THE RELATIONSHIPS BETWEEN MULTIFACETED DIVERSITY AND FUNCTIONING OF CANADIAN FORESTS UNDER GLOBAL ENVIRONMENTAL CHANGE

By

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ABSTRACT

Human activities have caused biodiversity simplification at local and global scales and raised concerns about potential effects on ecosystem functions and biodiversity conservation. In the past decades, there have been increasing efforts to better understand the relationships between biodiversity (loss) and ecosystem functions, mainly primary productivity, carbon storage, and temporal stability of productivity. However, there remain important aspects that are still debated and understudied. Under the ongoing global environmental change, herein, (i) I reviewed and examined the predictors, drivers and mechanisms of forest background and acute tree mortality under global environmental change and particularly the interactions between drivers within and between two mortality modes; (ii) I tested the relationships between multifacet diversity (functional, phylogenetic and taxonomic) and biomass and stem mortality rates as well as the underlying mechanisms including biotic damage, stand density index and size inequality in natural forests, in British Columbia, Canada; (iii) I mechanistically studied the relationship between multifacet diversity relationship with temporal stability of productivity in natural temperate and boreal forests across Canada.

In order to holistically understand forest tree mortality, different from previous syntheses focused on a single or two factors, I reviewed a diverse range of the triggers and factors influencing background and acute tree mortality, respectively. Specifically, I reviewed different processes by which rising atmospheric CO2 concentration, warming, and changes in water availability and radiation affect background and acute tree mortality, and their influences on drivers such as competition, tree longevity, and species composition, in addition to well acknowledged hydraulic failure, carbon starvation, fire, insects, and diseases. The influences of global change drivers on tree mortality may differ among forests of different ages, diversity, background climates, and disturbance history. We also explored the feedback between background and acute tree mortality. The issue of reliable future projections of biomass loss caused by tree mortality should be of the highest priority, which can be better accomplished by integrating monitoring, experimentation, and modelling efforts to better understand the diversity and functioning of global forests.

Tree mortality is a natural process of forest dynamics, but excessive tree mortality not only has negative consequences on the economy but also strongly reduces the potential of forests as sinks for carbon. Yet, our understanding of the roles of functional and phylogenetic diversity and their influences on the mechanisms underlying tree mortality remains unexplored. Using inventory data of natural forests in British Columbia, Canada, I examined the relationship between biomass and stem mortality rate with functional and phylogenetic diversity and the three mechanisms, including biotic damage, stand density index (representing competition) and size inequality (inferring niche partitioning). This study shows that after controlling the effects of climate and stand age, biomass mortality rate and stem mortality rate increased with tree functional diversity but decreased with phylogenetic diversity. Specifically, increasing functional diversity from its minimum to maximum increased the tree biomass and stem mortality rates by 250% and 131%, respectively. Increasing phylogenetic diversity from its minimum to maximum decreased biotic damage by 60% and decreased tree biomass and stem mortality rates by 70% and 78%, respectively. Biotic damage from the pool of 143 types of insects and pathogens was the main driver of tree mortality, and it decreased with tree phylogenetic diversity. Tree mortality was lower in stands of high size inequality that was positively related to tree phylogenetic and functional diversity; however, the effect of stand density index on mortality was negligible, indicating that the nearly century-old theory using stand density index to quantify competition

developed for monocultures might not be relevant to natural forests of varying tree diversity. Our finding suggests that conserving phylogenetically diverse natural forests or planting tree mixtures of phylogenetically distant species will lower tree mortality, safeguard the forest economy, and enhance the role of forests in mitigating climate change.

The temporal stability of productivity in natural forests is essential for humanity. Stability measures the temporal variation of productivity and is defined as the ratio of mean productivity and standard deviation within the same timeframe. Biodiversity experiments with observations up to 20 years indicate that plant diversity increases stability under various environmental changes. However, it remains debated whether short-term experimental findings are relevant to the long-term stability of natural forests. Using inventory data of temperate and boreal forests across Canada from 1951 to 2016, I revealed the relationship between temporal stability of productivity with functional and phylogenetic diversity. The study provides strong evidence that higher stability is consistently associated with greater functional and phylogenetic diversity across all lengths of observations. Specifically, increasing functional diversity from its minimum to maximum values improves stability, mean productivity, and the temporal standard deviation of productivity by 14%, 36%, and 28%, respectively. Increasing the phylogenetic diversity increases stability by an additional 1%. Our results highlight that the promotion of functionally and phylogenetically diverse forests could enhance long-term productivity and the stability of natural forests.

The findings of this dissertation provide us with knowledge in a deeper mechanistic understanding of the relationship between biodiversity and ecosystem functioning under global environmental change. Multifacet biodiversity is important for climate mitigation, and the

conservation of diverse functional traits and phylogenetic distant species in natural forests is vital for healthy and stable forest ecosystems.

Keywords: functional diversity; phylogenetic diversity; productivity stability; tree mortality; biotic damage

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This is a manuscript-based thesis. Formatting and reference style may differ because chapters were written to suit the submission requirements of the targeted journals. Individual chapters reflect the joint contributions of myself and my collaborators, I use ‘we’ instead of ‘I’ for individual chapters.

1. Chapter 2: Global environmental change and tree mortality: An overview. Submitted to *Canadian Journal of Forest Research*.
2. Chapter 3: Phylogenetic diversity reduces tree mortality by decreasing biotic damage. *Submitted to Natural Ecology and Evolution*.
3. Chapter 4: Long-term stability of productivity increases with tree diversity in Canadian forests. Submitted to *Proceedings of the National Academy of Sciences of the United States of America*.

CHAPTER 1: GENERAL INTRODUCTION

Global environmental change has reduced forest area, led to unintegral habitat and threatened forest health, carbon sequestration, and commodity supply through shifting forest dynamics (Brecka et al. 2018; Curtis et al. 2018; McDowell et al. 2020; Pan et al. 2011). Tree mortality has been observed to increase rapidly in the 21st century, causing uncertainties and shifts in forest dynamics and stability, influencing carbon cycling and contributing to the pace of climate change (Anderegg et al. 2012; Forzieri et al. 2022; McDowell et al. 2020). Recent studies have advanced the understanding of triggers of and factors that influence tree mortality, for example, warming or drought (Allen et al. 2010; Choat et al. 2018; McDowell et al. 2022b; Reich et al. 2022) and enhanced biotic damage from insects and pathogens (Anderegg et al. 2015; Koontz et al. 2021; Kozlov et al. 2015; Kurz et al. 2008), as well as increased tree competition and shortened tree longevity (Brienen et al. 2015; Luo and Chen 2011; Ma et al. 2023; Searle et al. 2022). Global warming and increased acute droughts (Dai 2012) have led to more frequent and severe fires (Jolly et al. 2015; Kasischke and Turetsky 2006; Westerling et al. 2006) and insect and disease outbreaks (Kautz et al. 2017; Kurz et al. 2008). The increasing disturbances and tree mortality also influence tree growth and the long-term temporal stability of productivity. Biodiversity loss is one major global change (Newbold et al. 2015) and has profound effects on ecosystem functioning such as productivity (Hooper et al. 2012). Although tree mortality is as important as productivity to forest economy and carbon sequestration, few have studied the relationships between biodiversity loss and tree mortality and those did have reported mixed results with underlying mechanisms poorly understood. Moreover, despite the critical importance of the long-term stability of forest productivity, the assumption of extrapolating short-term experimental findings into the long-term stability of productivity in natural forests has not been tested.

In this dissertation, I first reviewed the triggers and mechanisms of background and acute tree mortality under global environmental change. Since the seminal synthesis of global scale tree mortality (Allen et al. 2010), the triggers and mechanisms of drought-related tree mortality have been comprehensively studied at the cell, organ, and tree level in the aspect of carbon starvation and hydraulic failure and physiological traits associated with drought-induced tree mortality (Choat et al. 2018; McDowell et al. 2022b). Increases in tree mortality induced by global environmental change can also arise from intensified competition, reduced tree longevity, and compositional changes. Furthermore, acute tree mortality can lead to younger forests and changes in species composition, which can feedback tree mortality processes (Mack et al. 2021; McDowell et al. 2020). This synthesis presents a framework to differentiate the effects of global environmental change on (*i*) background tree mortality due to press biotic and abiotic stresses, competition and aging in the absence of large-scale acute stresses, (*ii*) acute tree mortality (unusually high proportion of tree death) associated with major droughts, insect or pathogen outbreaks, and stand-replacing fires, and *(iii)* the feedback within and between background and acute drivers.

In the face of rapid biodiversity loss and rising tree mortality, recent studies have explored the relationships between species richness and tree mortality rate in natural forests but the results are mixed (Hisano et al. 2019; Liang et al. 2007; Pretzsch et al. 2023b; Searle et al. 2022). Meanwhile, short-term tree diversity experiments have reported non-significant relationships between species richness and sapling survival rate (King et al. 2023; Liu et al. 2022; Van de Peer et al. 2016). Functional and phylogenetic diversity, which help infer ecological mechanisms associated with ecological functioning, can provide a better way to understand biodiversity-ecosystem functioning relationships, support policymakers with practical suggestions (Cadotte et al. 2011; Srivastava et al. 2012), and constitute a part of the natural-based solution to mitigating climate change (Girardin et al. 2021). Yet, our understanding of the roles of functional and phylogenetic diversity and their influences on the mechanisms underlying tree mortality remains unexplored.

The temporal stability of ecosystem productivity is a key ecosystem function important to humanity and it is typically defined as the ratio of mean productivity (μ) and its temporal variation (standard deviation, σ), reflecting the resistance and resilience of an ecosystem to disturbances. The ongoing simplification of local communities due to anthropogenic disturbances has raised concerns about temporal stability for a long time. Recently, two decadal-length tree diversity experiments have also demonstrated that species richness stabilizes the temporal stability of forest productivity (Schnabel et al. 2019; Schnabel et al. 2021). However, it remains unclear whether these positive relationships between diversity and stability based on short-term, small-scale manipulation experiments can be extended to long-term, large-scale, complex natural forests, which experience major climate and biotic disturbances with cycles of multiple decades.

The objective of this dissertation was to enhance the knowledge of how the key processes of forest ecosystems respond to global change. I first reviewed the effects of diverse global change drivers on background and acute tree mortality and their interactions (Chapter 2). By identifying the key knowledge gap of the effect of biodiversity loss on tree mortality, I examined the relationship between multifacet (functional, phylogenetic and taxonomic) diversity and tree mortality and the underlying mechanisms in the natural forests of British Columbia, Canada

(Chapter 3). Following my effort on tree mortality, I explored the multicausal relationships between multifacet diversity and the long-term stability of productivity and its components in natural temperate and boreal forests across Canada (Chapter 4).

CHAPTER 2: GLOBAL ENVIRONMENTAL CHANGE AND TREE MORTALITY: AN OVERVIEW

2.1 Abstract

Tree mortality influences resource availability, biodiversity, and climate forcing. Recent studies have reported increases in tree mortality in most regions of the world. However, both the drivers for the increased tree mortality and the associated mechanisms are debated, due to an array of processes that simultaneously affect mortality dynamics. For this reason, here we review different processes by which rising atmospheric CO_2 concentration, warming, and changes in water availability and radiation affect background and acute tree mortality, and their influences on drivers such as competition, tree longevity, and species composition, in addition to well acknowledged hydraulic failure, carbon starvation fire, insects, and diseases. The influences of global change drivers on tree mortality may differ among forests of different ages, diversity, background climates, and disturbance history. We also explored the feedback between background and acute tree mortality. We argue that reliable future projections of biomass loss from tree mortality are an issue of the highest priority, which can only be achieved by integrating monitoring, experimentation, and modelling efforts to improve our understanding of global forest diversity and functioning.

Keywords: background tree mortality; acute mortality; drought; fire; insects; forest structure

2.2 Introduction

Land use and climate changes have reduced forest area, led to unintegral habitat and threatened forest health, carbon sequestration, and commodity supply through shifting forest dynamics, specifically increasing tree mortality (Brecka et al. 2018; Curtis et al. 2018; McDowell et al. 2020; Pan et al. 2011). Widespread tree mortality has resulted from drought and warming in different regions and forest types (Allen et al. 2010; Brando et al. 2014; Breshears et al. 2005; Hammond et al. 2022; Hartmann et al. 2022; Liu et al. 2023; Peng et al. 2011; Rukh et al. 2023; van Mantgem and Stephenson 2007; Williams et al. 2012; Zhang et al. 2017a; Zuleta et al. 2017). Global warming and increased acute droughts (Dai 2012) have led to more frequent and severe fires (Jolly et al. 2015; Kasischke and Turetsky 2006; Westerling et al. 2006) and insect and disease outbreaks (Kautz et al. 2017; Kurz et al. 2008). These disturbances are usually interactive and can amplify tree mortality (Anderegg et al. 2015; Brando et al. 2014; Caldeira 2019; Zhang et al. 2014).

Since the seminal synthesis of global scale tree mortality (Allen et al. 2010), the triggers and mechanisms of drought-related tree mortality have been comprehensively studied at the cell, organ, and tree levels (Choat et al. 2018; McDowell et al. 2022b). Multiple syntheses about individual global change drivers on tree mortality have been published, including acute drought and heat (Feng et al. 2023; Fernandez-de-Una et al. 2023; Hartmann et al. 2022; Hember et al. 2017; Ionita et al. 2021; McDowell et al. 2022a; McDowell et al. 2022b; O'Brien et al. 2017; Oliveira et al. 2021; Williams et al. 2022; Zhang et al. 2017a); fire (Büntgen et al. 2021; Dey and Schweitzer 2018; Faustini et al. 2015; Hood et al. 2018; Kane et al. 2017a; Michaletz and Johnson 2007; Moritz et al. 2012; Pellegrini et al. 2021), biotic disturbances (Flower and Gonzalez-Meler 2015; Gely et al. 2020; Jactel et al. 2021; McCullough et al. 1998), and compound events (Markonis et al. 2021; Mukherjee and Mishra 2021; Ridder et al. 2022; Vogel et al. 2021). It is well recognized that species functional traits, including wood density, specific leaf area, physiological characteristics, root system, and stature, all contributed to their sensitivity to environmental and biotic stresses (Adams et al. 2017; Anderegg et al. 2020a; Anderegg et al. 2016; Dickman et al. 2023; Feng et al. 2023; Greenwood et al. 2017; Hember et al. 2017; Hoffmann et al. 2011; King et al. 2006; Liang et al. 2021; O'Brien et al. 2017; Stephenson et al. 2011; Trugman 2022; Zhang et al. 2017a).

Hydraulic failure and carbon starvation are mutually non-exclusive, and their roles in inducing tree mortality tend to be dependent on species groups (isohydric and anisohydric), drought intensity and duration, and concurrent biotic attacks (insect infestations and pathogens) (Anderegg et al. 2015; McDowell et al. 2008; McDowell et al. 2022b). Increases in tree mortality induced by global environmental change can also arise from intensified competition, reduced tree longevity, and compositional changes (Table 2-1). Furthermore, acute tree mortality can lead to younger forests and changes in species composition, which can feedback tree mortality processes (Mack et al. 2021; McDowell et al. 2020). This synthesis presents a framework to differentiate the effects of global environmental change on (*i*) **background tree mortality** due to press biotic and abiotic stresses, competition and aging in the absence of large-scale acute stresses (see Glossary), (*ii*) **acute tree mortality (unusual high proportion of tree death)** (see Glossary) associated with major droughts, insect or pathogen outbreaks, and stand-replacing fires, and (*iii)* the feedback within and between background and acute mortality drivers (Figure 2-1).

Table 2-1. Mechanisms and global change drivers underlying temporal increases in tree mortality identified by recent studies.

Mortality types	Mechanisms	Global change driver	Biomes observed	References
Background mortality				
	Hydraulic failure	Press drought, insects and pathogens	Global	(Anderegg et al. 2016; Anderegg et al. 2018; Morcillo et al. 2022; Oliveira et al. 2021; Rowland et al. 2015)
	Carbon starvation	Press drought, insects and pathogens	Global	(Choat et al. 2018; McDowell et al. 2022b)
	Intensified competition	Rising CO_2 and warming	Boreal and Temperate	(Luo and Chen 2015; Young et al. 2017)
	Shortened longevity	Rising CO_2 and warming	Boreal and Tropical	(Brienen et al. 2015; Locosselli et al. 2020; Searle and Chen 2018)

	Compositional shift	Rising CO2 and warming	Boreal and Tropical	(Feeley et al. 2011; Hisano et al. 2021; Laurance et al. 2004; Searle and Chen 2017)
Acute mortality				
	Hydraulic failure	Acute drought	Global	(Klos et al. 2009; Michaelian et al. 2011; Powers et al. 2020; Trugman et al. 2018)
	Direct killing	Heat, fire, insects and pathogens	Global	(Abatzoglou and Williams 2016; Allen et al. 2010; Anderegg et al. 2015; Brando et al. 2014; Breshears et al. 2005; Caldeira 2019; Fei et al. 2019; Flower and Gonzalez-Meler 2015; Jolly et al. 2015; McCullough et al. 1998; Nelson et al. 2013; Swinfield et al. 2012)

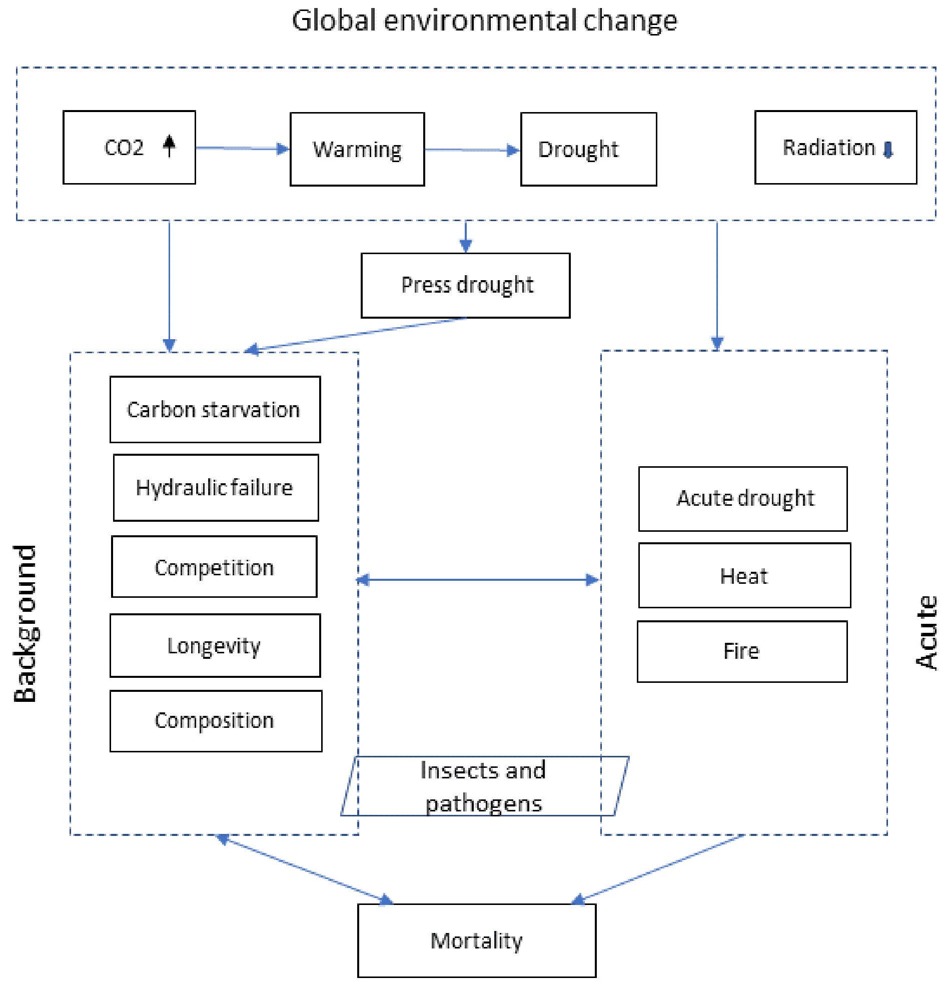

Figure 2-1. Multi-facet of interacting mechanisms influencing background and acute tree mortality.

Warming refers to the temporally systematic increase in atmospheric temperature since industrialization, and drought represents a decrease in climate water availability (IPCC 2021; Sheffield et al. 2012). The sunlight received by plants (radiation), is influenced by cloudiness and pollution, and affects photosynthesis and thus tree carbon balance and tree mortality dynamics (Durand et al. 2021).

Glossary

Background tree mortality: the typically low rates of tree mortality found in forests due to competition and aging in the absence of large-scale acute stresses.

Canopy transition: The intense competition among stems comes to an end. As trees start to decline and die because of longevity or damage from non-stand-replacing disturbances, shade-tolerant trees from the understory and intermediate canopy now take over the main canopy.

Acute tree mortality: large-scale tree mortality resulting from acute stresses like fire, logging, insect outbreak, hurricane, or acute drought.

Gap dynamics: Trees established through self-perpetuation dominate the stand. Growing space is available in all strata because of the death of individual trees. Structurally, it is characterized by a mosaic canopy dominated by shade-tolerant tree species.

Longevity: The time elapsed from regeneration to death of a tree without an acute disturbance.

Press drought: chronic reductions in water availability due to warming, reduced precipitation, or both.

Acute drought: an occurrence of the drought indices, e.g., annual Palmer Drought Severity Index of less than two standard deviation units below the long-term average (Williams et al. 2012) or an absolute threshold of –3 (Sheffield et al. 2012).

Stem exclusion: Following the initiation stage after a stand-replacing disturbance, this stage occurs as soon as all growing space is occupied, trees compete intensively for space and resources due to their rapid growth, and new shade-intolerant tree species are excluded from regenerating.

2.3 Background tree mortality

Background tree mortality occurs endogenously through competition among individual trees, aging, and fungal pathogens (Das et al. 2016; Hill et al. 2005; Luo and Chen 2011; Lutz and Halpern 2006). There are two peaks of tree mortality along with stand development following establishment, one at the **stem exclusion** stage due to the competition among rapidly growing trees and the other at **the canopy transition** stage as short-lived pioneer species reach their longevities (see Glossary) (Chen and Popadiouk 2002; Oliver and Larson 1996). At the **gap dynamics** or old-growth stage (see Glossary), biomass loss from tree mortality is assumed to equal biomass growth from surviving trees and the ingrowth of new recruits (Chen and Popadiouk 2002; Odum 1969; Oliver and Larson 1996). However, it is quite uncertain what happens if stands remain undisturbed for long periods of time, past the longevity of the post-fire species in boreal forests.

For a long time, background tree mortality seems to have little consequences and attracts minimal attention in detecting the mechanism of forest die-offs. However, a substantial portion of growth and ingrowth is lost from tree mortality (Chen and Luo 2015; McDowell et al. 2018). The background tree mortality rate can be as high as 1% to 5% annually, varying between tree species (Luo and Chen 2013; Pretzsch and Grote 2023; Pretzsch et al. 2022; Pretzsch et al. 2023a). Although the background tree mortality rate may be low on an annual basis, the accumulated tree loss can be greater than acute tree mortality over a long period (Hicke et al. 2013; van Mantgem and Stephenson 2007; van Mantgem et al. 2009). For example, in the same period (14 years) in the western US, 340 Tg carbon was lost from insect outbreak (Hicke et al. 2013), while rising background mortality (0.5% / yr) caused at least 720 Tg carbon loss (van Mantgem et al. 2009).

Several mechanisms underlying background tree mortality include biotic damage without insect or pathogen outbreaks, competition, and environmental stresses. In the next subsections, we explore how non-outbreak insects and pathogens, competition, climate change, and climate change-induced alterations in competition, tree longevity and composition influence background tree mortality.

2.3.1 Non-outbreak insects and pathogens and competition

Through stand development, insect herbivory, pathogens (diseases), and competition can occur independently or interactively (Andrus et al. 2021; Chen and Popadiouk 2002; Zhu et al. 2015). The relative contributions of biotic damage and resource competition to tree mortality differ with stand development, with a greater role of resource competition in the early stages and diseases in the later stages (Chen and Popadiouk 2002; Lutz and Halpern 2006). On the other hand, damage from insects and pathogens tends to become a more dominant factor for tree mortality in older stands, particularly in larger trees (Das et al. 2016; Hill et al. 2005).

The Janzen-Connell effect, which was proposed to explain the high species richness in tropical forests, is important for understanding the community-level biotic damages and predicting tree mortality (Janzen 1970). There are two main mechanisms underlying the Janzen-Connell effect, host-plant specificity and reduced resource competition. Specifically, host-plant specificity generates a rare species advantage by disproportionately reducing recruitment in seedlings occurring at high conspecific densities or near their parent trees (Bell et al. 2006; Chen et al. 2019; Johnson et al. 2012). Reduced resource competition also contributes to the Janzen-Connell effect because species with functional trait differences tend to occupy different ecological niches temporally, spatially, chemically, or biologically. The vulnerable trees are weak in producing defence chemicals against biotic agents (McDowell et al. 2022b). Within limited carbohydrate storage and water transport restrictions, plants divide it into survival, growth, and defence. With carbohydrate consumption, trees die of starvation or biotic agents before starving.

2.3.2 Climate change

Global warming can cause chronic reductions in water availability (**press droughts**) (see **Glossary**). Insufficient water under warming is directly related to heat stress, since lack of water limits tree evapotranspiration, a process that reduces tree temperatures (Percival 2023; Wang and Wang 2023). During the past decade, press droughts and direct heat stress have been recognized as drivers for temporal increases in background tree mortality, with the rate of increases being 3% to 5% annually (Allen et al. 2010; Andrus et al. 2021; Brienen et al. 2015; Luo and Chen 2013; Peng et al. 2011; Trugman et al. 2018; van Mantgem and Stephenson 2007; van Mantgem et al. 2009). Carbon starvation and hydraulic failure are acknowledged as the mechanisms underlying background tree mortality under press drought (Choat et al. 2018; McDowell et al. 2022b) (Table 2-1, Figure 2-1). Clearly, more intensive press droughts lead to higher tree mortality, and drier regions may be more vulnerable to further reductions in water availability with a more pronounced consequence in tree mortality (Luo et al. 2019).

Global change has influenced tree physiology and morphology, insects, pathogens, and their interactions (Hamann et al. 2021; Milici et al. 2020; Simler-Williamson et al. 2019). The effects of insects and pathogens on seedling survival can be influenced by environmental change (Figure 2-1). For example, density-dependent mortality driven by fungal pathogens was reduced at drier sites (Swinfield et al. 2012). In a wetter environment, increased root exudates support nutrients for spore germination and transmission over a longer distance and expose the susceptible host to being attacked (Garrett 1970; Short and Lacy 1974). Root exudates may decrease under drought, but this has been questioned or even contradicted by newer publications (Brunn et al. 2022; de Vries et al. 2019; Preece et al. 2018; Williams and de Vries 2020). Warming has also been shown to increase the negative effects of soil pathogens on plants by increasing the abundance of pathogen fungi (Liu and He 2021).

Young forest stands may be more vulnerable to droughts, possibly because water scarcity due to intense competition among trees at the stem exclusion stage reduces their ability to withstand additional stresses (Luo and Chen 2013). Furthermore, shallow root systems of smaller trees limit their ability to access deep soil water. In contrast, old trees can also be at higher risk due to their greater inherent vulnerability to hydraulic stress and the greater probability of pathogens and insect attacks (Bennett et al. 2015). However, most previous studies did not separate the effects of global environmental change from individual tree aging, increases in tree size and/or stand development (Chen and Popadiouk 2002; Oliver and Larson 1996), masking the estimates of global environmental change effects (Brown et al. 2011).

An emerging question is whether tree species diversity may reduce tree mortality under global environmental change. By combining eddy covariance measurements from 40 forest sites, remote sensing observations of plant water content, and plant functional traits data, a study demonstrated that the hydraulic diversity of trees increases ecosystem resilience to drought (Anderegg et al. 2018). However, others have reported that tree mixtures do not increase resilience to drought (Ovenden et al. 2022). Additionally, higher tree neighbourhood diversity reduces water competition due to their differences in water niches or facilitative interactions to improve carbon assimilation under drought, likely decreasing the probability of tree mortality (O'Brien et al. 2017). A recent analysis indicates that tree species diversity reduces the damage of specialist insect herbivores (Jactel et al. 2021). In boreal forests, species-rich forests suffer less tree mortality in response to global environmental change (Hisano et al. 2019). Hydraulic diversity and reduced damage from specialist insect herbivores in species-rich boreal forests may have contributed to their lower mortality loss. These findings offer optimism that promoting high tree diversity may reduce forest vulnerability to ongoing global environmental change. However, deforestation, the driver of global biodiversity loss, is ongoing at a rapid pace, particularly in tropical regions, and will increase the rate of global environmental change (Curtis et al. 2018; Pan et al. 2011). Furthermore, the global conversion of species-rich natural forests to species-poor plantations decreases biodiversity (Newbold et al. 2015) and these species-poor plantations, especially those under intensively managed plantations through vegetation management, may suffer more tree mortality due to greater intraspecific than interspecific competition under global change (Luo and Chen 2015).

Although the water availability of terrestrial ecosystems has decreased and is predicted to decrease further on average, some areas have experienced and will experience increased water availability (IPCC 2021; Sheffield et al. 2012). Increased precipitation may reduce solar radiation for trees (Durand et al. 2021; Knohl and Baldocchi 2008) and affect tree mortality. However, our understanding of the direct and indirect effects of increased water availability on tree mortality is limited.

2.3.3 Climate change-induced alterations in competition, longevity, and composition

Observational and experimental studies have found positive responses of tree growth to rising CO_2 and warming when water is not limiting (Girardin et al. 2016; Norby et al. 2005; Pretzsch et al. 2014), but modelling studies suggest that forest productivity could decrease under future climates (Sperlich et al. 2020). Increased tree growth amplifies tree-to-tree competition, particularly conspecific competition, in boreal forests, increasing tree mortality (Luo and Chen 2015) (Table 2-1, Figure 2-1). Increased tree growth can also lead trees to reach their hydraulic limitation heights sooner, increasing mortality from reduced longevity (Brienen et al. 2015; Locosselli et al. 2020). Rising CO_2 concentrations are believed to cause background compositional shifts toward faster-growing and drought-tolerant tree species (Feeley et al. 2011; Hisano et al. 2021; Laurance et al. 2004; Searle and Chen 2017) with more species reaching their dry or warm limits (Taccoen et al. 2022). Large surveys of plant communities in North, Central and South America also found an increase in heat-tolerant species associated with rising temperature, but the relative abundances of water-demanding or drought-tolerant species are less consistent and are not correlated with changes in precipitation (Feeley et al. 2020). These compositional shifts may also be responsible for temporally increasing tree mortality since faster-growing tree species are associated with shorter longevities (Brienen et al. 2020; Stephenson and Das 2020). However, our understanding of the implications of increasing heat-tolerant or drought-tolerant species for tree mortality remains limited.

2.4 Acute tree mortality

Acute tree mortality occurs exogenously from fire, insects, diseases, and climate events, such as hurricanes, heat and acute droughts (Figure 2-1). The influences of these drivers on tree mortality vary temporally and spatially across forests around the world. Between 1970 and 2017, Canada experienced an average of 8,000 wildfires burning 2.25 million hectares per year; the area burned varies from 289,000 hectares in 1978 to 7.56 million hectares in 1989; in recent decades, the frequency of large forest fires has increased, on average 0.7% of the forested land burning annually (Tymstra et al. 2020). Meanwhile, moderate and severe insect and/or disease defoliation, including bark beetles, occurs on average approximately 23 million ha annually, representing 6.6% of Canada's forested land area (Canadian Council of Forest Ministers 2021). This defoliation-induced tree mortality is estimated to be 1.3 to 2 times the mortality due to fires in Canada (Volney and Fleming 2000). As a net carbon sink, forests can become a large net carbon source both during and immediately after an insect outbreak (Kurz et al. 2008). In these high-latitude forests, the sum of acute tree mortality from fires (0.7% per year of the forested land) and insects (1.2% per year) (Brecka et al. 2018; Stocks et al. 2002; Volney and Fleming 2000; Wang et al. 2022c) is lower than background tree mortality (the median of 1% to 5% of all trees of the forest land) (Luo and Chen 2013).

2.4.1 Climate events and fire

Global warming can also increase the frequency, intensity, and duration of short-term extreme drought events (**acute droughts**) (see Glossary). Chronic and acute droughts are expected to correlate because temporal increases in temperatures affect both types of droughts simultaneously, but they can occur independently. Acute droughts have long been recognized as a cause of widespread tree mortality (Breshears et al. 2005; Michaelian et al. 2011; Powers et al. 2020; Senf et al. 2020; Young et al. 2017) (Table 2-1, Figure 2-1). Large-scale acute droughts can cause massive tree mortality and have the potential to shift forest biomes into grasslands or savannas (Allen and Breshears 1998). Furthermore, subsequent acute droughts generally lead to a more deleterious impact than initial droughts that cause trees under water stress, with a more pronounced effect on conifer-dominated ecosystems (Anderegg et al. 2020a). Large trees are believed to die twice the rate of small trees during extreme drought (Stovall et al. 2019); however, height-dependent responses can be confounded with species composition and differ with local site conditions (Au et al. 2022; Koontz et al. 2021). However, these studies suggest that projected more frequent and more intensive acute droughts in the future will have profound consequences on global forests, the extent of which depends on how human society will reduce fossil emissions and conserve and restore global forests. Furthermore, although climate events such as hurricanes, storms, and flooding are major risks to ecosystems and human society (Johnston et al. 2020), their influences on tree mortality on a regional and global scale are poorly understood.

Forest fires dramatically influence tree mortality, diversity, ecosystem functioning, and human well-being. Global fire activity is projected to increase based on the global climate model and decrease probability in the tropics and differentiated on biomass resources to burn, atmosphere conditions conducive to combustion and ignition (Moritz et al. 2005; Moritz et al. 2012; Patacca et al. 2023; Pausas and Keeley 2021). In recent decades, many regions have seen increases in forest fires due to warming and drying (Abatzoglou and Williams 2016; Kasischke and Turetsky 2006; Westerling et al. 2006). Between 1997 and 2016, the burned area increased in many tropical, temperate, and boreal closed-canopy forests, although fire activities have decreased in regions with low and intermediate levels of tree cover (Andela et al. 2017). From 1979 to 2013, fire weather seasons have lengthened across 25% of the vegetated surface of the Earth, resulting in a 19% increase in global mean fire weather season length, a double of the global burnable area, and an increased global frequency of long fire weather seasons (Jolly et al. 2015). Climate variability strongly influences fire activity worldwide (Abatzoglou et al. 2018), suggesting that projected increasing climate extremes in the 21st century will amplify forest fire activities and tree mortality. The rates of warming increase with latitude, exerting greater water stress in forests at high latitudes accordingly (IPCC 2021). It remains unclear how the different warming rates across the globe are linked to increased fire activities and how this may play out in the future.

The process underlying fire-caused tree mortality is similar to drought-induced tree mortality. Usually, there are first- and second-order type effects. The first-order effects are nonlethal; it is the immediate transfer of heat to plant tissues (Michaletz and Johnson 2007). The first-order effect is similar to drought-stress plants or makes trees vulnerable. In defence of the first-order effect, bark insulation related to bark thickness is important for thermal protection (Bär and Mayr 2020). Plant water and carbon are also found to influence plant combustion and heat transfer to plants that affect fire behaviour and effect (Dickman et al. 2023). Between first- and second-order effects induced mortality, plants' response to post-fire effects has the same importance. In field and lab experiments, post-fire species *Picea abies*, *Pinus sylvestris*, and *Fagus sylvatica*, showed changes and impairment of hydraulic efficiency and safety. The second-order effect is the following disturbances, such as insect attacks and pathogen infections. The changed environment could even drive non-virulence pathogens to be virulent.

2.4.2 Biotic disturbances

Insect herbivory and pathogens regulate species coexistence and the forest carbon cycle (Das et al. 2016; Kurz et al. 2008; Schowalter et al. 1986). In temperate forests, pests and pathogens are considered the biotic agents that are capable of causing similar magnitude consequences of climate change (Flower and Gonzalez-Meler 2015). In the Northern Hemisphere, the consequence of biotic disturbances was the same magnitude as fire, with annual damage of forests and associated carbon fluxes of about 43.9 million hectares and 129.9 Mt C/year due to biotic disturbances (Kautz et al. 2017). Invasive pathogens and pests have a wider host range and cause different scale and intensity impacts (Wang et al. 2022b). In the Northern Hemisphere, Blister rust, the introduced fungal pathogen, has threatened the survival of whitebark pine (Ellison et al. 2005; McDonald 2001). Most of the research on blister rust had mountain pine beetles occurring together (Kendall and Keane 2001; Shanahan et al. 2016; Smith et al. 2008). The effects of native and invasive biotic agents decreased with decreasing precipitation (Wong and Daniels 2017). Invasive pathogens not only cause a decrease in tree growth and increased tree mortality but also impair belowground microbial community and the cycle of nutrients and result in habitat loss and species replacement (Diaz-Yanez et al. 2020; Gomez-Aparicio et al. 2022).

Climate change has changed forest pathogen and insect habitats and induced distribution range and outbreak range expansion, such as white pine blister rust, Canker pathogens, Armillaria root disease (Sturrock et al. 2011) and bark beetle guilds, such as mountain pine beetle, spruce bark beetle and pine processionary moth (Pureswaran et al. 2018). Climate change also increased the frequency and intensity of insect and pathogen outbreaks over the past decades (Haynes et al. 2014; McCullough et al. 1998; Nelson et al. 2013). Climate change also accelerates the occurrence of novel disturbances in forests in recent decades (Allen et al. 2015; Aukema et al. 2010) and can cause novel associations between fungi pathogens and their host trees (Wingfield et al. 2017). Furthermore, the effects of invasive pests on tree mortality have increased over time in US forests (Fei et al. 2019).

Studies demonstrating the direct link between global warming, drought, and widespread insect and pathogen activities remain limited (Sturtevant et al. 2023). There are several reasons. First, mechanistically, warming does not only increase insect activities but can also have negative effects on insects, such as the lethal effects of heat waves or more abundant predators and parasites (Harvey et al. 2020; Jactel et al. 2019). Second, insect and pathogen responses to drought intensity and duration varied among species or guilds. Third, natural enemies and resource competition also play an important role in insect outbreaks by influencing the larva stage. The prediction of the jack pine budworm model from observational and experimental data showed that at low and intermediate budworm densities, parasitoid attacks were the main source of larval budworm mortality, while resource competition became dominant at high density and the strength of the effect increased with host age (Gallagher and Dwyer 2019). Lastly, insect outbreaks vary in cycles because of differences in host abundance and migration speeds and environmental requirements of the insects, with the cycle of several decades for some insects, including spruce budworms *(Choristoneura fumiferana* Clemens.) in Canadian boreal forests (Canadian Council of Forest Ministers 2021). In defense, some species are able to attract the parasitoids of their attackers (Turlings and Erb 2018). Due to the long cycles, we lack the data to demonstrate that insect outbreaks increase temporally over time, but a study in Finland shows that Lymantria *monachal*, a major pest in Central Europe, has expanded northward in the past three decades, in response to higher minimum winter temperatures (Fält-Nardmann et al. 2018).

2.4.3 Interactions among acute mechanisms

Acute tree mortality is highly sensitive to climate change. Warmer and drier climates facilitate fire, drought, and insect outbreaks, while warmer and wetter conditions promote pathogens and wind disturbances (Seidl et al. 2017; Sommerfeld et al. 2018). Both insect and fire activities are positively associated with climate-driven acute droughts (Abatzoglou et al. 2018; Brando et al. 2014; Gely et al. 2020; Koontz et al. 2021; Mattson and Haack 1987). Insects and drought interactions have been well recognized in temporal increases in tree mortality because drought-stressed trees are more susceptible to dying once attacked by insects (Anderegg et al. 2015; Jactel et al. 2019; McDowell et al. 2011). Alternatively, heavily defoliated trees with little carbon reserves are more prone to fail with additional heat or water stress (Mediavilla et al. 2022; Morcillo et al. 2022; Yi et al. 2022). The interaction effects of insects and droughts on tree mortality depend on the severity and longevity of droughts and the types of insects (Gely et al. 2020). Although acute drought and insects interact and contribute to increased tree mortality, it is less understood how an increase in precipitation or high precipitation extremes may interact with insect or pathogen activities.

Insect and fire activities are also interactively linked. Changes in tree species composition, density, and size after a stand-replacing fire are related to fuel availability, flammability, and susceptibility to insects and pathogens (Chen and Popadiouk 2002; Oliver and Larson 1996). For example, young stands established after fires have limited fuel availability, particularly dominated by broadleaf trees, and are less susceptible to subsequent fires (Cumming 2001). Insect-killed trees may become more susceptible to fire due to higher fuel availability (Kane et al. 2017b).

2.5 Feedback between background and acute mechanisms

The background and acute mechanisms for tree mortality are not mutually exclusive (Figure 2-1). Due to heat and press drought, weakened trees can become more vulnerable under acute droughts. With reduced investments in defence compounds, they can endure greater damage from insects. Similarly, warming and drying from press drought increase fire activities (Abatzoglou and Williams 2016). Together, warming and press drought increase forest vulnerability to acute disturbances.

Faster-growing trees with lower wood density induced by rising CO_2 may be more susceptible to acute damage such as acute droughts and insects, but the impacts seem species-specific and may be related to allocation strategies (Arsić et al. 2021). Since another effect is a shift into higher root/leave ratios (Li et al. 2019), the impact of CO_2 might rather be beneficial by decreasing drought vulnerability. Meanwhile, shorter tree longevities are associated with shorter times for pathogens and insects to accumulate, reducing their damage to trees. The background change in composition due to rising CO_2 (Brienen et al. 2015; Hisano et al. 2021; Searle and Chen 2018) may contribute to acute disturbances. For example, an increase in the deciduous broadleaf composition can reduce fire activities and alter insect dynamics and forest susceptibility to both press and acute droughts (Cumming 2001). Future efforts are needed to better understand the extent of these feedback mechanisms and represent these processes in mechanistic vegetation models to predict changes in tree mortality in response to future global environmental changes.

Acute tree mortality events reinitiate forest stands (Figure 2-1). As stands develop after the events, tree mortality processes are highly dynamic in response to stem exclusion and canopy transition, including changes in tree species composition (Bergeron 2000; Chen and Popadiouk 2002; Oliver and Larson 1996). Tree mortality rates are inherently different between tree species (Luo and Chen 2011), and their responses to global environmental change also differ in boreal forests (Luo and Chen 2013; Luo and Chen 2015). Stands dominated by early-successional tree species suffer less tree mortality due to warming and droughts than those dominated by late-successional tree species (Chen and Luo 2015). Increased stand-replacing disturbances from fires and insect outbreaks will increase the composition of broadleaf and early successional species and decrease forest ages (Chen and Taylor 2012; Chen et al. 2009; Mack et al. 2021). Frequent burning favours trees with low nitrogen and phosphorus content, the resource-conservative species, and consequently affects tree mortality (Pellegrini et al. 2021). Our understanding of how these early successional stands differ in response to global environmental change from older stands remains incomplete.

2.6 Concluding Remarks and Future Perspectives

Recent studies have shown that ongoing global environmental change has increased background and acute tree mortality around the world, presenting risks to biodiversity, ecosystem functioning, and the global carbon cycle. In this review, we examined the mechanisms underlying temporal increases in tree mortality such as intensified competition, reduced tree longevity, and species compositional shift, in addition to well acknowledged hydraulic failure, carbon starvation fire, insects, and diseases. Moreover, we explored the feedback between background and acute tree mortality. However, it is unclear the extent to which various causes contribute to increased tree mortality. For example, across temporal and spatial scales, does global environmental change affect background tree mortality more than acute tree mortality, and vice versa? What are the patterns and mechanisms of forest insects and pathogens and their influences on tree mortality in response to global environmental change drivers? How can we better predict future background and acute tree mortality on a regional, biome, and global scale?

We suggest that several avenues can help us improve our understanding of tree mortality in response to global environmental change drivers, including rising atmospheric CO_2 concentration, warming, reduced water availability and changes in radiation. First, we suggest that our framework that simultaneously incorporates background and acute tree mortality (Figure 2-1) will help identify future research questions by focusing on how different causes may interact. Second, we suggest that evaluating simultaneous direct and indirect mechanisms will better predict the response of background tree mortality to a gradient of environmental change in global forests. We argue that assessing regional and global forest mortality responses to global environmental change requires accounting for background and acute tree mortality. Finally, society must act to reduce fossil emissions, deforestation, and ecosystem simplification to combat the rapid increase in tree mortality.

CHAPTER 3: PHYLOGENETIC DIVERSITY REDUCES TREE MORTALITY BY DECREASING BIOTIC DAMAGE

3.1 Abstract

Tree mortality is a natural process of forest dynamics, but excessive tree mortality not only has negative consequences on the economy but also strongly reduces the potential of forests as sinks for carbon (Anderegg et al. 2020b). Although biodiversity loss is at an alarming rate in all taxa, including trees (Newbold et al. 2015), few have examined the relationships between species richness and tree mortality and found mixed results. Furthermore, we lack a mechanistic understanding of the roles of biotic damage, competition (quantified by stand density index) and niche partitioning (measured by size inequality) in regulating the relationship between tree diversity and mortality. Here, we show that after controlling the effects of climate and stand age, biomass mortality rate and stem mortality rate increased with tree functional diversity but decreased with phylogenetic diversity in the natural forests of British Columbia, Canada. Specifically, increasing functional diversity from its minimum to maximum increased the tree biomass and stem mortality rates by 250% and 131%, respectively. Increasing phylogenetic diversity from its minimum to maximum decreased biotic damage by 60% and decreased tree biomass and stem mortality rates by 70% and 78%, respectively. Biotic damage from the pool of 143 types of insects and pathogens was the main driver of tree mortality, and it decreased with tree phylogenetic diversity. Tree mortality was lower in stands of high size inequality that was positively related to tree phylogenetic and functional diversity; however, the effect of stand density on mortality was negligible, indicating that the nearly century-old theory using stand density index to quantify competition developed for monocultures (Reineke 1933) might not be relevant to natural forests of varying tree diversity. Our finding suggests that conserving

phylogenetically diverse natural forests or planting tree mixtures of phylogenetically distant species will lower tree mortality, safeguard the forest economy, and enhance the role of forests in mitigating climate change.

3.2 Introduction

Tree mortality has been observed to increase rapidly in the 21st century, causing uncertainties and shifts in forest dynamics and stability, influencing carbon cycling and contributing to the pace of climate change (Anderegg et al. 2012; Forzieri et al. 2022; McDowell et al. 2020). Recent studies have advanced the understanding of triggers of and factors that influence tree mortality, for example, warming or drought (Allen et al. 2010; Choat et al. 2018; McDowell et al. 2022b; Reich et al. 2022) and enhanced biotic damage from insects and pathogens (Anderegg et al. 2015; Koontz et al. 2021; Kozlov et al. 2015; Kurz et al. 2008), as well as increased tree competition and shortened tree longevity (Brienen et al. 2015; Luo and Chen 2011; Ma et al. 2023; Searle et al. 2022). Biodiversity loss is one major global change (Newbold et al. 2015) and has profound effects on ecosystem functioning such as productivity (Hooper et al. 2012). Previous studies have shown negative (Hisano et al. 2019; Pretzsch et al. 2023b) and positive (Searle et al. 2022), and non-significant (Liang et al. 2007) relationships between species richness and tree mortality rate in natural forests. Meanwhile, short-term tree diversity experiments found non-significant relationships between species richness and tree survival rate (King et al. 2023; Liu et al. 2022; Van de Peer et al. 2016). Functional and phylogenetic diversity, which help infer ecological mechanisms associated with ecological functioning, provide a better way to understand biodiversity-ecosystem functioning and can support policymakers with practical suggestions (Cadotte et al. 2011; Srivastava et al. 2012) and constitute a part of the natural-based solution to mitigating climate change (Girardin et al. 2021).

Yet, our understanding of the roles of functional and phylogenetic diversity and their influences on the mechanisms underlying tree mortality remains unexplored.

Tree mortality may decrease with tree diversity due to reduced biotic damage. Insects and pathogens are part of the terrestrial ecosystem and drive the ecosystem process and functioning (Boyd et al. 2013; Yang and Gratton 2014). For example, a modelling analysis demonstrated that massive tree mortality from the mountain pine beetle outbreak between 2000-2020 in British Columbia, Canada shifted the forests from a small carbon sink to a large carbon source (Kurz et al. 2008). During the non-outbreak phase, insects and pathogens can also cause substantial loss of tree foliage and damage to the stems and roots, resulting in tree mortality (Das et al. 2016; Hill et al. 2005; Kozlov et al. 2015). Although the effects of functional traits or diversity on biotic damage vary with traits and species (Barrere et al. 2023; Haase et al. 2015; Moreira et al. 2016; Schuldt et al. 2014; Schuldt et al. 2012), lower host-plant abundance in diverse forests, combined with the volatile from non-host plants, and the increased natural enemies can usually decrease biotic damage, reducing tree mortality (Guyot et al. 2016; Jactel and Brockerhoff 2007; Matevski et al. 2023; Stemmelen et al. 2022; Vehvilainen et al. 2007). However, when generalist herbivores are dominant leaf damage agents in species-rich (sub)tropical forests, the higher probabilities of palatable hostplants for generalist insects and associated susceptibility in more diverse forests can lead to a positive relationship between herbivory and species richness (Barbosa et al. 2009; Schuldt et al. 2010; Wang et al. 2019; Wang et al. 2022a).

Higher tree diversity is usually associated with higher stand density due to canopy packing (Jucker et al. 2015) and higher tree size inequality (Zhang and Chen 2015), both of which can affect tree mortality. High stand densities are known to cause greater resource competition and increase tree mortality (Kulha et al. 2023; Luo and Chen 2011; Lutz and

Halpern 2006). However, tree mortality can be unrelated to stand density (Koontz et al. 2021) or is associated negatively during wetter periods but positively during drier periods (Van Gunst et al. 2016). As an indicator of niche partitioning, tree size inequality in species-rich forest stands due to the inherent difference in growth rates among species could increase above-ground light interception and below-ground resource utilization and therefore reduce the resource competition-induced mortality (Luo and Chen 2015; Morikawa et al. 2022; Searle et al. 2022). Moreover, in species-rich stands of high size inequality, trees overshadowed by tall neighboring trees could experience lower mortality due to lower exposure to solar radiation and lower water demand from evapotranspiration (Ma et al. 2023). Therefore, we expect that tree diversity influences tree mortality by its effects on stand density and size inequality, and the extent to which stand density and size inequality influence mortality can determine the relationships between tree diversity and mortality.

Herein, we compiled the dataset of 10826 natural forest plots across British Columbia with at least two measurements, among which 1219 plots were last measured between 2007 to 2019 when damage by insects and pathogens was explicitly documented for all dead trees (Extended Data Figure 3-1). We assessed how functional and phylogenetic diversity influenced tree mortality rate at the stand level by regulating biotic damage, stand density, and size inequality. Tree mortality was measured as annual biomass loss divided by stand biomass in the previous census (or annual stem loss divided by the total number of stems). Biotic damage was quantified as the proportion of dead biomass or stems with field-recorded insect and/or pathogen loads. Stand density was estimated as Reinek’s Stand density index in metric units (Reineke 1933), and the size inequality was the ratio of stand deviation and mean diameter at breast height (DBH) (Zhang and Chen 2015). We employed the Hill functional, phylogenetic, and taxonomic diversity (Chao et al. 2014a) to allow a meaningful comparison of their relationships with tree mortality, biotic damage, stand density, and size inequality. Because Hill taxonomic diversity had a variance inflation factor of 3.54 (VIF 95% CI: 3.22, 3.90) when it was included along with the other two diversity indices in the biomass mortality rate model, we developed a separate Hill taxonomic diversity model. Since across a large spatial scale, both diversity and tree mortality can be codetermined by climate, soil, and stand age (Hamann et al. 2021; Searle et al. 2022; Van Gunst et al. 2016), we included mean annual temperature and precipitation, continentality index, soil drainage and stand age as covariates in our models to account for their influences (see *Methods*). All predictors were scaled (minus mean and divided by one standard deviation) to enable their direct comparisons. The distributions of mortality rate and biotic damage show zeros and positive continuous values, which belong to the Compound Poisson-Gamma distribution under Tweedie distribution (1 < variance power < 2) (Bonat and Kokonendji 2017) (Extended Data Figure 3-2), and thus generalized linear model was applied to mortality rate and biotic damage (*see Methods*).

3.3 Methods

3.3.1 Study area and available data

To quantify temporal trends in mortality of the natural forests in British Columbia, we selected permanent sampling plots (PSPs) established by the Government of British Columbia using the following criteria: (i) natural origin and without management; (ii) with known stand age; (iii) have all trees marked with their diameter at breast height (DBH) measured; (iv) have two or more censuses of repeated measurements. To explore the relationships between tree diversity, mortality and the underlying mechanisms, we selected PSPs with their last census taken after 2007 when the insect and pathogen loads were explicitly documented for all trees within PSPs.

We quantified tree mortality based on each census interval that consisted of two consecutive censuses of a given PSP. Specifically, we calculated the annual biomass loss rate from tree mortality at the plot level as the ratio of the aboveground biomass of dead trees at the second census divided by the standing biomass of the first census and the number of years between the two censuses. Aboveground biomass of dead trees was estimated based on biomass allometric equations developed and used in other Canadian studies (Hisano and Chen 2020; Hisano et al. 2019). We also calculated the annual rate of tree mortality based on dead stems and dead basal area, which were highly correlated with the annual biomass loss rate (r = 0.70 and 0.96, respectively).

3.3.2 Hill number of taxonomic, functional and phylogenetic diversity, and functional composition

To test the relative importance of three diversity metrics on mortality and their role on underlying mechanisms, we calculated the Hill numbers of taxonomic, functional, and phylogenetic diversity using instructions of '*HillR*' package (Li et al. 2014). We calculated the species-specific relative basal area and phylogenetic tree and collected ten functional traits of fifty-three tree species. The phylogenetic tree was produced via the '*phylo.maker*' function from '*PhyloMaker*' package (Jin and Qian 2019). These ten functional traits were related to tree growth and competitive ability (Kunstler et al. 2016; Niinemets and Valladares 2006; Wright et al. 2010), which are leaf nitrogen content per leaf dry mass (Nmass, in milligrams per gram), leaf phosphorus content per leaf dry mass (Pmass, in milligrams per gram), specific leaf area (SLA, in square millimetres per milligram), wood density (WD, in grams per cubic centimetre), maximum tree height (Hmax, meter) and root depth, drought tolerance (DT, categorical class 1-5), shade tolerance (ST, categorical class 1-5), leaf habit (deciduous or evergreen, equals 1 or 0) and leaf structure (broadleaves or conifers, equals 1 or 0). Traits were obtained from the TRY database (Kattge et al. 2020). Hill numbers were compared, the ones q = 1 yielded the lowest values of Akaike information criteria of the mortality model, and were thus used for further analysis (Extended Data Table 3-1).

To quantify functional composition, we performed a principal component analysis with the community-weighted means (CWMs) of the ten traits to represent them due to the high correlations between the traits. The first axis (PC1) explained 36.95% of the variation of functional traits, representing a change from conifer to deciduous broadleaves, such as lower wood density and higher specific leaf area; the second axis (PC2) accounted for 25.58% of the variation, indicating an increase from a gradient of increasing drought tolerance (Extended Data Figure 3-5).

3.3.3 Biotic damage, stand density index and size inequality

In the field, up to three possible causes including insects, pathogens, small mammals, abiotic such as physical breakage, and unknown for each dead tree were identified during the measurements between 2007 and 2019 (British Columbia Forest Inventory and Monitoring Program 2007; Henigman et al. 1999). In our analysis, we treated the primary one as the cause of mortality. We quantified biotic damage as the proportion of dead stems with insect and/or pathogen loads within a plot. Insects and pathogens were aggregated to the family level (Extended Data Figure 3-1). We did not consider the severity of the damage since it can vary between agent types and was not comparable among different agents (British Columbia Forest Inventory and Monitoring Program 2007).

Similar to the previous study (Searle et al. 2022), we calculated the stand basal area as the sum of the basal area of all living stems and divided by the plot area in hectares. We also calculated Reineke's stand density index (Reineke 1933), which was highly correlated with stand basal area ($r = 0.82$) and showed the same results. Size inequality was the coefficient of variation of tree diameter at breast height (DBH), calculated as the ratio of the standard deviation of all DBH measurements to the mean DBH within each plot at each census (Zhang and Chen 2015).

3.3.4 Climate factors, local soil conditions, and stand age

To derive the plot-level mean annual temperature (MAT, °C) and mean annual precipitation as well as the continentality index, we employed the BioSIM, which generates weather from near weather stations (Fortin et al. 2022). Specifically, we generated the monthly values of total precipitation, maximum and minimum and mean temperature via the '*generateweather*' function. The mean annual precipitation (MAP, mm) and mean annual temperature (MAT, °C) were the average annual values of monthly total precipitation and mean temperature, respectively. For the calculation of the continentality index, the '*climate*' function was applied to the list of monthly values and then followed with the '*contin*' function. Among the generated indexes, we selected the Conrad-based metrics following a previous study (Hamm et al. 2023). We obtained soil drainage level (increasing soil water availability from 1 to 7) from SoilGrids to represent local soil characteristics (Hengl et al. 2017). Stand ages in PSP data were available in the PSP datasets provided by the provincial government. Ages were either based on known fire history or by coring at least three dominant/codominant trees of each tree species inside or outside the plot at the plot establishment (Senici et al. 2010).

3.3.5 Statistical analysis

We first followed the protocol from (Zuur et al. 2010) and examined the distribution of all calculated variables and the relationships between mortality rate and other variables. All statistical analyses were performed in R 4.3.2 (R Core Team 2024). The mortality rate and biotic damage fit the compound Poisson-Gamma distribution, whose variance power is located between 1 and 2, a case of Tweedie distribution, a flexible distribution for continuous positive data that can adequately handle zero inflation (Bonat and Kokonendji 2017). The stand density index and size inequality followed the Gaussian distribution (Extended Data Figure 3-2). Next, we modelled the temporal biomass mortality trend along measurement years from 1939 to 2019 using the generalized additive model in the application of the Tweedie family (Hastie 2017). Similar to previous studies (Guinet et al. 2023), we applied the generalized linear model using function glmmTMB (Brooks et al. 2017) to deal with Tweedie distribution variables in the R platform. The random effect of the unique plot was removed because of the reported model overfit and convergence problem. To improve normality and homogeneity, the Hill diversity, stand density index, size inequality, and stand age were log-transformed. All predictors were scaled (centred on the mean and divided by one unit of standard deviation) to allow them to be directly comparable.

When modelling the relationships between Hill diversity and mortality rate and underlying mechanisms, we included climates (MATave, MAPave, continentality index), soil drainage, and stand age as covariates. For all fitted models, model assumptions were examined using the R package DHARMa (Florian Hartig 2022), which uses a simulation approach to test the Q-Q plot of residuals, residuals vs. predicted, nonparametric dispersion, and zero inflation (Extended Data Figure 3-6, 7, 8, 9). Using this DHARMa package, we also tested residual temporal autocorrelation and showed a non-significant correlation at the level of 0.05. For all parsimonious models we selected for interpretation, predictor collinearity was low and all predictors had variance inflation factor (VIF) < 2. Similar to previous studies (Aguirre-Gutierrez et al. 2022), we checked the spatial autocorrelation of residuals using the Moran test and found significant effects of spatial autocorrelation for stand density index and size inequality models. Subsequently, we calculated the spatial distance at which such spatial effect decreased to nonsignificant for those models. We found that a distance of 0.3 km was the most appropriate and generated an identification for each group of plots (groupID) as the random factor in the models mentioned above (Extended Data Table 3-3).

3.4 Results and Discussion

The generalized additive model shows an overall temporal increase in biomass mortality rate in British Columbia forests from 1939 to 2019 (Figure 3-1). The temporal increase we observed is consistent with observations elsewhere across global forests (Allen et al. 2010; McDowell et al. 2022b). We found the peaks at the years of 1939, 1960s, and around 2013 in the mortality rate, which corresponded with the drought events that occurred in Canada (Bonsal et al. 2011).

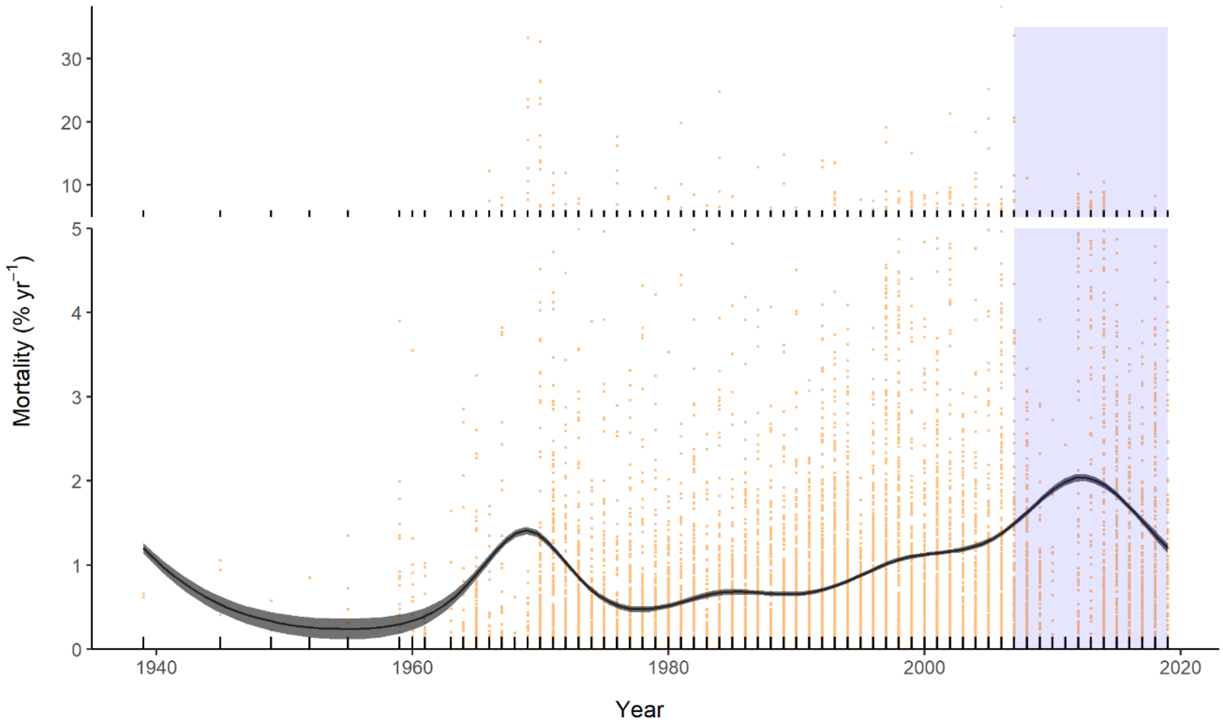

Figure 3-1. Trends in biomass mortality rate across all plots in British Columbia. The black line indicates the best model fit for the long-term trend from 1939 to 2019 using a general additive mixed model (GAMM) with 95% confidence intervals (ribbons). Points represent individual mortality rate values (*n* = 10826). The shaded area highlights the last observations that occurred between 2007 to 2019 when damage by insects and pathogens was explicitly documented for all dead trees.

The generalized linear model ($R^2 = 0.31$), which was developed based on the dataset with the last measurements from 2007 to 2019, showed that biomass mortality rate increased with functional diversity ($r = 0.18$, $p < 0.001$, Figure 3-2a) while decreased with phylogenetic diversity ($r = -0.10$, $p < 0.001$, Figure 3-2b). Such relationships were consistent in models with or without including mean annual temperature and precipitation, continentality index, soil drainage class and stand age as covariates (Extended Data Table 3-1). The summed effect size of functional and phylogenetic diversity was concordant with a positive taxonomic diversity relationship with biomass mortality found in the model with taxonomic diversity in substitute of functional and phylogenetic diversity (Extended Data Figure 3-3a). Our finding of the higher biomass mortality rate in taxonomically diverse forests resulted from a greater positive effect of functional diversity than a negative effect of phylogenetic diversity. The positive relationship between tree diversity and mortality found in our study differs from a negative relationship between biomass mortality rate and tree diversity found in western boreal forests of Canada (Hisano et al. 2019). In the boreal forests, higher diversity results predominantly from the mixture of broadleaves and conifers, signaling a dominant role of phylogenetic diversity in reducing tree mortality, which is concordant with our finding of the negative relationship between phylogenetic diversity and biomass mortality. The positive relationship between mortality and functional diversity could be attributed to that functional diversity increases productivity and higher mortality is associated with higher productivity (Searle et al. 2022; Stephenson et al. 2011).

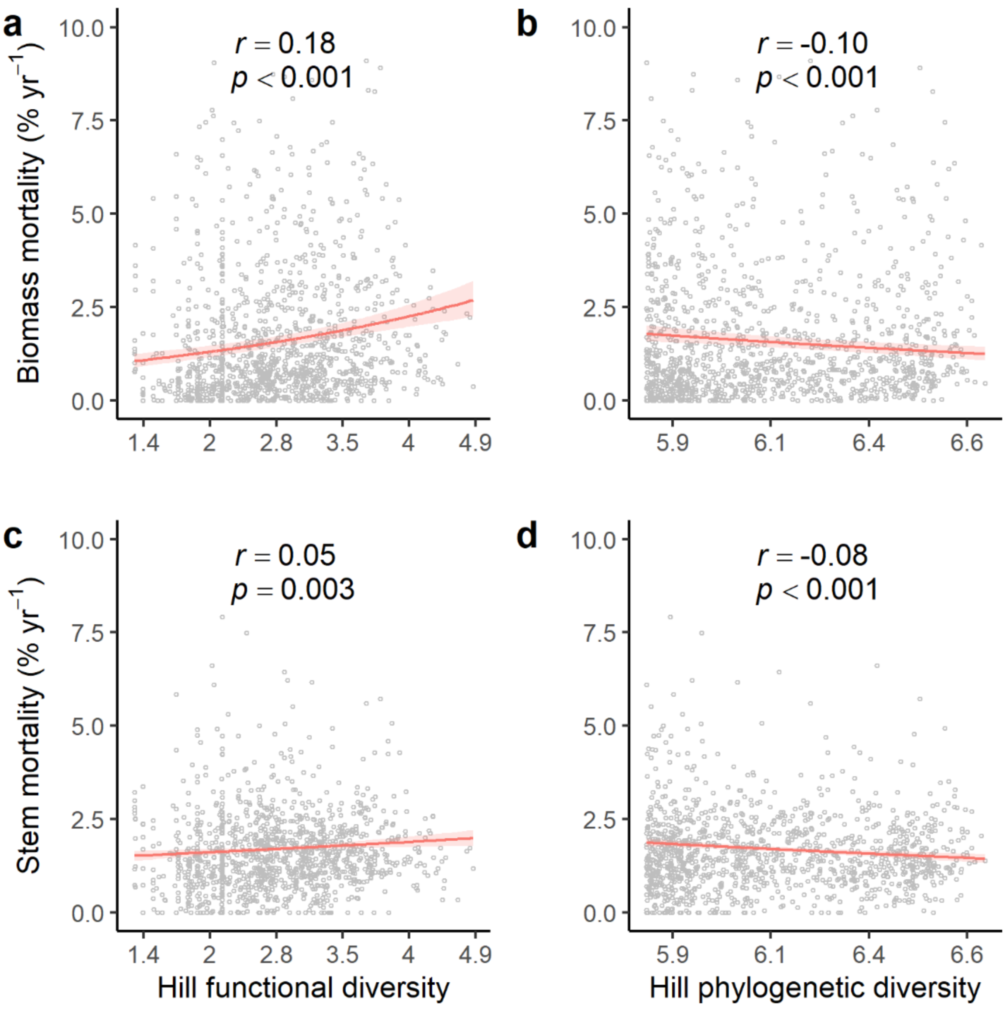

Figure 3-2. Relationships between tree mortality rate and Hill functional and phylogenetic diversity.

a-b, Biomass mortality rate measured as annual biomass loss divided by stand biomass in the previous census in relation to functional diversity (**a**) and phylogenetic diversity (**b**). **c-d**, Stem mortality rate measured as annual stem loss divided by the total number of stems in relation to functional diversity (**c**) and phylogenetic diversity (**d**). Red lines are the fixed-effect slopes with the 95% confidence interval (shaded ribbons), after accounting for the effects of functional composition, climate indices, soil drainage and stand age.

The stem mortality rate model ($R^2 = 0.1$) showed a similar relationship with functional diversity ($r = 0.05$, $p = 0.003$, Figure 3-2c) and phylogenetic diversity ($r = -0.08$, $p < 0.001$, Figure 3-2d). An additional analysis with taxonomic diversity in substitute of functional and phylogenetic diversity showed that stem mortality rate had no statistically significant relationship with taxonomic diversity (Extended Data Figure 3-3b). Our non-significant taxonomic diversity effect differs from a previous study that found a higher mortality probability in diverse temperate and boreal natural forests (Searle et al. 2022) but is similar to those reported for stem mortality rate and diversity in young experimental plantations (King et al. 2023; Liu et al. 2022; Van de Peer et al. 2016). Collectively, our findings and previous results suggest that the divergent relationships between taxonomic diversity and tree mortality could be attributed to the differences in the relative contributions of functional and phylogenetic diversity to taxonomic diversity in a study forest.

We quantified biotic damage, stand density index and size inequality as corresponding mechanisms of biotic feedback from other trophic levels, competition and niche partitioning, respectively (Barry et al. 2019; Reineke 1933). We found that biotic damage had a dominant positive effect on both biomass and stem mortality rates ($r = 0.51$, $p < 0.001$, Figure 3-3a; $r = 0.18$, $p < 0.001$, Figure 3-3d). Biomass mortality rate decreased with stand density index ($r = -0.14$, $p < 0.001$, Figure 3-3b) while stem mortality rate had no significant relationship with stand density index ($r = -0.01$, $p = 0.9$, Figure 3-3e). Both biomass and stem mortality rates decreased with size inequality (Figure 3-3c and 3-3f). In contrast with previous results that high canopy packing and resource competition, represented by stand density and stand basal area, acted as the primary mechanisms causing tree mortality in natural forests (Kulha et al. 2023; Luo and Chen 2011; Searle et al. 2022; Zhang et al. 2015), by simultaneously assessing the three mechanisms, our study highlights that biotic damage serves as the strongest mechanism for tree mortality in large-scale natural forests.

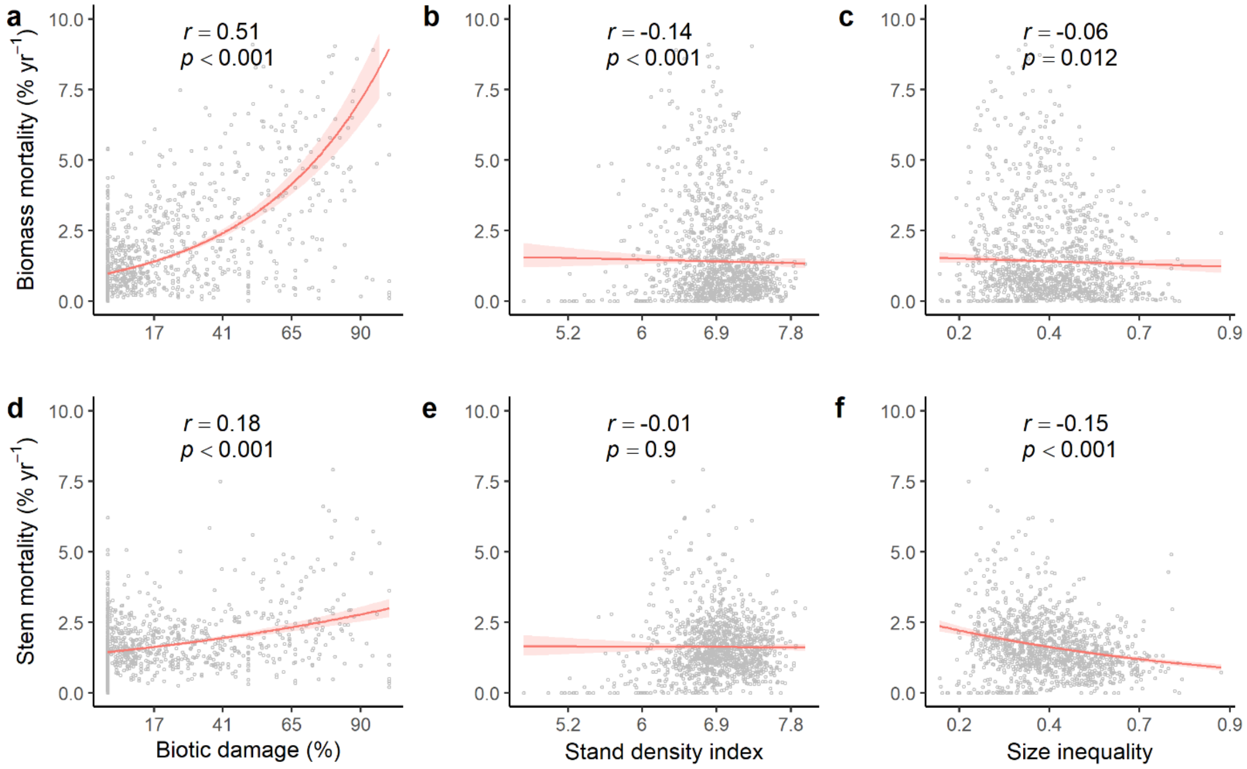

Figure 3-3. Relationships between mortality rate and biotic damage, stand density index, and size inequality.

a-c, Biomass mortality rate in relation to biotic damage (the proportion of dead stems with field-recorded insect and pathogen load) (**a**), stand density index (the Reineks' Stand density index in metric unit) (**b**), and size inequality (the ratio of stand deviation and mean diameter at breast height (**c**). **d-f**, Stem mortality rate in relation to biotic damage (**d**), stand density index (**e**), and size inequality (**f**). Red lines are the fixed-effect slopes with their 95% confidence intervals (shaded ribbons).

The relationships between mortality rate and biotic damage and size inequality are in agreement with our expectations and consistent with previous studies (Koontz et al. 2021; Kurz et al. 2008; Ma et al. 2023; Searle et al. 2022). In contrast, the relationships between biomass and stem mortality and stand density index were unexpected. These relationships suggest that the nearly century-old theory using stand density index to quantify competition developed for monocultures (Reineke 1933) might not be relevant to natural forests where tree diversity could alter the relationship between stand density and competition. For instance, trees in species mixture of a given stand density, in which different species occupy different crown and root positions and have different water and nutrient niches (Brassard et al. 2013; McKane et al. 2002; Silvertown et al. 1999; Williams et al. 2017), might have lower competition intensity than those in a monoculture of the same stand density. Alternatively, the mean stand density index in our study (Extended Data Figure 3-2) was lower than the threshold of maximum density index to become mortality agents based on theory and previous empirical findings (Long 1985; Reineke 1933), and this could explain the non-significant relationship between stem mortality and stand density index. Furthermore, plots of higher biomass mortality are distributed predominantly in interior British Columbia, where both climate water availability and stand density index are low (Extended Data Figure 3-4), and trees in these plots could suffer from greater exposure to solar radiation load (Ma et al. 2023) and exacerbated water stress (Forrester and Bauhus 2016), together contributing to a nonsignificant or even negative relationship between mortality rates and stand density index.

To examine how diversity might influence mortality via the three mechanisms, we modeled the relationships between these mechanisms and diversity. Phylogenetic diversity had negative ($r = -0.15$, $p < 0.001$, Figure 3-4b) and positive ($r = 0.018$, $p < 0.001$, Figure 3-4f) associations with biotic damage and size inequality, respectively, but had no significant association with stand density index ($p = 0.967$, Figure 3-4d). These results indicate that the negative relationship between mortality and phylogenetic diversity ($r = -0.10$, $p < 0.001$, Figure

3-2b) was attributed to the effects of phylogenetic diversity on biotic damage ($r = -0.15 * 0.51 = -0.077$) and size inequality ($r = 0.018 * -0.06 = -0.001$). Lower biotic damage in phylogenetically diverse stands is attributable to lower hostplant abundance (Gilbert and Webb 2007; Gougherty and Davies 2021; Janzen 1970). Our finding extends our understanding of that phylogenetic diversity reduces biotic damage from limited insect or pathogen types observed in local-scale natural forests (Schuldt et al. 2014) and biodiversity experiments (Wang et al. 2019) to a large number of insects and pathogen types across large-scale natural forests (Extend Data Figure 3-1). Higher size inequality in phylogenetically diverse forests could be attributed to the inherent ecological difference among species, which is shaped by evolutionary history (Srivastava et al. 2012). For example, species with different growth rates and shade tolerance could increase above-ground light interception and below-ground abiotic facilitation as well as the shelter to lower layer trees (Ma et al. 2023; Morikawa et al. 2022; Valladares and Niinemets 2008). Our findings highlight that phylogenetic diversity is an important part of a natural-based solution for climate mitigation through reducing tree mortality under ongoing climate change.

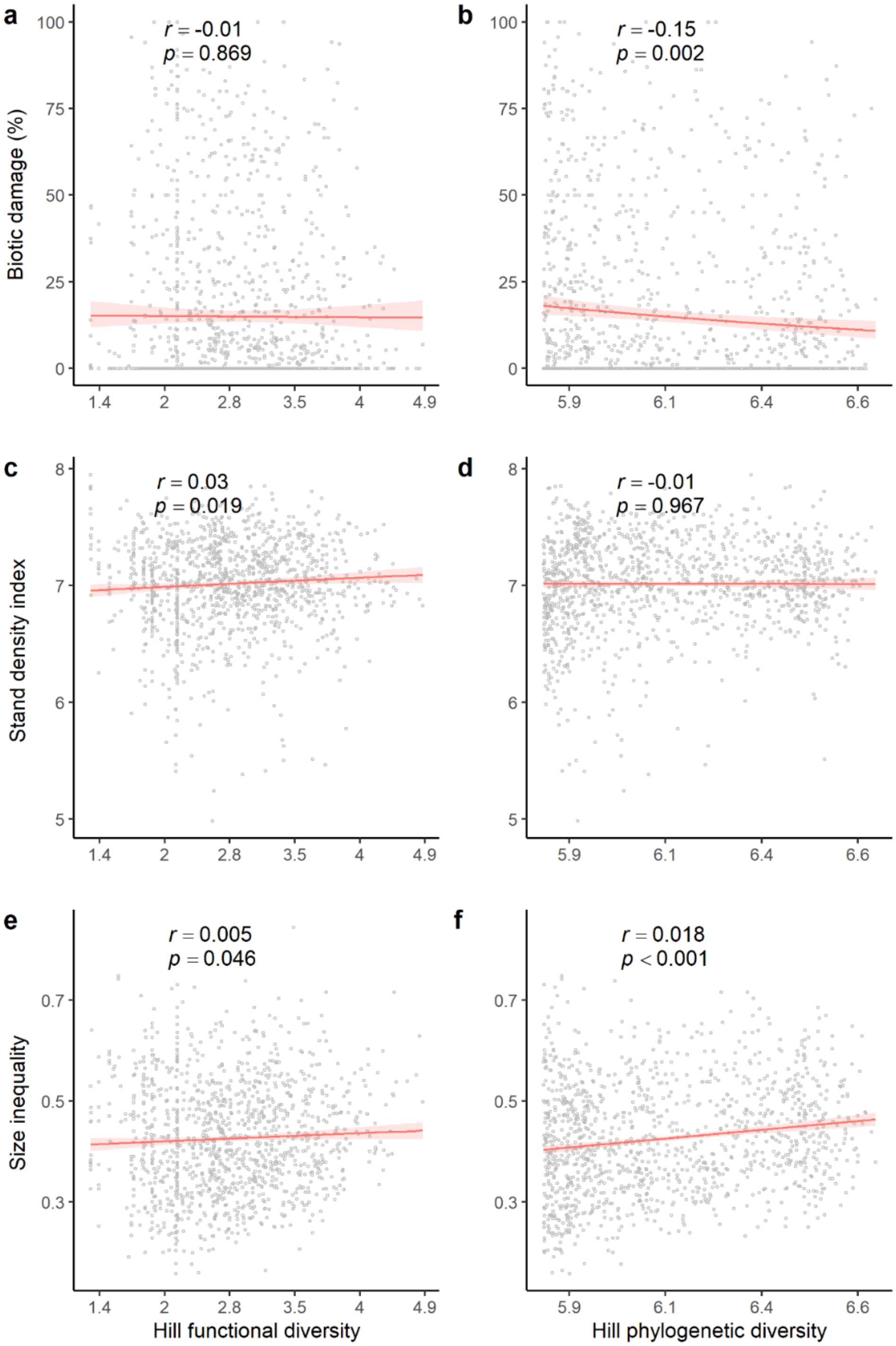

Figure 3-4. Biotic damage, stand density index, and size inequality in relation to Hill functional and phylogenetic diversity.

a-b, Biotic damage in relation to functional diversity (**a**) and phylogenetic diversity (**b**). **c-d**, Stand density index in relation to functional diversity (**c**) and phylogenetic diversity (**d**). **e-f**, Size inequality in relation to functional diversity (**e**) and phylogenetic diversity (**f**). Red lines are the fixed-effect slopes with the 95% confidence interval (shaded ribbons), after accounting for the effects of functional composition, climate indices, soil drainage and stand age.

Functional diversity had no significant relationships with biotic damage (p = 0.9, Figure 3-4a) and was only weakly associated with stand density index and size inequality (r = 0.03, p = 0.019, Figure 3-4d; r = 0.005, p = 0.046, Figure 3-4e). We found the relationship between biotic damage and functional diversity was not influenced even when phylogenetic diversity was excluded from the model (r = -0.07, p = 0.122). Previous biodiversity experiments showed no effect of functional diversity on insect herbivory from one to a few different feeding guides (Haase et al. 2015; Wang et al. 2019). Our study showed that functional diversity had a poor predictable effect on biotic damage from the pool of 143 types of insects and pathogens in natural forests. The lack of an effect of functional diversity on biotic damage quantified for all relevant insects and pathogens was expected because the effects of functional traits on different insect herbivores can vary (Haase et al. 2015; Schuldt et al. 2014). Meanwhile, the positive associations between stand density index and size inequality with functional diversity are related to trees occupying different niches having different growth rates and plasticity abilities (Jucker et al. 2015; Searle et al. 2022; Williams et al. 2017).

The inclusion of functional composition (higher PC1 represents resource acquisitive (broadleaf dominance) and higher PC2 represents drought tolerance) (Extended Data Figure 3-5) improved the variance explained for mortality and other dependent variables (Extended Data

Tables 3-1, 3-2). Higher values of resource acquisitive and drought tolerance traits were associated with higher mortality, higher biotic damage and lower size inequality (Figure 3-5). Specifically, mortality rate increased linearly with PC1 ($r = 0.05$, $p = 0.045$, Figure 3-5a) and increased in a quadratic form with PC2 ($r = 9.54|-4.52$, $p < 0.001$, Figure 3-5b). Biotic damage had no significant relationship with PC1 ($r = 0.01$, $p = 0.796$) but was positively related to PC2 ($r = 0.31$, $p < 0.001$, Figure 3-5c-d). Size inequality had a negative association with PC1 ($r = -0.03$, $p < 0.001$, Figure 5g) and PC2 ($r = -0.04$, $p < 0.001$, Figure 3-5h). Stand density index had no significant associations with PC1 or PC2 (Figure 3-5e, f).

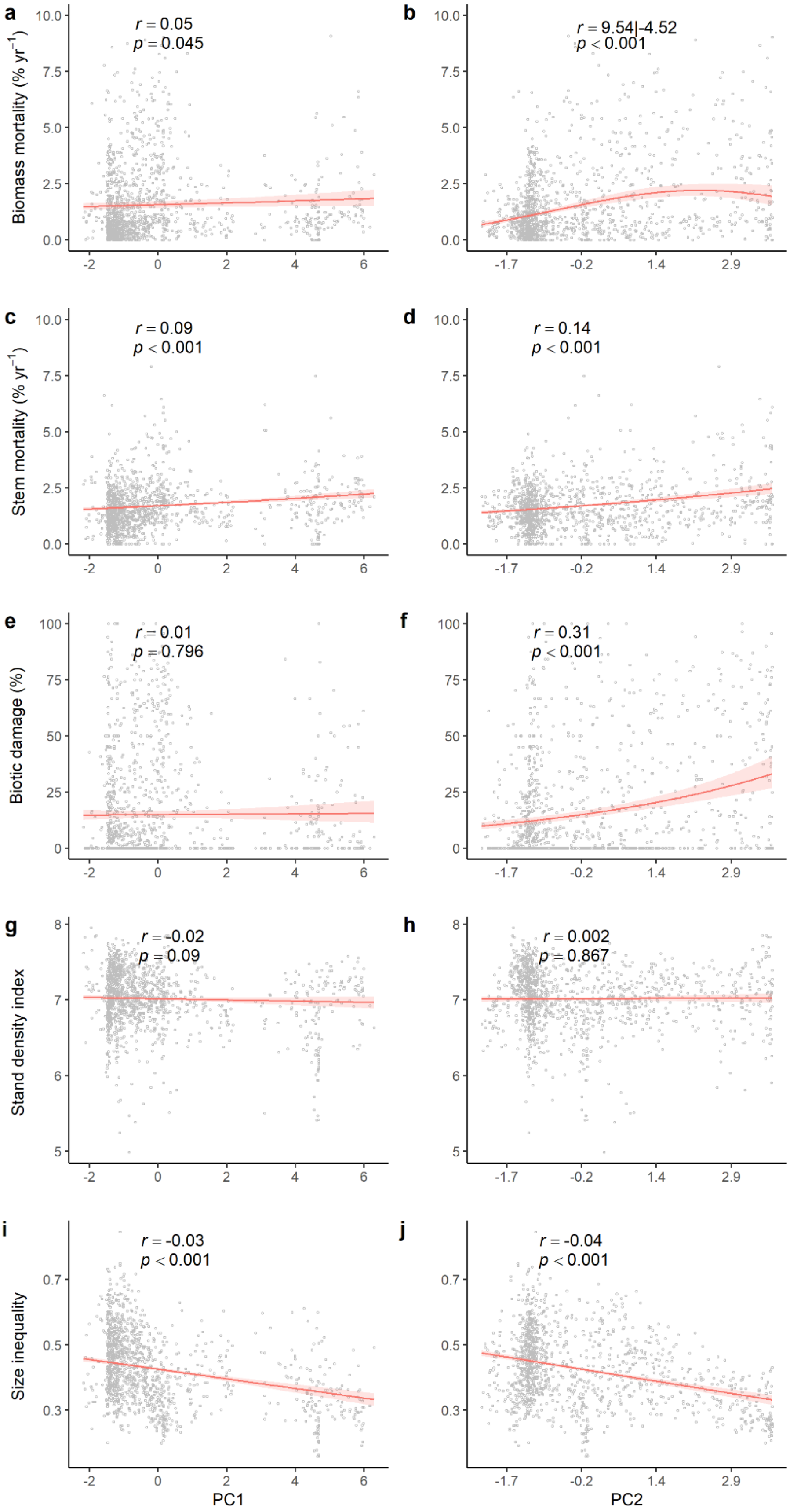
a
r = 0.05
p = 0.045
b
r = 9.54|-4.52
p < 0.001
Biomass mortality (% yr⁻¹)
10.0
7.5
5.0
2.5
0.0
c
r = 0.09
p < 0.001
d
r = 0.14
p < 0.001
Stem mortality (% yr⁻¹)
e
r = 0.01
p = 0.796
f
r = 0.31
p < 0.001
Biotic damage (%)
100
75
50
25
0
g
r = -0.02
p = 0.09
h
r = 0.002
p = 0.867
Stand density index
8
7
6
5
i
r = -0.03
p < 0.001
j
r = -0.04
p < 0.001
Size inequality
0.7
0.5
0.3
-2
0
2
4
6
PC1
-1.7
-0.2
1.4
2.9
PC2

Figure 3-5. Relationships between mortality rate, biotic damage, stand density index, and size inequality and functional composition.

Higher PC1 represents resource acquisitive (broadleaf dominance) and higher PC2 represents drought tolerance (Extended Data Figure 3-6). Red lines are the fixed-effect slopes with the 95% confidence interval (shaded ribbons), after accounting for the effects of functional and phylogenetic diversity, climate, soil drainage and stand age.

Our finding of the slightly higher mortality rate in broadleaves-dominated forests, which have lower values of wood density and higher specific leaf area (Extended Data Figure 3-5), is congruent with a previous global meta-analysis (Greenwood et al. 2017). Simpler vertical structures of broadleaf dominant forests may have contributed to their higher mortality (Ma et al. 2023). Meanwhile, mortality rates are lower in communities of more shade-tolerant coniferous species because shade-tolerant species can better resist pathogens in the shade, and species with different shade tolerance can form a deep and multilayered crown (Valladares and Niinemets 2008). Higher mortality in the communities of drought-tolerant species is consistent with a previous finding that drought-induced mortality is higher in drier populations at sites with high historical drought variability (Anderegg et al. 2019). Geographically in our study, drought-tolerant species were distributed in the interior of British Columbia, where water availability is low with correspondingly high mortality (Extended Data Figure 3-4).

3.5 Conclusion

An improved understanding of the relationships between biodiversity, biotic damage, and tree mortality has important implications on policy decisions tightly related to biodiversity conservation and human welfare (Anderegg et al. 2012; Forzieri et al. 2022; McDowell et al.

2020). We studied the relationships between 143 types of insects and pathogens-induced mortality relationship with different facets of tree diversity across large-scale natural forests while accounting for the influences from climate, soil drainage class, and stand age. Our study provides new direct evidence that phylogenetic diversity reduces tree mortality by decreasing biotic damage from a wide range of forest insects and pathogens in natural forests. Our result extends the previous findings of the phylogenetic diversity effect from single or limited insect herbivory type studied in local scale grassland (Parker et al. 2015), natural forests (Schuldt et al. 2014), biodiversity experiments (Wang et al. 2019) to multiple types of insects and pathogens across large scale natural forests.

Our findings add a new dimension to understanding the relationships between diversity and ecosystem functioning by illustrating how tree mortality decreases with increasing tree phylogenetic diversity. Furthermore, our study demonstrates that feedback at the other trophic level, that is, insects and pathogens, is a key mechanism underlying the relationship between phylogenetic diversity and tree mortality in natural forests, complimenting previous experimental findings of the key role of other trophic organisms played in the relationships between tree diversity and productivity (Laforest-Lapointe et al. 2017; Li et al. 2023; Liang et al. 2019). Our finding suggests that conserving phylogenetic diversity in natural forests or establishing plantations consisting of tree species of greater phylogenetic distances could reduce biotic damage and tree mortality. Such management strategies can help safeguard the forest economy and forests as strong carbon sinks in the era of unprecedented challenges of global warming that the Earth faces.

CHAPTER 4: LONG-TERM STABILITY OF PRODUCTIVITY INCREASES WITH TREE DIVERSITY IN CANADIAN FORESTS

4.1 Abstract

The temporal stability of productivity is a key ecosystem function and an essential service to humanity. Biodiversity experiments with observations up to 20 years indicate that plant diversity increases stability under various environmental changes. However, it remains debated whether short-term experimental findings are relevant to the long-term stability of natural forests. Using natural forest plots across Canada monitored over the past 65 years, we provide strong evidence that higher stability is consistently associated with greater functional and phylogenetic diversity across all lengths of observations. Specifically, increasing functional diversity from its minimum to maximum values improves stability, mean productivity, and the temporal standard deviation of productivity by 14%, 36%, and 28%, respectively. Increasing the phylogenetic diversity increases stability by an additional 1%. Our results highlight that the promotion of functionally and phylogenetically diverse forests could enhance long-term productivity and the stability of natural forests.

4.2 Introduction

The temporal stability of ecosystem productivity, often defined as the ratio of mean productivity (μ) and its variation in time (standard deviation, σ), is a concern due to the ongoing simplification of local communities (i.e., loss of local biodiversity) from anthropogenic disturbances (Hooper et al. 2005; Tilman et al. 2006; Wagg et al. 2022). Recently, two decadal-length tree diversity experiments have also demonstrated that species richness stabilizes the temporal stability of forest productivity (Schnabel et al. 2019; Schnabel et al. 2021). However, it remains unclear whether these positive relationships between diversity and stability based on short-term, small-scale manipulation experiments can be extended to long-term, large-scale, complex natural forests, which experience major climate and biotic disturbances with cycles of multiple decades. For example, moderate to severe droughts (measured as Palmer's drought severity index < 2 units of the standard deviation below the long-term mean) occur only once in several decades (Bonsal et al. 2011; Trenberth et al. 2014). Meanwhile, outbreaks of major forest insects, such as spruce budworms (*Choristoneura fumiferana* [Clem.]) and mountain pine beetles (*Dendroctonus ponderosae* Hopkins) in North America, take place every 30 to 40 years (Boucher et al. 2018; Canadian Council of Forest Ministers 2021). Variations in ecological properties, including productivity, can increase with the occurrence of major climate and biotic disturbances (Gaiser et al. 2020; Lindenmayer et al. 2012), probably weakening relationships between diversity and stability. Long-term, large-scale data from natural communities could help reveal real-world relationships between diversity and stability and demonstrate the utility of science to the development of forest management policies such as forest management planning manuals and silviculture guidelines.

The temporal stability of productivity can increase with diversity through the so-called insurance effect in two ways (Yachi and Loreau 1999). First, mean productivity can increase with diversity (i.e., 'performance-enhancing effect') due to complementarity among species, including resource partitioning, abiotic facilitation and biotic feedback, and the positive selection effect (Barry et al. 2019; Grossiord 2020). Second, the σ is composed of the components of variance (individual species) and covariance (correlation between species). While the variance scaled with productivity increases with diversity, the covariance component can decrease because other species compensate for the loss of biomass from some species ('buffering effect'), that is, community-wide species asynchrony (thereafter, asynchrony) (Loreau and de Mazancourt

2008). This is because species can respond asynchronously to environmental fluctuations due to the different intrinsic traits and response time among species, that is, compensatory dynamics, as well as statistical-averaging effects, both of which can correlate with taxonomic, functional and phylogenetic diversity at the community level (de Bello et al. 2021; Loreau and de Mazancourt 2013; Tilman 1999; Zhao et al. 2022).

Species can also respond asynchronously to other trophic organisms due to attacks from species- or genus-specific insects and pathogens, which occur periodically in nature (Barrett and Heil 2012), which can be predicted based on the phylogenetic signal in the insect- and pathogen-host range (Gilbert and Webb 2007; Gougherty and Davies 2021; Jactel et al. 2021). For example, plant species abundance and their phylogeny distance relatedness influence insect and pathogen damage and plant productivity (Liang et al. 2019; Parker et al. 2015). In phylogenetically diverse plant communities, plant productivity can be greater on average due to reductions in biotic damage, while its temporal standard deviation may be smaller due to asynchronous responses of plants to their respective insects and pathogens (Flower and Gonzalez-Meler 2015; Jactel et al. 2021). Accordingly, we hypothesized that diversity would increase mean productivity due to complementarity among species and increase the temporal standard deviation of productivity but to a lesser extent due to asynchrony induced by taxonomic, functional, and phylogenetic diversity, offsetting the increased variance scaling to higher productivity (Figure 4-1).

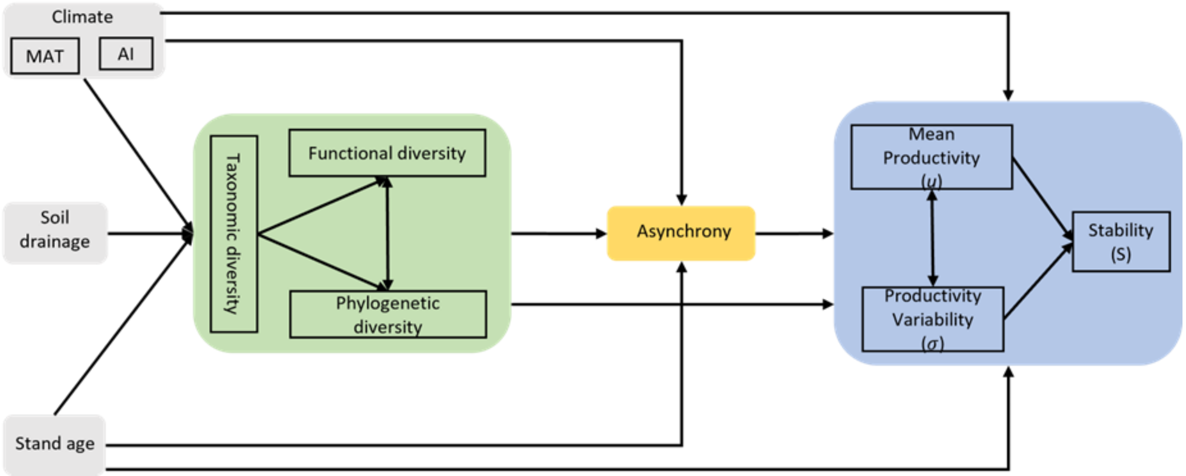

Figure 4-1. A priori causal pathways of tree diversity, climate and soil conditions, and stand age on asynchrony, mean productivity, temporal standard deviation of productivity and temporal stability of productivity.

Previous studies in natural forests have reported positive (del Rio et al. 2017; Jucker et al. 2014; Ouyang et al. 2021), negative (Dolezal et al. 2020) and nonsignificant (Li et al. 2022) relationships between tree species richness and productivity stability. These divergent findings can arise for several reasons. First, different lengths of observation (the number of years between the initial and last censuses) can influence the estimation of diversity and stability relationships. For example, diversity experiments have shown that the positive effects of diversity on productivity increase over stand development (Reich et al. 2012; Zhang et al. 2012), suggesting an enhanced positive diversity and stability relationship with a longer census duration. However, long temporal scales can increase the standard deviation of productivity (Gaiser et al. 2020; Lindenmayer et al. 2012). Second, species richness per se provides limited information to predict asynchrony and stability (Dolezal et al. 2020; Valencia et al. 2020; Xu et al. 2021). Although functional diversity and phylogenetic diversity have been shown to promote ecosystem stability in experimental systems (Cadotte et al. 2012; Craven et al. 2018), their roles are largely ignored in studies in natural forests (Dolezal et al. 2020; Yuan et al. 2019), where environmental fluctuations and natural enemies (which may be more in tune with phylogenetic diversity than taxonomic diversity) such as insect herbivores prevail and have pivotal influences on forest productivity (Canadian Council of Forest Ministers 2021; Jactel et al. 2021; Ma et al. 2012). Third, in natural forests, both diversity and stability are likely determined by climate factors, local site conditions, and stand development, whose effects need to be taken into account (and standardized) when quantifying their relationships between diversity and ecosystem functions (Chen et al. 2023; Grace et al. 2016) (Figure 4-1). Therefore, these confounding factors need to be studied and accounted for to achieve the generality of the relationship between diversity and stability in long-term and large-scale natural forests.

Our objective was to examine the relationship between long-term stability of productivity and multifacet diversity and its underlying mechanisms in natural forests across Canada. We determined the relationships between temporal stability of productivity and tree diversity using 65 years (1951-2016) of data collected from 7498 repeatedly measured unique plots of aboveground live biomass across Canada (*see* Methods for plot selection criteria, Figure S4-1). We calculated aboveground biomass and derived (interval-averaged) annual biomass growth for each tree and then summed all individual tree growth, including those from recruits that appeared between two consecutive censuses, to the stand level on a per hectare basis (see *Methods*). We calculated the mean and standard deviation of productivity for each plot over temporally repeated measurements (Tilman et al. 2006), whose lengths of observation (the number of years between the first and last census, that is, the census length thereafter) varied from 8 to 52 years. The μ and σ dependence on diversity was also tested. To produce a meaningful comparison of their dependence on diversity, we employed unified Hill diversity indices. Our initial model included Hill taxonomic diversity, functional diversity, and phylogenetic diversity as well as covariates, but the model had large values of variance inflation factor (Table S1). As recommended (Zuur et al. 2010), we developed two models, one included Hill functional and phylogenetic diversity, and the other included Hill taxonomic diversity to reduce collinearity and overfitting. We selected Hill functional diversity (FDq1), Hill phylogenetic diversity (PDq1), and Hill taxonomic diversity (Divq1), with q =1 based on Akaike's information criterion (Table S4-2). Temporal stability, μ and σ were detrended by including the year (middle calendar year of the initial and last measurement years) of each plot as a covariate in the statistic models to account for the variation attributable to temporal trends of productivity, similar to previous studies (Lepš et al. 2019; Tilman et al. 2006). Stability, μ and σ, and diversity, stand age were log-transformed to improve normality and their linear relationships. All variables were scaled prior to analyses to enable direct comparison between different models using standardized coefficients. We first show the relative importance of predictors (standardized coefficients) and their partially predicted relationship with linear mixed models (Table S4-3). Then, we presented the results of structural equation models (SEM) to show their casual relationships.

4.3 Materials and Methods

4.3.1 Study area and available data

To examine the long-term stability of productivity, we used a network of permanent sampling plots (PSPs) established by the provincial governments of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Nova Scotia and Newfoundland and Labrador since 1940s (Figure S4-1). The selected PSPs followed these criteria: (i) unmanaged, with known stand age; (ii) have all trees marked with their diameter at breast height (DBH) > 9 cm; (iii) have

≥ three censuses of repeated measurements; (iv) plot size ≥ 400m^2; (v) have at least 20 trees with DBH ≥ 9 cm on average between the first and last measurement. Since the provinces used different DBH thresholds for measurement, we standardized all plots by accounting for only trees with the largest threshold used (Saskatchewan), DBH ≥ 9 cm. Following these criteria, a total of 7498 unique permanent sampling plots (PSP) with 29430 observations between 1951 and 2016 were selected. The selected plots have an average plot size of 528 m^2, ranging from 400 m^2 to 2023 m^2. Mean annual temperature and aridity index varied from -4.3℃ to 9.7℃ and from 0.3 to 6.6, respectively. Their total measurement length, the number of years between the first and last census, ranged from 8 to 52 years, and the mean length was 36.1 years. The number of censuses ranged from 3 to 8, and the mean was 4.

For each plot, we calculated the temporal stability of productivity as μ/σ, where μ is the mean value of the annual increase in aboveground biomass over each census interval (Mg ha^{-1} yr^{-1}), including the growth of surviving trees and new recruitments over repeated measures (Chen et al. 2016) and σ as their temporal standard deviation over its repeated measurements (Tilman et al. 2006). The aboveground live biomass (Mg ha^{-1}) was the sum of biomass from stem, bark, leaves, and branches that applied specific allometric equations to different parts of species in Canada and was standardized by plot size per hectare (Lambert et al. 2005).

4.3.2 Hill number of phylogenetic diversity, functional diversity, taxonomic diversity

We employed the unified diversity indices, including Hill functional, phylogenetic, and taxonomic diversity, to enable a meaningful and complementary comparison of their relative importance on temporal stability (Chao et al. 2014a; Chao et al. 2014b). Using the '*HillR*' package, we prepared the community data of the relative basal area of each tree species for each plot at each census, functional traits and the phylogenetic tree of the 84 species that appeared in our study. We obtained eight functional traits related to species growth and reproduction for each tree species from the TRY database (Kattge et al. 2020). These traits are leaf nitrogen content per leaf dry mass (Nmass), leaf phosphorus content per leaf dry mass (Pmass), specific leaf area (SLA), wood density (WD), shade tolerance (ST) (class 1–5), drought tolerance (DT) (class 1–5), leaf habit (Habit) (deciduous = 1 versus evergreen =0), and leaf structure (broadleaf = 1 versus conifer =0) (Niinemets and Valladares 2006). Euclidean distance was used to calculate functional diversity. We obtained the phylogenetic tree via the '*phylo.maker*' function from '*PhyloMaker*' package (Jin and Qian 2019). The Hill diversity of taxonomic, functional, and phylogenetic diversity at q = 0 is simply species richness. For q = 1, it is the (exponential) Shannon entropy and for q =2, it is the inverse Simpson index (Chao et al. 2014b). The Hill diversity metrics of q = 1 and 2 are influenced by the dominant species that are not biased due to the sample size and are sufficiently accurate in estimating diversity without the need for rarefaction (Chao et al. 2021). Because Hill taxonomic, phylogenetic and functional diversity varied temporally over censuses within each plot, we used their average values, respectively, similar to previous studies (Tilman et al. 2006).

4.3.3 Asynchrony, compensatory dynamics, and statistical averaging

Asynchrony was calculated at the community level and defined as 1- synchrony. Synchrony was calculated as $\frac{\sigma_{x_T}^2}{\left(\sum_i \sigma_{x_i}\right)^2}$, the ratio between the variance of the aggregated community productivity and the summed variances of the productivity of individual species (Loreau and de Mazancourt 2008). We calculated the synchrony index using the package '*codyn*' (Hallett et al. 2016) and selected the metric of 'Loreau', which was not sensitive to variable species richness across communities. This community-wide species asynchrony is standardized between 0 (perfect synchrony, that is, for monocultures) and 1 (perfect asynchrony).

Compensatory dynamics is the reduction in productivity of some species being compensated by other species. It is determined by the negative species covariance and measured as the summed standard deviation of individual species productivity divided by the standard deviation of the community productivity, $\frac{\sqrt{\sum_i \sigma_i^2}}{\sigma_{comm}}$ (Zhao et al. 2022). Values above 1, reflecting compensatory dynamics, correspond to great community stability. Statistical averaging, or the portfolio effect, assumes that species within communities are independent, and the scaled variance decreases with species richness (1/ species richness) (Doak et al. 1998). It was measured as $\frac{\sum_i \sigma_i}{\sqrt{\sum_i \sigma_i^2}}$ (Zhao et al. 2022).

4.3.4 Climate factors, local soil conditions, stand age, and middle calendar year

Similar to the previous study (Searle et al. 2022), we used plot spatial locations to derive plot climate and soil condition. We extracted the mean annual temperature (MAT, °C) from the WorldClim dataset (Fick and Hijmans 2017) and the aridity index (AI) from CGIAR Consortium (Zomer et al. 2022) (https://cgiarcsi.community/) for each plot location between 1951 and 2016 for each plot as proxies for the site-specific local historical climate. We obtained the soil drainage level (increasing soil water availability from 1 to 7) from SoilGrids to represent the local soil characteristics (Chen et al. 2002; Hengl et al. 2017). Stand age for each plot was determined based on the last recorded stand-replacing fire or by coring at least three dominant/codominant trees of each species inside or outside the plot when the plots were established. The average ring counts of the oldest tree samples provided a conservative estimate of the time since stand establishment (Vasiliauskas and Chen 2002). During the long-term sampling, we estimated stand age and year as the middle age and middle year between the first and last census, respectively, to account for the temporal difference among plots.

4.3.5 Statistical analysis

All statistical analyses were performed in R 4.3.2 (R Core Team 2024). The Hill taxonomic, functional, and phylogenetic diversity at q = 1 was best to predict stability, μ and σ, based on the lowest Akaike's information criterion (AIC), obtained by the '*dredge*' function using the package "*MuMIn*" (Table S4-2). We included census length as the covariate and the number of censuses as the random variable to minimize the influence of random sampling efforts. Similar to previous studies, we tested the spatial autocorrelation of residuals using Moran's I test and found significant effects of spatial autocorrelation for μ , Hill functional and phylogenetic diversity models. Subsequently, similar to previous studies (Aguirre-Gutierrez et al. 2022), we calculated the spatial distance at which such spatial effect decreased to nonsignificant for those models. We found that a distance of 0.3 km was the most appropriate and generated an identification for each group of plots (groupID) as the random factor in the models mentioned above (Table S4-2). The normality of all component model residuals was met (Figure S4-6).

The coefficient plot showed the relative importance of predictors in stability and its components. The regression plot showed the partial relationships between predictors and stability as well as its components. We also employed structural equation modelling (SEM) to show a full view of the direct and indirect paths involved in the component models. We started from the full model based on the prior path diagram (Figure 4-1) and modified the model based on the theoretical assumption and statistical estimation. SEMs that achieved a good fit were selected based on the recommended evaluation parameters, the chi-square test ($p > 0.05$ for a satisfactory fit) (Kenny et al. 2015). The lower Akaike information criterion (AIC) was used to select SEM alternatives. We used the ‘PiecewiseSEM’ package for our structural equation model analyses (Lefcheck 2016).

Because functional and phylogenetic diversity were correlated, we investigated phylogenetic signals within functional traits, following (Keck et al. 2016) (Figure S4-5). Following the previous study (Carol Adair et al. 2018), we calculated the range change as the difference between the maximum value of predictor times standardized effect size and the minimum value of predictor times standardized effect size. The percentage change was calculated as the range change divided by the unscaled mean value of each response variable, such as stability, μ and σ.

To address the mechanisms associated with species asynchrony in the diversity-stability relationship (Tilman 1999), we examined the relationship between stability (also its components) and compensatory and statistical averaging effects, following the method described previously (Zhao et al. 2022). Furthermore, we examined how compensatory and statistical averaging effects were related to Hill functional and phylogenetic diversity.

The inclusion of all three diversity indices (functional, phylogenetic, and taxonomic diversity) resulted in high values of variable inflation factor (VIF) for taxonomic diversity (Table S4-1). To minimize collinearity (Zuur et al. 2010), we modeled the effects of taxonomic diversity separately from those of functional and phylogenetic diversity. The taxonomic diversity SEM explained a similar magnitude of variation in stability (Figure S4-3). To facilitate comparisons among predictors and models, we scaled all variables, that is, minus their respective means and divided by their standard deviations, prior to analysis.

4.4 Results

The linear mixed models based on FDq1 and PDq1 explained conditional variance from 0.42 to 0.88 for stability, mean productivity, and standard deviation of productivity (Table S4-3). Asynchrony was the dominant predictor of greater stability (standardized coefficient $r = 0.72$), while stability decreased with FDq1 and PDq1 ($r = -0.23$ and -0.07, respectively) (Figure 4-2A). Mean productivity increased with FDq1 and asynchrony ($r = 0.20$ and 0.05, respectively) (Figure 4-2B). Standard deviation showed a dominant negative association with asynchrony ($r = -0.61$) and positive relationships with FDq1 and PDq1 ($r = 0.35$ and 0.08, respectively, Figure 4-2C). The same pattern was found in the models predicted by Divq1 (Figure S4-3, Table S4-4). The sum effects of FDq1 and PDq1 on stability (sum $r = -0.29$) were slightly greater than that of Divq1 ($r = -0.25$), while they had a smaller effect on mean productivity than (sum $r = 0.20$; Divq1 $r = 0.23$), but greater effects on standard deviation (sum $r = 0.43$; Divq1 $r = 0.38$) and asynchrony (sum $r = 0.53$; Divq1 $r = 0.50$) (Tables S3 and 4).

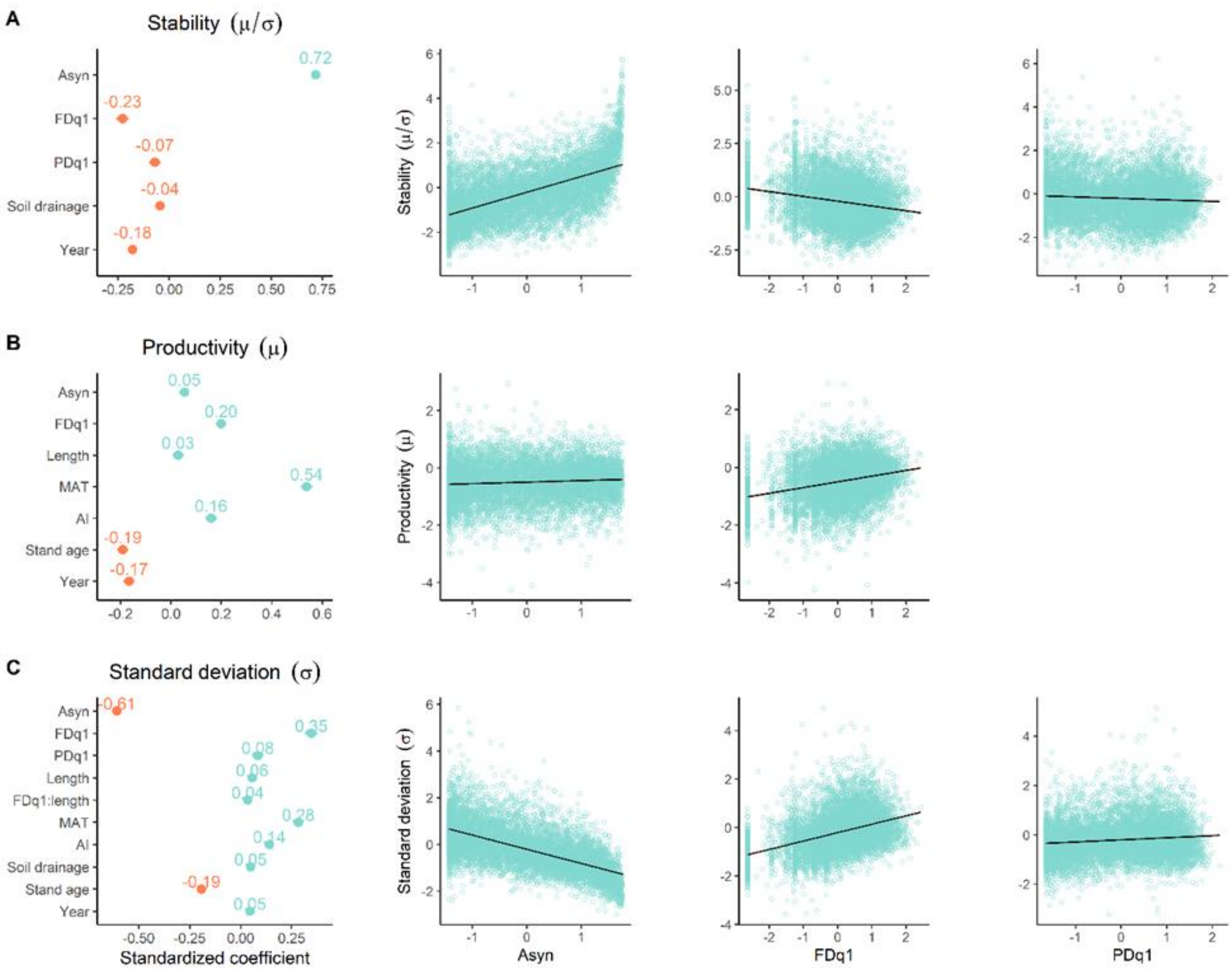

Figure 4-2. Relationship between stability, mean productivity, and standard deviation and asynchrony, diversity, and covariates.

The scatterplots are partial relationships between variables. Asyn: community-level species asynchrony; FDq1: Hill functional diversity at q = 1; PDq1: Hill phylogenetic diversity at q =1; MAT, AI, and stand age are the long-term averaged mean annual temperature, the long-term averaged aridity index, and the average stand age from the first to last measurement. Soil drainage indicates how rapidly water is removed from soil in relation to supply ranging from 1 (very rapidly drained) to 7 (very poorly drained). Census length (length) is the number of years between the first and last measurement of each sample plot. The year is the middle calendar year of all measurement years of each sample plot; Stability, mean productivity, standard deviation, and stand age were log-transformed. All variables were scaled.

The SEM based on FDq1 and PDq1 conformed well with data and explained 42% of the stability variances (Figure 4-3A). Stability was positively related to asynchrony (standardized coefficient $r = 0.72$, Figure 4-3A). Both FDq1 and PDq1 were positively related to stability through their influence on asynchrony, and the positive association between asynchrony and FD was more than three times stronger than between asynchrony and PD ($r = 0.30$ and 0.08, respectively) (Figure 4-3A). Meanwhile, FDq1 and PDq1 had direct negative relationships with stability ($r = -0.23$ and -0.08, respectively) (Figure 4-3A). As a result, the total effect of FDq1 was 0.07, and that of PDq1 was 0.01 (Figure 4-3A). Based on SEM, stability increased by 14% and 1%, increasing FDq1 and PDq1, respectively, from their minimums to maximums. In addition, stability showed the same dependence on Divq1 directly and indirectly. The total effect of Divq1 on stability ($r = 0.09$, Figure S4-3) was almost the sum of the effects of FDq1 and PDq1 on stability ($r = 0.07$ and 0.01, respectively).

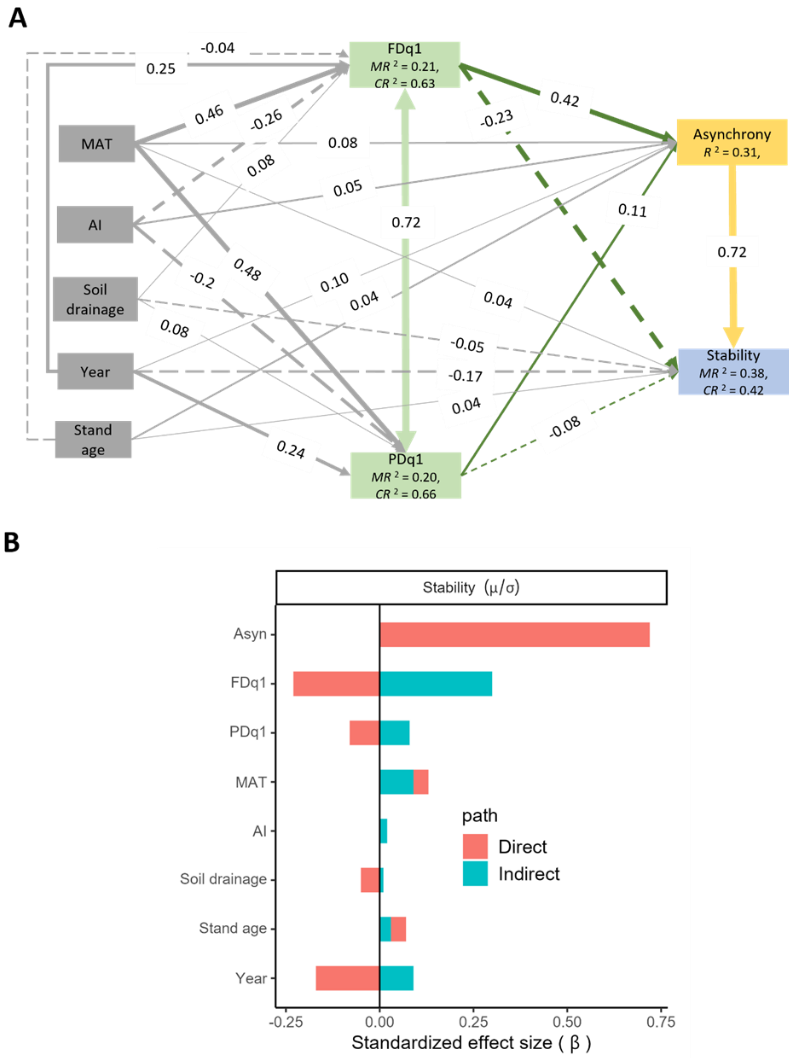

Figure 4-3. Structural equation model showing tree diversity, climate, soil conditions, and stand age on the long-term stability of productivity in natural forests.

A, Path diagram of attributes influencing stability. **B**, Direct and summed indirect effects. Numbers adjacent to arrows are standardized path coefficients analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. The proportions of marginal and conditional variance explained (MR^2 and CR^2, respectively) appear alongside every response variable. The goodness-of-fit statistics for panel a are Fishers' C = 5.4 and P = 0.492, indicating a close model-data fit. All variables are described in Figure 4-2.

The SEM for the stability components also conformed well to the data and explained 88% and 71% of the variance in μ and σ, respectively (Figure 4-4). Specifically, FDq1 had a direct association with μ ($r = 0.20$, Figure 4-4A), while σ was directly associated with FDq1 and PDq1 ($r = 0.35$ and 0.09, respectively, Figure 4-4B). Meanwhile, μ increased with FDq1 and PDq1 ($r = 0.02$ and 0.01, respectively), while σ decreased with FDq1 and PDq1 indirectly through asynchrony ($r = -0.25$ and -0.07, respectively, Figures. 4-4, 4-5). Overall, FDq1 had a greater total effect on μ than PDq1 ($r = 0.22$ and 0.01, respectively), and σ decreased with FDq1 and PDq1 ($r = 0.10$ and 0.02, respectively) (Figures. 4-4, 4-5). Increasing the value of FDq1 from minimum to maximum increased 36% and 28% in μ and σ, respectively. Increasing the PDq1 value from minimum to maximum increased μ and σ by 1% and 4%, respectively.

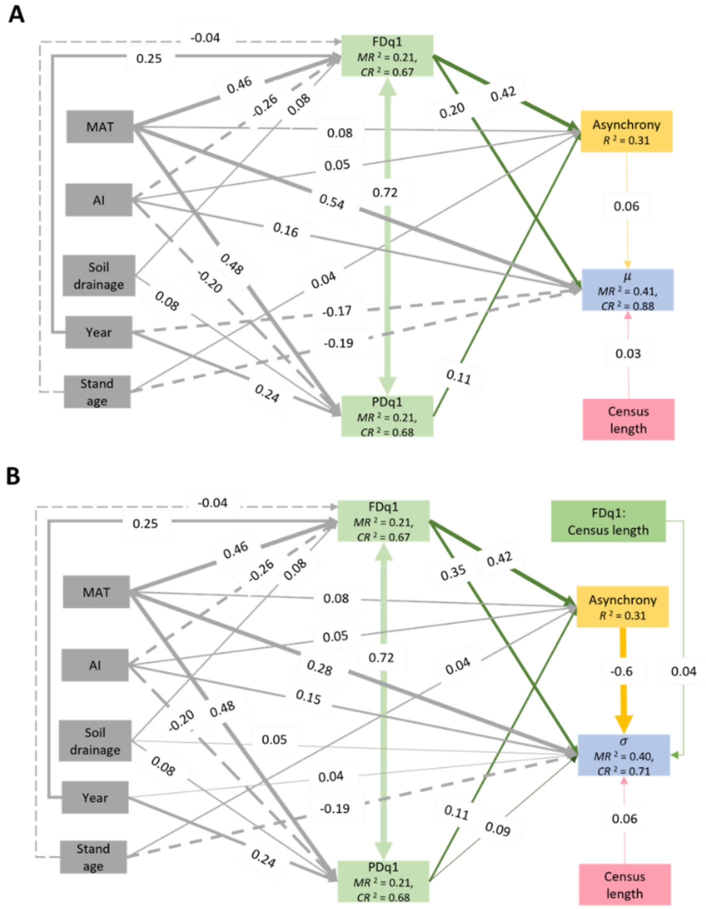

Figure 4-4. Structural equation model showing tree diversity, climate and soil conditions, and stand age on mean productivity (μ) and productivity standard deviation (σ) in long-term natural forests.

A, Path diagram of attributes influencing μ. **B**, Path diagram of attributes influencing σ. Numbers adjacent to arrows are standardized path coefficients analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. The proportions of marginal and conditional variance explained (MR^2 and CR^2, respectively) appear alongside every response variable. The goodness-of-fit statistics for panel a and b is Fishers'C = 18.2 and P = 0.196, indicating a close model-data fit. All variables are described above.

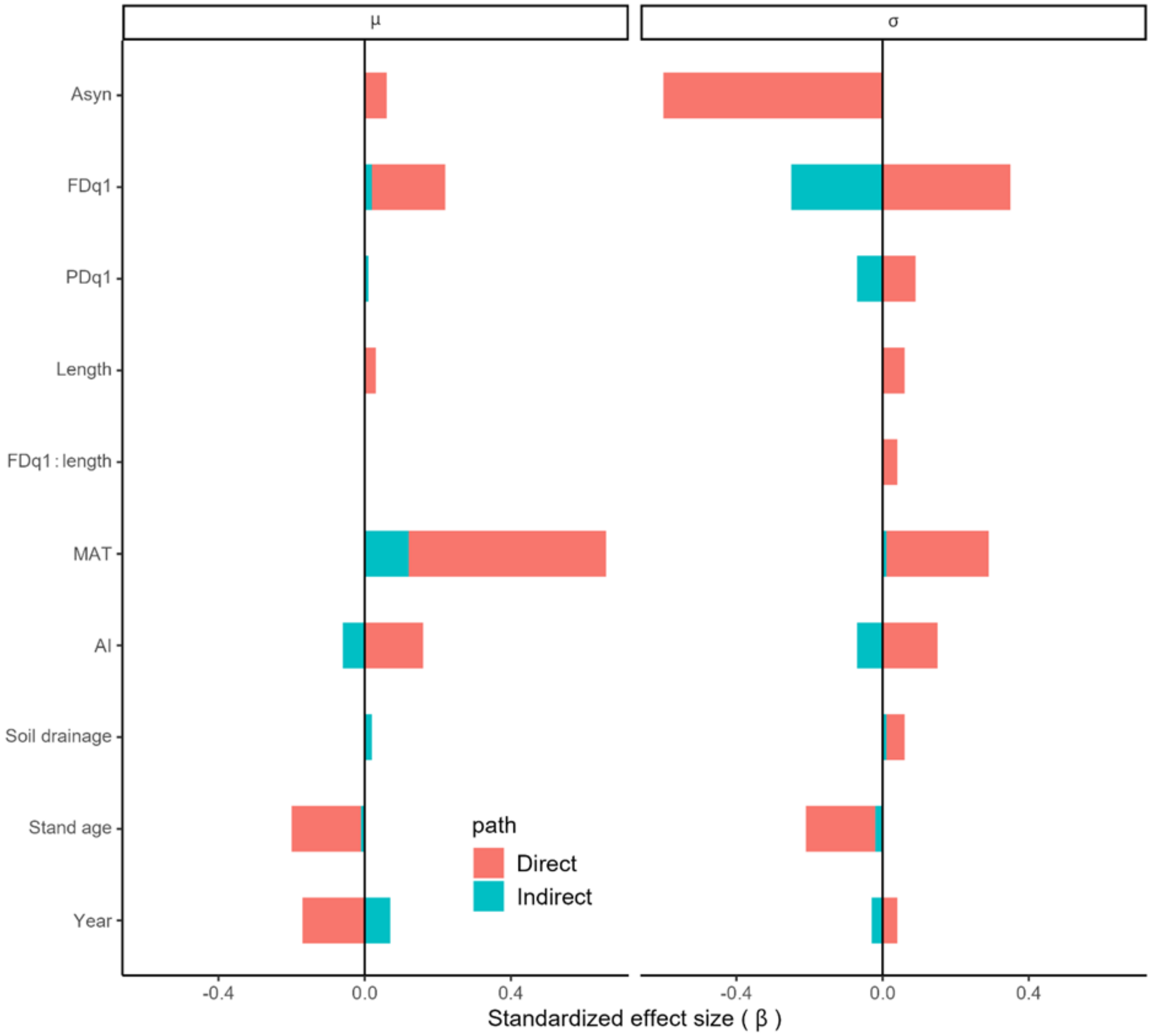

Figure 4-5. The bar plot of summarized direct and indirect paths by predictors on mean productivity (μ) and productivity standard deviation (σ) in long-term natural forests. All variables are described in Figure 4-4.

Diversity indices were higher in warmer sites (i.e., higher mean annual temperature, MAT) and lower in humid sites (i.e., higher aridity index, AI) (Figure 4-3, Figure S4-1). Stability was positively related to MAT and AI when both direct and indirect effects were included (Figure 4-3b). Meanwhile, μ increased more with MAT and AI than σ did (Figure 4-5). Soil drainage class had minor influences on stability, μ and σ (Figures. 4-3, 4-5). Stand age had a positive relationship with stability, corresponding with a stronger negative association with σ than μ (r = 0.07, -0.22, and -0.20, respectively, Figures. 4-3, 4-5). The middle calendar year of the sample plots had a negative relationship with stability due to a greater decrease in μ and a weak increase in σ (r = -0.08, -0.10, 0.01, respectively, Figures. 4-3, 4-5). Stability did not change with census length. However, μ and σ were greater for plots with longer census lengths (Figures. 4-3, 4-5).

4.5 Discussion

Our analysis indicates that species asynchrony served as the dominant mechanism underlying the positive relationship between diversity and the long-term stability of our studied natural forests. This finding is consistent with those previously reported in short-term experimental and observational studies (Craven et al. 2018; Hautier et al. 2014; Schnabel et al. 2021; Tilman et al. 2006; Wagg et al. 2022). By decomposing species asynchrony into compensatory and statistical averaging effects following a method described previously (Zhao et al. 2022), we found that the compensatory dynamics had twice as large an effect on stability as the statistical averaging (r = 0.60 and 0.34, respectively) by increasing mean productivity and decreasing standard deviation (Figure S4-4). However, the compensatory effect was only weakly associated with functional diversity (r = 0.05), while the statistical averaging effect was more positively associated with both functional and phylogenetic diversity (r = 0.59 and 0.21, respectively) (Figure S4-4). Our findings provide new evidence supporting the theoretic expectation that compensatory dynamics play a strong role in ecosystem stability in heterogenous environments (Loreau and de Mazancourt 2013), such as in the natural forests we studied. Nevertheless, similar to a previous grassland study (Zhao et al. 2022), statistical averaging contributed more to the relationship between diversity and stability than did compensatory dynamics.

We found that functional diversity served as a strong predictor for stability. This finding is in agreement with the theoretical expectation that functionally diverse communities have a high probability of containing species that occupy different ecological niches, showing different preferences for internal or external factors, leading to asynchronous responses between species and resulting in more stable community productivity (Loreau and de Mazancourt 2013). Our finding of a stronger effect of functional diversity than phylogenetic diversity on stability differs from those of some prior studies of experimental grasslands (Craven et al. 2018) and natural forests (Dolezal et al. 2020). One of the possible reasons for the difference in their relative importance could be how they were quantified. Previous studies quantified functional diversity as the sum of dissimilarity in the trait space of pairwise species and phylogenetic diversity as the mean pairwise distance, while we employed the unified Hill functional, phylogenetic and taxonomic diversity, which arguably allows a more meaningful comparison of their relative importance in ecosystem functions (Chao et al. 2014b). However, similar to previous studies (Paquette et al. 2015), higher functional diversity was associated with higher phylogenetic diversity in our data set ($r = 0.72$, Figure 4-3), suggesting that the effects of functional diversity estimated in our statistical models accounted in part for those from phylogenetic diversity. This view was supported by the strong phylogenetic signals in leaf structure and leaf habitat traits (Figure S4-5).

We found that diversity increased mean productivity and, to a lesser extent, productivity standard deviation. Numerous studies have reported higher mean productivity in diverse ecosystems (Feng et al. 2022; Liang et al. 2016; Zhang et al. 2012). The positive diversity-productivity relationship is usually contributed by the positive selection effect and more so by complementarity effects of niche partitioning and facilitation related to functional and phylogenetic diversity (Barry et al. 2019; Grossiord 2020). Higher diversity is associated with higher mean productivity due to increased utilization and retention of aboveground and belowground resources (Brassard et al. 2013; Chen et al. 2022; Chen et al. 2023; Williams et al. 2017). Furthermore, given the longer time intervals on average for our study than for most experiments in grasslands or forests, our positive diversity and mean productivity relationship likely reflect stronger diversity impacts that develop with longer periods (Reich et al. 2012; Zhang et al. 2012). As expected and previously demonstrated in short-term studies of natural grasslands and forest plantations (Hautier et al. 2014; Schnabel et al. 2021), we found that higher diversity was associated with higher asynchrony, resulting in a lesser increase in long-term standard deviation than mean productivity in natural forests. The greater decrease in standard deviation through asynchrony related to functional and phylogenetic diversity could be attributed to the asynchronous responses of different tree species to temporal environmental fluctuations (Loreau and de Mazancourt 2008) and to their respective insects and pathogens (Flower and Gonzalez-Meler 2015; Jactel et al. 2021).

Our finding that higher temperatures promoted diversity and mean productivity is consistent with previous studies (Chen et al. 2023; Zhang et al. 2017b). Furthermore, higher temperatures promote stability through diversity and asynchrony, as suggested previously (Oliveira et al. 2022). However, increasing the aridity index (higher moisture) decreased functional and phylogenetic diversity. This is related to the less diverse plots with overlapping traits distributed in the wet western region of Canada, as demonstrated in our study (Figure S1) and a previous study (Chen et al. 2023). Furthermore, older stands are associated with higher stability but low mean productivity, consistent with previous studies (Chen et al. 2016; Li et al. 2022).

In our study, stability did not change significantly with census length while both mean productivity and productivity standard deviation increased, as expected (Gaiser et al. 2020; Lindenmayer et al. 2012; Reich et al. 2012; Zhang et al. 2012). Moreover, there were no significant interaction effects of census length and functional, phylogenetic or taxonomic diversity on stability (Figure 4-2, Figure S4-2), indicating a consistent relationship between diversity and stability over the census lengths from 8 to 52 years in our studied forests. Our finding of the strong positive relationship between long-term stability and tree diversity of natural forests generalizes the result of short-term experimental and observational studies to long temporal, large spatial real-world Canadian natural forests, which had experienced various major climate and biotic disturbances during the study period from 1951 to 2016 (Boucher et al. 2018; Canadian Council of Forest Ministers 2021; Trenberth et al. 2014). Collectively, our results together with previous findings demonstrate that biodiversity acts as a strong force in stabilizing the productivity of various ecosystems under a wide range of abiotic and biotic environments.

Human activities have led to the loss of biodiversity and ecosystem functioning and services that are vital for human existence and well-being (Watson et al. 2019). Two short-term tree diversity experiments have shown that a greater number of tree species leads to greater temporal stability of productivity (Schnabel et al. 2019; Schnabel et al. 2021), but the results from natural forests are mixed (del Rio et al. 2017; Dolezal et al. 2020; Jucker et al. 2014; Li et al. 2022; Ouyang et al. 2021). Several reasons could explain the previously divergent findings. First, species evenness plays an important role in ecosystem functioning (Hillebrand et al. 2008; Zhang et al. 2012). The lack of positive diversity effects in previous studies could be attributed to the fact that most studies in natural forests used only species richness to represent diversity. Our analysis shows that species richness (i.e., Hill number with q =0) is not as effective as Shannon diversity (Hill number with q =1) in predicting stability (Table S2). Second, the magnitude (or range) of diversity can influence the outcome as we show that stability increases with diversity. A limited range of diversity such as comparing monocultures versus two species mixtures would likely find statistically insignificant results, in particular, combined with limited sample sizes. Third, the strength of the diversity and stability relationships is theoretically expected to increase with environmental heterogeneity and the variation of stand development stages and disturbances (Loreau and de Mazancourt 2013), and thus the lack of a positive relationship could result from sampling stands with limited variations in the environment, disturbances, and stand ages.

4.6 Conclusion

Our results build a consensus that when climate factors, soil conditions, and stand age were statistically controlled, the temporal stability of productivity was persistently positively associated with functional, phylogenetic, and taxonomic diversity at all census lengths we observed in large-scale Canadian natural forests, many of which have experienced major droughts (Bonsal et al. 2011) and moderate to severe defoliation due to various kinds of tree species-specific insects (Canadian Council of Forest Ministers 2021). Specifically, we found strong evidence that higher long-term stability was greater in functionally and phylogenetically diverse forests due to a greater increase in mean productivity than the standard deviation of productivity operating through species asynchrony, attributable to both compensatory dynamics and statistical averaging. Our findings highlight the importance of both functional and phylogenetic diversity in stabilizing long-term productivity in natural ecosystems.

CHAPTER 5 GENERAL CONCLUSION

Ecosystem functioning and services are vital to human welfare but become increasingly vulnerable to global environmental change and influenced by ongoing biodiversity loss, especially the simplification of local communities (Anderegg et al. 2020b; Newbold et al. 2015). The urgent call for climate mitigation via the nature-based solution, using biodiversity (Mori et al. 2021) has led to more exploration of the effects of biodiversity on productivity and mortality, which are highly related to carbon stock and cycling. In this dissertation, I examined the mechanisms underlying temporal increases in tree mortality such as intensified competition, reduced tree longevity, and species compositional shift, in addition to well-acknowledged hydraulic failure, carbon starvation fire, insects, and diseases. Moreover, I explored the feedback between background and acute tree mortality and offered suggestions of several avenues to help us improve our understanding of tree mortality in response to global environmental change drivers, including rising atmospheric CO2 concentration, warming, reduced water availability, and changes in radiation. I found phylogenetic diversity reduces biomass and stem mortality rates via decreasing biotic damage in natural forests. I also found functional diversity plays a more significant role than phylogenetic diversity in stabilizing long-term productivity in natural forests across Canada. Our long-term and large-scale studies provide strong evidence of multi-faceted biodiversity relationships with the stability of productivity and mortality and the mechanisms underlying these relationships. Our findings extended previous short-term biodiversity experiment results to long-term natural forests across a large spatial scale and offered insights into previous mixed results in natural forests. A summary of the key findings of each chapter of this dissertation are as follows:

1. In Chapter 2, by reviewing the mechanisms of tree mortality and the feedback between background and acute tree mortality influenced by global environment change drivers, I found it remains unclear the extent to which various causes contribute to increased tree mortality. For example, across temporal and spatial scales, does global environmental change affect background tree mortality more than acute tree mortality, and vice versa? What are the patterns and mechanisms of forest insects and pathogens and their influences on tree mortality in response to global environmental change drivers? How can we better predict future background and acute tree mortality on a regional, biome, and global scale? We suggest that several avenues can help us improve our understanding of tree mortality in response to global environmental change drivers, including rising atmospheric CO_2 concentration, warming, reduced water availability and changes in radiation. First, we suggest that our framework that simultaneously incorporates background and acute tree mortality will help identify future research questions by focusing on how different causes may interact. Second, we suggest that evaluating simultaneous direct and indirect mechanisms will better predict the response of background tree mortality to a gradient of environmental change in global forests. We argue that assessing regional and global forest mortality responses to global environmental change requires accounting for background and acute tree mortality. Finally, society must act to reduce fossil emissions, deforestation, and ecosystem simplification to combat the rapid increase in tree mortality.
2. In Chapter 3, by analyzing the relationship between tree mortality rate and functional and phylogenetic diversity in natural forests, I found that biomass and stem mortality rates were lower in phylogenetically diverse natural forests mainly due to reduced biotic

damage. The previously reported dominant cause of tree mortality, stand competition measured by stand density index, was less important when compared with biotic damage and size inequality (a surrogate measure of crown complementarity). Our study provided the first mechanistic test of the relationship between Hill taxonomic, functional, and phylogenetic diversity with biomass and stem mortality rates. Our findings suggest that conserving phylogenetically diverse forests could safeguard forests from biotic damage and benefit climate mitigation.

3. In Chapter 4, by modelling the long-term relationship between temporal stability of productivity and Hill taxonomic, functional, and phylogenetic diversity across a large-scale natural forest of Canada, I found that functional diversity performed better than phylogenetic diversity in stabilizing productivity in all observation lengths (8 – 52 years). Functional diversity stabilizes productivity via increased mean productivity and reduces standard deviation via asynchrony. In addition, the statistical averaging effect played a dominant role in the diversity-stability relationship, although compensatory dynamics showed a stronger positive relationship with stability. Our study showed that the positive effects of biodiversity on stability reported from short-term experiments are applicable to natural forests. Meanwhile, we offered insights into the mixed results from natural forest observations.

Our findings emphasize the importance of both functional and phylogenetic diversity in lowering the attack from insects and pathogens and consequently reducing tree mortality. This finding suggests that functional and phylogenetic diversity might reduce the vulnerability of forests in response to climate change, and stabilize forests in the long term. The findings of this dissertation will aid governmental agencies and private stakeholders in generating scientific-based natural forests conversation and sustainable management that can help cope with global environmental change and meet the policy requirements on carbon sequestration. Future studies can focus on the relationship between multifaceted biodiversity and net biomass change, which quantifies forest biomass accumulation by integrating productivity and mortality. An improved understanding of the processes and their conditional operation will help us anticipate the consequences of biodiversity loss on biomass accumulation, forest economy, and carbon sequestration and develop strategies to cope with these changes.

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APPENDIX I: SUPPLEMENTARY INFORMATION FOR CHAPTER 3

Extended Data Table | 3-1 Alternative models for the relationships between tree diversity and tree mortality rate.

Model	Predictors							Explained variance	Akaike information criterion
	FD	PD	PC1	PC2 (1^{st}|2^{nd})	Age	MAP (1^{st}|2^{nd})	Soil		
1 (q = 1)	0.21	-0.12						0.05	3885
2 (q = 1)	0.20	-0.13	0.13	12.12|-5.38				0.23	3692
3 (q = 1)	0.18	-0.10	0.05	9.53|-4.52	-0.15	-8.86|4.75		0.31	**3648**
4 (q = 2)	0.15	-0.08	0.03	9.05|-4.71	-0.17	-9.45|4.87		0.31	3668
5 (q = 0)	0.19	-0.15		9.29|-5.02	-0.18	-9.80|4.74		0.30	3675

Alternative models with Tweedie distributed mortality rate were developed based on the dataset of repeatedly measured permanent sample plots by the government of British Columbia. Models 1, 2, and 3 showed that the relationships between mortality rate and functional diversity (FD) and phylogenetic diversity (PD) were similar with or without covariates including forest composition (PC1 and PC2), stand age (Age), climate variable (Mean annual precipitation, MAP), and soil drainage (Soil). Models 3, 4, and 5 showed that FD and PD at q = 1 had the lowest AIC. Accordingly, Model 3 was considered the most parsimonious for interpretation. All predictors were scaled and showed low collinearity (VIF < 2). Model 3 showed no significant temporal (*P* = 0.3) and spatial autocorrelation (*P* = 0.1). Second-order polynomials were used for PC2 and MAP with the first coefficient for the linear term and the second for the quadratic term. Values for predictors are mean standardized coefficients, which are statistically significant at α =0.05 unless noted with ns.

Extended Data Table | 3-2 Alternative models for the relationships between tree diversity and biotic damage.

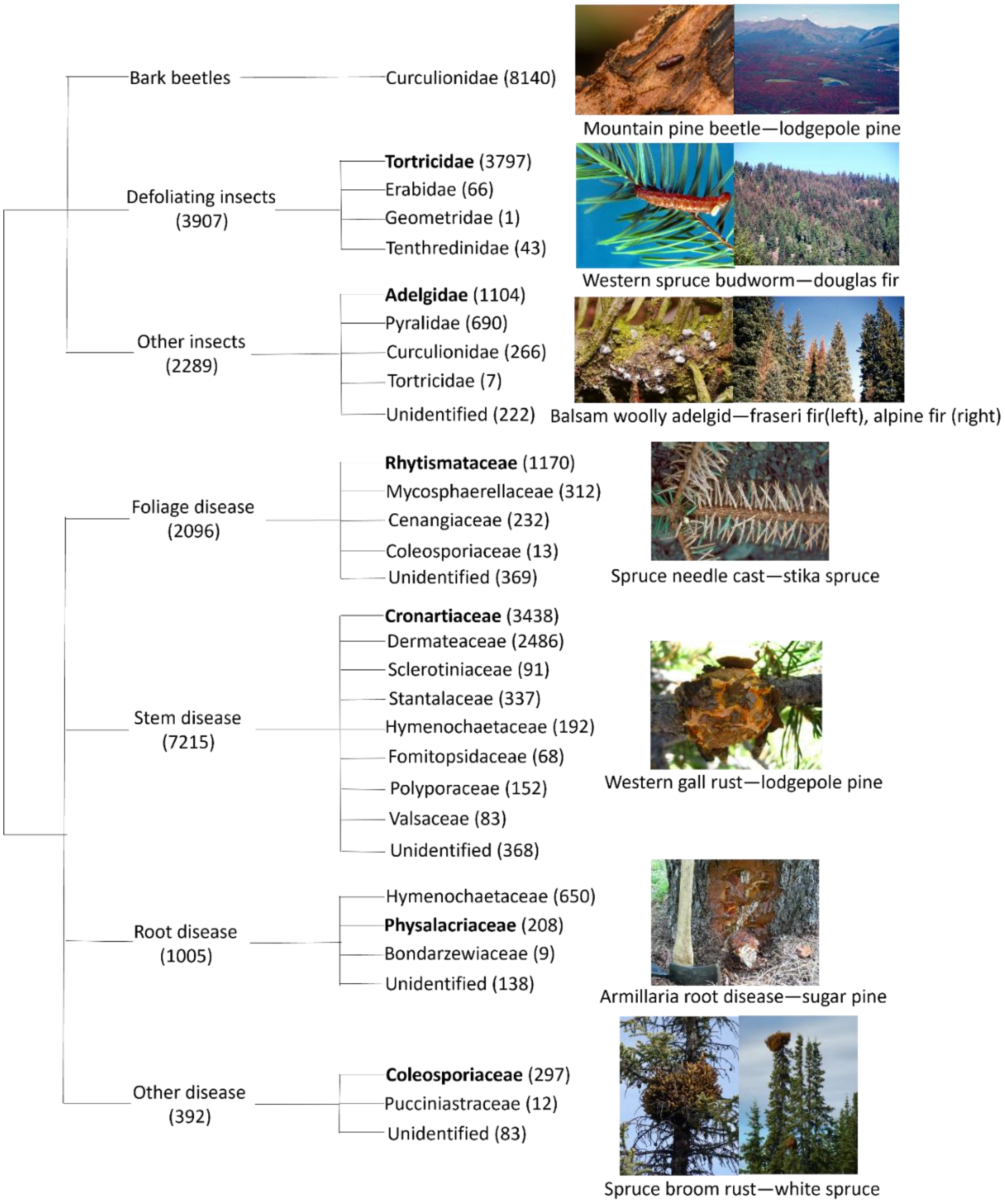
Model	Predictor							Explained variance	Akaike information criterion
	FD	PD	PC1	PC2	Age (1^{st}|2^{nd})	MAP	Soil		
1 (q = 1)	0.07 (ns)	-0.18						0.12	7428
2 (q = 1)	-0.01 (ns)	-0.15	0.01 (ns)	0.31	-12.02|-7.31	-0.54		0.94	**7202**
3 (q = 1)	-0.12 (ns)	-0.22			-9.9|-6.4			0.73	7201

Abbreviations are described in Extended Data Table 1. The inclusion of PC1 and PC2 improved the variance explained. Model 2 was considered the most parsimonious for interpretation. All predictors were scaled and showed low collinearity (VIF < 2). Model 2 showed no significant temporal (*P* = 0.9) and spatial autocorrelation (*P* = 0.2). Values for predictors are mean standardized coefficients, which are statistically significant at α =0.05 unless noted with ns (*P* > 0.05).

Extended Data Table | 3-3 Alternative models for the relationships between tree diversity and stand density index and size inequality.

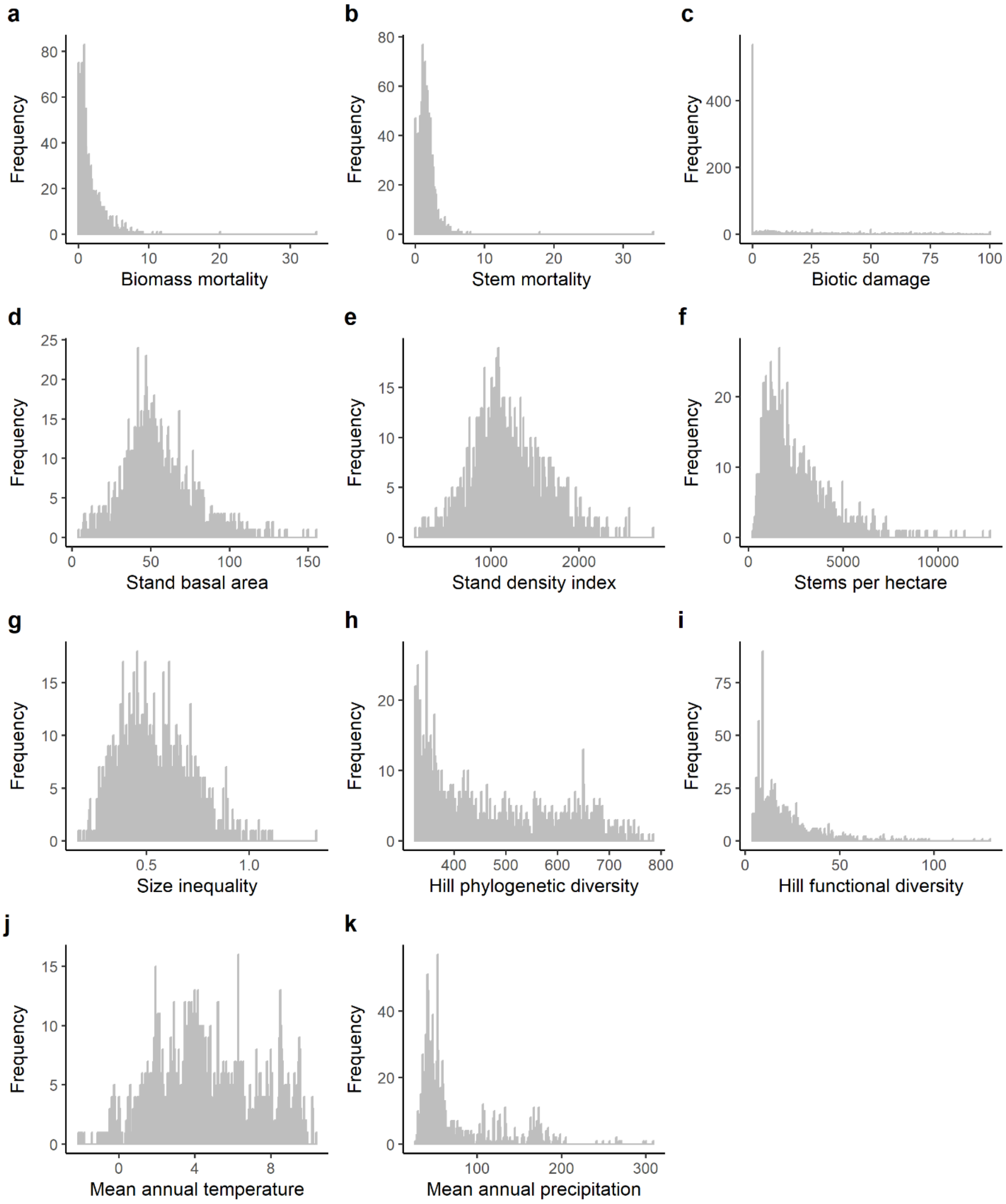
	Predictor							R2adj	Akaike information criterion
	FD	PD	PC1	PC2	Age	Climate	Soil		
Stand density index models									
1 (q = 1)	0.01(ns)	0.04						0.005	1174
2 (q = 1)	0.02(ns)	0.04	-0.08	-0.02(ns)				0.05	1122
3 (q = 1)	0.03	-0.01(ns)	0.02(ns)	0.002(ns)	0.16	MAT:-0.09 MAP:0.21 KC:0.08	0.03	0.17	**829**
Size inequality models									
4 (q = 1)	-0.002 (ns)	0.02						0.03	-1952
5 (q = 1)	0.03(ns)	0.02	-0.05	-0.04				0.34	-2421
6 (q = 1)	0.005	0.02	-0.03	-0.04	0.04	MAP:-0.02 KC:-0.02		0.45	**-2715**

Abbreviations are described in Extended Data Table 1. MAT is the mean annual temperature and KC is the continental index. Models 3 and 6 were considered the most parsimonious for stand density index and size inequality, respectively. All predictors were scaled and showed low collinearity (VIF < 2). Model 3 and Model 6 included the GroupID to account for the spatial autocorrelation. Model 3 and Model 6 showed no significant temporal ($P = 0.5$ and $P = 0.9$) and spatial autocorrelation ($P = 0.6$ and $P = 0.8$)

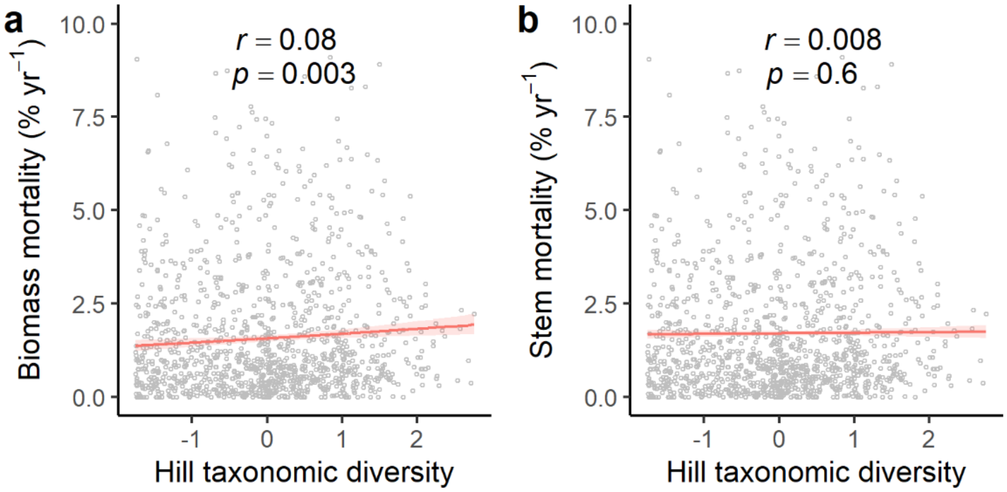


Extended Data Figure | 3-1. Insect and/or pathogen loads on dead trees based on the types of damage and families in natural forests in British Columbia, Canada.

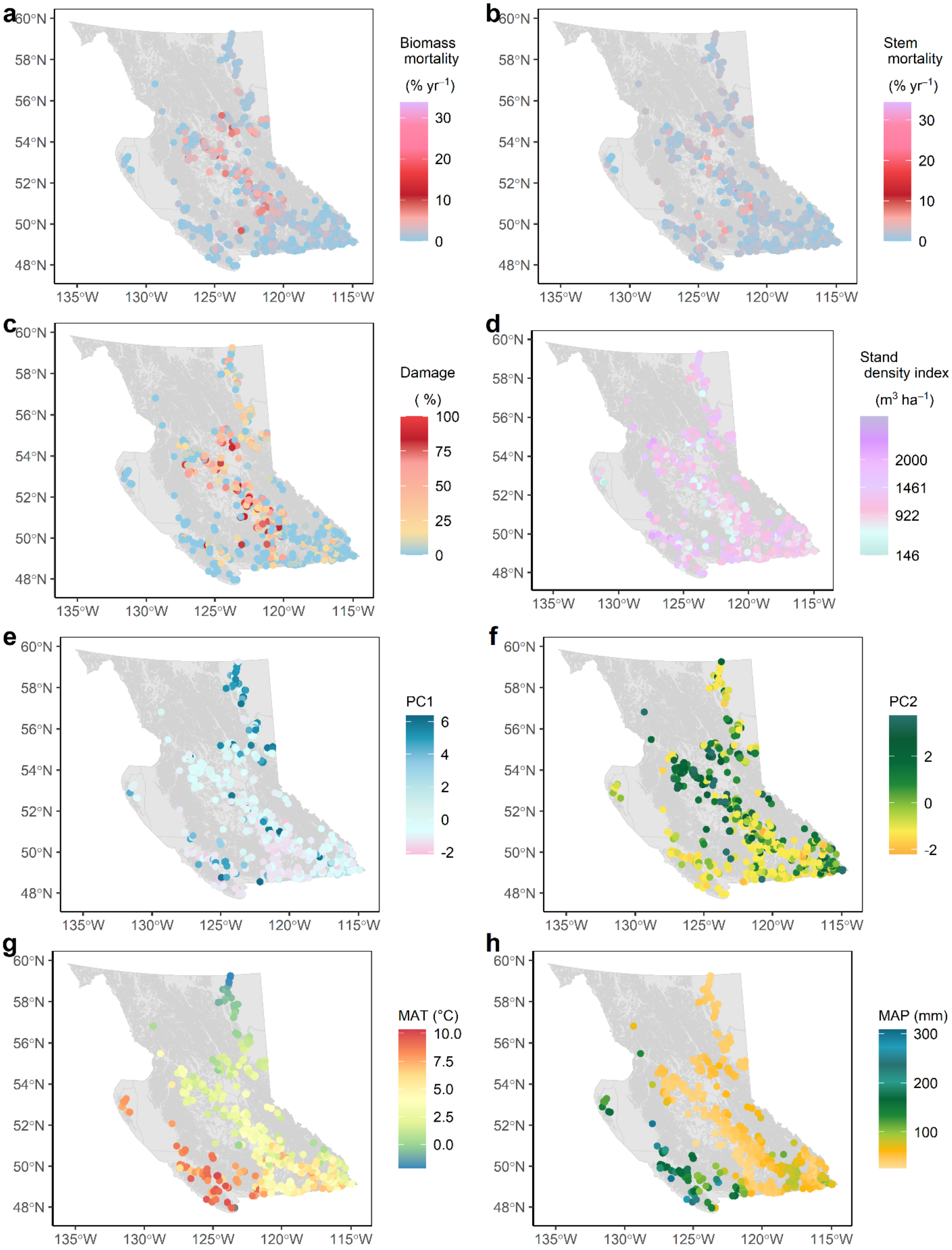
The values represent the number of dead trees with insect or pathogen loads of a total of 61,427 dead trees surveyed. We listed pictures, which are free for use based on the sources, belonging to the families in bold.



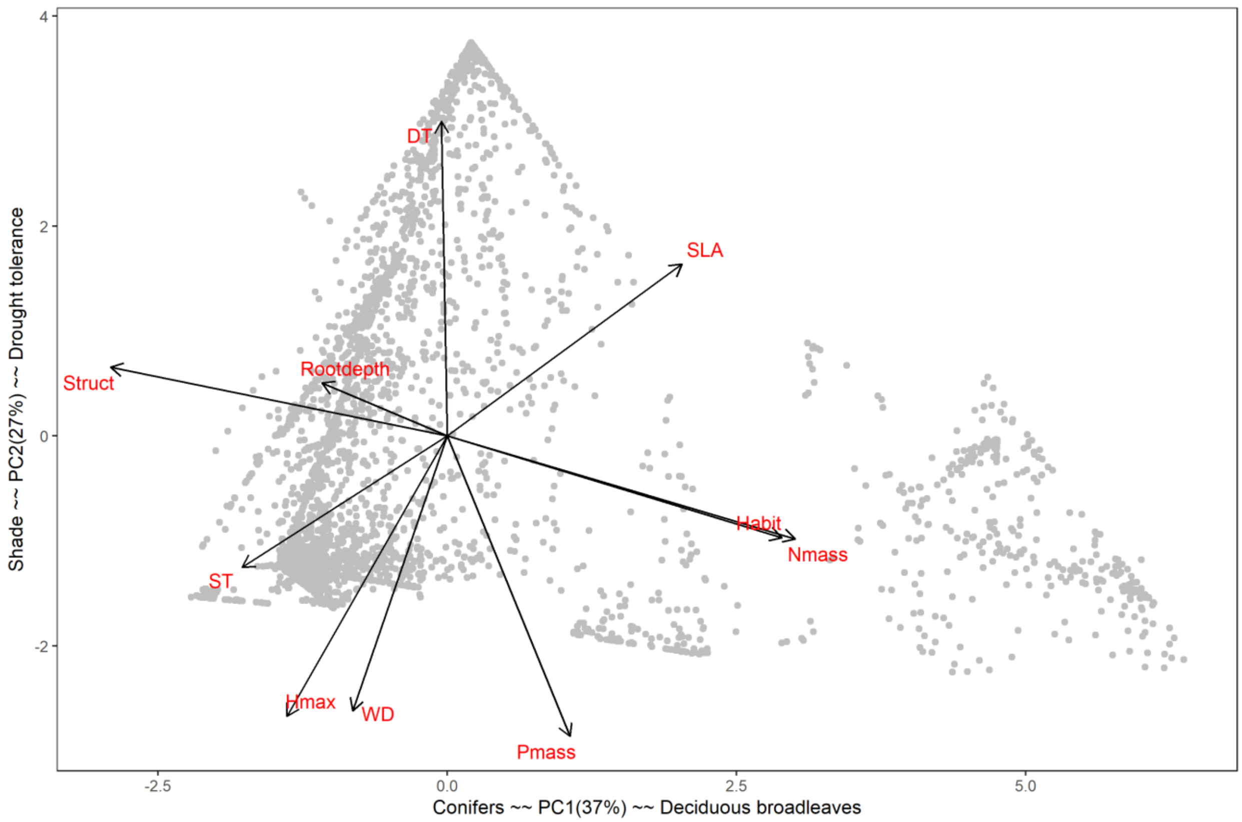
Extended Data Figure | 3-2. Frequency distributions of variables used in our analysis.



Extended Data Figure | 3-3. The relationship between morality rate and taxonomic diversity. a) biomass mortality rate (annual biomass loss divided by stand biomass in the previous census and b) stem loss rate (annual stem loss divided by total number of stems showed the slopes and 95% confidence intervals and *P*-values.

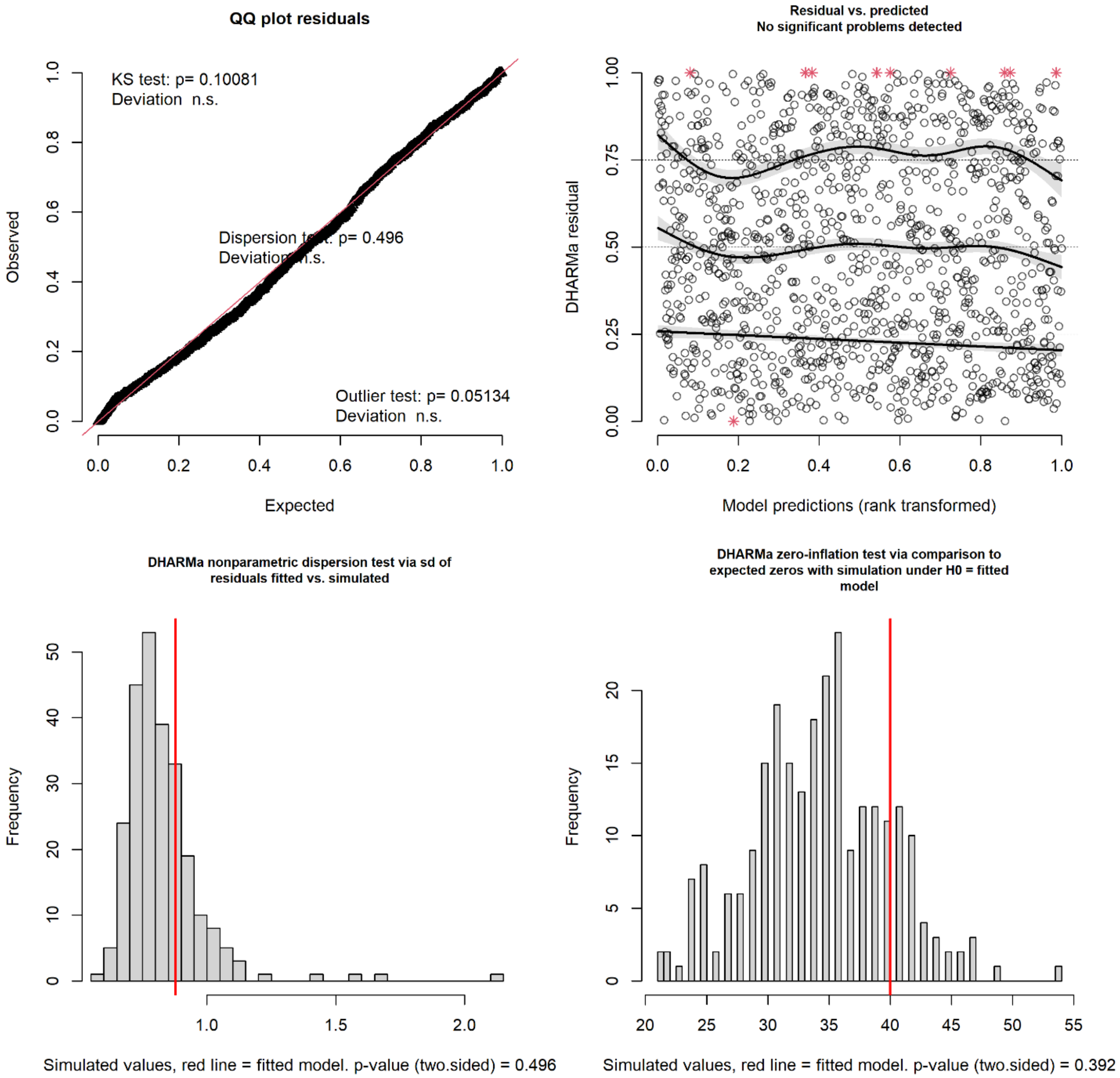


Extended Data Figure | 3-4. Spatial distribution of selected variables used in models.

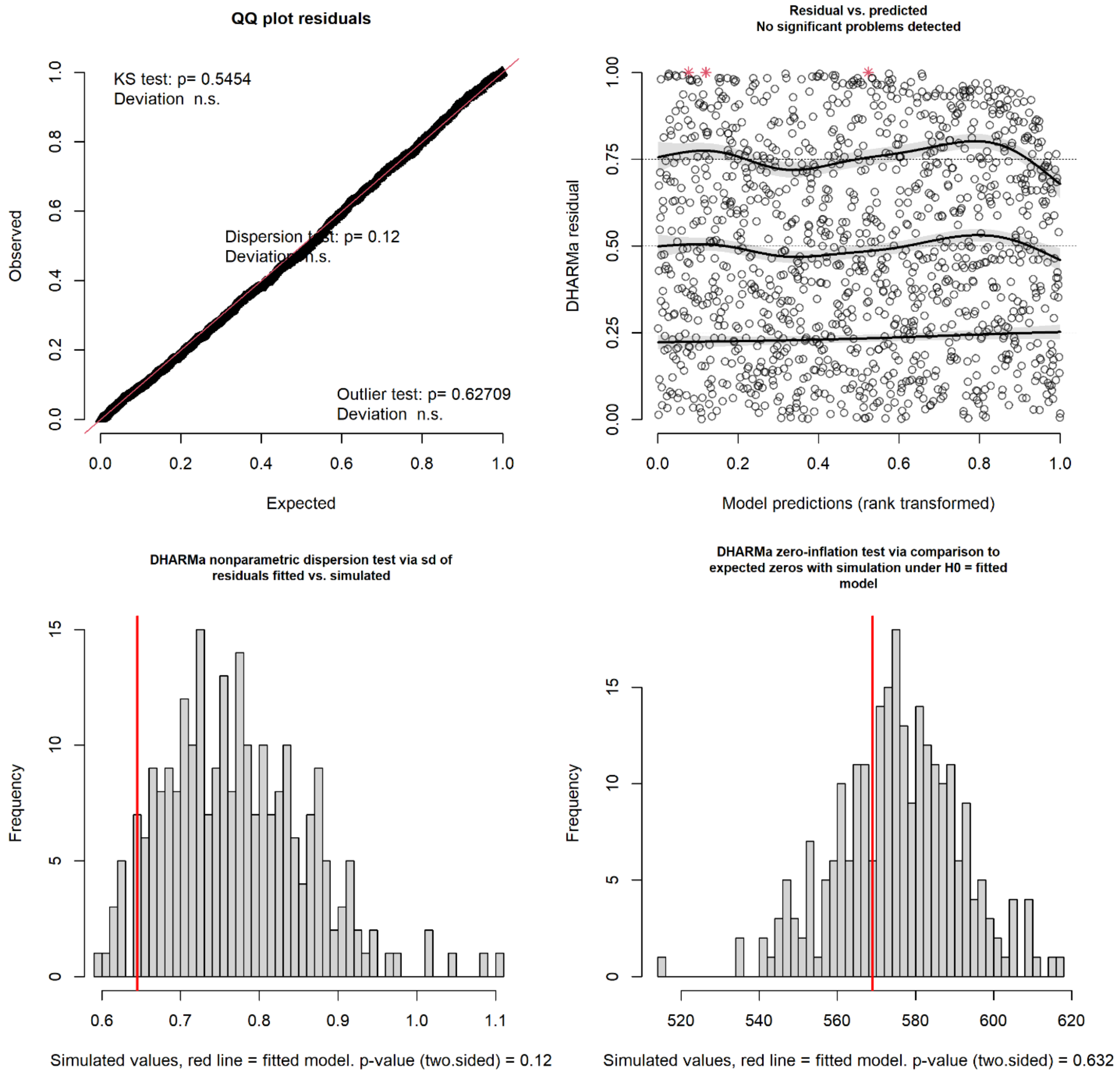


Extended Data Figure | 3-5. Principal component analysis of ten functional traits in our study.

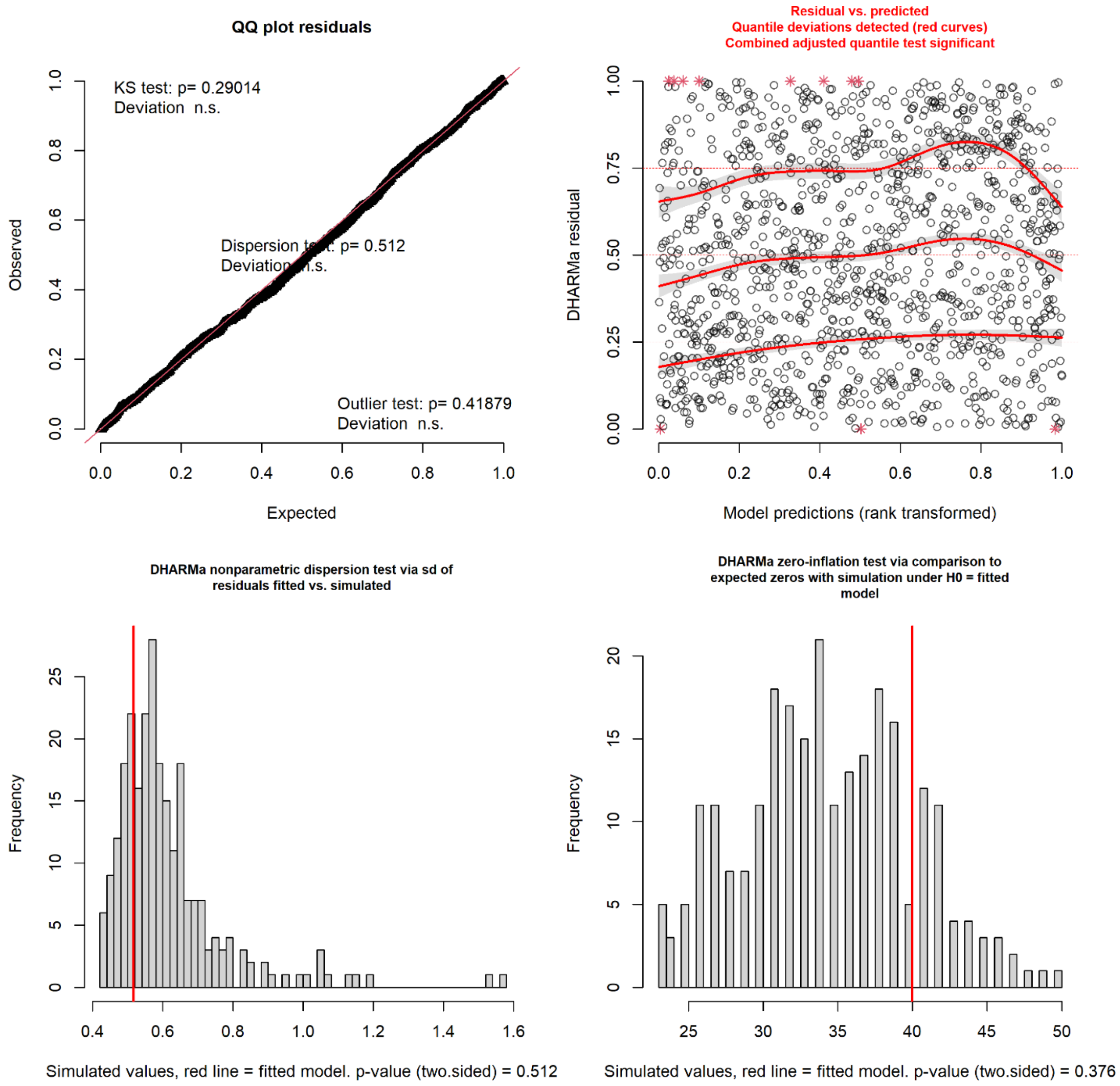
Leaf nitrogen content per leaf dry mass (Nmass, in milligrams per gram), leaf phosphorus content per leaf dry mass (Pmass, in milligrams per gram), specific leaf area (SLA, in square millimetres per milligram), wood density (WD, in grams per cubic centimetre), maximum tree height (Hmax, meter); root depth, drought tolerance (DT, ranking in increasing tolerance from 1 to 5), shade tolerance (ST, ranking in increasing tolerance from 1 to 5), leaf habit (Habit, deciduous =1, evergreen =0); leaf structure (Struct, broadleaves = 1, conifers = 0).



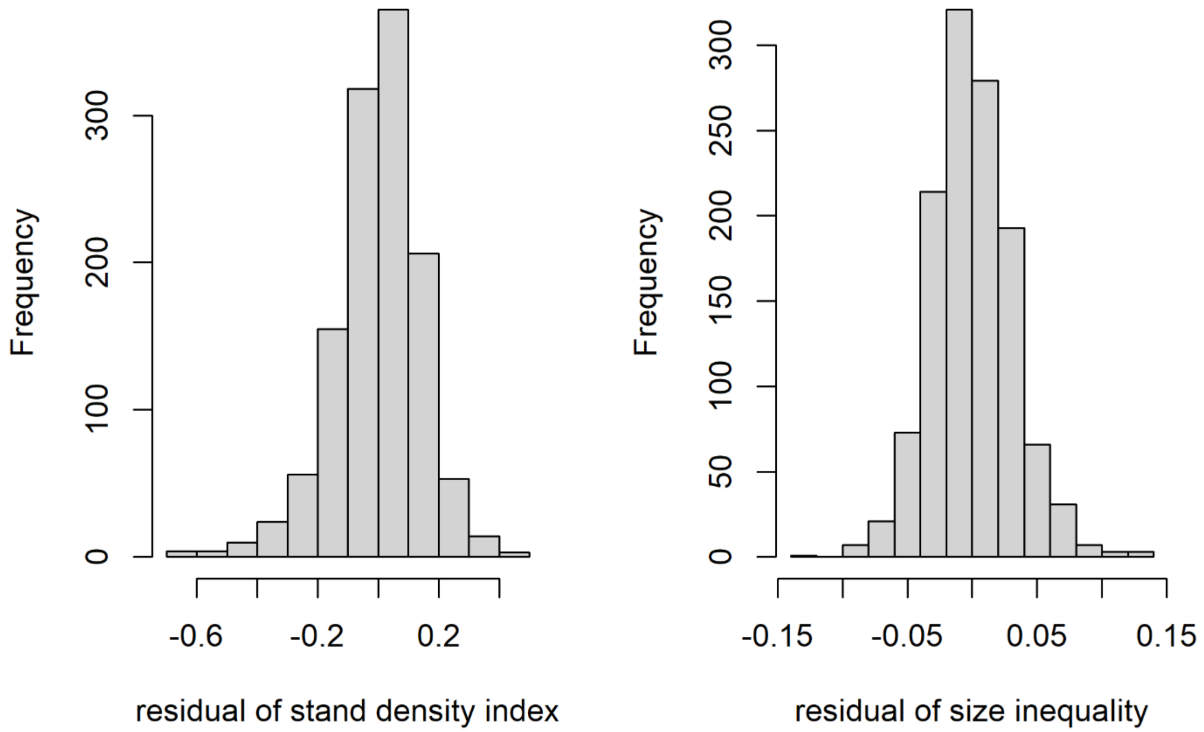
Extended Data Figure | 3-6. Diagnostic plot of Model 3 in Extended Data Table 3-1 using DHARMa.



Extended Data Figure | 3-7. Diagnostic plot of Model 2 in Extended Data Table 3-2 using DHARMa.



Extended Data Figure | 3-8. Diagnostic plot of biomass mortality rate predicted by biotic damage and stand density index and size inequality using DHARMa.



Extended Data Figure | 3-9. Histogram of residuals of Model 1 and Model 2 in Extended Data Table 3-3.

APPENDIX II: SUPPLYMENTARY INFORMATION FOR CHAPTER 4

Table S4-1. *P*-values and variance inflation factor (VIF) of covariates in temporal stability models.

Covariates	Full model q = 0		Full model q = 1		Full model q = 2	
	P-value	VIF	*P*-value	VIF	*P*-value	VIF
Asyn	< 0.001	1.45	< 0.001	1.46	<0.001	1.44
Div	< 0.001	24.85	0.338	7.27	0.049	4.88
FD	< 0.001	24.36	< 0.001	4.89	<0.001	3.39
PD	0.545	5.98	<0.001	4.11	<0.001	3.15
Stand age	0.282	1.25	<0.001	1.21	<0.001	1.21
MAT	0.692	1.52	<0.001	1.47	0.003	1.45
AI	0.003	1.46	0.257	1.41	0.353	1.40
Soil drainage	< 0.001	1.18	<0.001	1.18	<0.001	1.18
Census length	0.135	1.21	0.020	1.20	0.029	1.20
Year	<0.001	1.46	<0.001	1.49	<0.001	1.48

All predictors' coefficient estimates are statistically significant at $\alpha = 0.05$.

Asynchrony is the community-level species asynchrony; Hill taxonomic, functional and phylogenetic diversities were assessed at q =0, 1, and 2 (Divq0, Divq1, Divq2, FDq0, FDq1, FDq2, PDq0, PDq1, and PDq02, respectively). MAT, AI, and stand age are the long-term averaged mean annual temperature, the long-term averaged aridity index, and the average stand age from the first to last measurement; Soil drainage indicates how rapidly water is removed from soil in relation to supply ranging from 1 (very rapidly drained) to 7 (very poorly drained). Census length (length) is the number of years between the first and last measurement of each unique sample plot. Year is the middle calendar year of all measurement years; the total number of censuses (n.cens) was the random effect. Stability, mean productivity, standard deviation, and stand age were log-transformed. All variables were scaled.

Table S4-2. Hill diversity selection and the determination of the most parsimonious models of stability, mean productivity, standard deviation, and asynchrony.

Model	AIC	Moran.I (p-value)
Stability ~ Asyn + FDq0 + AI + Soil drainage + Year + (1|census number)	17370	
Stability ~ Asyn + FDq1+ PDq1 + Soil drainage + Year + (1|census number)	**17215**	**0.07**
Stability ~ Asyn + FDq2+ PDq2 + Soil drainage + Year + (1|census number)	17203	
Productivity ~ Asyn + FDq0 + Length + MAT + AI + Stand age + Year + (1|census number)	16190	
Productivity ~ Asyn +FDq1 + Length + MAT + AI + Stand age + Year +(1|GroupID) + (1|census number)	**16041**	**1**
Productivity ~ Asyn +FDq2 + Length + MAT + AI + Stand age + Year + (1|census number)	16370	
Productivity ~ Asyn × Length + FDq0 + MAT + AI + Stand age + Year + (1|census number)	16177	
Productivity ~ (Asyn) × Length+FDq1 + MAT + AI + Stand age + Year + (1|census number)	16316	
Productivity ~ (Asyn) × Length+FDq2 + MAT + AI + Stand age + Year + (1|census number)	16356	

SD ~ Asyn +PDq0+ Length + MAT + AI + Soil drainage + Stand age + Year + (1|census number)	17658	
SD ~ Asyn + FDq1 + PDq1 +Length + MAT + AI + Soil drainage + Stand age + Year + (1|census number)	17124	
SD ~ Asyn + FDq2 + PDq2 +Length + MAT + AI + Soil drainage + Stand age + Year + (1|census number)	17158	
SD ~ Asyn +PDq0* Length + MAT + AI + Soil drainage + Stand age + Year + (1|census number)	17658	
SD ~ Asyn + FDq1 × Length + PDq1+ MAT + AI + Soil drainage + Stand age + Year +(1|GroupID) + (1|census number)	**17116**	**0.09**
SD ~ Asyn +FDq2 × Length +PDq2 + MAT + AI + Soil drainage + Stand age + Year + (1|census number)	17148	
Asynchrony ~ PDq0 + MAT + AI + Stand age + (1|census number)	19173	
Asynchrony ~ FDq1+ PDq1 + MAT + AI + Stand age + (1|census number)	**19019**	**0.2**
Asynchrony ~ FDq2+ PDq2 + MAT + AI + Stand age + (1|census number)	19129	

The full models for the respective variables were the conceptual models described in Figure 1. GroupID: the lag distance setting at 0.3 km to mitigate spatial autocorrelation. All variables are described in Table S1.

Table S4-3. Linear mixed model summary of the most parsimonious models derived from the model selection.

	Stability	**Mean productivity**	**Standard deviation**	**Asynchrony**
Predictors	*Estimates*	*Estimates*	*Estimates*	*Estimates*
Asyn	0.71	0.05	-0.61	
FDq1	-0.22	0.20	0.35	0.42
PDq1	-0.07		0.08	0.11
Length		0.03	0.06	
FDq1:Length			0.04	
MAT		0.54	0.28	0.08
AI		0.16	0.14	0.05
Soil drainage	-0.05		0.05	
Stand age		-0.19	-0.19	0.04
Year	-0.18	-0.17	0.05	0.10
Random Effects				
σ^2	0.58	0.21	0.31	
τ_{00}	$0.05_{\text{n.cens}}$	$0.31_{\text{y\_m\_x\_m03}}$	$0.26_{\text{y\_m\_x\_m03}}$	

		$0.53_{\text{n.cens}}$	$0.17_{\text{n.cens}}$	
ICC	0.08	0.80	0.58	
N	$6_{\text{n.cens}}$	$6533_{\text{y\_m\_x\_m03}}$	$6533_{\text{y\_m\_x\_m03}}$	
		$6_{\text{n.cens}}$	$6_{\text{n.cens}}$	
Observations	7498	7498	7498	7498
Marginal R^2 / Conditional R^2	0.372 / 0.420	0.405 / 0.883	0.399 / 0.749	0.309 / 0.309

All predictors' coefficient estimates are statistically significant at α = 0.05. Variables and abbreviations are described in Table S4-1.

Table S4-4. Linear mixed model summary of the most parsimonious models derived based on Hill taxonomic diversity (q = 1).

	Stability	**Mean productivity**	**Standard deviation**	**Asynchrony**
Predictors	*Estimates*	*Estimates*	*Estimates*	*Estimates*
Asyn	0.69	0.06	-0.59	
Divq1	-0.25	0.19	0.38	0.50
Length		0.04	0.04	
Asyn:Length		0.04		
MAT		0.54	0.30	0.08
AI		0.14	0.11	
Soil drainage	-0.05		0.05	
Stand age	0.05	-0.21	-0.22	
Year	-0.17	-0.17	0.04	0.09
Random Effects				
σ^2	0.59	0.20	0.59	
τ_{00}	$0.04_{\text{n.cens}}$	$0.31_{\text{y\_m\_x\_m03}}$	$0.22_{\text{n.cens}}$	
		$0.65_{\text{n.cens}}$		

ICC	0.06	0.83	0.27	
N	$6_{\text{n.cens}}$	$6552_{\text{y\_m\_x\_m03}}$ $6_{\text{n.cens}}$	$6_{\text{n.cens}}$	
Observations	7498	7498	7498	7498
Marginal R^2 / Conditional R^2	0.365 / 0.401	0.383 / 0.892	0.372 / 0.542	0.301 / 0.301

All predictors' coefficient estimates are statistically significant at α = 0.05. Variables and abbreviations are described in Table S4-1.

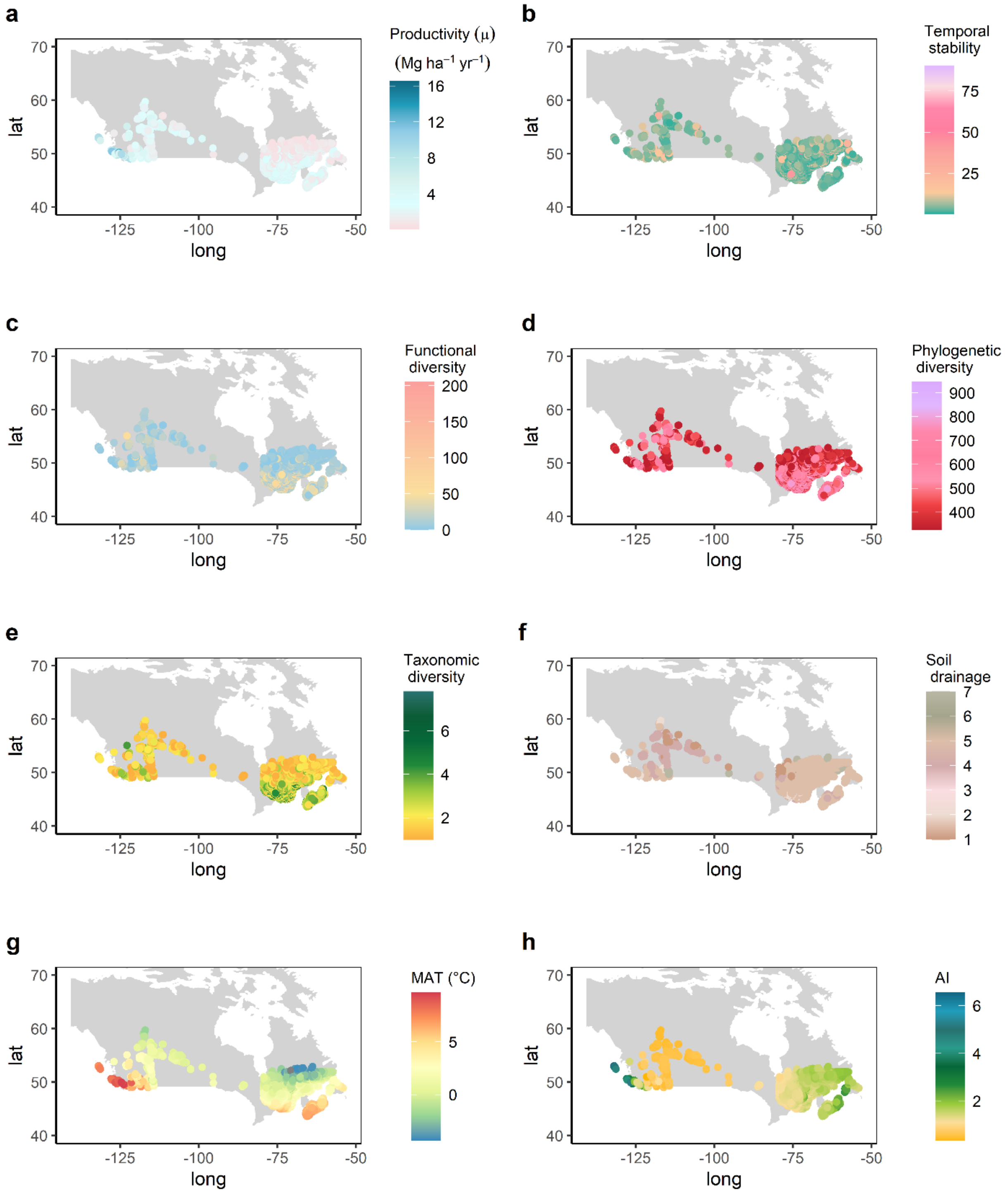


Figure S4-1. Spatial distribution of plots. Variables and abbreviations are described in Table S4-1.

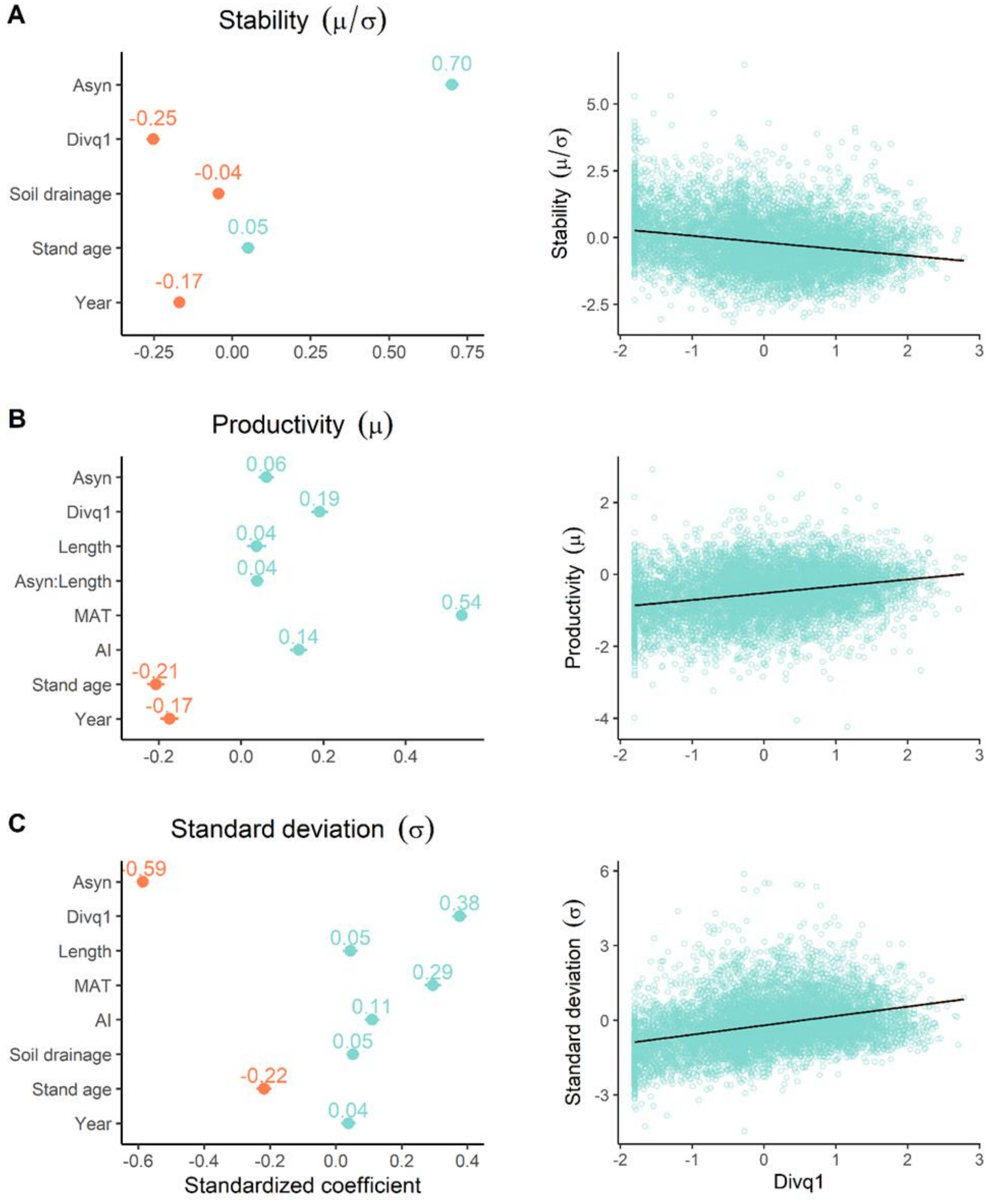


Figure S4-2. Coefficient plots and partial dependence plots of the three most parsimonious linear mixed models based on Hill taxonomic diversity (q =1).

Variables and abbreviations are described in Table S4-1.

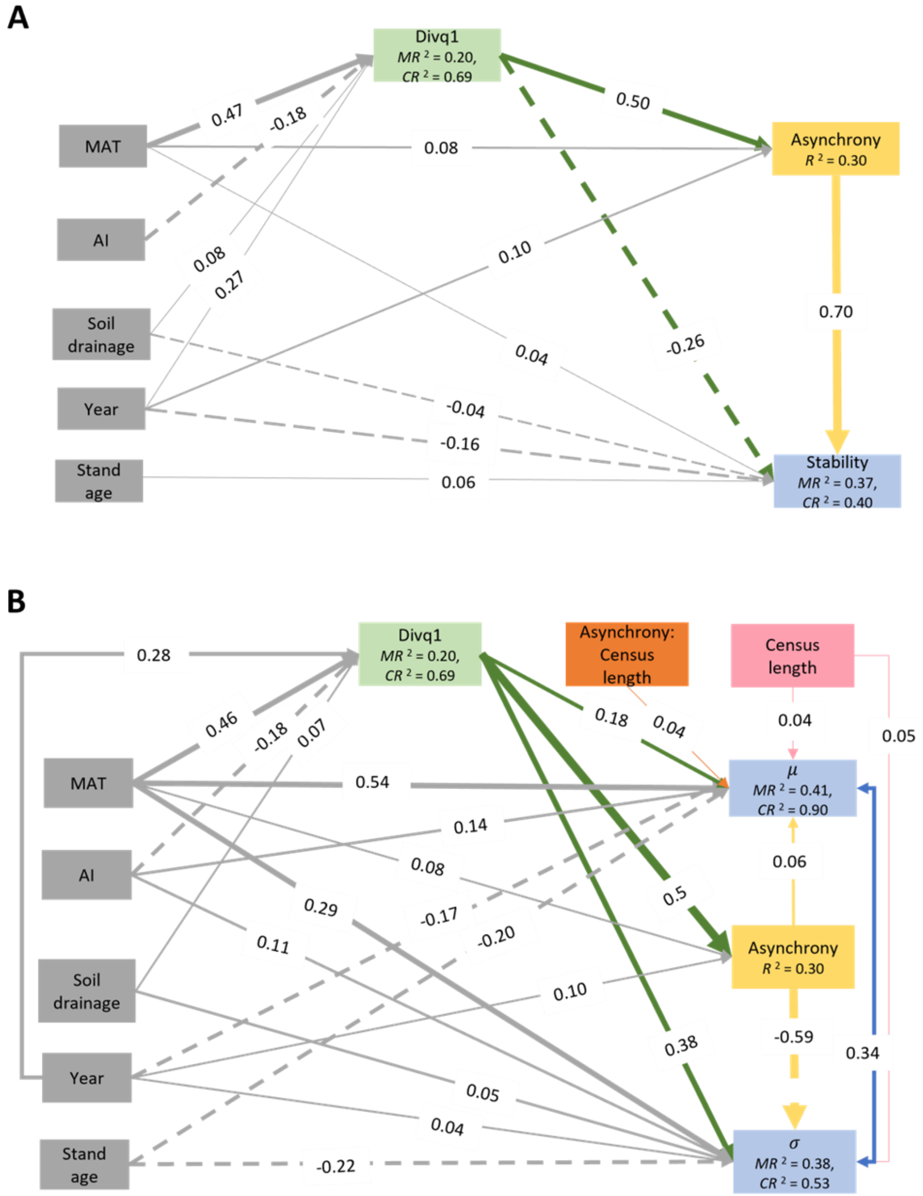


Figure S4-3. Structural equation model showing tree diversity, climate and soil conditions, and stand age on mean productivity (μ) and productivity standard deviation (σ) in long-term natural forests.

A, Path diagram of attributes influencing stability. **B**, Path diagram of attributes influencing m and s. Numbers adjacent to arrows are standardized path coefficients analogous to relative regression weights. Solid and dashed arrows represent positive and negative relationships, respectively. The proportion of marginal and conditional variance explained (R2) appears alongside every response variable in the model. The goodness-of-fit statistics for panel a is Fishers'C = 13.574 and P = 0.193, and b is Fishers'C = 14.922 and P = 0.383, indicating a close model-data fit. All variables are described above.

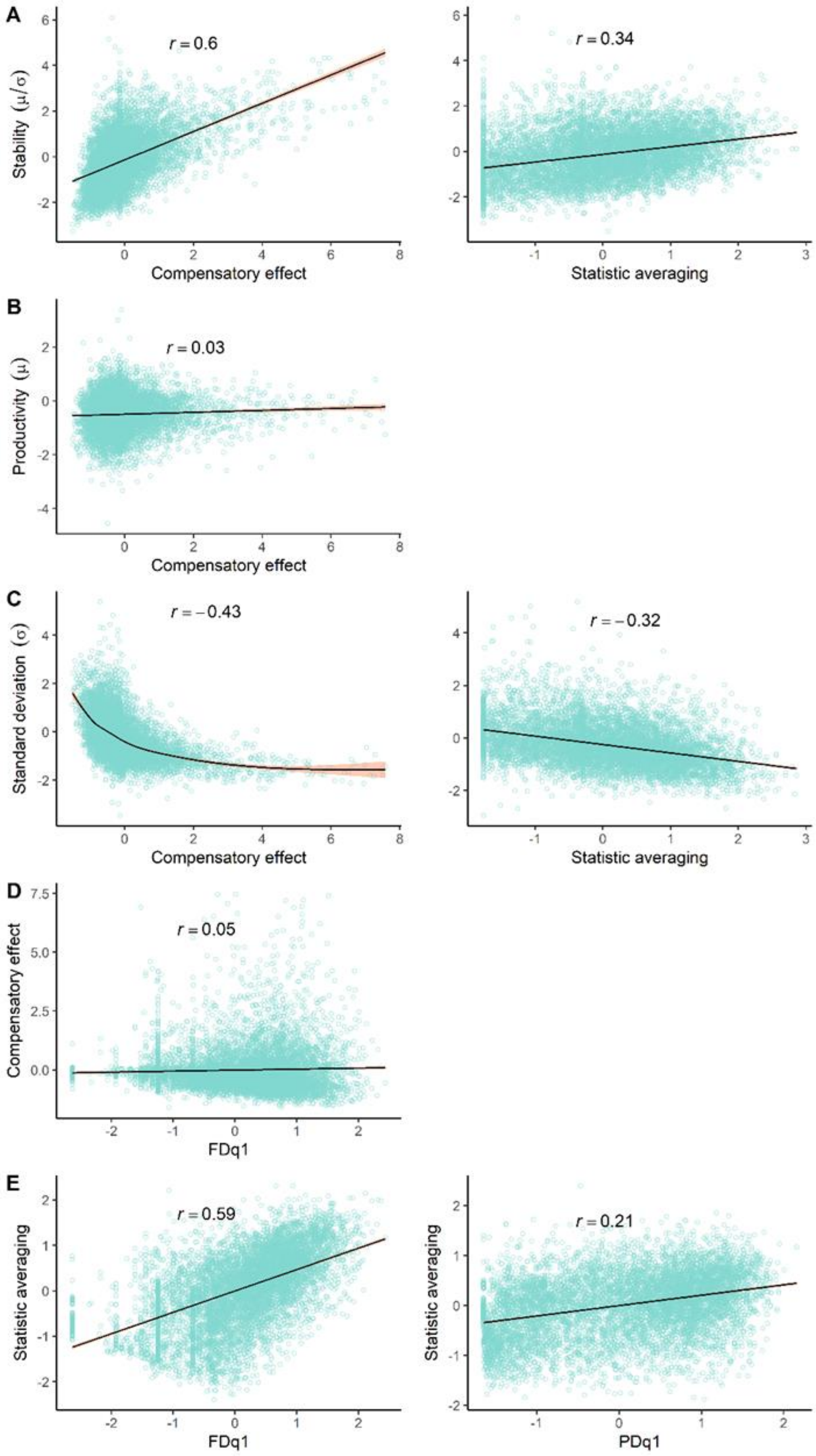


Figure S4-4. Partial relationship between stability (also mean productivity and standard deviation) and compensatory and statistical averaging and diversity in long-term natural

forests.

Effects of compensatory and statistical averaging on **A**, stability, **B**, mean productivity, and **C** standard deviation. Effects of diversity on D compensatory and E statistical averaging. *r* is standardized coefficient.

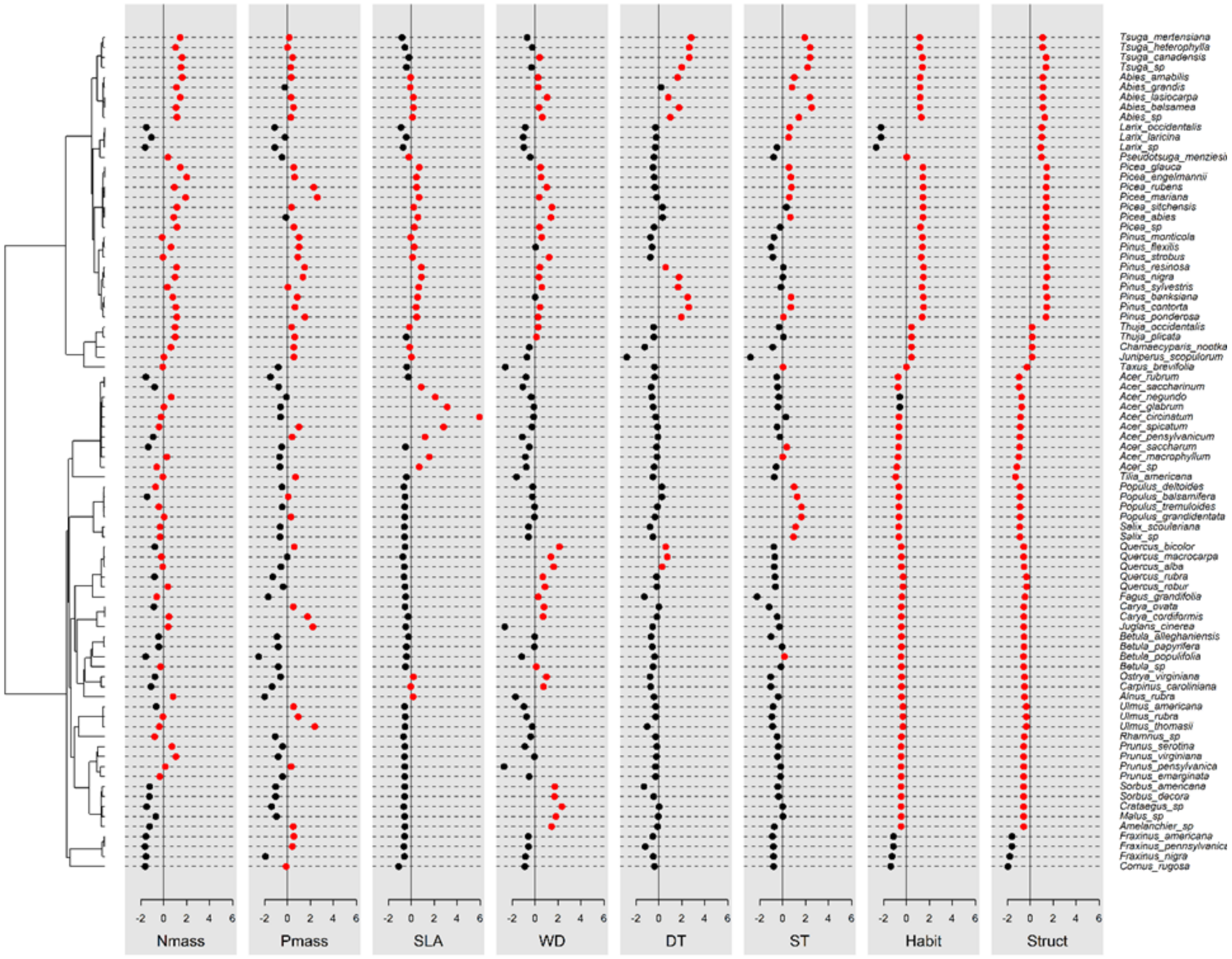


Figure S5-5. Phylogenetic signal within eight functional traits in regional species pools of eighty-four species.

Red points indicate significant phylogenetic signals and black points indicate no phylogenetic signals. Nmass: leaf nitrogen content per leaf dry mass, Pmass: leaf phosphorus content per leaf dry mass, SLA: specific leaf area, WD: wood density, ST: shade tolerance (class 1–5), DT: drought tolerance (class 1–5), leaf habit (deciduous versus evergreen), and leaf structure (broadleaves versus coniferous).

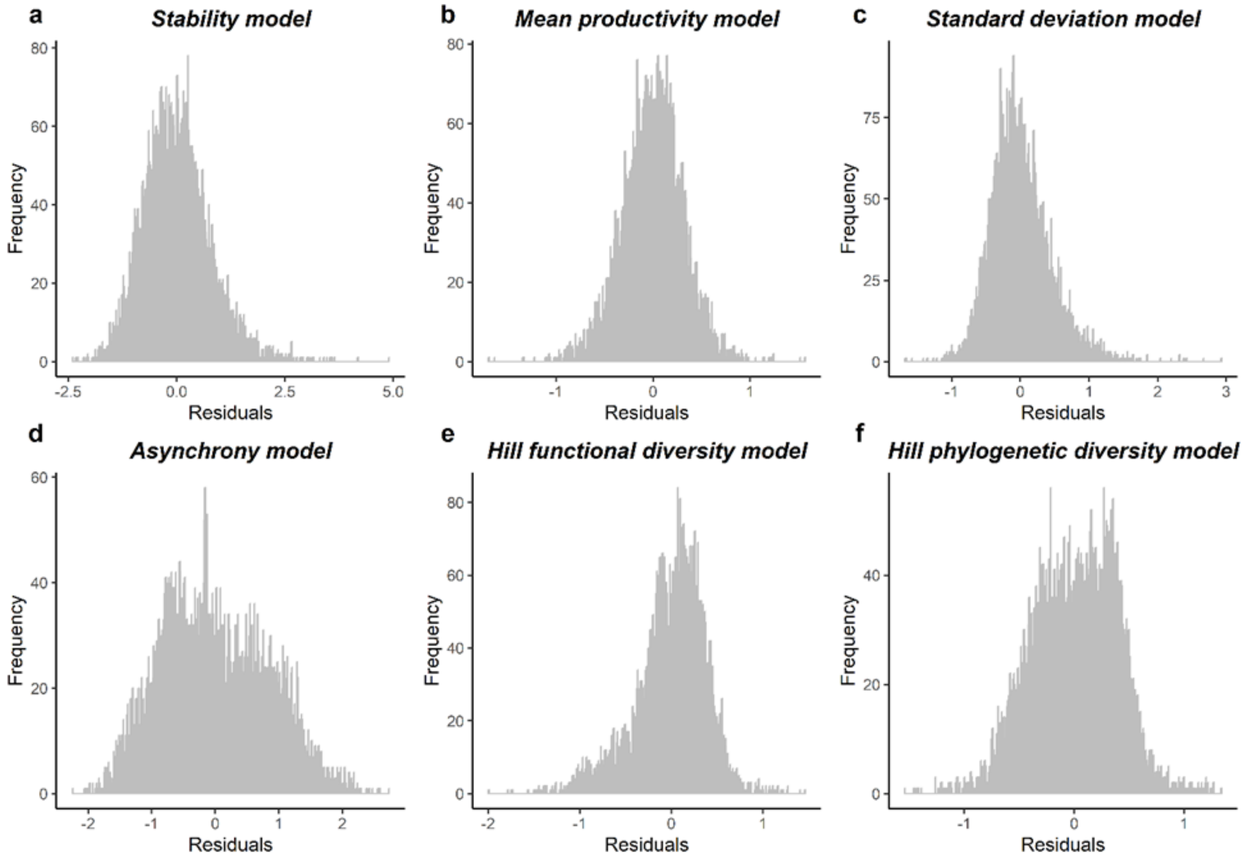


Figure S4-6. Histogram of model residual distribution.

Hill functional and phylogenetic diversity at q =1.