There is widespread support for local stabilizing CDD at local scales, most often realized as a disproportionate negative effect on conspecific performance relative to heterospecific performance (Comita et al., 2014). This type of stabilizing CDD provides locally less dominant species with an advantage by limiting locally dominant species, potentially contributing to the maintenance of species diversity if other conditions are met (Chesson, 2000; Levi et al., 2019; Smith, 2022).. However, local stabilizing CDD can also be destabilizing (also known as positive CDD) when host-specific interactions enhance individual conspecific performance relative to heterospecific performance (Delavaux et al., 2023; Zahra et al., 2021). Destabilizing CDD advantages locally dominant species and can promote the erosion of species diversity under certain conditions (Chesson, 2000; Levi et al., 2019; Smith, 2022). Importantly, host-specific interactions need only be relatively host-specific to contribute to local stabilizing CDD; that is, they cause disproportionately strong effects on primary plant hosts relative to other hosts (Spear & Broders, 2021).

In plants, local stabilizing CDD is increasingly attributed to the outcomes of these relatively host-specific interactions with antagonistic and mutualistic fungi (Chen et al., 2019; Liang et al., 2021; Packer & Clay, 2000). Pathogenic fungi contribute to local stabilizing CDD by aggregating where conspecific density is high and reducing individual plant performance (Freckleton & Lewis, 2006; Ricklefs, 1977). Mutualistic mycorrhizal fungi, on the other hand, are thought to counteract local stabilizing CDD by aggregating where conspecific density is high and improving plant performance by aiding in nutrient acquisition and pathogen resistance, among other potential benefits (Delavaux et al., 2017, 2023; Jiang et al., 2021). Therefore, pathogenic and mycorrhizal fungi can generate opposing forces influencing the net strength and directionality (stabilizing or destabilizing) of local CDD.

There is clear evidence that abiotic stress alters the composition of the root-associated microbiome (Hartman & Tringe, 2019), which suggests that changes to pathogenic and mycorrhizal root-fungal interactions may relate to shifts in local stabilizing CDD along environmental stress gradients. To date, empirical studies have found general support for the hypothesis that local CDD shifts predictably from stabilizing to neutral or destabilizing with chronic stressors such as depleted nutrient availability, harsh climates, and light limitation (LaManna et al., 2022; Lebrija-Trejos et al., 2023; Liu & He, 2021; Uriarte et al., 2018). Despite evidence that local CDD shifts predictably with abiotic stress gradients, we lack a framework and direct tests of how the underlying mechanisms generating CDD, such as host-specific pathogenic and mycorrhizal interactions, are impacted by abiotic stress and alter the strength and direction of CDD.

To synthesize recent studies of local stabilizing CDD along abiotic gradients with predictions of the SGH, we present the Stress Gradient Feedback Hypothesis (SGFH). The SGFH posits that relatively host-specific plant-microbe interactions become more facilitative with increases in abiotic stress – contributing to less stabilizing (i.e., more destabilizing) conspecific density-dependent feedback (Table 4-1; Figure 4-1B). Conversely, in abiotically benign environments, where nutrients are widely available and mutualists are potentially less necessary to plant survival and growth, the SGFH predicts stronger stabilizing CDD will be generated through increased importance and host-specificity of plant antagonists such as fungal pathogens. By formulating the SGFH, we explicitly link the SGH to host-specific interactions and their consequences for individual conspecific performance as well as population growth rates and species diversity along abiotic gradients.

Here, we use an observational approach to begin to evaluate predictions derived from the SGFH. Specifically, we relate the spatial structure of pathogenic, mycorrhizal, and saprotrophic fungal communities to patterns of tree community composition along a 690-meter elevation stress gradient in old-growth forests of the central Cascade Range of Oregon, USA (Table 4-1). As elevation increases along this gradient, nutrient availability declines and microclimates become harsher. Using this elevational stress gradient, we assess predictions from the SGFH by pairing high-resolution forest inventory plots with chemical analyses and amplicon sequencing in both the mineral soils and litter layer of the forest floor. We predict that mycorrhizal fungi are more spatially aggregated, clustering in association with specific tree communities in higher elevations with harsher abiotic conditions. We predict the opposite pattern for pathogenic fungi; that spatial aggregation and associations with tree communities are highest in low elevation, abiotically benign forests. In addition to our focal guilds of pathogenic and mycorrhizal fungi, which are often invoked as an important driver of local CDD, we tested the spatial aggregation and associations of tree communities with saprotrophic fungi. Saprotrophic fungal communities functionally provide a control group, as they are not thought to contribute to local CDD in similar ways to pathogens and mycorrhizal fungi. Therefore, we expected weaker patterns between elevational stress and saprotrophic fungal spatial aggregation or associations with tree communities than patterns observed for pathogenic and mycorrhizal fungi. Understanding the implications of interactions between fungal guild communities and trees along stress gradients is increasingly important to explaining the maintenance of species diversity under climate change and climate-driven changes to environmental stress.

Materials & Methods

Site Description

This study took place across a 690-meter elevation gradient (500-meters to 1190-metres) at the Andrews Experimental Forest LTER near Blue River, Oregon. Climatic conditions vary across this gradient, with generally shorter growing seasons at high elevations due to persisting spring/summer snowmelt, dry summers, and freezing temperatures during the wet season. A detailed description of the tree communities and climatic conditions at the Andrews Experimental Forest LTER is available in Appendix S4-1: Section S4-1.

Sample Collection

To test predictions generated by the SGFH, we collected and examined the soil, fungi, and tree communities at 6 old-growth forest dynamics plots (Franklin et al., 2024) that were recently expanded in 2019-2023. In 5 of these plots (ranging in size from 2 – 12 ha; Table S4-1), all trees ≥ 1 cm DBH were measured and mapped between 2019 and 2023 using TOPCON laser surveying equipment (Topcon Positioning Systems Inc., Livermore, CA). These long-term forest plots are part of the Smithsonian ForestGEO network (Andrews Forest Dynamics plots;

https://forestgeo.si.edu/sites/usa/andrews) and co-located with historical inventory censuses dating back to the 1970s.

While most root-associated fungi interact with trees in mineral soil, the litter layer also harbors fungi capable of mediating plant performance (Prescott & Grayston, 2013; Veen et al., 2019). Additionally, litter layer fungal communities may partially reflect foliar fungal communities which can enhance or reducing plant performance (Jia et al., 2020). To account for the ecological relevance of both mineral soil and litter layers for tree-fungi interactions, we sampled fungi at two depths (litter layer: O horizon; mineral soil: top 10-cm of A horizon) at each forest inventory plot between July and August of 2021 (Carpenter et al., 2014). Soil and litter were sampled along a 25x25-meter grid within each 2-12ha inventory plot, excluding plot edges (Table S4-1). Within every other grid square (in a checkerboard pattern), we collected 9 samples in a square pattern, 8 spaced evenly in 5-meters increments from the perimeter, and 1 from the square center. These samples were pooled and homogenized at each grid square. Pooled samples were air dried for 24-48 hours, split into two equal 100g samples for separate chemical and microbial analyses, and stored in -20°C freezers until processed.

Soil Chemical Analyses, Microbiome Sequencing, & Bioinformatics

To quantify both abiotic properties and fungal communities we utilized chemical analyses performed at the Soil Health Laboratory in the Crop and Soil Science Department of Oregon State University in the Fall of 2021 as well as amplicon sequencing on the PacBio Sequel IIe (Pacific Biosciences of California, California, USA) platform at the Functional Genomic Center in Zurich, Switzerland (FGCZ, Zürich, CH). A detailed description of the chemical nutrient assays is available in Appendix S4-1: Section S4-2. We performed amplicon sequencing of the ITS region using the forward primer ITS9munngs and the reverse primer ITS4ngUni (Tedersoo & Anslan, 2019). Procedures for international soil shipment as well as DNA isolation, amplification, and sequencing are available in Appendix S4-1: Section S4-3.

To process raw CCS sequences, we followed an adapted cutadapt pipeline developed for demultiplexing PacBio and our specific ITS primer sequences (Martin, 2011). Using cutadapt, we removed primers before denoising, quality filtering, and checking for chimeras using Dada2 (Callahan et al., 2016). Once demultiplexed and processed, we assigned taxonomic identity of amplicon sequence variants (ASVs) using the ‘probable’ and ‘highly probable’ filter of FUNGuild as recommended by Nguyen et al., (2016). FUNGuild assignments are often inclusive of life-histories, which led to many cases in our dataset where a given ASV was categorized in overlapping guilds (i.e., “saprotrophic” and “ectomycorrhizal” or “saprotrophic” and “pathogenic). In many cases these overlapping assignments are informative, especially for some ectomycorrhizal fungi that have retained saprotrophic nutrient acquisition strategies. We allowed ectomycorrhizal and pathogenic guilds to contain ASVs that overlapped with saprotrophic life histories. No ASV was included in multiple focal guilds, meaning that if an ASV was categorized as “saprotrophic” and “ectomycorrhizal” it was only included in the “ectomycorrhizal” guild for subsequent analyses. All ASVs assigned to both “ectomycorrhizal” and “pathogenic” functional guilds were excluded. We observed a total of 11749 unique ASVs across litter layer and mineral soil samples. All categorized guild outputs from FUNGuild, including the “non-assigned” group, are listed in Table S4-2. Distribution of ASVs and reads by FUNGuild assignments are listed in Table S4-3.

Microbial sequencing data is inherently compositional and suffers from unequal sequencing depth, overdispersion, zero-inflation, and data redundancy (McMurdie & Holmes, 2014). Many traditional approaches, including rarefaction, treat all information in low-abundance samples as unreliable, discarding information potentially informative for ecological inference – especially community analyses that are predicated on accurately representing species distribution and abundance. This loss of microbial data through rarefaction is the subject of ongoing debate, especially when subsequent analyses are focused on determining distances between samples in multivariate space (Schloss, 2024; Warton et al., 2012).

Given our emphasis on distance-based analyses (e.g. PCoA, variation partitioning), we opted to use the denoising algorithm 'mbDenoise' (Zeng et al., 2022) instead of rarefaction as our primary method for minimizing inherent challenges with preparing fungal sequencing data. mbDenoise employs a zero-inflated probabilistic principal components negative binomial model that algorithmically distinguishes between biological and technical zeros (Zeng et al., 2022). The resulting denoised abundance matrix represents the estimated true abundance of each taxon in each sample after accounting for technical zeros, uneven sequencing depth, and overdispersion and performs favorably when fungal community data are used for spatial analyses (Busato et al., 2023; Sato et al., 2024). A detailed description of mbDenoise is available in Appendix S4-1: Section S4-4. We used denoised ASV matrices in all downstream analyses except for beta-deviation analyses for which we utilize an established bootstrapping method (Kraft et al., 2011) that relies on untransformed ASV counts. All ASV matrices were Hellinger transformed when used in distance-based analyses due to the poor performance of ecological data in Euclidean space (Legendre & Gallagher, 2001).

Statistical Analyses

We used several complementary analyses of spatial aggregation as a proxy for measuring relative preference for soil location or tree communities among pathogenic, ectomycorrhizal, and saprophytic fungal communities. Evidence of spatial aggregation, while not an explicit test of host-specificity, indicates that environmental factors and/or interactions are shaping the compositions of fungal guilds. Given the grid-based and compositional nature of our sampling design, we could not directly measure host-specificity in 1-1 relationships between host trees and fungi. All analyses were 3completed in R version 4.1.1 (R Core Team, 2021). Generally, our analyses were completed using the R packages ‘phyloseq’ (McMurdie & Holmes, 2013) and ‘vegan’(Oksanen et al., 2025). Data preparation was performed with the ‘tidyverse’ packages (Wickham et al., 2023). For hypothesis testing we used permutational analysis of variance (PERMANOVA) and mixed linear models (LMM) in the ‘vegan’ and ‘lme4’ (Bates et al., 2003) packages, respectively. Model fits were assessed using the ‘DHARMa’ package (Hartig, 2016). All figures were generated using ‘tidyverse’ (ggplot2) and ‘ggpubr’ (Kassambara, 2016) packages.

Relative abundance and compositional differences

To test how elevation influences the composition of pathogenic, ectomycorrhizal, and saprotrophic fungal communities we used the ‘adonis2’ function of the vegan package to perform permutational multivariate analyses of variance (PERMANOVA) on denoised PCoA vectors across forest plots. Then, to assess how the relative abundance of pathogenic and mycorrhizal fungi varies with elevation and soil layer we used LMMs with a ln-transformed ectomycorrhiza-to-pathogen read ratio as the response variable. We fit our models with elevation as a predictor, and a random effect of site to control for spatial non-independence of samples.

Spatial aggregation relative to random assortment

First, to demonstrate that ectomycorrhizal and pathogenic fungi are more spatially aggregated than expected under null community assembly, we adapted the approach for calculating β-deviations outlined in Kraft et al. (2011). β-deviations (SES β) are standardized effect sizes of the difference between pairwise sample Bray-Curtis dissimilarities and dissimilarities derived from randomly assorted null communities. Since β-diversity is inherently a product of $\alpha\ (local)$ and $\gamma\ (regional)$ diversity (Whittaker, 1960), calculating SES β allows us to compare spatial aggregation across sites independent of site-level differences in local and regional richness. A detailed description of this analysis, including equations and parameters for approximating null community assembly are available in Appendix S4-1: Section S4-5. We tested for significant differences between mean β-deviations at each elevation and guild using a 2-way ANOVA in each layer of soil (i.e., litter and mineral soil layers).

Spatial aggregation relative to outgroup

We further tested spatial aggregation of pathogenic and ectomycorrhizal fungal communities by comparing the spatial aggregation of focal guilds to the observed spatial aggregation of fungi without an assigned functional guild from FUNGuild (β-dispersion; Anderson et al., 2006). Unlike the β-deviation analysis described above, our β-dispersion analysis of focal guilds relative to non-focal guilds provides a metric of how spatially aggregated certain fungal guilds are in relation to the fungal community that does not fall into one of our focal guilds for which we have no *a priori* hypotheses of spetial aggregation. We calculated β-dispersion for each combination of layer, guild, and site using the 'betadisper' function in Vegan (Oksanen et al., 2025), and then calculated β-dispersion from iteratively resampled the non-focal community at the observed richness and sample depth. We ran this analysis with 1000 permutations and a standardized non-focal community (non-assigned guilds) across all tests. Similarly to our β-deviation analyses, we present β-dispersions as standardized effect sizes between the focal guild dispersions and non-focal dispersions, where positive values indicate higher dispersion among focal guilds relative to non-focal communities, and negative values indicate over-dispersion relative to non-focal communities. We tested for significant differences between mean β-dispersion at each elevation and guild using a 2-way ANOVA in each layer of soil (i.e., litter and mineral soil layers).

Assessing associations between fungal communities and tree communities

Finally, we utilized variation partitioning to assess associations between fungal guild communities and tree composition across elevation. While β-deviation and β-dispersion tests provide insight into the spatial aggregation of fungal communities, variation partitioning goes one step further by relating changes in community composition of different fungal guilds with correlated changes in tree compositions using distance-based redundancy analysis (dbRDA). We consider this to be a measure of relative or functional host-affinity within each fungal guild community, since high R^2 means that site-to-site differences in tree and fungal guild community composition are highly correlated, and low R^2 values indicate that site-to-site differences in tree and fungal guild community composition are unrelated. We included pathogenic, ectomycorrhizal, saprotrophic fungi as an out-group, and soil chemistry in our variation partitioning analysis with the basal area of all trees from the sampled region of each forest inventory plot as a Hellinger transformed, Bray-Curtis dissimilarity matrix as the multidimensional response (Legendre & Legendre, 2012).

Since soils were sampled and sequenced on a checkered grid within each forest plot, we used inverse distance weighted (IDW) interpolation to estimate the denoised PCoA vector for non-sampled quadrats. IDW interpolation is a simple interpolation method that explicitly assumes a negative relationship between distance and site relatedness and performs favorably when compared to other interpolation methods for fungal community datasets (Janowski & Leski, 2023). While our original soil collection involved 6 forest inventory stands, two of these stands were incompletely surveyed before a wildfire in 2023. To avoid making inference on overly interpolated data, we restricted this analysis to the 4 forest inventory plots for which we had the largest number of quadrats with overlapping tree inventory and sequencing data (RS38, RS02, RS31, and RS21; Table S4-1). A detailed description of variation partitioning including the selection of predictor matrices is available in Appendix S4-1: Section S4-6.

Results

Variation in soil properties with elevation

Soil chemistry differed across the elevational gradient, with declines in nutrient availability at higher elevations (Figure S4-1; Table S4-2). PC axis 1 and PC axis 2 explained 39.8% and 15.9% of variability in soil chemical composition, respectively (Figure S4-1A). Many of the measured chemical properties varied significantly with elevation, especially between the lower five sites and the two highest sites on the elevation gradient (1090 and 1190-meters, Figure S4-1).

Relative abundance and compositional changes with elevation among key fungal guilds

Both relative abundance of ectomycorrhizal to pathogenic fungi and community composition of ectomycorrhizal, pathogens, and saprotrophic fungi changed with elevation. In the litter layer, we found that pathogenic fungi are relatively more abundant compared to ectomycorrhizal fungi, at high elevations (Figure S4-2A; Table S4-5; $t = -3.167$, $p = 0.0164$). In contrast, we find that ectomycorrhizal fungi trend towards relatively more abundant at higher elevations in mineral soils, although the trend is insignificant (Figure 4-2B; Table S4-5; $t = 1.698$, $p = 0.159$). Along with read ratios, we find that the composition of ectomycorrhizal, pathogenic, and saprotrophic fungal guilds varied significantly with elevation (Figure 4-3; Table S4-6)

Spatial aggregation of pathogenic, ectomycorrhizal, and saprophytic fungi

Our β-deviation analysis, which iteratively re-assembles fungal communities assuming random community assembly from all ASVs available at the plot-scale in a particular focal guild, showed that ectomycorrhizal, pathogenic, and saprotrophic fungal communities were more spatially aggregated than expected from a null model with random assembly of communities (higher standardized effect size of β-deviations; Figure 4-4). Ectomycorrhizal fungi in the mineral soil were increasingly spatially aggregated at higher elevations relative to aggregation expected under random assembly. However, β-deviations declined for ectomycorrhizal fungi in the litter layer with increasing elevation (Figure 4-4; Table S4-7; Table S4-8). Saprotrophic β-deviations were lowest in both mineral soil and litter layers at mid elevations and increased at each end of the elevation gradient (Figure 4-4; Table S4-7; Table S4-8). We found no evidence for elevation trends in β-deviations among pathogenic fungal communities.

Our β-dispersion analysis, which compares spatial aggregation of focal fungal guilds to non-focal guilds, showed that ectomycorrhizal fungi were the most spatially aggregated (relative to other non-focal fungal guilds) in both mineral and litter soil layers, and saprotrophic fungi were the least aggregated relative to non-focal fungal guilds, even showing evidence of overdispersion relative to non-assigned fungi (Figure 4-5). We found a small but significant elevational trend in the spatial aggregation of ectomycorrhizal fungi in mineral soil, which become relatively less spatially aggregated towards the higher end of our elevation relative to non-assigned fungi (Table S4-9, Table S4-10). There were no elevational patterns in beta-deviations of pathogenic or saprotrophic fungi.

Association between Conspecific Densities and Fungal Composition

Our dbRDA-based variation partitioning analysis, which examines correlations between spatial changes in tree community composition with changes in fungal guild community compositions and soil chemistry, revealed that key fungal guilds were more associated with tree community compositions than nutrient availability (Figure 4-6). Additionally, pathogenic fungi community composition was more correlated with tree community composition at low than at high elevations (Figure 4-6; Table S4-11). We also find that ectomycorrhizal fungi and saprotrophic fungi are most associated with tree composition at high elevations, although there is not a clear elevational trend across all four sites. Importantly for assessing our hypotheses, we find that the ratio of the proportions of tree community compositional differences explained by pathogenic and ectomycorrhizal fungal communities flips with increasing elevation. In other words, at lower elevations, within plot site-to-site differences in tree composition were more associated with site-to-site differences in pathogenic fungi than site-to-site differences in ectomycorrhizal fungi. However, at higher elevations, within plot site-to-site differences in tree composition were more associated with site-to-site differences in ectomycorrhizal fungi than site-to-site differences in pathogenic fungi.

Discussion

Our findings provide multiple lines of observational evidence that support the Stress Gradient Feedback Hypothesis (SGFH). Specifically, our results support the idea that increasing abiotic stress promotes the host-specificity of mutualistic interactions over antagonistic interactions. That is, we find evidence that ectomycorrhizal fungi are more spatially aggregated relative to both randomly assembled communities (Figure 4-4) and non-host associated fungi (Figure 4-5). This spatial aggregation becomes more pronounced at higher elevations under local conditions that are thought to be more abiotically stressful to plants. Finally, we found that pathogen fungal composition was more strongly associated with tree composition than ectomycorrhizal composition at low elevations, while ectomycorrhizal fungal composition was more strongly associated with tree composition than pathogenic composition at high elevations (Figure 4-6). Together, these findings suggest that interactions between trees and pathogenic fungi are more functionally host-specific at lower elevations whereas interactions between trees and ectomycorrhizal fungi are more functionally host-specific at higher elevations. Furthermore, stabilizing CDD has already been shown to go from stabilizing to less stabilizing or even neutral with increasing elevation in our study system (LaManna et al., 2022). Such observations lend initial support to some fundamental predictions of the SGFH framework and suggest this framework may be useful for assessing local stabilizing CDD in the context of abiotic stress.

We find evidence that ectomycorrhizal fungi are relatively more spatially aggregated compared to randomly assembled communities at higher elevations in the mineral layer (Figure 4-4). Elevational trends in spatial aggregation among focal fungal guilds (ectomycorrhizal, pathogenic, and saprotrophic fungal guilds) are strongest in comparison to randomized null and weakened or disappeared entirely when compared to non-focal community aggregation (Figure 4-5). Increasing β-deviations (spatial aggregation relative to random assembly) with elevation indicates that ectomycorrhizal communities are responding independent of other fungal guilds, and independent to the total abundance and functional composition of the greater fungal community.

Independent responses of ectomycorrhizal communities to elevation relative to other functional guilds may indicate a divergence between host selection of ectomycorrhizal fungi and abiotic filtering of non-ectomycorrhizal fungi in stressful environments (Lumibao et al., 2020). Abiotically stressful environments theoretically alter aggregation around hosts in all organisms

(Grime, 1977). However, we only recover spatial aggregation patterns for ectomycorrhizal fungi (Figure 4-4) – which could indicate that host selection of ectomycorrhizal fungi outweighs abiotic stress as a predictor of fungal composition. Alternatively, similar patterns may arise due to understory plant heterogeneity and co-aggregation of trees and fungi around downed woody debris (Tedersoo et al., 2003). Decreased decomposition rates lead to increased downed woody biomass in high elevation forests, which may in turn attract both seedlings and fungi seeking limited nutrients from downed logs (i.e., nurse logs). One interpretation of our result that spatial aggregation of ectomycorrhizal fungi increases with elevation (Figure 4-4) is that fungi are more likely to aggregate around downed logs when mineral soil nutrient availability is poor. However, we find this interpretation unlikely given that elevational trends in spatial aggregation are only evident in mineral soil where fungi-root interactions occur, and the same trends are not present for saprotrophic fungi which also would be expected aggregate around debris. Finally, tree hosts in our system alter local soil nutrient availability and surface conditions for centuries, factors which have demonstrated impacts on the spatial arrangement and abundance of ectomycorrhizal fungi (Otsing et al., 2021). We conclude that changing spatial aggregation of ectomycorrhizal fungi – which occurs independent of saprotrophic fungi and litter layer fungi – is indicative that aggregation is occurring in locations with dense tree hosts (conspecifics) as opposed to locations with dense nutrients or understory plants.

In contrast to our present observations, some prior studies suggest that ectomycorrhizal communities under extreme abiotic stress, such as at the arctic range-limits of vascular plants, are dominated by generalists (Botnen et al., 2014). Others indicate that the SGH may not be supported at extreme high levels of abiotic stress (He & Bertness, 2014; Michalet et al., 2014). To explain these differences, we hypothesize that our stress gradient is not extreme enough to capture antagonistic and mutualistic plant-fungal interactions occurring at the limits of our focal tree species' niche space. Moreover, we hypothesize that increasing host-affinity of ectomycorrhizal fungi in nutrient-poor environments may be a result of strong selective pressures for trees to upregulate mutualistic associations that bolster nutrient acquisition (Kiers et al., 2011). Additionally, ectomycorrhizal fungi may rely more on resource exchanges with trees in nutrient-stressed environments and therefore form stronger, or more frequent, associations. We emphasize that our results in support of the SGFH are representative of environmental stressors that are generally tolerable for host trees, and not intolerably extreme environmental stressors which may become more common under climate change.

In contrast to ectomycorrhizal fungi, we find that the correlations between tree and pathogenic fungi community composition declines with increasing elevation in the mineral soil (Figure 4-6), despite unchanging spatial aggregation (Figure 4-4). Several potential explanations for these results deserve future attention. First, we hypothesize that communities of pathogenic fungi may be equally relatively host-specific across elevation and simply less abundant at higher elevations (Větrovský et al., 2019) – thereby contributing less to local stabilizing CDD with increasing stress. In this case, the fundamental host-pathogen relationships may remain consistent across elevation, and overall effects on composition at high elevation are muted by reduced relative pathogen abundances independently of other factors. Alternatively, chronic stress, such as nutrient depletion at high elevations, may select for generalist pathogens that do not contribute to relatively host-specific feedbacks resulting in tree compositions that do not reflect underlying pathogen aggregation (Gostinčar et al., 2022). However, these explanations depend on pathogenic fungi being more susceptible to environmental stress than other fungal guilds, which remains uncertain in forest systems. Finally, another potential explanation for declining correlations between tree and pathogenic fungi community composition with increasing elevation is that the harmful effects of pathogenic fungi may be increasingly offset by stronger facilitation under nutrient stress, known as mycorrhizal induced resistance (Cameron et al., 2013; Mauch-Mani et al., 2017). Ectomycorrhizal resistance to pathogens includes buffering against nutrient stressors that lead to downregulated investment in defenses, as well as physical sheathing of root structures that limits infection from nearby pathogens (Bonfante & Anca, 2009). As elevation increases, increased spatial aggregation and abundance of ectomycorrhizal fungi may prevent relatively host-specific pathogens from associating with hosts, potentially generating selection pressure for pathogens that are less host-specific and therefore contribute less to stabilizing CDD.

In addition to finding support for the SGFH in spatial aggregation of pathogenic and ectomycorrhizal fungi, we also find abiotic stress patterns in relative abundance. Specifically, we find increasingly more pathogenic fungi relative to ectomycorrhizal fungi in the litter layer with increasing elevation, and an insignificant opposing trend towards more ectomycorrhizal fungi than pathogenic fungi in mineral soils at high elevations (Figure 4-2). These contrasting patterns suggest that different processes may be contributing to compositions of root-associated fungi across the litter and shallow mineral soil layers and may relate to decomposition rates across elevation. Both at our study site, and more broadly across the Pacific Northwest, decomposition rates decline with increasing elevation (Kirschbaum, 1995). At low elevations, where high-moisture and low snowpack contribute to faster decomposition rates, ectomycorrhizal and saprotrophic fungi may more aggressively compete for organic matter in the litter layer (Steidinger et al., 2019). Alternatively, the efficiency and abundance ectomycorrhizal fungi in the litter layer at higher elevations may be limited by prolonged extreme cold conditions in the winter (Castaño et al., 2017; Klimek & Niklińska, 2024). The difference between the abundance of pathogenic and ectomycorrhizal fungi across soil layers suggests either that mineral soil fungi play a more dominant role in tree performance than litter soil fungi or that the SGFH may need refinement when applied to interactions between trees and fungi in multi-layered soils where resource gradients and competitive environments vary significantly with soil depth (Warren et al., 2005). Vertical stratification of litter and soil fungal communities may affect local stabilizing CDD, particularly in local communities with both shallow and deep-rooting tree species. We emphasize the need to investigate the root-associated microbiome in a wider range of soil layers and assess their contribution to local stabilizing CDD along stress gradients.

While historical explanations for conspecific density effects on individual performance centered the role of natural enemies in the form of herbivores, parasites, and pathogens (Janzen, 1970; Connell, 1971; Ricklefs, 1977), our results add to a growing body of evidence emphasizing the importance of mutualistic interactions as counterbalances to the influence of natural enemies (Delavaux et al., 2023; Jiang et al., 2020). In formulating the SGH, Bertness & Callaway (1994) noted that “Positive interactions deserve increased empirical attention and should be incorporated into models of community organization”. The work presented here suggests that increased empirical attention is not only necessary among facilitative interspecific plant-plant interactions, but also among relatively host-specific mutualisms between plants and fungi that may contribute to patterns of diversity along abiotic stress gradients.

Our findings center on ectomycorrhizal and pathogenic fungi due to their ecological relevance and well documented role in contributing to local stabilizing CDD (Delavaux et al., 2023; Janzen, 1970; Connell, 1971; Jiang et al., 2020; Liang et al, 2021). Nevertheless, there are many other taxa that may contribute to local stabilizing CDD that we did not test for – including arbuscular mycorrhizal fungi, oomycetes, and aboveground organisms such as insects and foliar fungal communities (LaManna et al., 2024). Each of these potential drivers may alter how host individuals experience abiotic stress – which could generate complex feedback loops altering local CDD effects on individual performance. The relative importance of these diverse taxa in driving local CDD patterns across environmental gradients, and how their effects may shift with increasing abiotic stress, remains an important avenue for future research.

Conclusions

Together, our observations lend support to the idea that the relative importance of ectomycorrhizal fungi in shaping CDD increases, relative to that of pathogenic fungi, as environmental stress increases. In other words, plants are increasingly associated with ectomycorrhizal fungi as elevation increases, which we may contribute to stronger destabilizing conspecific density effects at high elevations – which are well-documented at our study site and along other elevational gradients. In our system, these patterns also correlate with declining tree richness, further corroborating evidence that stress-mediated communities of relatively host-specific mutualists and antagonists may contribute to species diversity along abiotic gradients. These results in support of the SGFH highlight the importance of understanding tree-fungal interactions in their abiotic contexts. Future studies should consider how other abiotic stressors, including extreme abiotic stress events such as ecological disturbances, may influence community dynamics by altering the relative importance of relatively host-specific antagonistic and facilitative interactions. In conclusion, the SGFH presents a viable framework for testing the role that host-specific interactions play under abiotic stress, with preliminary evidence in tree-fungal systems, and potential for application across community ecology.

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Tables and Figures

Table 4-1: Definition and Tests of the Stress Gradient Feedback Hypothesis

<table>
<tr><td colspan="3"><u>Stress Gradient Hypothesis (SGH):</u> Competitive interactions are more important, or more intense, in benign, low-stress environments, whereas facilitative interactions are more important in harsh, high-stress environments (Bertness & Callaway 1994, Maestre et al. 2009).

<u>Stress Gradient Feedback Hypothesis (SGFH):</u> Increased importance or intensity of relatively host-specific antagonistic interactions contributes to negative conspecific density-dependent feedback in benign, low stress environments, whereas increased importance or intensity of relatively host-specific facilitative plant-microbe interactions contributes to increased positive conspecific density-dependent feedback in harsh, high-stress environments.</td></tr>
<tr><th>Prior findings</th><th>SGFH prediction</th><th>Test of prediction in study</th></tr>
<tr><td>Climatic and chemical nutrient limitations to plant performance are strongest at high elevations (Lomolino, 2001).</td><td>At high levels of abiotic stress facilitative plant-microbe interactions become increasingly abundant relative to antagonistic plant-microbe interactions.</td><td>Compare the relative abundance of mycorrhizal and pathogenic fungi across a stress gradient associated with elevation.</td></tr>
</table>

Local CDD is primarily generated by relatively host-specific associations including between trees and pathogenic and mycorrhizal fungi, which generate differential affects across tree species (Jiang et al., 2021; Mangan et al., 2010; Packer & Clay, 2000; Song & Corlett, 2022).	1. Antagonistic plant-microbe interactions are relatively more host-specific and/or more intense in abiotically benign environments than in abiotically stressful environments. 2. Facilitative plant-microbe interactions are relatively more host-specific and/or more intense in abiotically stressful environments than in abiotically benign environments.	Compare the absolute and relative spatial aggregation of pathogenic and mycorrhizal fungi along an elevational stress gradient: 1. Spatial aggregation of pathogenic and ectomycorrhizal fungal communities relative to a randomly assorted null community (Kraft et al. 2011). 2. Spatial aggregation of pathogenic and ectomycorrhizal fungal communities relative to other fungal functional guilds.
The strength of local CDD correlates with tree diversity across elevation (stronger stabilizing CDD associated with higher tree diversity; (Fibich et al., 2021; LaManna et al., 2022).	1. Conspecific tree compositions are associated with compositions of ectomycorrhizal fungi more than compositions of pathogenic fungi in abiotically stressful environments. 2. Conspecific tree compositions are associated with compositions of pathogenic fungi more than compositions of ectomycorrhizal fungi in abiotically benign environments.	Relate changes to the spatial structure of tree communities (analogous to changing conspecific abundances) with changes to pathogenic, ectomycorrhizal, and saprotrophic fungal communities using variation partitioning (Legendre & Legendre 2012). Compare differences between guild R^2 values along an elevational stress gradient.

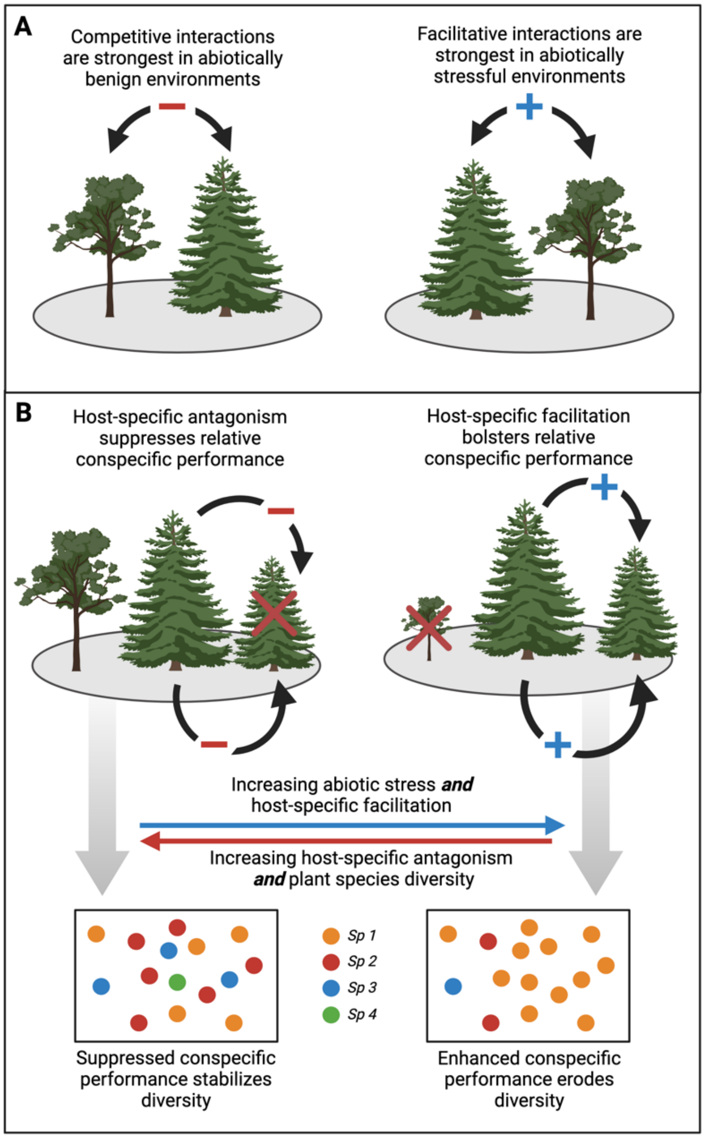

Figure 4-1: The Stress Gradient Hypothesis (A) and the Stress Gradient Feedback Hypothesis (B). The Stress Gradient Hypothesis (SGH, A) posits that competitive interactions are more important, more intense, or more frequent in benign, low-stress environments, whereas facilitative interactions are more important, intense, or frequent in harsh, high-stress environments. Here, we expand the SGH to relatively host-specific antagonists and mutualists (B). Relatively host-specific above- and belowground plant-microbe interactions may explain shifts in net conspecific density-dependent feedback and correlated patterns of species diversity across abiotic stress gradients. All else being equal, antagonistic conspecific feedbacks may increase fitness differences under abiotic stress and promote species diversity by preventing competitive dominance of a single species (spatial patterns of species represented by colored circles). Alternatively, relatively host specific facilitative feedbacks, also generated by root- or leaf-associated microbes, may bolster conspecific performance and erode diversity – particularly under regimes of high abiotic stress.

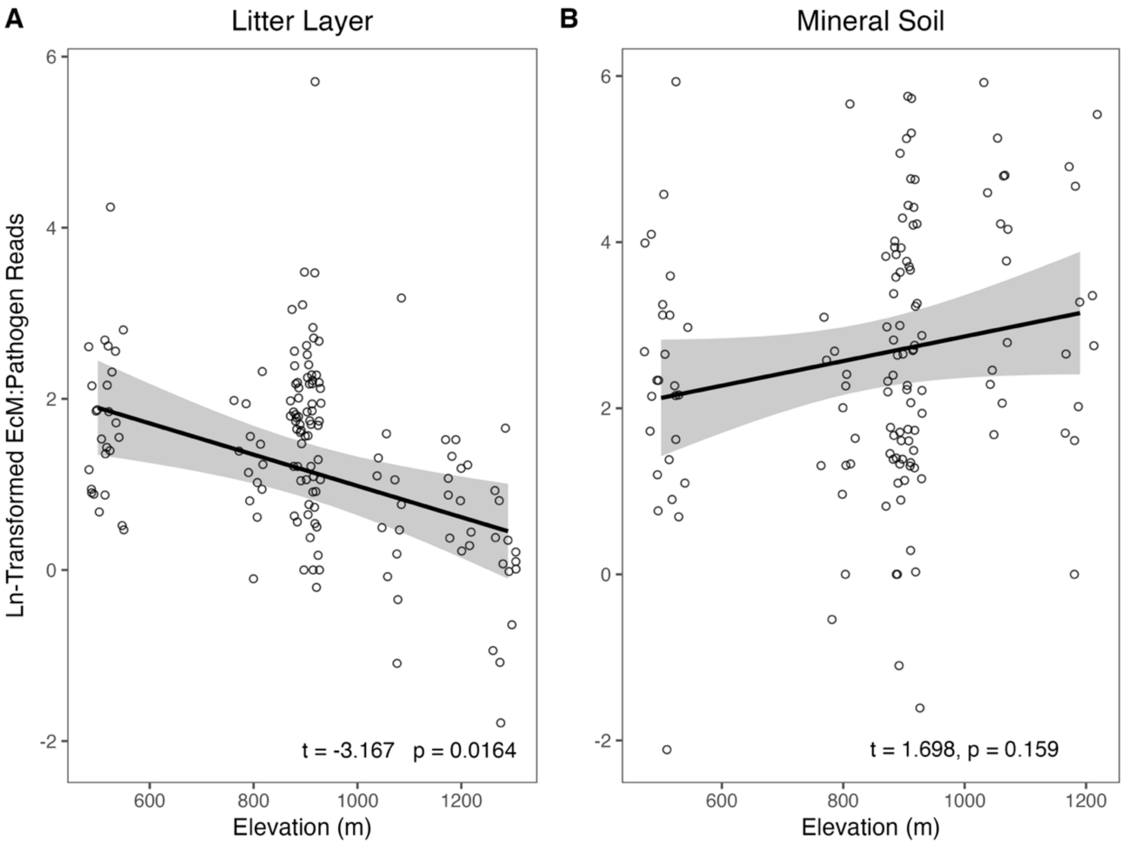

Figure 4-2: Ratio of ectomycorrhizal to pathogenic fungi across elevation in the (A) litter layer and (B) mineral soil. In the litter layer (A), natural log transformed EcM to pathogen ratios decline with increasing elevation (t = -3.167, p = 0.0164). In the mineral soil (B), EcM to pathogen ratios trend towards increasing with elevation, although this effect was insignifcant (t = 1.698, p = 0.159). Circles represent individual soil samples; positions are jittered on the X axis to show sample size. Black lines represent best fit from LMM allowing site-level random intercepts. Shaded areas indicating 95% confidence intervals. Model statistics are presented in Table S4-4.

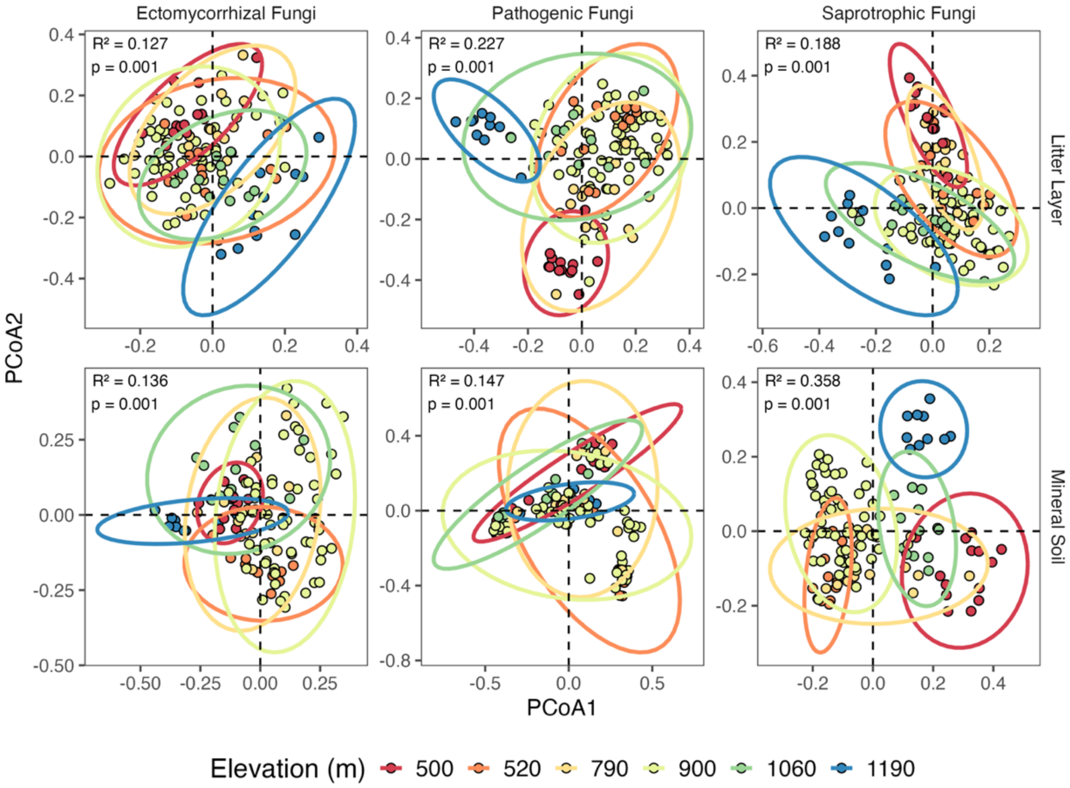

Figure 4-3: Compositional probabilistic PCoA analysis of (A) ectomycorrhizal, (B) pathogenic, and (C) saprotrophic fungal communities. Each point represents a sample, and points are color-coded by elevation (500 m, 520 m, 790 m, 900 m, 1060 m, 1190 m). The axes (PCoA1 and PCoA2) explain the highest proportion of variance in denoised community composition data, which distinguishes between technical and biological zeros to account for the composition and incomplete nature of sequencing for fungal compositional estimations (see methods). Fungal guild communities are distinctly clusted by elevation. R^2 and p values for elevational associations are presented in each combination of guild and layer as assessed using PERMANOVA (Figure S4-5).

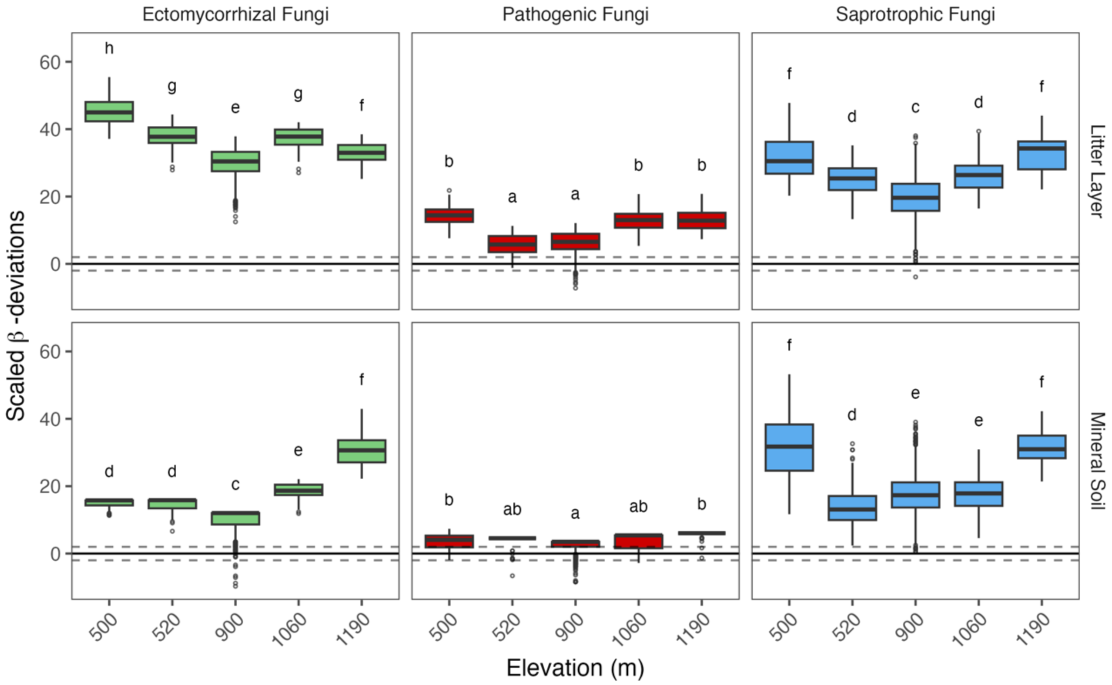

Figure 4-4: Standardized comparisons of beta-deviations among fungal functional guilds in litter layer and mineral soil. Boxplots depict results of iterative testing of beta-deviations (SES β) for ectomycorrhizal fungi (green), pathogenic fungi (red) and saprotrophic fungi (blue) across elevations from 500-m to 1190-m. Dotted lines depict null envelope (+/- 2 SD), above and below which are considered to be assorting non-randomly (above 2, spatially aggregating; below 2, spatially over-dispersed). SES β compare beta diversity to expected beta diversity under random community assembly an accounting for regional (plot) and local (sample) richness. We find contrasting patterns for ectomycorrhizal fungi between the litter layer and mineral soil, particularly for the highest two plots where nutrients are the least available (Fig S1). Ectomycorrhizal fungi are most aggregated in litter layers at low elevation, and most aggregated in mineral soil at high elevations. No strong elevational trends exist for pathogenic fungi, which are generally the least spatially aggregated across elevation. Saprotrophic fungi show strong evidence of spatial aggregation at low and high elevations with generally lower spatial aggregation at mid elevations.

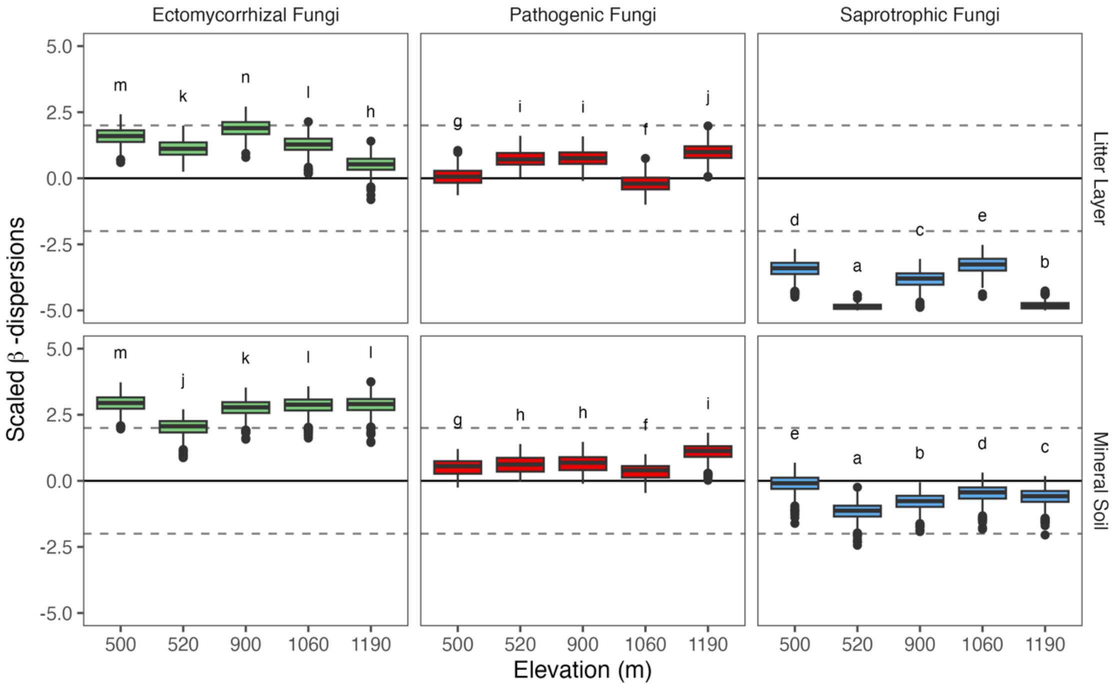

Figure 4-5: Standardized comparisons of beta-dispersions among fungal functional guilds in litter layer and mineral soil. Boxplots depict results of iterative testing of beta-dispersions for ectomycorrhizal fungi (green), pathogenic fungi (red) and saprotrophic fungi (blue) across elevations from 500-m to 1190-m. Dotted lines depict null envelope (+/- 2 SD), above and below which we considered to be evidence of non-random spatial aggregation (above 2, spatially aggregating; below 2, spatially over-dispersed). Whereas SES β compare beta diversity to expected beta diversity under random community assembly, beta-dispersions compare against an outgroup of fungi that were unassigned to any focal guild. This provides a measure of whether focal guilds are more spatially aggregated than the larger fungal communities. For ectomycorrhizal fungi in the litter layer, beta-deviations peak at 500-m and decreases with elevation, while pathogenic fungi fall generally within the null envelope and saprotrophic fungi show evidence of overdispersion. In mineral soil, beta dispersion patterns generally fell within the null envelope for pathogenic and saprotrophic communities but were positive, indicating spatial aggregation, for ectomycorrhizal communities. This figure provides evidence that ectomycorrhizal fungi are generally more spatially aggregated than non-assigned fungi, although the magnitude of aggregation is less than when compared to null assembly (SES β).

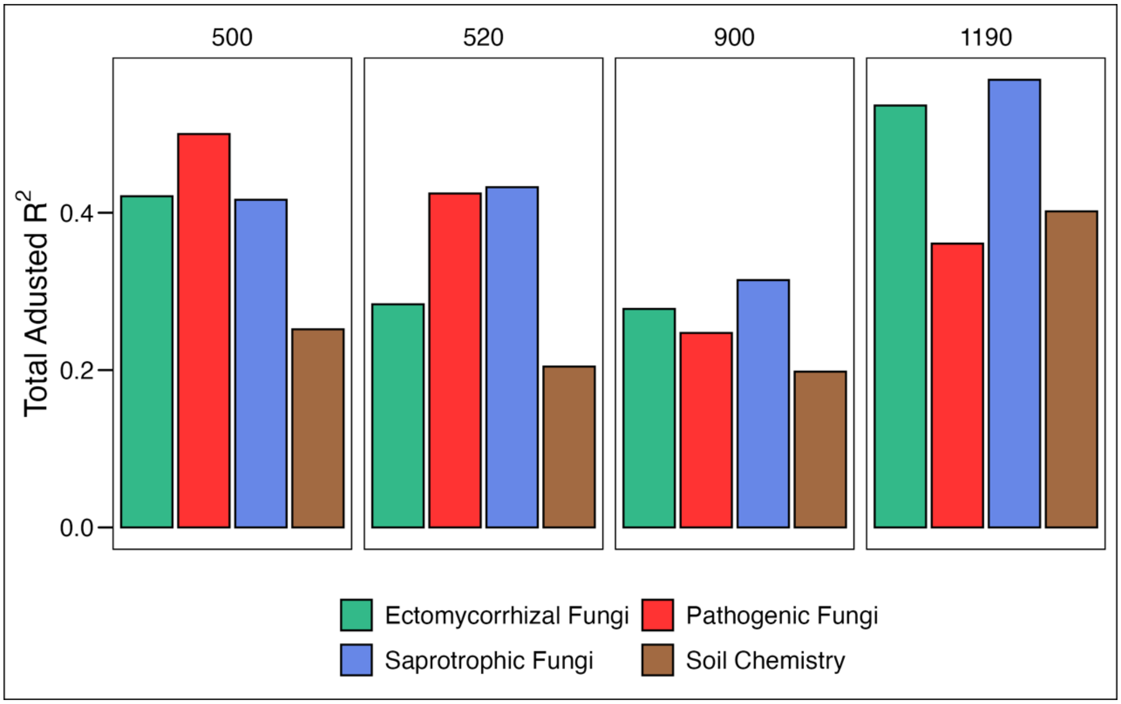

Figure 4-6: Correlated changes in tree community composition (species basal area), soil nutrients, and fungal communities across 4 large ForestGEO plots spanning 690 meters of elevation. Top axis represents elevation in meters. Color indicates study factor, being either a focal fungal guild or soil chemistry. Within each forest plot, adjusted R-squared values represent the result of dbRDA-based variation partitioning and describe the total correlated changes between fungal guild and tree community compositions. We find general support for the SGFH in the relative change in adjusted R^2 between pathogenic and ectomycorrhizal fungal communities along the elevation gradient. Soil chemistry and saprotrophs also become more important to determining tree compositions our highest elevation site, which has the most distinct soil chemical composition (Fig S4-1).

Supplemental Information (Appendix S4-1)

Section S4-1: Detailed Site Description

This study took place across a 700-meter elevation gradient (500-meters to 1190-metres) at the Andrews Experimental Forest LTER near Blue River, Oregon. Climatic conditions vary across this gradient, with temperature ranging from 7.4°C to 10.3°C and annual precipitation from 2,040 to 2,354 mm/yr (Wang et al., 2016). Long-term meteorological data from stations at lower (436 m) and higher (1,268 m) elevations reveal that lower valleys typically experience higher mean-spring temperatures, greater relative humidity, and more moderate year-long temperatures that provide extended growing seasons for evergreen species, even during winter (Waring & Franklin, 1979). In contrast, higher elevations face shortened growing seasons due to spring/early summer snowmelt, dry summers, and freezing temperatures during the wet season. The forest communities at Andrews LTER exemplify old-growth Pacific Northwest temperate rainforests, which are home to some of the world's tallest trees and highest aboveground biomass. The canopy is predominantly composed of Douglas-fir (*Pseudotsuga menziesii*), Western red-cedar (*Thuja plicata*), Western hemlock (*Tsuga heterophylla*), and various *Abies* species including Silver fir (*Abies amabilis*) and Noble fir (*Abies procera*). The mid-canopy and understory layers feature numerous broadleaf and conifer species, notably Big-leaf maple (*Acer macrophyllum*) and Pacific dogwood (*Cornus nuttallii*).

Section S4-2: Detailed Soil Chemistry Methodology

To address the role of soil chemistry in mediating fungal and tree compositional patterns, chemical analyses on macro- and micro-nutrients were performed on mineral soil samples at the Soil Health Laboratory in the Crop and Soil Science Department of Oregon State University in the Fall of 2021. C and N content was measured using dry combustion using an Elementer Vario Macro Cube (Elementar Americas Inc., Ronkonkoma, NY USA). OM was calculated as twice the total carbon content (Pribyl, 2010). pH was measured in Sikora buffer solution on Hanna HI5522 benchtop meter (Hanna Insturments, Inc.). PO4-P extractions were performed using Bray P1 and measured on VWR V1200 spectrophotometry (VWR International, LLC, Vienna, Austria). Ca, Mg, and K were measured through a 1M ammonium acetate extraction measured on Agilent 5110 ICP-OES (Agilent Technologies, Inc., Santa Clara, CA, USA). NO3-N and NH4-N were both extracted with KCl and measured on a VWR V1200 spectrophotometer using Griess reagents and a Lachat QuikChem 8500 Series 2 flow injection analyzer, respectively. B, Cu, Fe, Mn, and Zn content were all extracted with DTPA-sorbitol and measured on Agilent 5110 ICP-OES.

Section S4-3: Detailed Amplicon Sequencing Methodology

To quantify the composition of fungal communities, we used amplicon sequencing on the PacBio Sequel IIe (Pacific Biosciences of California, California, USA) platform at the Functional Genomic Center in Zurich, Switzerland (FGCZ, Zürich, CH). 100g samples of both mineral soil and litter layers were air-dried for 24-48 hours and were checked for dryness before being packaged. Samples were stored in a 3° C fridge before being shipped overnight to ETH Zurich, Switzerland for sequencing. We isolated microbial genomic DNA from 250 mg of soil using DNeasy Power Soil Pro Kits (Qiagen, Hilden, Germany). To amplify ITS regions, we performed PCR on each sample with the forward primer ITS9munngs and the reverse primer ITS4ngUni at a concentration of 12.5 µM (Tedersoo & Anslan, 2019; Tedersoo & Lindahl, 2016). The fungal PCR reaction was performed with 0.5 µl of each primer, 1 µl of extracted DNA template, 13 µl of GoTaq G2 Hot Start Colorless Master Mix (Promega, CH, REF M743B) and 10 µl PCR grade ddH2O (REF P119C). Thermocycling was performed with the following procedure: 15-minutes at 95°C, 30 cycles of (30-seconds at 95°C, 30-seconds at 57°C, 60-seconds at 72°C), and a final 10-minute extension step at 72°C with subsequent cooling at 4°C until sample collection. Before sequencing, we estimated the relative quantity of PCR products by running samples on 1% agarose gel for 25-minutes and pooling based on band intensity. These pools were cleaned with AMPure beads (Beckman Coulter, Brea, California, USA) and DNA was quantified with Qubit (Invitrogen/Thermo Fisher Scientific, Massachusetts, USA).

Section S4-4: Accounting for technical confounding factors using mbDenoise

mbDenoise employs a sophisticated zero-inflated probabilistic principal components analysis negative binomial model (ZIPPCA-nb) that algorithmically distinguishes between biological and technical zeros in microbial abundance data (Zeng et al., 2022). This methodology addresses a fundamental challenge in microbiome sequencing data: distinguishing between true biological absences (where a taxon is genuinely not present in a sample) and technical zeros (where a taxon is present but undetected due to sampling limitations, sequencing depth constraints, or other technical artifacts).

The model architecture incorporates a two-part noise model with latent indicator variables $z_{ij} \sim Bernoulli(\eta_{ij})$ for each sample i and taxon j. The zero-inflation probability η_{ij} is modeled through a logistic regression: $\eta_{ij} = {e^{(c_i + \tau_j)}}/{1 + e^{(c_i + \tau_j)}}$, where c_i are sample-specific parameters and τ_j are taxon-specific parameters. This formulation allows both sample-level and taxon-level factors to influence the probability of biological zeros. When z_{ij} = 1, the observation represents a biological zero indicating true absence of the taxon. When z_{ij} = 0, the observation follows a negative binomial distribution $\text{NB}(\mu_{ij}, \varphi_j)$ that explicitly accounts for overdispersion commonly observed in sequence count data, where φ_j are taxon-specific overdispersion parameters. The mean parameter follows: $\log(\mu_{ij}) = \alpha_{i0} + \beta_{0j} + f_i^T \beta_j$, where α_{i0} handles uneven sequencing depth across samples, β_{0j} represents taxon-specific baseline abundance, and $f_i^T \beta_j$ captures the low-dimensional latent structure.

Rather than making definitive binary classifications of zeros based on arbitrary thresholds, the ZIPPCA-nb model estimates the posterior probability of each zero being biological through variational inference. The variational approximation assumes $q(z_{ij}) \sim \text{Bernoulli}(\pi_{ij})$, where π_{ij} represents the approximate posterior probability that zero observation (i,j) is biological. This inference procedure leverages complex patterns across the entire dataset through the latent factor structure $f_i \sim N(0, I)$ and factor loadings β_j, where samples with similar environmental conditions are expected to have similar latent factor profiles f_i. A zero is assigned higher probability of being biological if a taxon is consistently absent across samples that share similar latent factor profiles, while zeros for taxa frequently present in ecologically similar samples are more likely classified as technical artifacts. The low-rank representation ${f_i}^T \beta_j$ captures intrinsic redundancy in microbial communities, consistent with ecological theory that microbial communities are constrained by local environmental conditions (Kraft et al., 2015). This allows the model to "borrow strength" across samples when making zero classifications, which is particularly valuable for rare taxa where individual sample information may be limited.

Probabilistically determining biological versus technical zeros offers substantial advantages for spatial pattern analysis in microbial data, as demonstrated in fungal community studies (Busato et al., 2023; Sato et al., 2024). This approach allows for information sharing via the low-rank representation while addressing multiple sources of technical variation: uneven sequencing depth (through α_{i0}), overdispersion (through φ_j), and excess zeros (through the zero-inflation component). Given our emphasis on spatial and correlative community analyses we used denoised ASV matrices in all downstream analyses except for beta-deviation analyses, which utilize an established bootstrapping method (Kraft et al., 2011) requiring untransformed counts. All ASV matrices were Hellinger transformed for distance-based analyses due to poor performance of ecological data in Euclidean space (Legendre & Gallagher, 2001).

Section S4-5: Calculating β-deviations

First, to demonstrate that ectomycorrhizal and pathogenic fungi are more spatially aggregated than expected under null community assembly, we adapted the approach for calculating β-deviations outlined in Kraft et al. (2011). β-deviations (SES β) are standardized effect sizes of the difference between pairwise sample Bray-Curtis dissimilarities and Bray-Curtis dissimilarities derived from randomly assorted null communities. Since β-diversity is inherently a product of α $(local)$ and γ $(regional)$ diversity (Whittaker, 1960), calculating SES β allows us to compare spatial aggregation across sites independent of site-level differences in local and regional richness. The formula for β-deviations (SES β) of a given site s, focal fungal guild g, and number of samples n is as follows:

$$\text{SES } \beta_{sg} = \frac{\left(\frac{\text{Observed } \beta_{sg} - \text{Null } \beta_{sg}}{sd(\text{Null } \beta_{sg})}\right)}{\sqrt{\text{n}}}$$

Our null assembly resorted all ASVs from a given site into new communities for each sample while retain sample ASV richness α and total site richness γ. Neutral β-deviations are indicative that fungal communities are assorting stochastically (e.g., assembled into each 25x25-m grid square at random from all fungal species available in the entire plot). while positive β-deviations indicate that fungal communities are spatial aggregated (clustering) relative to random assembly and negative β-deviations indicate that fungal communities are spatially over-dispersed relative to random assembly (Kraft et al., 2011; Myers et al., 2013). While this approach does not account for sample completeness, β-deviations are comparable across sites when sample size differences are accounted for by dividing SES β by the square root of sample size n (Xing & He, 2021). We tested for significant differences between mean β-deviations at each elevation and guild using a 2-way ANOVA in each layer of soil (i.e., litter and mineral soil layers).

Section S4-6: Estimating associations between fungi and tree communities using variation partitioning

Variation partitioning is a multivariate statistical technique that decomposes the total variation in a response dataset into fractions explained by different sets of predictor variables, including their unique contributions and shared effects (Borcard et al., 2011; Legendre & Legendre, 2012). This method extends the concept of R^2 from simple regression to complex multivariate datasets, examining how much variation in community composition can be attributed to different environmental factors while accounting for correlations among predictors (Peres-Neto et al., 2006). The method works by fitting constrained ordination models (in our case, distance-based redundancy analyses; dbRDA) to calculate the variation explained by each predictor set individually and in combination. The total variation is then partitioned into: (1) variation uniquely explained by each predictor set, (2) variation jointly explained by combinations of predictor sets, and (3) unexplained variation (Legendre & Legendre, 2012). This approach is especially useful when predictor variables are correlated, as it separates their independent effects from their shared contributions to explaining patterns in the response data.

The predictors of our variation partitioning analyses were denoised PCoA axes retained from forward selection of species-by-site matrices for fungal pathogens, ectomycorrhizal fungi, and soil chemistry using the 'forward.sel' function of the 'adespatial' package (Dray, 2016; Legendre & Legendre, 2012). Axes were retained up to the adjusted-R^2 of the overall predictor matrix, although we also found similar results with p-value limits (Legendre & Legendre, 2012). Principal coordinates were calculated using the 'vegdist' and 'cmdscale' functions in the Vegan package (Oksanen et al., 2025). Using this approach, we estimate the total variation in the response matrix (tree species distance matrix) that is explained by each explanatory matrix (i.e., soil chemistry matrix, ectomycorrhizal fungi matrix, pathogenic fungi matrix) as well as the proportion of variation that is shared among explanatory matrices (Legendre & Legendre, 2012). Here, we report the total variation in the response matrix explained by each predictor as our metric of host affinity. We additionally report the individual variation explained by each predictor in Table S12, although we consider this to be less ecologically relevant since we are interested in total associations and expect some degree of overlap since ectomycorrhizal and pathogenic fungi both associate with tree hosts.

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Supplemental Tables and Figures

Table S4-1: Site elevation, soil sample information, and proportion EcM tree basal area. Sites are distributed along nearly 700 m of elevation at the Andrews Forest in the central Cascade Range of Oregon, USA. Samples were collected on a 25 m^2 grid, and varied in number based on the size of the plot. Forest inventory reference stands are larger than listed sample area as samples were only selected from the central region to avoid edge effects. Proportion of EcM tree basal area (>1 cm diameter trees) in each plot was calculated from the region of each forest inventory plot from which soil samples were collected. Because at plot RS27, only stems >5 cm diameter were measured, basal area is based on these stems only at this plot. Due to the lower resolution of this plot compared to other plots, it was excluded from spatial analyses.

Site	Mean Plot Elevation (m)	Sample Area (hectares)	Sample Number	Proportion EcM Basal Area
RS38	500	1.875	15	0.936
RS02	520	1.875	14	0.615
RS27	790	1.875	14	0.856
RS31	900	9.375	70	0.947
RS28	1060	1.875	12	0.995
RS21	1190	1.875	14	0.999

Table S4-2: Final FUNGuild assignments based on recommended quality filters for each focal guild. We separated each amplicon sequencing variant (ASV) into the following guilds: "ectomycorrhizal", "pathogenic", "saprotrophic" or "unassigned". Assignment was based on the probable and highly probable guild assignment filter and excluding any duplicate assignments (Nguyen et al. 2016). FUNGuild assignments are often inclusive of multiple life-history strategies (i.e., pathogenic and saprotrophic). Here, we generated mutually exclusive "ectomycorrhizal" and "pathogenic" guilds inclusive of overlapping saprotrophic guilds. The saprotrophic guild was defined as saprotrophic assignments that did not overlap with "ectomycorrhizal" or "pathogenic". All guilds that did not fall into one of our focal categories, either for not including "ectomycorrhizal", "pathogenic", "saprotrophic", or for not being retained at probable and highly probable filters, were grouped into "unassigned". Each FUNGuild assigned guild as assigned to each focal category is listed below.

Ectomycorrhizal	Pathogenic	Saprotrophic	Unassigned
Ectomycorrhizal	Plant.Pathogen-Wood.Saprotroph	Undefined.Saprotroph	-
Ectomycorrhizal-Undefined.Saprotroph-Wood.Saprotroph	Animal.Pathogen-Fungal.Parasite-Undefined.Saprotroph	Dung.Saprotroph-Undefined.Saprotroph-Wood.Saprotroph	Endophyte-Litter.Saprotroph-Soil.Saprotroph-Undefined.Saprotroph
Dung.Saprotroph-Ectomycorrhizal	Animal.Pathogen	Endophyte-Litter.Saprotroph-Soil.Saprotroph-Undefined.Saprotroph	Ericoid.Mycorrhizal
Ectomycorrhizal-Undefined.Saprotroph	Animal.Pathogen-Endophyte-Epiphyte-Fungal.Parasite-Plant.Pathogen-Wood.Saprotroph	Wood.Saprotroph	Animal.Pathogen-Soil.Saprotroph
Ectomycorrhizal-Endophyte-Ericoid.Mycorrhizal-Litter.Saprotroph-Orchid.Mycorrhizal	Leaf.Saprotroph-Plant.Pathogen-Undefined.Saprotroph-Wood.Saprotroph	Dung.Saprotroph	Endophyte
	Plant.Pathogen	Soil.Saprotroph	Lichenized
	Endophyte-Plant.Pathogen-Undefined.Saprotroph	Plant.Saprotroph-Wood.Saprotroph	Soil.Saprotroph
	Fungal.Parasite-Wood.Saprotroph	Endophyte-Litter.Saprotroph-Wood.Saprotroph	Animal.Pathogen-Endophyte-Epiphyte-Undefined.Saprotroph
	Algal.Parasite-Bryophyte.Parasite-	Litter.Saprotroph-Soil.Saprotroph-Wood.Saprotroph	Endophyte-Epiphyte-Fungal.Parasite-Insect.Parasite

Ectomycorrhizal	Pathogenic	Saprotrophic	Unassigned
	Fungal.Parasite-Undefined.Saprotroph		
	Fungal.Parasite	Dung.Saprotroph-Endophyte-Undefined.Saprotroph	Animal.Pathogen-Clavicipitaceous.Endophyte-Fungal.Parasite
	Endophyte-Plant.Pathogen-Wood.Saprotroph	Ectomycorrhizal-Fungal.Parasite-Plant.Pathogen-Wood.Saprotroph	Ectomycorrhizal-Orchid.Mycorrhizal-Root.Associated.Biotroph
	Insect.Pathogen	Dung.Saprotroph-Plant.Saprotroph	Ectomycorrhizal-Wood.Saprotroph
	Fungal.Parasite-Lichen.Parasite	Soil.Saprotroph-Undefined.Saprotroph	Dung.Saprotroph-Ectomycorrhizal-Soil.Saprotroph-Wood.Saprotroph
	Plant.Pathogen-Plant.Saprotroph	Undefined.Saprotroph-Undefined.Symbiotroph	Ectomycorrhizal
	Endophyte-Plant.Pathogen	Lichenized-Undefined.Saprotroph	Animal.Pathogen-Endophyte-Lichen.Parasite-Plant.Pathogen-Soil.Saprotroph-Wood.Saprotroph
	Animal.Pathogen-Endophyte-Endosymbiont-Epiphyte-Soil.Saprotroph-Undefined.Saprotroph	Dung.Saprotroph-Soil.Saprotroph-Undefined.Saprotroph	NULL
	Animal.Pathogen-Undefined.Saprotroph	Dung.Saprotroph-Wood.Saprotroph	Ectomycorrhizal-Endophyte-Plant.Pathogen-Wood.Saprotroph
	Bryophyte.Parasite-Leaf.Saprotroph-Soil.Saprotroph-Undefined.Saprotroph-Wood.Saprotroph	Litter.Saprotroph	Animal.Pathogen-Endophyte-Fungal.Parasite-Lichen.Parasite-Plant.Pathogen-Wood.Saprotroph
	Fungal.Parasite-Plant.Pathogen-Plant.Saprotroph	Dung.Saprotroph-Undefined.Saprotroph	Bryophyte.Parasite-Ectomycorrhizal-Ericoid.Mycorrhizal-Undefined.Saprotroph-Wood.Saprotroph
	Endophyte-Lichen.Parasite-	Endophyte-Undefined.Saprotroph-Wood.Saprotroph	Bryophyte.Parasite-Ectomycorrhizal-

Ectomycorrhizal	Pathogenic	Saprotrophic	Unassigned
	Plant.Pathogen-Undefined.Saprotroph		Ericoid.Mycorrhizal-Undefined.Saprotroph
	Animal.Pathogen-Plant.Pathogen-Undefined.Saprotroph	Leaf.Saprotroph	Animal.Pathogen-Endophyte-Plant.Pathogen-Wood.Saprotroph
	Dung.Saprotroph-Plant.Parasite-Soil.Saprotroph-Undefined.Saprotroph-Wood.Saprotroph	Dung.Saprotroph-Soil.Saprotroph-Wood.Saprotroph	Bryophyte.Parasite-Dung.Saprotroph-Ectomycorrhizal-Fungal.Parasite-Leaf.Saprotroph-Plant.Parasite-Undefined.Saprotroph-Wood.Saprotroph
	Endophyte-Fungal.Parasite-Lichen.Parasite-Plant.Pathogen-Wood.Saprotroph	Dung.Saprotroph-Plant.Saprotroph-Wood.Saprotroph	Animal.Pathogen-Plant.Pathogen-Soil.Saprotroph-Undefined.Saprotroph
	Animal.Pathogen-Endophyte-Plant.Saprotroph-Soil.Saprotroph	Dung.Saprotroph-Plant.Saprotroph-Soil.Saprotroph	Animal.Pathogen-Endophyte-Fungal.Parasite-Plant.Pathogen-Wood.Saprotroph
	Bryophyte.Parasite-Litter.Saprotroph-Wood.Saprotroph	Undefined.Saprotroph-Wood.Saprotroph	Dung.Saprotroph-Ectomycorrhizal-Litter.Saprotroph-Undefined.Saprotroph
	Fungal.Parasite-Soil.Saprotroph-Undefined.Saprotroph-Wood.Saprotroph	Dung.Saprotroph-Nematophagous	Endophyte-Plant.Pathogen-Wood.Saprotroph
	Endophyte-Leaf.Saprotroph-Plant.Pathogen	Dung.Saprotroph-Soil.Saprotroph	Ectomycorrhizal-Fungal.Pathogen-Undefined.Saprotroph
	Fungal.Parasite-Litter.Saprotroph	Endophyte-Undefined.Saprotroph	Animal.Pathogen-Endophyte-Plant.Pathogen-Dung.Saprotroph-Undefined.Saprotroph
	Animal.Endosymbiont-Animal.Pathogen-Plant.Pathogen-Undefined.Saprotroph	Litter.Saprotroph-Wood.Saprotroph	Animal.Pathogen-Plant.Pathogen-Undefined.Saprotroph
	Lichen.Parasite	Dung.Saprotroph-Ericoid.Mycorrhizal-Lichenized	Undefined.Saprotroph

Ectomycorrhizal	Pathogenic	Saprotrophic	Unassigned
	Plant.Pathogen-Undefined.Saprotroph	Leaf.Saprotroph-Wood.Saprotroph	Endomycorrhizal-Plant.Pathogen-Undefined.Saprotroph
	Animal.Pathogen-Endophyte-Wood.Saprotroph	Epiphyte-Undefined.Saprotroph	Ectomycorrhizal-Fungal.Parasite-Soil.Saprotroph-Undefined.Saprotroph
	Plant.Pathogen-Undefined.Parasite-Undefined.Saprotroph	Lichenized-Wood.Saprotroph	Epiphyte-Plant.Pathogen-Wood.Saprotroph
	Dung.Saprotroph-Endophyte-Plant.Pathogen-Undefined.Saprotroph	Plant.Saprotroph	Animal.Pathogen-Endophyte-Plant.Pathogen-Undefined.Saprotroph
	Animal.Endosymbiont-Animal.Pathogen-Undefined.Saprotroph		Animal.Pathogen-Dung.Saprotroph-Endophyte-Lichen.Parasite-Plant.Pathogen-Undefined.Saprotroph
	Animal.Pathogen-Lichen.Parasite-Plant.Pathogen-Undefined.Saprotroph-Wood.Saprotroph		Epiphyte
	Fungal.Parasite-Litter.Saprotroph-Undefined.Saprotroph		Animal.Pathogen-Endophyte-Ericoid.Mycorrhizal-Plant.Pathogen-Wood.Saprotroph
	Fungal.Parasite-Undefined.Saprotroph		Dung.Saprotroph-Endophyte-Litter.Saprotroph-Undefined.Saprotroph
	Animal.Endosymbiont-Animal.Pathogen-Endophyte-Plant.Pathogen-Undefined.Saprotroph		Orchid.Mycorrhizal
	Dung.Saprotroph-Plant.Pathogen		Animal.Pathogen
	Plant.Parasite-Wood.Saprotroph		Lichen.Parasite-Lichenized
			Animal.Pathogen-Endophyte-Epiphyte-Plant.Pathogen-Undefined.Saprotroph

Ectomycorrhizal	Pathogenic	Saprotrophic	Unassigned
			Endophyte-Soil.Saprotroph-Undefined.Saprotroph
			Epiphyte-Leaf.Saprotroph-Lichen.Parasite-Lichenized-Plant.Pathogen-Wood.Saprotroph
			Endophyte-Lichen.Parasite-Undefined.Saprotroph
			Fungal.Parasite-Undefined.Saprotroph
			Bryophyte.Parasite-Lichen.Parasite-Ectomycorrhizal-Ericoid.Mycorrhizal-Undefined.Saprotroph
			Arbuscular.Mycorrhizal
			Endophyte-Plant.Pathogen
			Endophyte-Plant.Pathogen-Undefined.Saprotroph
			Ectomycorrhizal-Undefined.Saprotroph
			Lichen.Parasite
			Wood.Saprotroph
			Nematophagous
			Plant.Pathogen
			Endophyte-Dung.Saprotroph-Lichen.Parasite-Litter.Saprotroph-Plant.Pathogen-Soil.Saprotroph-Wood.Saprotroph
			Animal.Associated.Biotroph-Root.Associate.Biotroph
			Dung.Saprotroph-Endophyte-Wood.Saprotroph
			Soil.Saprotroph-Undefined.Saprotroph

Table S4-3: Distribution of common fungal guilds across sites sorted by number of amplicon sequence variants (ASVs) and sequence read counts. Assignments were made using the 'probable' and 'highly probable' filters of FUNGuild as recommended by Nyugen et al. (2016). Here, we present all guilds for which the number of observed reads was greater than 0.1% of all observed reads. Many reads were not assigned to any guild (23.02% of ASVs), with saprotrophs and ectomycorrhizal fungi being the next most common guilds. For information on how FUNGuild outputs were assigned into focal guilds, see methods and Table S2. Sequences in FASTQ format are available on NCBI under project number PRJNA1210581.

		ASV Counts							**Read Abundance**						
		Site-Specific Values							Site-Specific Values						
Guild	% of Total	RS38	RS02	RS27	RS31	RS28	RS21	Totals	RS38	RS02	RS27	RS31	RS28	RS21	Totals
Unassigned	23.35	772	453	580	1464	347	599	4215	23261	12722	14128	69238	12999	22335	154683
Undefined.Saprotroph	22.69	342	247	263	644	214	266	1976	12159	15870	13169	82432	12861	13840	150331
Ectomycorrhizal	18.86	337	260	311	924	236	264	2332	15670	13271	11011	62306	8046	14597	124901
Dung.Saprotroph-Undefined.Saprotroph-Wood.Saprotroph	10.28	73	31	47	84	35	43	313	13989	2750	7271	26937	5306	11819	68072
Ericoid.Mycorrhizal	6.66	18	21	31	60	24	55	209	2102	3092	4664	22194	3991	8065	44108
Endophyte-Litter.Saprotroph-Soil.Saprotroph-Undefined.Saprotroph	4.11	43	14	51	69	26	34	237	2724	1198	3175	16857	1074	2203	27231
Wood.Saprotroph	2.08	31	25	33	112	37	70	308	576	411	571	5135	1759	5333	13785
Animal.Pathogen-Soil.Saprotroph	1.34	8	6	8	31	14	6	73	496	99	526	5184	839	1760	8904
Leaf.Saprotroph-Plant.Pathogen-Undefined.Saprotroph-Wood.Saprotroph	1.32	33	14	28	89	53	57	274	739	469	552	4240	1542	1210	8752
Endophyte	1.26	19	13	19	30	17	18	116	907	568	820	3835	606	1624	8360
Ectomycorrhizal-Orchid.Mycorrhizal-Root.Associated.Biotroph	1.13	30	19	29	39	35	27	179	991	761	914	2454	1193	1172	7485
Other	1.11	111	58	79	184	44	76	552	1385	711	978	2580	417	1313	7384
Endophyte-Plant.Pathogen-Undefined.Saprotroph	0.91	22	13	17	29	20	20	121	762	424	512	1783	978	1589	6048
Lichenized	0.75	8	7	5	20	7	8	55	140	341	85	3738	316	364	4984

Animal.Pathogen-Fungal.Parasite-Undefined.Saprotroph	0.65	8	9	9	31	4	10	71	60	435	316	3096	236	162	4305
Ectomycorrhizal-Wood.Saprotroph	0.52	10	6	9	23	4	8	60	632	487	197	1405	432	327	3480
Plant.Pathogen	0.46	28	11	27	33	14	14	127	816	119	1024	432	482	158	3031
Soil.Saprotroph	0.43	3	2	6	10	3	2	26	92	19	1046	1536	69	68	2830

Table S4-4: Elevational shifts in soil nutrient availability. We examined variation in key macro- and micro-nutrients across elevation using linear models for each variable accounting for site-level random effects. Model estimates for elevation and intercepts are presented with standard error in parentheses.

	Dependent variable:						
	K	Mg	Na	Mn	Cu	Fe	Zn
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Elevation	-0.309***	-0.487***	-0.081*	0.083***	0.0005***	0.052***	-0.023***
	(0.036)	(0.064)	(0.042)	(0.016)	(0.0001)	(0.012)	(0.006)
Intercept	667.914***	756.339***	339.746***	-1.405	0.335***	56.664***	34.439***
	(33.123)	(59.403)	(39.048)	(14.488)	(0.077)	(11.210)	(5.150)
Observations	239	237	239	238	238	238	237
R^2	0.240	0.198	0.015	0.108	0.113	0.074	0.070
Adjusted R^2	0.237	0.195	0.011	0.104	0.109	0.070	0.066
Residual Std. Error	132.178 (df = 237)	236.572 (df = 235)	155.821 (df = 237)	57.711 (df = 236)	0.306 (df = 236)	44.651 (df = 236)	20.379 (df = 235)
F Statistic	74.861*** (df = 1; 237)	58.066*** (df = 1; 235)	3.726* (df = 1; 237)	28.449*** (df = 1; 236)	30.009*** (df = 1; 236)	18.828*** (df = 1; 236)	17.590*** (df = 1; 235)

	Dependent variable:					
	OM	N	NO3.N	NH4.N	PO4.P	CEC
	(1)	(2)	(3)	(4)	(5)	(6)
Elevation	0.012***	0.0003***	-0.001***	0.002***	-0.056***	-0.021***
	(0.002)	(0.00003)	(0.0002)	(0.0003)	(0.008)	(0.003)
Intercept	5.322***	0.078***	1.506***	0.743**	90.557***	35.454***
	(1.448)	(0.026)	(0.197)	(0.300)	(7.467)	(2.481)
Observations	239	239	239	234	239	236
R^2	0.201	0.262	0.110	0.109	0.169	0.206
Adjusted R^2	0.198	0.259	0.106	0.105	0.165	0.202
Residual Std. Error	5.778 (df = 237)	0.102 (df = 237)	0.787 (df = 237)	1.182 (df = 232)	29.797 (df = 237)	9.880 (df = 234)
F Statistic	59.610*** (df = 1; 237)	84.205*** (df = 1; 237)	29.150*** (df = 1; 237)	28.315*** (df = 1; 232)	48.096*** (df = 1; 237)	60.600*** (df = 1; 234)

*p**p***p<0.01

Table S4-5: Model results for EcM:pathogen read ratios. We tested for a relationship between natural-log transformed sequencing EcM:pathogen read ratios across elevation. We found a significant negative relationship in the litter layer samples (relatively more pathogens at high elevations). While insignificant, mineral soil ratios trended positive (relatively more ectomycorrhizae at high elevations).

	Sample Layer:	
	Ln EcM:Path Ratio	
	Litter Layer	Mineral Soil
	(1)	(2)
Elevation	-0.002***	0.001*
	(0.001)	(0.001)
Intercept	2.809***	1.384*
	(0.540)	(0.754)
Observations	147	133
Log Likelihood	-203.295	-255.265
Akaike Inf. Crit.	414.590	518.530
Bayesian Inf. Crit.	426.551	530.092
Note:		*p**p***p<0.01

Table S4-6: PERMANOVA test for differences in composition of key fungal guilds by elevation. We found significant variation in site-level guild composition using the 'adonis2' function from the Vegan package set to 1000 permutations. P-value and R^2 results are presented in Figure 4-3.

Group	Statistic	N	Mean	St. Dev.	Min	Max
Mineral Soil Ectomycorrhizal Fungi	Df	3	82.667	66.463	6	124
	SumOfSqs	3	35.158	24.507	7.163	52.737
	R^2	3	0.667	0.465	0.136	1.000
	F	1	3.091	-	3.091	3.091
	Pr(>F)	1	0.001	-	0.001	0.001
Mineral Soil Pathogenic Fungi	Df	3	82.667	66.463	6	124
	SumOfSqs	3	32.566	22.274	7.182	48.848
	R^2	3	0.667	0.456	0.147	1.000
	F	1	3.390	-	3.390	3.390
	Pr(>F)	1	0.001	-	0.001	0.001
Mineral Soil Saprotrophic Fungi	Df	3	82.667	66.463	6	124
	SumOfSqs	3	12.466	6.012	6.703	18.698
	R^2	3	0.667	0.322	0.358	1.000
	F	1	10.989	-	10.989	10.989
	Pr(>F)	1	0.001	-	0.001	0.001
Litter Layer Ectomycorrhizal Fungi	Df	3	93.333	75.692	6	140
	SumOfSqs	3	32.095	22.705	6.117	48.143
	R^2	3	0.667	0.472	0.127	1.000

Group	Statistic	N	Mean	St. Dev.	Min	Max
	F	1	3.251	-	3.251	3.251
	Pr(>F)	1	0.001	-	0.001	0.001
Litter Layer Pathogenic Fungi	Df	3	93.333	75.692	6	140
	SumOfSqs	3	28.588	17.046	9.722	42.882
	R²	3	0.667	0.398	0.227	1.000
	F	1	6.547	-	6.547	6.547
	Pr(>F)	1	0.001	-	0.001	0.001
Litter Layer Saprotrophic Fungi	Df	3	93.333	75.692	6	140
	SumOfSqs	3	23.622	15.060	6.664	35.433
	R²	3	0.667	0.425	0.188	1.000
	F	1	5.173	-	5.173	5.173
	Pr(>F)	1	0.001	-	0.001	0.001

Table S4-7: Post-hoc comparisons of mineral soil β deviation (SES β) across site and guilds. Statistical comparisons of SES β across elevation for different fungal guilds in mineral soil. SES β relates the observed spatial patterns of each focal guild to expectations from null model (see methods). Rows depict estimated marginal means and standard error for site and guild combinations.

Site	Guild	Est. Marginal Mean	SE	df	lower.CL	upper.CL
RS02	Ectomycorrhizal Fungi	14.173610	0.37032840	10,651	13.447698	14.899523
RS21	Ectomycorrhizal Fungi	31.237612	0.44848997	10,651	30.358488	32.116736
RS28	Ectomycorrhizal Fungi	18.503035	0.34065258	10,651	17.835293	19.170778
RS31	Ectomycorrhizal Fungi	10.086868	0.07032884	10,651	9.949011	10.224726
RS38	Ectomycorrhizal Fungi	15.038630	0.31538301	10,651	14.420420	15.656839
RS02	Pathogenic Fungi	3.668454	0.40567444	10,651	2.873256	4.463652
RS21	Pathogenic Fungi	5.478209	0.50142703	10,651	4.495318	6.461099
RS28	Pathogenic Fungi	3.635899	0.65652209	10,651	2.348993	4.922805
RS31	Pathogenic Fungi	2.494404	0.09781679	10,651	2.302665	2.686144
RS38	Pathogenic Fungi	3.923274	0.40567444	10,651	3.128077	4.718472
RS02	Saprotrophic Fungi	14.542992	0.37032840	10,651	13.817080	15.268905
RS21	Saprotrophic Fungi	31.515150	0.44848997	10,651	30.636026	32.394274

Site	Guild	Est. Marginal Mean	SE	df	lower.CL	upper.CL
RS28	Saprotrophic Fungi	17.843697	0.34065258	10,651	17.175955	18.511440
RS31	Saprotrophic Fungi	17.490296	0.07032884	10,651	17.352439	17.628154
RS38	Saprotrophic Fungi	31.580029	0.31538301	10,651	30.961819	32.198238

Table S4-8: Post-hoc comparisons of litter layer β deviation (SES β) across site and guilds. Statistical comparisons of SES β across elevation for different fungal guilds in the litter layer. SES β relates the observed spatial patterns of each focal guild to expectations from null model (see methods). Rows depict estimated marginal means and standard error for site and guild combinations. See figure 4-4 for more details.

Site	Guild	Est. Marginal Mean	SE	df	lower.CL	upper.CL
RS02	Ectomycorrhizal Fungi	37.905332	0.36751174	14,519	37.184962	38.625702
RS21	Ectomycorrhizal Fungi	33.168545	0.43766032	14,519	32.310675	34.026415
RS28	Ectomycorrhizal Fungi	37.286571	0.39952738	14,519	36.503446	38.069695
RS31	Ectomycorrhizal Fungi	30.227317	0.07008174	14,519	30.089948	30.364686
RS38	Ectomycorrhizal Fungi	45.353758	0.36751174	14,519	44.633388	46.074127
RS02	Pathogenic Fungi	5.886065	0.36751174	14,519	5.165695	6.606435
RS21	Pathogenic Fungi	13.008541	0.43766032	14,519	12.150671	13.866411
RS28	Pathogenic Fungi	12.819573	0.39952738	14,519	12.036448	13.602697
RS31	Pathogenic Fungi	6.636112	0.07116834	14,519	6.496613	6.775611
RS38	Pathogenic Fungi	14.377052	0.36751174	14,519	13.656682	15.097422
RS02	Saprotrophic Fungi	25.154997	0.36751174	14,519	24.434627	25.875367
RS21	Saprotrophic Fungi	32.383838	0.43766032	14,519	31.525968	33.241708
RS28	Saprotrophic Fungi	26.205378	0.39952738	14,519	25.422254	26.988503
RS31	Saprotrophic Fungi	19.746159	0.06902782	14,519	19.610855	19.881462
RS38	Saprotrophic Fungi	31.886454	0.36751174	14,519	31.166085	32.606824

Table S4-9: Mineral soil standard effect size of beta dispersions by site and guild. Statistical comparisons of standardized beta dispersion effect sizes across elevation for different fungal guilds in mineral soil. Model-estimated marginal means relate the similarity of samples within a site and focal guild to "non-assigned" fungi. Rows depict estimated marginal means and standard error for site and guild combinations.

Site	Guild	Est. Marginal Mean	SE	df	lower.CL	upper.CL
RS02	Ectomycorrhizal Fungi	2.0322093	0.01	14,985	2.0126081	2.05181051
RS21	Ectomycorrhizal Fungi	2.8687436	0.01	14,985	2.8491424	2.88834482
RS28	Ectomycorrhizal Fungi	2.8533142	0.01	14,985	2.8337130	2.87291545
RS31	Ectomycorrhizal Fungi	2.7543018	0.01	14,985	2.7347005	2.77390298
RS38	Ectomycorrhizal Fungi	2.9277036	0.01	14,985	2.9081023	2.94730479
RS02	Pathogenic Fungi	0.6097220	0.01	14,985	0.5901207	0.62932318
RS21	Pathogenic Fungi	1.0839996	0.01	14,985	1.0643984	1.10360087
RS28	Pathogenic Fungi	0.3302925	0.01	14,985	0.3106913	0.34989374
RS31	Pathogenic Fungi	0.6551912	0.01	14,985	0.6355900	0.67479245
RS38	Pathogenic Fungi	0.5041421	0.01	14,985	0.4845408	0.52374329
RS02	Saprotrophic Fungi	-1.1520288	0.01	14,985	-1.1716300	-1.13242754
RS21	Saprotrophic Fungi	-0.5998084	0.01	14,985	-0.6194096	-0.58020719
RS28	Saprotrophic Fungi	-0.4746059	0.01	14,985	-0.4942071	-0.45500465
RS31	Saprotrophic Fungi	-0.7908606	0.01	14,985	-0.8104618	-0.77125939
RS38	Saprotrophic Fungi	-0.1115682	0.01	14,985	-0.1311694	-0.09196695

Table S4-10: Litter layer standard effect size of beta dispersions by site and guild. Statistical comparisons of standardized beta dispersion effect sizes across elevation for different fungal guilds in litter layer. Model-estimated marginal means relate the similarity of samples within a site and focal guild to "non-assigned" fungi. Rows depict estimated marginal means and standard error for site and guild combinations.

Site	Guild	Est. Marginal Mean	SE	df	lower.CL	upper.CL
RS02	Ectomycorrhizal Fungi	1.11808382	0.01	14,985	1.09848260	1.13768504

Site	Guild	Est. Marginal Mean	SE	df	lower.CL	upper.CL
RS21	Ectomycorrhizal Fungi	0.51911640	0.01	14,985	0.49951518	0.53871763
RS28	Ectomycorrhizal Fungi	1.26639205	0.01	14,985	1.24679083	1.28599327
RS31	Ectomycorrhizal Fungi	1.88887874	0.01	14,985	1.86927752	1.90847997
RS38	Ectomycorrhizal Fungi	1.58189439	0.01	14,985	1.56229316	1.60149561
RS02	Pathogenic Fungi	0.74435256	0.01	14,985	0.72475133	0.76395378
RS21	Pathogenic Fungi	0.99077717	0.01	14,985	0.97117595	1.01037839
RS28	Pathogenic Fungi	-0.20422191	0.01	14,985	-0.22382313	-0.18462068
RS31	Pathogenic Fungi	0.76185826	0.01	14,985	0.74225704	0.78145949
RS38	Pathogenic Fungi	0.06224491	0.01	14,985	0.04264369	0.08184613
RS02	Saprotrophic Fungi	-5.23172732	0.01	14,985	-5.25132854	-5.21212610
RS21	Saprotrophic Fungi	-5.10781819	0.01	14,985	-5.12741941	-5.08821696
RS28	Saprotrophic Fungi	-3.28204424	0.01	14,985	-3.30164546	-3.26244302
RS31	Saprotrophic Fungi	-3.82209821	0.01	14,985	-3.84169943	-3.80249699
RS38	Saprotrophic Fungi	-3.42013634	0.01	14,985	-3.43973756	-3.40053511

Table S4-11: Total contribution of each predicting factor to variation partitioning estimates. We used dbRDA-based variation partitioning to determine correlations between changes in predictor matrices (fungal guilds or soil chemistry) and tree distance matrices at each site.

Site	Elevation (m)	Factor	Total Fraction (R^2)
RS02	520	Ectomycorrhizal Fungi	0.284
RS02	520	Pathogenic Fungi	0.424
RS02	520	Saprotrophic Fungi	0.432
RS02	520	Soil Chemistry	0.204
RS21	1,190	Ectomycorrhizal Fungi	0.536
RS21	1,190	Pathogenic Fungi	0.361
RS21	1,190	Saprotrophic Fungi	0.569
RS21	1,190	Soil Chemistry	0.402
RS31	900	Ectomycorrhizal Fungi	0.278
RS31	900	Pathogenic Fungi	0.247
RS31	900	Saprotrophic Fungi	0.314
RS31	900	Soil Chemistry	0.198
RS38	500	Ectomycorrhizal Fungi	0.421

Site	Elevation (m)	Factor	Total Fraction (R^2)
RS38	500	Pathogenic Fungi	0.500
RS38	500	Saprotrophic Fungi	0.416
RS38	500	Soil Chemistry	0.252

Table S4-12: Individual contribution of each predicting factor to variation partitioning estimates. While we consider the total fraction R^2 to be most informative for assessing changing associations across elevation, we present here the individual contribution of each factor unique from other factors. These individual R^2 values represent the non-overlapping contribution of each predictor to the response (tree composition distance matrix).

Site	Elevation (m)	Factor	Individual Fraction (R^2)
RS02	520	Ectomycorrhizal Fungi	0.054
RS02	520	Pathogenic Fungi	0.136
RS02	520	Saprotrophic Fungi	0.107
RS02	520	Soil Chemistry	0.058
RS21	1,190	Ectomycorrhizal Fungi	0.187
RS21	1,190	Pathogenic Fungi	0.128
RS21	1,190	Saprotrophic Fungi	0.235
RS21	1,190	Soil Chemistry	0.201
RS31	900	Ectomycorrhizal Fungi	0.380
RS31	900	Pathogenic Fungi	0.449
RS31	900	Saprotrophic Fungi	0.517
RS31	900	Soil Chemistry	0.315
RS38	500	Ectomycorrhizal Fungi	0.220
RS38	500	Pathogenic Fungi	0.279
RS38	500	Saprotrophic Fungi	0.213
RS38	500	Soil Chemistry	0.081

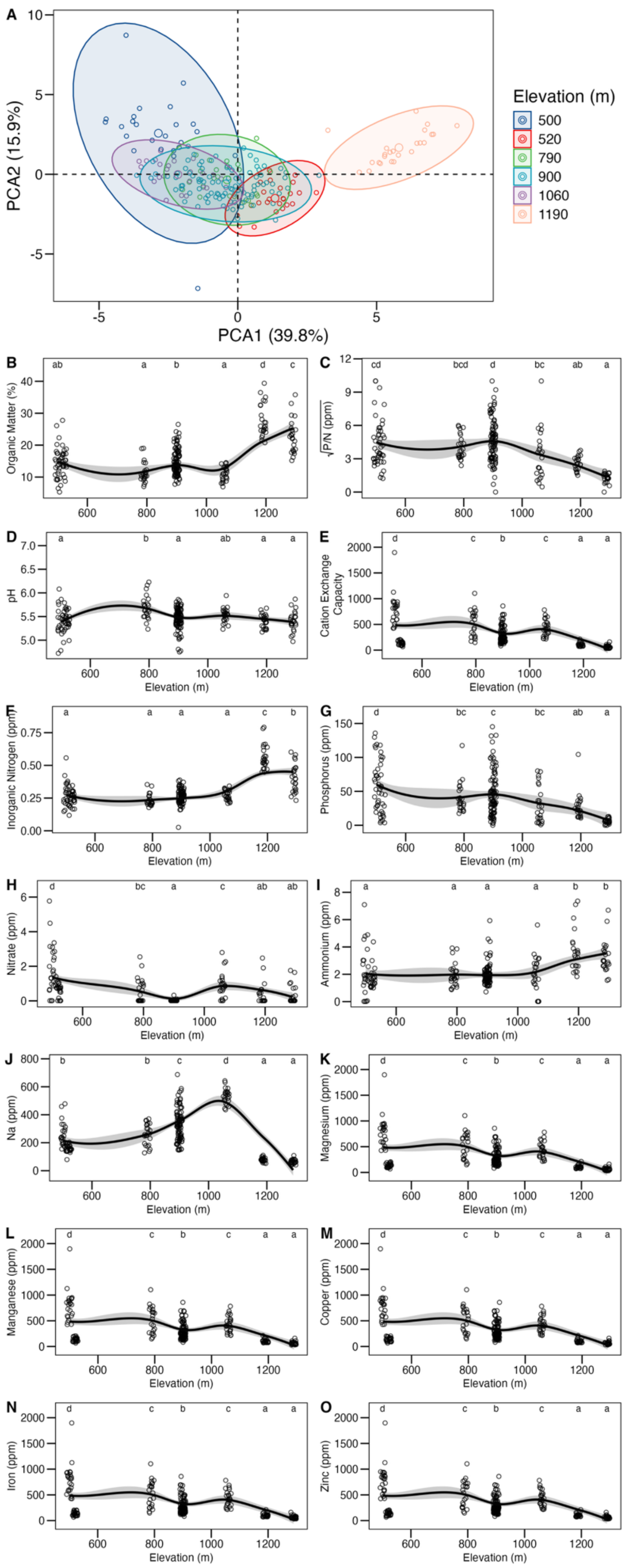
A
PCA1 (39.8%)
PCA2 (15.9%)
Elevation (m)
500
520
790
900
1060
1190
B
Organic Matter (%)
ab a b a d c
C
√P/N (ppm)
cd bcd d bc ab a
D
pH
a b a ab a a
E
Cation Exchange Capacity
d c b c a a
F
Inorganic Nitrogen (ppm)
a a a a c b
G
Phosphorus (ppm)
d bc c bc ab a
H
Nitrate (ppm)
d bc a c ab ab
I
Ammonium (ppm)
a a a a b b
J
Na (ppm)
b b c d a a
K
Magnesium (ppm)
d c b c a a
L
Manganese (ppm)
d c b c a a
M
Copper (ppm)
d c b c a a
N
Iron (ppm)
d c b c a a
O
Zinc (ppm)
d c b c a a
Elevation (m)

Figure S4-1: Soil chemical properties change across elevation. (A) Principal Component Analysis (PCA) biplot showing the distribution of soil samples based on chemical properties at seven different elevations (500 m, 580 m, 790 m, 900 m, 1060 m, 1190 m, 1290 m). Ellipses represent the 95% confidence intervals for each elevation group. (B-O) Chemical analyses across elevation. The black lines represent loess lines with shaded areas indicating standard errors. Different letters above data points denote significant differences among elevations as determined by ANOVA and Tukey HSD post-hoc tests ($p < 0.05$).

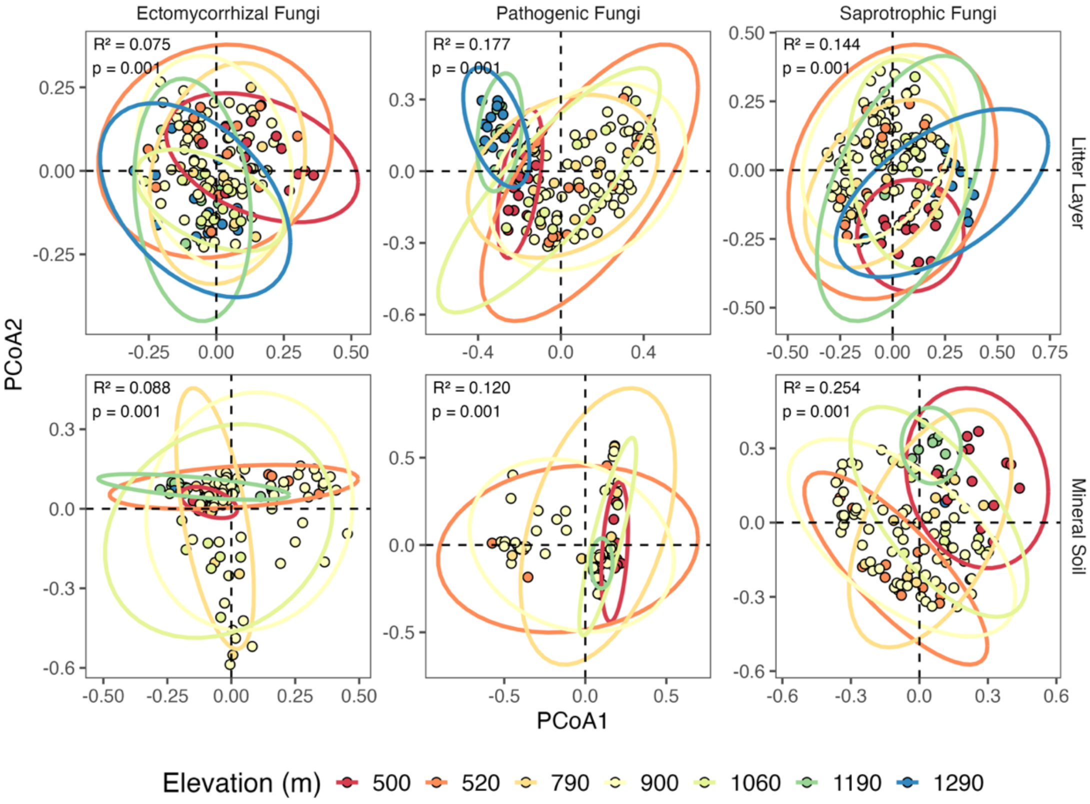

Figure S4-2: Alternative PCoA analysis of (A) ectomycorrhizal, (B) pathogenic, and (C) saprotrophic fungal communities using rarefied microbial sequencing data. As an alternative to denoising, we assessed differences in guild compositions across the elevation gradient using rarefied microbial sequencing data with a standardized library size of 2000 reads. Each point represents a sample, and points are color-coded by elevation (500 m, 520 m, 790 m, 900 m, 1060 m, 1190 m). The axes (PCoA1 and PCoA2) explained the highest proportion of fungal guild communities and are distinctly clustered by elevation, although clustered poorly relative to our primary denoising approach. Site elevation predictive significance was assessed with PERMANOVA (Table S6)

DISCUSSION

My dissertation makes several contributions to our collective understanding of how environmental stress and ecological disturbances influence the local neighborhood interactions thought to contribute to the stability and diversity of forest plant communities. By integrating theoretical frameworks with empirical study, I tested specific hypotheses regarding how local CDD responds to changing environmental conditions. Here, I briefly discuss how my empirical findings support the theoretical predictions developed in my conceptual work.

In Chapter 1, I developed a framework categorizing ecological disturbances based on their primary effects on forest structure, predicting that combined disturbances like wildfire would neutralize local CDD by simultaneously affecting competitive densities, resource availability, and tree-associated communities of natural enemies and mutualists. My empirical test of post-fire seedling mortality in Chapter 2 strongly supported this prediction, demonstrating that wildfires disrupt the stabilizing neighborhood feedbacks evident in nearby undisturbed forests. Additionally, I found that wildfires neutralize the relationship between stabilizing local CDD and extreme heat. While several underlying factors may contribute to these findings, I find most compelling the hypothesis that neutralized local CDD in burned forests is the result of wildfire-induced mortality and erosion of tree-associated microbes which otherwise contribute to a positive relationship between abiotic stress and local CDD (more positive, destabilizing). Together, these empirical findings generally support the central predictions of my disturbance framework, most evidently the prediction that combined disturbances like wildfire neutralize local CDD and decouple neighborhood interactions from climate-related stress.

My empirical findings from Chapters 3 and 4 provide complementary insights into the Stress Gradient Feedback Hypothesis (SGFH) by testing how environmental stress alters the drivers and outcome of local CDD along an elevation gradient. The SGFH predicts that increased importance or intensity of relatively host-specific antagonistic interactions contribute to stabilizing local CDD in benign, low stress environments, whereas increased importance or intensity of relatively host-specific facilitative plant-microbe interactions contributes to destabilizing local CDD in harsh, high-stress environments.

In Chapter 3, my dendrochronological analysis revealed species-specific responses to climate that align with key predictions of the SGFH. For Douglas-fir (*P. menziesii*), local CDD became increasingly destabilizing (positive) in cooler years, suggesting that lower temperatures constitute a form of stress for this canopy-dominant, shade-intolerant species that enhances the importance of conspecific facilitation. Conversely, Western hemlock (T. *heterophylla*) exhibited stronger stabilizing local CDD in wetter years, indicating that reduced water stress (relatively un-stressful conditions) may enhance the effects of host-specific antagonists for this shade-tolerant, co-dominant species. The differences in my main findings between focal species likely relates to individual tolerances to different stressors (temperature, precipitation) based on life-history and canopy position. Overall, we find broad support for the hypothesis that climate-induced stress temporarily alters local CDD on an interannual basis in adult trees, which represents a key advancement in the field by demonstrating that temporal patterns observed in short-term and seedling-focused studies can scale to influence growth in the largest members of forest communities across multiple decades.

In Chapter 4, I explore a mechanistic explanation for my findings of climate-mediated shifts in local CDD among large adult trees by examining the spatial aggregation of soil fungal communities in relation to tree communities across elevation. As predicted by the SGFH, site-to-site differences in tree community composition were more strongly associated with pathogenic fungal composition at lower, more resource-abundant elevations, while associations with ectomycorrhizal fungal communities predominated at higher, more stressful elevations. The increasing spatial aggregation of ectomycorrhizal fungi with elevation provides additional evidence that trees rely more heavily on these mutualistic relationships under stressful conditions, and that observed changes to local CDD with environmental stress are likely driven by changes to underling tree-microbe interactions.

Collectively, these findings provide empirical support, and reveal important nuances, for my frameworks of explaining local CDD in the context of environmental change and ecological disturbances. This work demonstrates that local CDD is not a static property of forest communities but rather responds dynamically to both acute disturbances and chronic environmental stress. The dendrochronological analyses from Chapter 3 demonstrates that local CDD varies not only across space (as shown in Chapter 4) but also through time, as interannual climate fluctuations temporarily shift the balance between antagonistic and mutualistic neighborhood interactions. This temporal dimension adds considerable complexity to understanding how forest communities will respond to climate change, as future climates are expected to be defined not only by increasing mean temperatures but also increasing variance. Temporal shifts in the directionality and magnitude of local CDD may alternately accelerate or buffer compositional changes depending on the specific climate variables involved and the life histories of dominant species.

In summary, this dissertation has made important contributions to our theoretical and empirical understanding of how local conspecific density dependence (CDD) varies in changing environments, with important implications for the maintenance of species diversity and forest ecosystem resilience. By integrating conceptual frameworks with field studies in a variety of taxa ranging from soil fungi to adult trees, this work revealed that differences in the strength of conspecific and heterospecific neighborhood interactions are a dynamic factor influencing individual responses to both acute disturbances and chronic environmental stressors.