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Spatiotemporal effects of climate on the relationship between tree diversity and forest ecosystem functioning

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SPATIOTEMPORAL EFFECTS OF CLIMATE ON THE RELATIONSHIP BETWEEN TREE DIVERSITY AND FOREST ECOSYSTEM FUNCTIONING

By

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ABSTRACT

Worldwide, forest ecosystem functioning and plant diversity have been altered by global environmental change. Understanding the relationship between biodiversity and ecosystem functioning with long-term environmental change is important because maintaining diversity can mitigate the impacts of environmental change on ecosystem functioning. Here, I i) developed a concept that can elucidate how enhancing plant diversity may help mitigate global environmental change impacts on ecosystem functioning; ii) empirically tested this concept in natural forest systems by examining whether higher tree diversity enhances and reduces positive and negative impacts of long-term environmental change on forest biomass dynamics (biomass growth, loss, and net biomass change); iii) explored effects of spatial variations in climate on the relationship between tree functional diversity and forest biomass dynamics; and iv) investigated how spatial variations in climate mediate the impacts of long-term environmental change on tree functional composition.

In order to establish the concept of how tree diversity can mitigate the impacts of global environmental change on forest ecosystem functioning, I reviewed the field of climate change effects on biodiversity-ecosystem functioning. I found mixed evidence for positive diversity effects on ecosystem functioning persistent before and after experiencing changes in climates within grassland communities, but strong support in the few studies conducted in forest ecosystems which are more stable and resilient at higher levels of diversity. I identify the importance of future research combining investigations into climate change impacts on ecosystem functionality with the B-EF. I concluded that biodiversity can hold certain potential to be a solution to mitigate environmental change impacts.

Using inventory data of boreal forests of western Canada from 1958-2011, I revealed that aboveground biomass growth of species-rich forests increased with the calendar year but that of species-poor forests decreased. Moreover, species-rich forests experienced less aboveground biomass loss from tree mortality than species-poor forests. I found that the growth of species-rich forests, but not species-poor forests, was positively associated with elevated CO_2. Mortality in species-poor forests increased more with decreasing water availability than species-rich forests. In contrast, growth decreased, and mortality increased as the climate warmed regardless of species diversity. The results of this study suggest that promoting high tree diversity may help reduce the climate and environmental change vulnerability of boreal forests.

Using inventory data of temperate and boreal forests across Canada, I examined how the effects of plant functional diversity and identity on biomass dynamics are dependent on environmental contexts. I found that positive effects of functional diversity on net biomass change (ΔAGB) were consistent across the gradient of temperature but were strengthened by increasing water availability. The functional identity of resource acquisition shifted from negative in colder sites to positive in warmer sites but had negative effects on ΔAGB regardless of water availability. To increase stand-level live biomass, promoting higher functional diversity is important, especially in humid sites, while enhancing the functional identity of resource acquisition is particularly important in warmer sites.

By utilizing extensive spatial and long-term forest inventory data of Canada, I showed that the functional composition of forests in colder plots experienced greater

impacts from global environmental change. Further, over time, it shifted more rapidly toward fast-growing deciduous broadleaved trees and higher drought tolerance, due to temporally increasing CO_2, warming, and changes in water availability. My findings suggest the importance of taking local historic climate into account toward the development of forest management strategies that facilitate the sustainability of functional composition, as well as ecosystem functioning and the services of forests under ongoing global environmental change.

The findings of this dissertation provide us with the knowledge in developing effective forest management and conservation strategies to cope with global environmental change impacts on forest ecosystem functioning and tree diversity that can meet international standards for carbon sequestration. This dissertation has impacts on multidisciplinary studies because biodiversity and ecosystem functioning are ultimately related to ecosystem services and benefits that improve human welfare.

Keywords: biodiversity; biomass dynamics; climate change impacts; ecosystem functioning; functional shift; mitigation

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NOTE

This is a manuscript-based thesis. Formatting and reference styles may differ because the chapters were written to suit the submission requirements of the targeted journals (see below). Chapter 2 uses "climate change", while the rest of chapters uses "global environmental change" to refer to temporal changes in atmospheric carbon dioxide (CO_2) concentration, temperature, water availability, and nitrogen deposition (the two terms are used as essentially the same meaning in this dissertation). Since individual chapters reflect the joint contributions of myself and my academic supervisor, I use "we" instead of "I" for individual manuscripts.

Chapter 2: Hisano, M., Searle, E.B. & Chen, H.Y.H. (2018). Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews*, 93, 439-456.

Chapter 3: Hisano, M., Chen, H.Y.H., Searle, E.B. & Reich, P.B. (2019). Species-rich boreal forests grew more and suffered less mortality than species-poor forests under the environmental change of the past half-century. *Ecology Letters*, 22, 999-1008.

Chapter 4: Hisano, M. & Chen, H.Y.H. Spatial variations in climate modify effects of functional diversity on biomass dynamics in natural forests across Canada. Submitted to *Global Ecology and Biogeography*.

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CHAPTER 1: GENERAL INTRODUCTION

Human-induced environmental changes have significantly impacted global ecosystem functioning and biodiversity (Chapin III et al. 2000; Lewis & Maslin 2015). A rapid rise in atmospheric carbon dioxide (CO_2) concentration has been observed with increased dependency on fossil fuel during the 20th century, which has caused an unusual rate of global warming (IPCC 2014). Terrestrial ecosystem functioning is responding to these environmental change drivers both positively and negatively (Arrow B in Fig. 1-1). For example, rise in CO_2 and global warming increased tree growth (Coomes et al. 2014; Pretzsch et al. 2014)), while warming and/or a decrease in water availability increased tree mortality (van Mantgem et al. 2009; Luo & Chen 2015) and reduced tree growth (Barber et al. 2000) over the decades. In the face of this, the United Nations Intergovernmental Panel on Climate Change (IPCC) has highlighted the importance of making efforts to prevent global warming from exceeding 1.5°C from pre-industrial levels in order to avoid drastic alteration in biodiversity and ecosystem functioning (IPCC 2018). Therefore, coping with the impacts of environmental change, that is, taking a "climate action" (Overpeck & Conde 2019), is now a globally important task.

In this dissertation, I focus on plant diversity and terrestrial ecosystem functioning, and their relationship (biodiversity-ecosystem functioning (Arrow E in Fig. 1-1), B→EF (Huang et al. 2018)) with relation to environmental factors (Arrows A-D in Fig. 1-1) because plant diversity has been hypothesized to improve ability of ecosystem functioning to mitigate impacts of global environmental change (Reich et al. 2001; Isbell et al. 2015). Plant diversity can increase productivity (i.e., biomass growth in this dissertation) in terrestrial ecosystems primarily through 'niche complementarity' and 'selection effects'. The former involves interspecific niche partitioning and facilitative interactions, while the latter results from inherent performances of individual species/traits (Isbell et al. 2017; Huang et al. 2018). Based on this relationship, biodiversity is expected to i) enhance positive impacts, and ii) reduce negative impacts of, global environmental change on ecosystem functioning. However, this perspective has been mainly tested in experimental grassland systems (Reich et al. 2001; Isbell et al. 2015; Cowles et al. 2016), and it is unclear whether plant diversity can also mitigate impacts of global environmental change in natural systems.

Besides temporal changes in the environment, spatial variation in the abiotic context also determines plant diversity and ecosystem functioning (Arrows C and D in Fig. 1-1). Plant diversity and forest productivity typically increase with a warmer climate and higher moisture availability (Keeling & Phillips 2007; Zhang et al. 2014). These spatial variations in climate are also thought to influence the relationship between diversity and productivity (Forrester 2014). The positive diversity effects on productivity tend to be strengthened in environments unfavourable for growth in both experimental and natural systems (Garcia-Palacios et al. 2018; Kardol et al. 2018) because of the extent of niche complementarity among species changes with environmental stress (Maestre et al. 2009). However, how spatial variations in environmental factors can affect diversity effects on mortality (biomass loss from dead trees) is unknown, although mortality is an important component to determine net biomass change (the difference between biomass growth and mortality), and thus terrestrial carbon cycles.

Spatial variations in climate can also affect the impacts of temporal change on forest ecosystems. For example, growth of colder boreal forests that experienced less or no changes in water availability was less negatively affected by long-term climate change compared to warmer boreal forests in eastern Canada (D'Orangeville et al. 2016). Moreover, regionally more humid boreal forests suffered less extent of loss in biomass with long-term changes in climate in western Canada (Luo et al. 2019). While global environmental change has substantially affected regional diversity and composition of forest ecosystems (Searle & Chen 2017; Fadrique et al. 2018; Esquivel-Muelbert et al. 2019), whether spatial variations in climate (i.e., local historic climate) also modifies the effects of temporal change in the environment on forest composition is largely unclear (Aguirre-Gutiérrez et al. 2019), especially at larger-scale across biomes. Understanding how fast compositional shifts occur on a larger scale across biomes is essential for developing globally applicable strategies for 'climate action' (Overpeck & Conde 2019).

The general objective of this dissertation was to enhance knowledge on the relationship between tree diversity/composition and forest ecosystem functioning in relation to spatiotemporal environmental factors. Firstly, I established a concept of how plant diversity can mitigate global environmental change impacts on ecosystem functioning of natural forests (Chapter 2). Secondly, to empirically test this concept, I examined whether species-rich forests grew more and suffered less mortality in natural forest systems (Chapter 3). Thirdly, I explored spatial variations in climate effects on the relationship between tree functional diversity and forest biomass dynamics (Chapter 4). Lastly, I investigated whether spatial variations in climate determine the rate and directionality of functional shifts of natural forests induced by global change environmental change (Chapter 5). To achieve these specific objectives, I conducted extensive literature review (Chapter 2) and analysed large-spatial and long-term forest inventory data spanning boreal forest, temperate coniferous forest, and temperate broadleaf and mixed forest of Canada (Chapters 3-5).

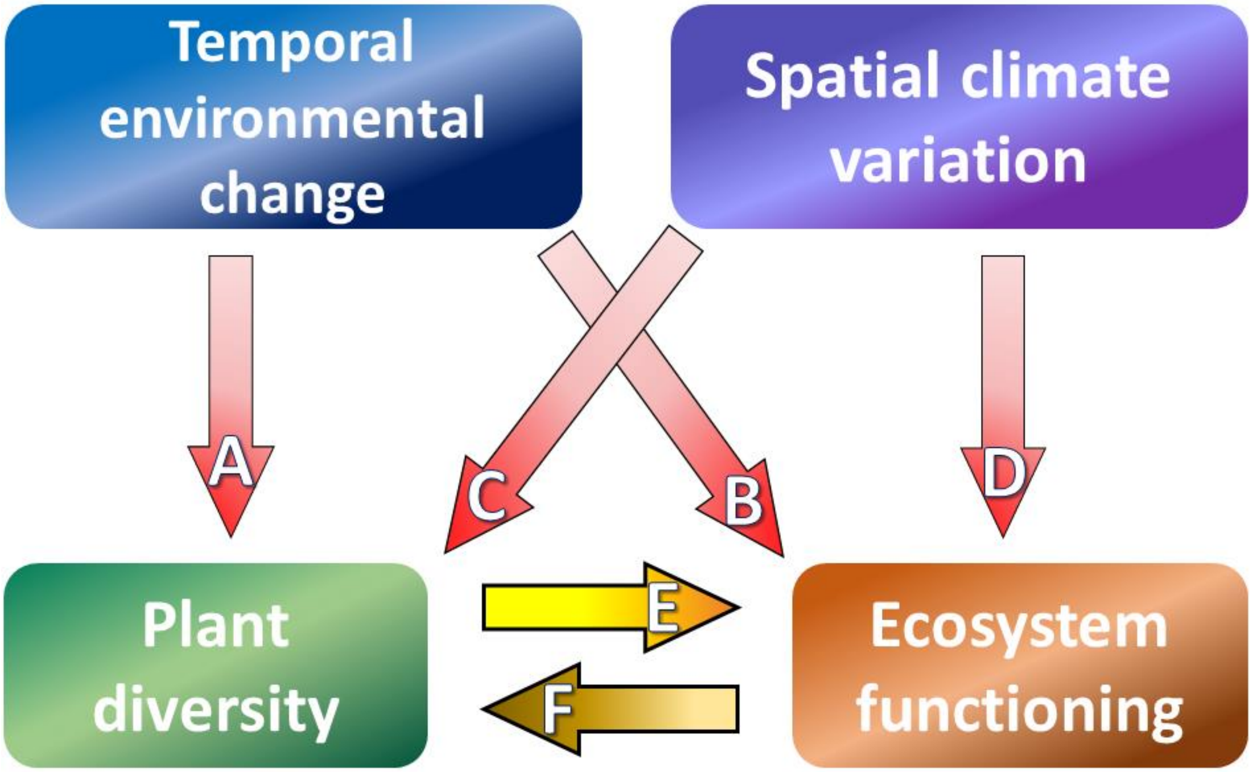

Figure 1-1: A conceptual figure demonstrating the hypothesized causal paths examined in this dissertation. The arrows indicate potential causal relationships. Chapter 2 refers to Arrows A, B, E, and F. Chapter 3 mainly explores Arrows B and E and touches on Arrow A, as well. Chapter 4 investigates Arrows C, D, and E. Chapter 5 deals with Arrows A and C with an implication to Arrow E.

CHAPTER 2: BIODIVERSITY AS A SOLUTION TO MITIGATE CLIMATE CHANGE IMPACTS ON THE FUNCTIONING OF FOREST ECOSYSTEMS

2.1 Abstract

Forest ecosystems are critical to mitigating greenhouse gas emissions through carbon sequestration. However, climate change has affected forest ecosystem functioning in both negative and positive ways and has led to shifts in species/functional diversity and losses in plant species diversity which may impair the positive effects of diversity on ecosystem functioning. Biodiversity may mitigate climate change impacts on (I) biodiversity itself as more-diverse systems could be more resilient to climate change impacts, and (II) ecosystem functioning through the positive relationship between diversity and ecosystem functioning. By surveying the literature, we examined how climate change has affected forest ecosystem functioning and plant diversity. Based on the biodiversity effects on ecosystem functioning (B→EF), we specifically address the potential for biodiversity to mitigate climate change impacts on forest ecosystem functioning. For this purpose, we formulate a concept whereby biodiversity may reduce the negative impacts or enhance the positive impacts of climate change on ecosystem functioning. Further B→EF studies on climate change in natural forests are encouraged to elucidate how biodiversity might influence ecosystem functioning. This may be achieved through the detailed scrutiny of large spatial/long temporal scale data sets, such as long-term forest inventories. Forest management strategies based on B→EF have strong potential for augmenting the effectiveness of the roles of forests in the mitigation of climate change impacts on ecosystem functioning.

2.2 Introduction

Forest ecosystems cover more than 4.1 billion ha of the Earth's surface and greatly contribute to the global carbon cycle as carbon sequestration reservoirs (Dixon et al. 1994; Pan et al. 2011; Körner 2017). They are also the primary elements for atmospheric carbon dioxide (CO_2) absorption, functioning as massive terrestrial carbon sink systems (Canadell & Raupach 2008). The role that forests have in climate change mitigation is generally recognised, and their strategic management is imperative for maintaining, and ideally enhancing, their effectiveness (Canadell & Raupach 2008).

Global environmental changes have significantly affected functioning and biodiversity in forest ecosystems (Sala et al. 2000; Fig. 1). The degradation of the environment and climate change, due to anthropocentric factors, is rapidly leading to a significant reduction in global species diversity (Thuiller et al. 2005; Harley 2011; Hooper et al. 2012), changes in the global distribution of organisms (Chapin III et al. 2000), shifts in species composition (Bertrand et al. 2011; Fauset et al. 2012; Searle & Chen 2017a), and the alteration of species interactions (Harley 2011; Blois et al. 2013). Carbon dynamics in global forests have been affected by climate change both positively and negatively, contingent on the driver under examination (e.g., Boisvenue & Running 2006; Allen et al. 2010; Allen et al. 2015). Rising atmospheric CO_2 levels and increasing nitrogen deposition may increase tree growth and carbon storage in certain regions that are not constrained by water availability (Magnani et al. 2007; Thomas et al. 2010) (but see Norby & Zak 2011; Körner 2017), whereas water deficits, as well as enhanced competition induced by warming and rising CO_2 levels, have increased tree mortality and reduced net aboveground biomass change (the difference between biomass gain from growth and biomass loss from mortality) of forests on a global scale (Van Mantgem et al. 2009; Hooper et al. 2012;

Brienen et al. 2015; Chen & Luo 2015; Luo & Chen 2015; Chen et al. 2016). Climate change may also impact global commercial forestry *via* decreasing yields and affect market prices of timber products, and thus the economic value of woodlands (Kirilenko & Sedjo 2007; Hanewinkel et al. 2013; Zhou 2017). Therefore, the development of adaptive forest management practices against these degradative impacts of global environmental change is critical and relies on an improved understanding of the nature of climate change threats to biodiversity and ecosystem functioning (Dawson et al. 2011). To mitigate environmental changes effectively forest management strategies should (*a*) generate an annual sustained yield of timber, fibre, and energy; (*b*) maintain or increase forest carbon stocks; (*c*) preserve forest biodiversity (IPCC 2014).

Biodiversity has the potential to mitigate two important elements of climate change impacts: (I) on biodiversity itself as more diverse systems could be more resilient (e.g., Chapin III et al. 2000); and (II) on ecosystem functioning (Grossiord et al. 2014; Isbell et al. 2015; Ruiz‐Benito et al. 2017a; Sakschewski et al. 2016; Fig. 1). Global environmental change does not only affect ecosystem functioning and biodiversity, but also *vice versa*. Losses in biodiversity can directly reduce ecosystem functioning (e.g. losses in carbon stocks, arrow C in Fig. 2-1), which can accelerate global change (e.g. increased carbon emission, arrow E in Fig. 2-1). Moreover, increased biodiversity can mitigate the negative impacts of climate change on ecosystem functioning (arrow B in Fig. 2-1) by enhancing ecosystem functioning through the direct relationship between biodiversity and ecosystem functioning (arrow C in Fig. 2-1, mitigation type II) (Grossiord et al. 2014; Isbell et al. 2015; Ruiz‐Benito et al. 2017a; Sakschewski et al. 2016). Herein, we specifically review and synthesise the rapidly expanding literature on the potential of biodiversity to mitigate climate change impacts on ecosystem functioning.

Over the last two decades, much effort has been invested towards revealing the effect of biodiversity on ecosystem functioning (i.e. B–EF; but here termed as B→EF for clarification of directionality) (Huston 1997; Tilman 1997; Lavorel 1999; Yachi & Loreau 1999; Naeem et al. 2000; Loreau & Hector 2001; Hooper et al. 2005; Tilman et al. 2006; Paquette & Messier 2011; Cardinale et al. 2012; Hooper et al. 2012; Tilman et al. 2012; Zhang et al. 2012; Barrufol et al. 2013; Isbell et al. 2013; Jucker et al. 2014; Morin et al. 2014; Pedro et al. 2014; Tilman et al. 2014; Hautier et al. 2015; Liang et al. 2015; Grace et al. 2016; Liang et al. 2016), and the profound positive effects of diversity on ecosystem processes (e.g. productivity) have been well documented. Further, diversity provides higher levels multiple ecosystem services to society (i.e. B–ES) (Gamfeldt et al. 2013; Mori et al. 2016), hence, studies of B→EF ultimately aim to improve human wellbeing through enhanced ecosystem functioning by increasing biodiversity (Duffy 2009). Therefore, we anticipate that these positive effects of biodiversity may be employed in forest management strategies as a solution to reduce the negative impacts, or to enhance the positive impacts, of climate change on ecosystem functioning (here defined as the 'biodiversity-mitigation concept') (note that for the purposes of this study, 'biodiversity-mitigation concept' is exclusively used for mitigation type II: biodiversity as a solution to mitigate climate change impacts on ecosystem functioning; Fig. 2-1). Several studies have combined research on the effects of diversity loss on B→EF and impacts of climate change on ecosystem functioning, where diversity has been shown to enhance productivity, stability, resistance and/or resilience against the effects of climatic drivers in experimental grasslands (Reich et al. 2001; Isbell et al. 2015; Cowles et al. 2016). However, research into B→EF in the context of climate change in natural forest systems is largely lagging behind, with little evidence having emerged recently (Grossiord et al. 2014; Gazol & Camarero 2016; Ruiz - Benito et al. 2017a). Hence, a systematic framework is required to develop the biodiversity-mitigation concept and to orient future studies.

It should also be noted that ecosystem functioning can affect biodiversity (EF→B; arrow D in Fig. 2-1). This relationship has been found to be both positive and negative, and even linear or non-linear, with the most common relationship being unimodal (e.g., Grime 1973; Chase & Leibold 2002; Gillman & Wright 2006; Reich et al. 2012; Grace et al. 2016). A recent study using integrative modelling techniques revealed that species richness had a positive effect on productivity, while the accumulation of total biomass depressed richness (Grace et al. 2016). Consideration of both B→EF and EF→B is needed to disentangle the complex mechanism of B→EF. Studies have rarely addressed EF→B in forest ecosystems, although this relationship provides significant implications for forest management (Liang et al. 2016). Since integrative research is still in progress, here we focus on B→EF to address the biodiversity-mitigation concept.

In this paper, we review (*i*) how climate change has impacted forest ecosystem functioning and terrestrial plant diversity; (*ii*) the directionality of the B→EF relationship in plant communities; and (*iii*) B→EF under environmental changes/perturbations, in order to develop the perspective that ecosystems with greater biodiversity, by improving biomass production or stability, can modulate the rate of biomass loss imparted by negative climatic drivers (e.g. warming, drought), while promoting the biomass gains initiated by positive drivers (e.g. elevated CO_2, nitrogen deposition; Fig. 2-1). Finally, we emphasise the importance of combining the two fields of study, providing implications for forest management under climate change, and for future studies into the B→EF in natural forest systems facing a changing climate.

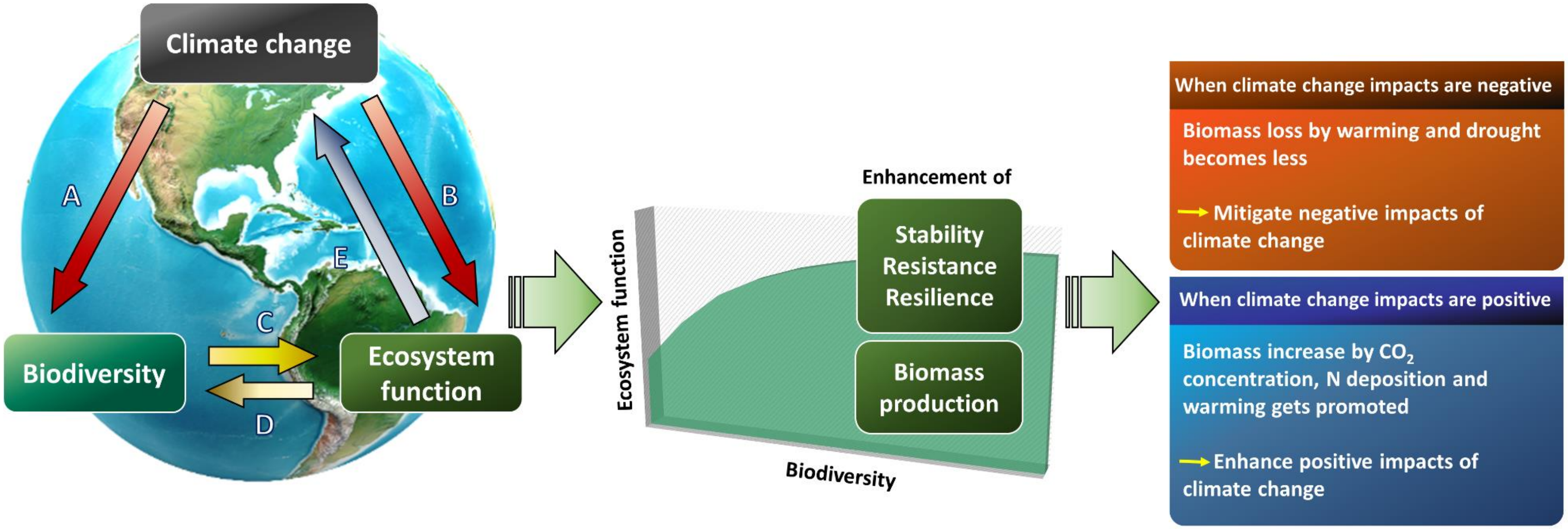

Figure 2.1: A conceptual diagram showing how biodiversity reduces the negative impacts and enhances the positive impacts of climate change on ecosystem functioning (the biodiversity-mitigation concept).

2.3 Materials and Methods

2.3.1 Term definitions

The Intergovernmental Panel on Climate Change (IPCC) defines 'mitigation' as a human intervention to reduce the sources of greenhouse gas and their cumulative impacts, or enhance the carbon sinks to sequester them (IPCC 2014). However, here we specify the term as an effort to reduce the negative impacts, or to enhance the positive impacts of climate change on ecosystem functioning (i.e. 'risk hedge' of ecosystem functioning against climate change impacts). 'Climate change' (and 'environmental change') encompasses both chronic climate change and particular climatic events. Among the 'climatic drivers' to affect ecosystem functioning, we particularly focus on global warming, altered moisture availability, CO_2 concentrations, and nitrogen deposition (Yuan & Chen 2015). 'Ecosystem functioning' here focuses primarily on aboveground productivity and net aboveground biomass in forest systems, including their associated components, i.e. mortality, recruitment, growth (Chen & Luo 2015; Chen et al. 2016), their temporal stability (ratio of the mean to standard deviation), resistance (proximity to normal levels), and resilience (rate of return towards normal levels) (Isbell et al. 2015). 'Biodiversity' includes variables of taxonomic diversity (e.g. species richness, evenness), functional diversity [e.g. functional dispersion (FDis), community-weighted mean (CWM) functional traits], and species/trait composition (Duncan et al. 2015).

2.3.2 Literature search

To obtain literature for Sections III and IV, we performed literature searches using *Web of Science* and *Google Scholar* and combinations of the following key words: "biodiversity", "biomass", "climate change", "CO_2", "compositional shift", "diversity", "drought", "ecosystem function", "forest", "functional shift", "growth", "mortality", "nitrogen addition", "nitrogen deposition”, “plant”, “productivity”, “species”, “tree”. We selected representative relevant English-written peer-reviewed literature to provide examples (Tables 2-1 and 2-2). Note that this search did not necessarily aim to cover all existing literature because these topics have been extensively reviewed elsewhere (e.g., Boisvenue & Running 2006; Allen et al. 2010; Bellard et al. 2012; Allen et al. 2015).

For the remaining sections, we again searched intensively for papers published from peer-reviewed journals written in English using *Web of Science* and *Google Scholar*. Various combinations of the following key words were used, to ensure that all relevant literature was obtained: “B-EF”, “biodiversity”, “biomass”, “climat* driver”, “climate change”, “CO_2”, “disturbance”, “diversity”, “DPR (diversity-productivity relationship)”, “drought”, “ecosystem function*”, “evenness”, “forest”, “functional diversity”, “grassland”, “growth”, “mediate”, “mitigate”, “modulate”, “mortality”, “nitrogen addition”, “nitrogen deposition”, “perturbation”, “plant”, “precipitation”, “productivity”, “recovery”, “resilience”, “resistance”, “richness”, “species diversity”, “stability”, “temperature”, “tree”, and “warming”. We examined all papers resulting from this search, and extracted those that satisfied at least one of the following criteria: (*a*) experimental B→EF studies conducted in terrestrial systems with control of climatic drivers [specifically, manipulating the conditions, or intensities, of temperature, drought (moisture availability in air or soil), CO_2 concentration, and N addition]; (*b*) B→EF studies conducted in natural terrestrial systems under chronic climate change (e.g. warming, chronic drought, rise in CO_2 levels) or climate events/disturbances (e.g. drought event); and (*c*) any studies (not necessarily within a B→EF framework) that compared ecosystem functioning between different levels of species/functional diversity, or different types of species/functional compositions (species/functional identity; e.g. species/trait relative abundance, CWM), in natural or experimental terrestrial systems, with explicit inclusion of climatic drivers. References cited by this literature were also included if they fitted our selection criteria. Studies focusing on belowground systems were excluded from our review.

2.4 Climate change impacts on forest ecosystem functioning

Climate change has impacted patterns of demography, productivity, and carbon storage in global forests (Table 2-1). Reduced water availability, caused by the combination of rising temperatures and altered precipitation, has increased tree mortality directly through the interaction of carbon starvation with hydraulic failure (McDowell et al. 2008; Hartmann et al. 2015) and/or indirectly through enhanced vulnerability to insects (McDowell et al. 2011; Anderegg et al. 2015). Even in regions without drought, other drivers of climate change have increased tree mortality by potentially reducing tree longevity (Brienen et al. 2015) or enhancing competition among trees (Luo & Chen 2015). Crucially, climate change-type increases in tree mortality are often associated with enormous losses in forest biomass (Lewis et al. 2011; Michaelian et al. 2011). Therefore, although mortality rates are not typically considered as an ecosystem function, they are a critical factor that influences global carbon storage.

In contrast to mortality rates, which universally increase due to climate change, responses of tree growth to climate change are inconsistent: both positive and negative impacts have been observed regardless of moisture availability. Tree growth and productivity have been enhanced by different combinations of the following drivers: rising temperatures that extend the growing season, increased moisture, nitrogen deposition, and elevated CO_2 concentrations (Hember et al. 2012; Coomes et al. 2014; Pretzsch et al. 2014). On the other hand, rising temperatures and increased frequency of drought have reduced the growth rates of trees (Barber et al. 2000; Feeley et al. 2007; Brzostek et al. 2014).

These climate change impacts on biomass loss, due to tree mortality, and biomass gain, by the growth of surviving trees and ingrowth by new recruitment trees, jointly affect net aboveground biomass change. The increase in mortality and decline in growth rates in some regions have substantially contributed to declining net aboveground biomass change (Hooper et al. 2012; Chen & Luo 2015; Chen et al. 2016). These declines have led to concerns that global forest ecosystems might be transformed from carbon sinks to carbon sources through global environmental change (Peng et al. 2011; Brienen et al. 2015). Furthermore, climate change-associated declines in net aboveground biomass change are speculated to occur without decreased water availability, where forests experience faster temporal increases in tree mortality than growth rates, resulting in a net aboveground biomass decline (Brienen et al. 2015).

In order to grasp these trends related to climate change impacts correctly, we need to assess several methodological considerations. It should be noted that studies on growth rate changes are conducted by two different methods: plot sampling and dendrochronology, whereas mortality and net aboveground biomass change are often measured solely by plot sampling. Dendrochronological studies typically focus on older/larger trees, while forest inventory studies generally include a wider age/size range of trees (Table 2-1). As larger trees are more susceptible to drought (Bennett et al. 2015), tree-ring data may be more likely to show negative growth rate responses, while forest inventory data may detect positive trends. Further, mortality must be examined through repeated measurements, as coring does not allow reliable sampling of dead trees. Therefore, contrasting reports on the responses of tree growth to climate change (both negative and positive) might result from the different characteristics of these survey methods.

Another important factor to consider when examining the results of climate change on forest ecosystems are endogenous processes, such as forest age effects. Stand aging is critical in the determination of forest dynamics (Chen et al. 2016; Poorter et al. 2016), particularly for temperate and boreal forests where stand-replacing disturbances such as fire occur. In the process of stand development, aging increases mortality (Luo & Chen 2011) while reducing growth and net aboveground biomass change (Pretzsch et al. 2014; Chen & Luo 2015; Chen et al. 2016). Among the literature that we reviewed, several studies from temperate/boreal forests did not take age effects into consideration (Barber et al. 2000; Van Mantgem et al. 2009) (Table 2-1), which might raise concerns that the observed temporal changes in stand dynamics might merely have reflected natural age-related processes and did not arise as the result of climate change. Hence, contrasting results that climate change may affect forest ecosystem functioning both positively and negatively might also be attributed to whether stand aging factors were considered.

Table 2-1: Positive and negative impacts of climate change on forest ecosystem functioning.

Source	Type of impact	Geographical location (biome[a])	Survey method[b]	Study period	Stand age	Threshold[c]	Climatic driver[d]
Growth change							
(Pretzsch et al. 2014)	Increased growth	Germany (Te)	FI	1870–2010	*	21–188 years; 5.4–54.4 cm	W
(Thomas et al. 2010)	Increased biomass	Northeastern-central USA (Te)	FI	Early 1980s–mid 1990s		> 12.7 cm	N
(McMahon et al. 2010)	Increased biomass	Eastern USA (Te)	FI	1987–2005	*	5–250 years; > 2 cm	C, N, W
(Fang et al. 2014)	Increased biomass	Japan (Te)	FI	1980–2005	*	5-80 years	C, N, IP, W
(Hember et al. 2012)	Increased production and growth	Western Canada (Te)	FI	1959–1998	*	20–160 years; > 4.0 cm	C, IP, W
(Laurance et al. 2004)	Increased growth	Amazon (Tr)	FI	1981–2000	†	≥ 10 cm	C
(Lewis et al. 2009)	Increased biomass	Africa (Tr)	FI	1968–2007		≥ 10 cm	C
(Coomes et al. 2014)	Increased production	New Zealand (Te)	FI	1980–2005		≥ 2.5 cm	W
(D'Orangeville et al. 2016)	Increased/decreased growth	Eastern Canada (Bo)	TR	1960–2004		Not shown	DP, W
(Prior & Bowman 2014)	Decreased growth	Southern Australia (Te)	FI	Not shown		10–150 cm	W
(Elliott et al. 2015)	Decreased growth	Eastern USA (Te)	TR	1935–2003		10.0–110.6 cm	DP
(Girardin et al. 2016)	Decreased growth	Across Canada	TR	1971–2004	*	> 5 cm	W
(Barber et al. 2000)	Decreased growth	Alaska (Bo)	TR, CI	1900–1996		≥ 85 years; ≥ 6.0 cm	W, DP
(Jump et al. 2006)	Decreased growth	Spain (Te)	TR	1960–2003	*	50–235 years; 25.8–118.4 cm	W

(Feeley et al. 2007)	Decreased growth	Panama and Malaysia (Tr)	FI	1981–2005 (Panama), 1989–2000 (Malaysia)		≥ 1.0 cm	W
(Brzostek et al. 2014)	Decreased growth	Eastern USA (Te)	FI	2000–2012		≥ 12.7 cm	DP
(Hogg et al. 2002)	Decreased growth, massive mortality	Western Canada (Bo)	TR	1950–1997	†	43–99 years; 11.0–23.0 cm	DP
(Hogg & Wein 2005)	Decreased growth	Western Canada (Bo)	TR	1951–2000	*	27–200 years	DP
Mortality change							
(Phillips et al. 2009)	Increased mortality, decreased growth/biomass	Amazon (Tr)	FI	1980–2005		≥ 10 cm	DP
(van Mantgem & Stephenson 2007)	Increased mortality	Western USA (Te)	FI	1983–2004		≥ 1.37 m	W, DP
(Van Mantgem et al. 2009)	Increased mortality, reduced biomass	Western USA (Te)	FI	1955–2007		≥ 0.1 cm	W, DP
(Peng et al. 2011)	Increased mortality	Canada (Bo)	FI	1963–2008	*	80–218 years	DP
(Luo & Chen 2013)	Increased mortality	Western Canada (Bo)	FI	1950–2007	*	17–243 years; ≥ 10 cm	DP
(McIntyre et al. 2015)	Increased mortality, reduced biomass	Western USA (Te)	FI	1920–1930s and 2001–2010		≥ 10.2 cm	W, DP
(Bennett et al. 2015)	Increased mortality and decreased growth	Global (Bo, Te, Tr)	MA-FI	–	–	–	DP
(Huang & Anderegg 2012)	Massive mortality, reduced biomass	Southwestern USA (Sub-al)	PS	2009–2011		1.0–39.6 cm	DP
(Hogg et al. 2008)	Increased mortality, decreased growth	Western Canada (Bo)	TR, PS	2000–2005	†	> 7.0 cm	DP
(Zhang & Liang 2014)	Increased mortality	Northeastern China (Te)	FI	1986–2006	†	≥ 5.0 cm	DP
(Luo & Chen 2015c)	Increased mortality	Western Canada (Bo)	FI	1984–2010	*	10–163 years; 5 cm	W, C

Net biomass change							
(Brienen et al. 2015)	Reduced biomass	Amazon (Tr)	FI	1983–2011		≥ 10 cm	W, C
(Ma et al. 2012)	Reduced biomass	Western Canada (Bo)	FI	1963–2008	*	80–218 years	DP, W
(Chen & Luo 2015)	Reduced biomass	Western Canada (Bo)	FI	1958–2011	*	17–174 years; ≥ 10 cm	DP, W
(Zhou et al. 2013)	Reduced biomass, decreased growth	Southern China (Sub-tr)	FI	1978–2010	*	≥ 1.0 cm; ≥ 1.5 m	W, DP
(Rolim et al. 2005)	Reduced biomass	Amazon (Tr)	FI	1978–2000		≥ 10 cm	DP
(Zhang et al. 2015)	Reduced biomass	Western Canada (Bo)	FI	1958–2009	*	≥ 50 years; ≥ 9.0 cm	DP
(Chen et al. 2016)	Reduced biomass	Western Canada (Bo)	FI	1958–2011	*	17–210 years; ≥ 10 cm	DP, W
(Malhi et al. 2015)	Net primary production stopped increasing	Amazon (Tr)	FI	2009–2012		≥ 10 cm	DP

[a] Bo: boreal; Sub-al: sub-alpine; Sub-tr: sub-tropical; Te: temperate; Tr: tropical.

[b] CI: carbon isotope data; FI: forest inventory data; MA-FI : meta-analysis of forest inventory studies; PS: plot sampling data; TR: tree-ring data.

[c] Initial forest/tree age (years); diameter at breast height (DBH; cm); height (m).

[d] C: rising CO_2; DP: decreased precipitation/moisture availability or drought; IP: increased precipitation/moisture availability; N: nitrogen deposition; W: warming.

[e] Green arrow: positive impacts of climate change on forest ecosystem functioning; red arrow: negative impacts of climate change on forest ecosystem functioning; yellow arrow: results showed mixed conclusions.

*Studies that accounted for stand-age effects.

†Studies that confirmed that stand-age effects were negligible.

2.5 Climate change impacts on plant diversity

On a geographic macroscale of biodiversity, climate change may initiate biome shifts, and is predicted to alter approximately 50% of global vegetation by the next century (Bergengren et al. 2011). Generally, biome shifts occur geographically along with changes in climatic conditions, causing present edges of species ranges to be most affected (Sala 2005). Species may track suitable climatic conditions at the regional scale (i.e. species response along the spatial axis), and much evidence supports latitudinal and altitudinal range shifts of plant species that are induced by climate change (Colwell et al. 2008; Bellard et al. 2012). Moreover, each species is assumed to respond to climate change independently, since they have variable environmental requirements and capacities to adapt (Sala 2005). Furthermore, species with traits that are sensitive to climatic drivers decrease in dominance within their range, while those with traits that are tolerant to environmental change prosper (Moradi et al. 2012). For example, warming has caused directional changes in the relative abundance of life-history traits across the Japanese archipelago (Suzuki et al. 2015), leading to increases in species around their colder range limits at the expense of the current occupants. Moreover, drought has favoured traits associated with rapid growth (Harrison et al. 2015) and drought tolerance (Feeley et al. 2011; Fauset et al. 2012). Similarly, increasing CO_2 concentration (Laurance et al. 2004) and nitrogen deposition (Bobbink et al. 2010; Duprè et al. 2010), or a combination of all climate drivers (Searle & Chen 2017a) have also caused shifts in functional traits or species composition by favouring species with certain functional traits that benefit them in their new climate reality. Thus, differences in vulnerability to climatic change between species or functional traits may lead to compositional shifts (Table 2-2).

Table 2-2: Impacts of climate change on plant biodiversity in natural systems.

Source	Type of impact	Community[a]	Geographic location (biome[b])	Survey method[c]	Study period	Climatic driver[d]
(Stevens et al. 2004)	Decreased species richness	H	UK (Te)	PS	2002–2003	N
(Harrison et al. 2015)	Decreased species richness	H	Western USA (Te)	PS	2000–2014	DP
(Pauli et al. 2012)	Decreased/increased species richness	H	Europe (Al)	PS	2001–2008	W, DP
(Duprè et al. 2010)	Shifted species composition	H	Northern Europe (Te)	PS	1960–2003 (UK), 1939–2006 (Netherlands), 1940–2007 (Germany), 2007 (Denmark), 2007 (Sweden)	N
(Fauset et al. 2012)	Shifted functional traits	T	Ghana (Tr)	FI	Early 1990s–2010 (functional trait), 1968–2010 (compositional change)	DP
(Feeley et al. 2011)	Shifted species composition	T	Panama (Tr)	FI	1981–2005	DP
(McIntyre et al. 2015)	Shifted species composition	T	Western USA (Te)	FI	1920–1930s and–2001-2010	W, DP
(Laurance et al. 2004)	Shifted species composition	T	Amazon (Tr)	FI	1981–2000	C
(Suzuki et al. 2015)	Shifted life-history traits	T	Japan (Te)	FI	2004–2012	W
(Soudzilovskaia et al. 2013)	Shifted functional traits	H	Russia (Al)	PS	1981–2009	W
(Li et al. 2015)	Shifted functional traits	T	Southern China (Sub-tr)	FI	1978–2010	DP, C, W, N
(Zhou et al. 2013)	Increased species richness, shifted species composition	T	Southern China (Sub-tr)	FI	1978–2010	W, DP

(Enquist & Enquist 2011)	Shifted functional traits	T	Costa Rica (Tr)	FI	1976–1996	DP
(Mueller et al. 2005)	Shifted species composition	T	Western USA (Te)	FI	1996–2002	DP
(Searle & Chen 2017)	Shifted life-history traits	T	Western Canada (Bo)	FI	1958–2013	W, C
(Grabherr et al. 1994)	Increased species richness	H	Central Europe (Al)	PS, HR	1895–1992	W

[a] H: herbaceous; T: tree.

[b] Al: alpine; Bo: boreal; Sub-tr: sub-tropical; Te: temperate; Tr: tropical.

[c] FI: forest inventory data; HR: historical data; PS: plot sampling data.

[d] C: rising CO_2; DP: decreased precipitation/moisture availability or drought; N: nitrogen deposition; W: warming.

At the taxonomic level, warming and decreased water availability have caused regional plant species extinction and decreases in species diversity (Thuiller et al. 2005). For instance, plant species richness of a grassland community in California declined with the loss of species that were sensitive to drought (Harrison et al. 2015). Additionally, nitrogen deposition has reduced species richness in global infertile grasslands and heathlands (Sala et al. 2000; Duprè et al. 2010). Elevated CO_2 levels acted to decrease species richness in experimental grasslands by delaying senescence of the dominant plant canopy, thereby covering late-emerging and shorter species (Zavaleta et al. 2003). Thus, multiple climatic drivers have reduced global plant species diversity in grasslands; however, studies relating to how environmental changes have affected species diversity in forest ecosystems are unavailable.

Climate change-induced shifts in community structure may affect regional species diversity not only negatively, but also positively. It is speculated that warming, increased precipitation, and enhanced CO_2 concentration may increase biodiversity by providing more favourable or productive habitats for certain plant species/communities (Bellard et al. 2012). In experimental grasslands, elevated CO_2 levels had the effect of increasing species richness and/or evenness by improving reproduction and survival, and decreasing the dominance of some species (Leadley et al. 1999; Niklaus et al. 2001). Additionally, regional diversity might increase with climate change-type compositional shifts if the number of immigrant species allowed by climate change exceeds that of extirpated species. Even though water deficiency decreased species richness on the summits of Mediterranean mountain regions, it increased on the summits of boreal and temperate mountain regions due to warming-induced range shifts (Pauli et al. 2012). If the direction of global climate change impacts on biodiversity can be both negative and positive, then climate change may not have an overall directional effect. Indeed, a global meta-analysis suggests that climate change does not actually change net plant biodiversity at local scales overall, with increases equally as probable as declines (Vellend et al. 2013) although Gonzalez et al. (2016) contends that these data should be re-analysed more carefully to include consideration of spatial bias, differences in timescale, and post-disturbance recovery. In light of this, we need to disentangle the complexity of the negative and positive interactions between climate change and biodiversity in order to understand their relationship.

Notably, lags occur between these biodiversity shifts and climate change when the biotic responses do not correspond to the assumption of complete synchrony with climate change (defined as ‘climatic debt’). For example, the forest plant composition in France responded to climate warming in highland areas more rapidly than in lowland areas due to differences in community tolerance to warming and the suitability of habitat for migration between the areas (Bertrand et al. 2011). Other than altitudinal differences, investigating latitudinal as well as moisture gradient differences in compositional responses will advance our understanding of climatic debt. Moreover, climatic debt in terms of plant species diversity should also be explored.

2.6 The role of biodiversity under environmental change

2.6.1 An overview of biodiversity–ecosystem functioning

Biodiversity influences the functioning of ecosystems (e.g. primary production, nutrient cycling, decomposition), and losses in diversity reduce the efficiency of communities in the uptake of resources (e.g. nutrients, water, light) and in conversion of those resources into biomass (Cardinale et al. 2012; Hooper et al. 2012; Tilman et al. 2012). The principle of this biodiversity–ecosystem functioning relationship (arrow C in Fig. 2-1) is based on the predictions of: (*i*) the niche complementary hypothesis, which predicts that niche partitioning and/or interspecific facilitation improves the utilisation of limited resources and nutrient retention; and (*ii*) the selection probability effect hypothesis, which is based on the inherent productivities of respective species, and predicts that sites with higher species diversity have a greater probability of containing more productive species (Huston 1997; Tilman 1997; Loreau & Hector 2001; Hooper et al. 2005; Tilman et al. 2014). In addition, the niche efficiency hypothesis, a recent theoretical model, proposes that diversity can improve overall resource utilisation efficiency and thereby enhance productivity, based on a link between resources and productivity (Liang et al. 2015). When considering environmental variability, the insurance hypothesis must also be discussed. This hypothesis states that each species has different ways of responding to disturbances, and sites with multiple species have greater guarantees of maintaining ecosystem functioning, in that certain species may work against certain disturbances even if others fail (Yachi & Loreau 1999). Based on these mechanisms, biodiversity enhances the ability of communities to utilise resources and to gain biomass from these resources. Biodiversity has been shown to increase ecosystem productivity significantly in experimental grasslands controlling herbaceous species diversity (Hooper et al. 2012; Tilman et al. 2014), natural grasslands (Grace et al. 2016), and global natural forest ecosystems (Paquette & Messier 2011; Zhang et al. 2012; Barrufol et al. 2013; Liang et al. 2016). Diversity also enhances ecosystem stability against environmental variability (Tilman et al. 2006; Cardinale et al. 2012), resistance to drought and invasive species (Naeem et al. 2000; Tilman et al. 2014), and resilience to disturbances (Lavorel 1999). The common relationship between species diversity and stability against disturbances is also observable in forest ecosystems (Jucker et al. 2014; Morin et al. 2014; Pedro et al. 2014). In this way, alteration of biodiversity affects ecosystem functions as strongly as (or even more strongly than) direct environmental changes (Hooper et al. 2012; Tilman et al. 2012).

Additionally, changes in biodiversity might even allow climatic drivers indirectly to affect ecosystem functioning (Fig. 2-1); for example, reduced species diversity by nitrogen addition decreases ecosystem productivity and stability (Isbell et al. 2013; Hautier et al. 2015). These findings imply that the positive relationship between diversity and ecosystem functioning might be leveraged to mediate the negative impacts of environmental changes (i.e. biomass production in ecosystems with greater diversity would be less adversely affected by negative climatic drivers), and enhance the positive impacts of climate change (i.e. increased growth rate by positive climatic drivers would be promoted in more diverse systems – a synergistic relationship; Fig. 2-1). To develop this concept, it is essential to understand how B→EF is affected under altered climate conditions, extremes, or perturbations.

2.6.2 Applying the diversity–productivity relationship under perturbation to the mitigation concept

Diversity may enhance or modulate the impacts of natural perturbations on ecosystem functions (Yachi & Loreau 1999; Pedro et al. 2014; Wright et al. 2015). We propose that this diversity–productivity relationship under perturbation is applicable in the context of climate change, since climate change may be regarded as a disturbance. Each type of disturbance (Lake 2013) might correspond to each type of climate change (i.e. climate extremes/events = 'pulse disturbance'; chronic/persistent climate changes = 'press disturbance' or 'ramp disturbance'). When perturbations have a positive influence on resource enrichment and productivity, biodiversity promotes the positive effect (Wright et al. 2015); on the other hand, when disturbance decreases productivity, diversity modulates biomass reduction, thereby increasing stability (Tilman et al. 2006; Pedro et al. 2014; Isbell et al. 2015). Here we illustrate how diversity affects the responses of ecosystem productivity to climate change, based on the framework for diversity–productivity relationships prior to or following perturbation (Wright et al. 2015).

When climate change impacts are positive, climatic drivers (i.e. warming, increased precipitation, CO_2 concentration, nitrogen deposition) enhance aboveground biomass, to an extent shown as blue arrows in Fig. 2-2A. Here, systems with greater diversity show additional enhanced aboveground biomass production compared to those with less diversity (the extent of the diversity effect on improved biomass is shown as a grey double-headed arrow in Fig. 2-2A). This means that more diverse systems may possess even more biomass after experiencing positive climate change impacts. On the other hand, when climate change impacts are negative, climatic drivers such as warming and drought reduce aboveground biomass, to the extent shown as red arrows in Fig. 2-2B-1. Here again, systems with greater diversity still show more aboveground biomass production than those with less diversity. That is, more diverse systems may retain a higher quantity of biomass even after experiencing negative climate change impacts.

In some cases, the effect of diversity may be altered after experiencing a climate change-induced modification (Fig. 2-2B-2). We assume that, even if the magnitude of B→EF is reduced (response slope of productivity associated with diversity becomes more gradual), it follows that the diversity effect mitigates climate change impacts as long as the productivity of polyculture sites is greater than that of monoculture following a climate change-induced alteration. In other cases, the magnitude of B→EF may become even greater after experiencing a climate change-induced modification (Fig. 2-2B-3), which may more effectively lessen negative impacts. However, if no effect of diversity is observed following a climate change-induced alteration, this will mean that diversity does not mitigate climate change impacts (Fig. 2-2B-4). The key assumption is whether diversity effects on ecosystem functioning are persistent after experiencing climate change-induced modifications. If they are persistent, then diversity is able to enhance/reduce climate change impacts as it does under other perturbations.

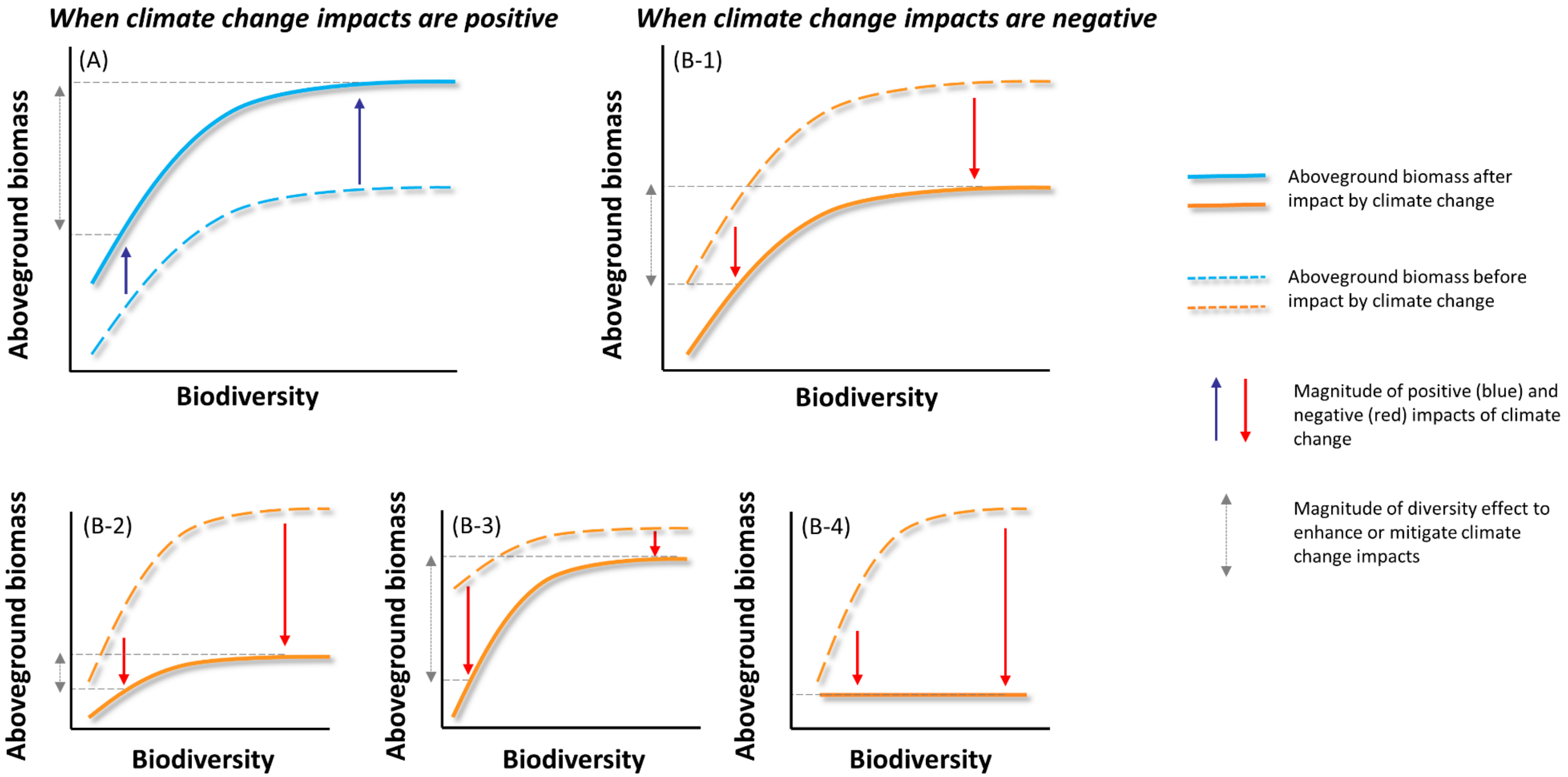

Figure 2-2: Theoretical diversity–productivity relationships under climate change based on Wright et al. (2015). Expected changes in productivity prior to and following climate change-induced modifications are shown: (A) when climate change impacts are positive; (B1–4): when climate change impacts are negative.

2.6.3 Biodiversity–ecosystem functioning under climate change

Our knowledge of B→EF is limited in the context of global environmental change; in order to put the mitigation theory into practice, we need to understand (*i*) whether diversity still promotes biomass production under environmental change, and (*ii*) whether the direction and extent of the diversity effects are influenced by climatic drivers. In recent years, research into B→EF under climate change has been increasing (Table 2-3). For example, in grassland systems, increased plant diversity promoted the effect of positive climatic drivers, such as elevated CO_2 levels(Reich et al. 2001; Isbell et al. 2013), nitrogen/nutrient addition (Reich et al. 2001; Isbell et al. 2013; Craven et al. 2016), and warming (Cowles et al. 2016), on productivity. Diversity may also increase ecosystem stability and resistance to drought (Tilman et al. 2006) and climate extremes (Isbell et al. 2015). These experimental results all meet the key assumption addressed above: the direction of biodiversity effects on grassland production was not affected even though grassland productivity was increased by nutrient enrichment and was reduced by drought (Craven et al. 2016). These findings support the potential of biodiversity to enhance increased productivity or modulate any reduction in productivity caused by climatic drivers.

Table 2-3: Biodiversity–ecosystem functioning (B→EF) studies linked to climatic changes or events.

Source	Biodiversity[a]	Ecosystem function (type of ecosystem[b])	Survey method[c]	Geographic location	Climatic driver[d]
Enhanced positive impacts					
(Reich et al. 2001)	SR	Above/belowground biomass (EG)	H	Central USA	C, N
(Cowles et al. 2016)	SR	Aboveground net primary production (EG)	H	Central USA	W
(Isbell et al. 2013)	SR	Aboveground net primary production (EG)	H	Central USA	C, N
(Coomes et al. 2014)	SI (FI)	Aboveground wood production (NF)	FI	New Zealand	W
Enhanced/reduced positive/negative impacts					
(Craven et al. 2016)	SR	Aboveground biomass (EG)	MA	Europe, North America	DP, N
Reduced negative impacts					
(Isbell et al. 2015)	SR	Stability/resistance/resilience of productivity (EG)	H	Europe, North America	DP, IP
(Gazol & Camarero 2016)	FD	Basal area increment (growth resilience) (NF)	TR	Spain	DP
(Van Ruijven & Berendse 2010)	SR	Recovery (production after drought) (EG)	H	Netherlands	DP
(Grossiord et al. 2014)	Sh	Resistance (increase in δ13C) (NF)	$\delta^{13}C$	Europe	DP
(Klaus et al. 2016)	Sh	Resistance (increase in δ13C) (NG)	$\delta^{13}C$	Germany	DP
(Mariotte et al. 2013)	DS	Resistance (increase in δ13C) (EG)	$\delta^{13}C$	Switzerland	DP
(Sakschewski et al. 2016)	FD	Resilience of aboveground biomass (EF)	MS	Ecuador, Amazon	C, W, DP
(Ruiz-Benito et al. 2017a)	FD, FI	Growth, mortality, sapling abundance (NF)	FI	Europe	DP, W

(Craine et al. 2013)	FD	Physiological drought tolerance (leaf water potential) (EG)	H	Central USA	DP
(Chen & Luo 2015)	LC	Aboveground biomass (NF)	FI	Western Canada	DP, W
(Elliott et al. 2015)	FI	Growth (NF)	TR	Eastern USA	DP
(Tilman & Downing 1994)	SR	Aboveground biomass, resistance (EG)	H	Central USA	DP
(Uriarte et al. 2016)	FI	Growth, mortality (NF)	PS	Costa Rica	DP, W
(Drobyshev et al. 2013)	SI (FI), SM	Aboveground biomass, resilience (NF)	TR	Eastern Canada	DP, W
Did not enhance positive impacts					
(Coomes et al. 2014)	Sh	Aboveground wood production (NF)	FI	New Zealand	W
Did not reduce negative impacts					
(Kahmen et al. 2005)	Sh	Aboveground biomass, resistance (increase in δ13C) (Semi-NG)	H	Germany	DP
(Vogel et al. 2013)	SR	Litter mass loss rates (and microbial properties) (EG)	H	Germany	DP
(Pfisterer & Schmid 2002)	SR	Resistance/resilience of aboveground biomass production (EG)	H	Switzerland	DP
(Grossiord et al. 2013)	Sh, SM	Water use efficiency, basal area increment (NF)	$\delta^{13}C$	Finland	DP
(Wang et al. 2007)	SR	Resistance of aboveground biomass (EG)	H	Southern China	DP
(De Boeck et al. 2008)	SR	Above/belowground biomass production (EG)	H	Belgium	DP, W
(Van Peer et al. 2004)	SR	Survival rate of herbaceous plants (EG)	H	Europe	DP, W

[a] DS: removal of dominant and subordinate species; FD: functional diversity (functional dispersion); FI: functional identity; LC: life-history trait composition; Sh: Shannon index; SI: species identity; SM: species mixture; SR: species richness.

[b] EF: experimental forest; EG: experimental grassland; NF: natural forest; NG: natural grassland; Semi-NG: semi-natural grassland.

[c] $\delta^{13}C$: carbon isotope ratio; FI: forest inventory data; H: harvesting; MA: meta-analysis; MS: model simulation; PS: plot sampling data; TR: tree-ring data.

[d] C: rising CO_2; DP: decreased precipitation/moisture availability or drought; IP: increased precipitation/moisture availability; N: nutrient enrichment; W: warming.

[e] Green arrow: diversity enhanced positive impacts or reduced negative impacts of climate change; red arrow: diversity did not enhance positive impacts or reduce negative impacts; yellow arrow: results showed mixed conclusions; 0: no relationship between diversity and ecosystem function was observed.

Despite this evidence, biodiversity does not always mitigate the negative impacts of climate change (Fig. 2-2B-2). For instance, experimental warming and drought have demonstrated reduced aboveground productivity in controlled grasslands, which suppressed the positive effects of B→EF, presumably due to intensified competition for resources among an increased number of species under stressed conditions (De Boeck et al. 2008). Moreover, no positive relationship between diversity and resistance has been found in many cases due to resistance being primarily driven by differences in pre-perturbation biomass, rather than diversity (Pfisterer & Schmid 2002; Wang et al. 2007; Vogel et al. 2012). Instead, a positive effect of diversity on recovery (change in biomass production following drought) has been detected (Van Ruijven & Berendse 2010). It appears that the ability of diversity to reduce the negative impacts of climate events/perturbations in grasslands may be dependent on whether climatic drivers influence the effects of B→EF and how ecosystem functions are measured (e.g. productivity, stability, resistance, resilience, recovery).

Diversity effects on ecosystem functions under climate change have also been examined in forest systems. For example, functional diversity ameliorates the negative impacts of warming on tree mortality and sapling abundance (Ruiz - Benito et al. 2017a). Diversity may also promote resistance and resilience in forest ecosystems. The growth response of silver fir (*Abies alba*) in stands with greater functional diversity was more resilient, recovering more rapidly from drought events and exhibiting higher growth (Gazol & Camarero 2016). Moreover, a recent simulation study revealed that plant trait diversity may improve the resilience of an Amazonian forest's carbon storage against increased CO_2 and its consequences (e.g. warming, water deficiency) (Sakschewski et al. 2016). Biodiversity has also been shown to enhance resistance to annual moisture differences, although the effect was contingent on community composition

(Grossiord et al. 2014). Hence, these studies suggest that biodiversity might reduce the negative impacts of climatic events or disturbances on tree growth in natural forests through the improvement of demographic patterns (i.e. productivity), stability, resistance or resilience.

2.6.4 Mechanisms of the biodiversity-mitigation concept in forest ecosystems

The key essence of the mitigation concept is the persistence of the positive effects of diversity on ecosystem functioning under climate change-induced stresses; that is, whether climatic drivers affect niche complementarity, selection, or insurance effects. The relative importance of niche complementarity is often examined by the effects of species/functional diversity (Ruiz-Benito et al. 2014; Ratcliffe et al. 2016; Ruiz‐Benito et al. 2017a). Higher heterogeneity in shade tolerance enhances forest productivity *via* more efficient light acquisition at the stand level (Morin et al. 2011; Zhang et al. 2012). Diversity of other traits, such as wood density (Lasky et al. 2014; Ruiz‐Benito et al. 2017a), seed mass (Ruiz-Benito et al. 2014; Ruiz‐Benito et al. 2017a) and root habits (Brassard et al. 2013), which are related to strategies of reproduction, resource exploitation or growth, may also be determinants in improving the efficiency of resource exploitation. In addition, mixed-species forests may use canopy space more efficiently than monocultures, due to greater diversity in maximum height (vertical stratification, i.e. coexistence of species with contrasting crown architectures and physiological adaptations to shade), or crown morphology/branching patterns (canopy plasticity, i.e. adjustment of crown shape/size in response to competition with neighbours) (Jucker et al. 2015). This diversity–canopy packing relationship is often referred to as an underlying mechanism of B–EF in forest systems (Morin et al. 2011; Zhang et al. 2012).

On the other hand, selection effects are related to species/functional identity (Ruiz-Benito et al. 2014; Ratcliffe et al. 2016; Ruiz‐Benito et al. 2017a), and the presence (or relative abundance) of certain species with key traits in the community is responsible for improving stand production. In regions under water stress, the presence of traits adapted to a dry environment (high drought tolerance) are favoured, which can promote productivity. Higher leaf mass per area (needle-leaved) is associated with greater productivity in Mediterranean forests (Ruiz-Benito et al. 2014), and the functional identity of productive pioneers (wood density, maximum lifespan, and maximum height) showed a higher relative importance for biomass productivity across European forests (Ratcliffe et al. 2016).

Based on the selection effect (the species/functional identity effect; e.g. Ruiz-Benito *et al.*, 2016; Ratcliffe *et al.*, 2016), species composition may be an additional critical component for the diversity-mitigation concept, as the loss or reduction of the relative abundance of key species/traits in a community may disproportionately affect ecosystem functioning (Chapin et al. 1997). For example, diffuse-porous species are more sensitive to drought events than ring-porous species in terms of basal area increment (Elliott et al. 2015) and the annual net aboveground biomass change of late-successional coniferous forest is more affected by climate change compared to other forest types in the Canadian boreal forest (Chen & Luo 2015). Consequently, the vulnerability of forest productivity to climate change might be dependent on the composition of species/traits. Moreover, heterogeneity in functional traits (e.g. shade tolerance, growth pattern) has positive effects on stability against disturbance (Morin et al. 2014) and resilience to water deficit (Drobyshev et al. 2013) in natural forest systems. Again based on the selection effect (the species/functional identity effect; e.g. Ruiz-Benito *et al.*, 2016; Ratcliffe *et al.*, 2016), we can assume that communities which contain key species/functional traits (e.g. those tolerant against environmental changes), or communities with greater relative abundance of such species/traits, are more resilient, resistant, and stable in the face of climate change (i.e. climate change effects are mitigated), while a composition without these key species/traits is not. In this manner, species/functional trait composition may be as important as species/functional diversity in the mitigation of climate change impacts. Hence, composition should be emphasised because relative abundances of species are more sensitive to environmental changes than the presence/absence of species (Chapin III et al. 2000).

Moreover, biodiversity may be able to mitigate climate change impacts on diversity itself (i.e. species loss and compositional shifts), which might also indirectly reduce climate change-induced biomass losses. Climate change and increased infestation by pests/pathogens (Kurz et al. 2008) can reduce the relative abundances of key species in a region, which may substantially affect overall diversity by altering biotic interactions (see Blois et al. 2013) and causing compositional shifts (Laurance et al. 2004; Fauset et al. 2012). Highly diverse ecosystems, however, may have more stable compositions than low-diversity systems, as even if key species are eliminated, other species could work to maintain the current composition types (i.e. insurance hypothesis). Furthermore, systems with greater diversity may experience less significant climate change-induced shifts simply because they contain a higher number of species/trait individuals (i.e. stochastically stable). Yet, whether biodiversity reduces climate change impacts on itself has not been tested, and forest inventory data, which are often employed for examining climate change-induced vegetation shifts, could be utilised to provide field-based evidence for this concept.

2.7 Implications for future research and forest management strategies

To date, most B→EF studies under controlled climates have been conducted in experimental grasslands. Experimental B→EF studies remain limited in terms of making inferences about the responses of biomass production in natural ecosystems to climate change drivers, such as chronic water deficiency, warming, CO_2 concentration, and drought events. Even though the positive effects of diversity are detectable in natural systems (Grace et al. 2016; Liang et al. 2016), it is still uncertain whether the B→EF relationship under climate change is similar to those observed in controlled experiments (Reich et al. 2001; Isbell et al. 2015; Cowles et al. 2016). Therefore, it is necessary to combine studies of B→EF and climate change impacts on ecosystem functioning (Ruiz‐Benito et al. 2017a) in order to demonstrate how climate mitigation theory operates in natural systems. Forest ecosystems dominated by long-lived trees may be used to examine how biodiversity impacts the responses of ecosystem functioning to long-term environmental change. As multiple studies have already used large spatial and long temporal scale data (i.e. those from long-term forest inventories) to investigate climate change impacts on ecosystem functioning, we anticipate that natural forest systems may also allow us to examine simultaneously how biodiversity can affect the responses of ecosystem functioning to environmental change. For these reasons, combining B→EF studies with assessments of climate change impacts on ecosystem functioning using long-term monitoring data from natural forest sites is highly encouraged.

This combined approach might provide us with knowledge towards the development of mitigation strategies against the impacts of global environmental change. For example, detection of the ideal diverse species assemblage required for mitigation would assist ecosystem managers or foresters in determining how many species are required to be conserved or planted for effective management. As functional trait diversity is an important factor to associate with ecosystem functioning, these aspects should also be included for the combined study of B→EF and climate change impacts. This can tell us which plant traits play key roles in mitigating the impacts of global environmental change, allowing us to determine which functional groups should be conserved or planted. Moreover, recent climate change-induced shifts in taxonomic or trait composition (Laurance et al. 2004; Fauset et al. 2012) may also affect the B→EF mechanism through changes in diversity and functional traits in the community. Besides, the inclusion of other abiotic factors such as stand age (Chen et al. 2016) and topography (soil moisture content) (Elliott et al. 2015), which may affect responses of site productivity to climate change, can also provide beneficial information on mitigation strategies. These factors and biodiversity could synergistically affect ecosystem functioning since diversity effects can increase through stand age (Zhang et al. 2012; Barrufol et al. 2013), and tree growth on mesic sites may be less affected by climate change (Elliott et al. 2015). Biodiversity could be a solution to lessen the negative economic impacts of climate change on ecosystem services while providing an effective forest-management strategy. A positive diversity–stability relationship would satisfy the objective 'to produce an annual sustained yield of timber and energy supplies'; while a positive diversity–productivity relationship would satisfy the objective 'to maintain or increase forest carbon stocks'. However, in order to realise this, carbon inputs should be greater than carbon outputs, and this condition of carbon fluxes must be maintained over centuries (Körner 2017). If diversity can mitigate climate change impacts on itself then the objective 'to preserve forest biodiversity' is also satisfied.

Productivity and carbon storage may not require maximum species richness, since diversity effects will be saturated when functional redundancy and niche overlaps occur (Cardinale et al. 2012; Zhang et al. 2012; Ruiz-Benito et al. 2014; Tilman et al. 2014). Based on the selection effect, there might arise an argument as to whether planting single species with higher productivity and resistance to climate change would be better than polyculture. However, since climate change is likely to increase environmental variability, the selection probability effect would dictate that more functionally diverse forests would still perform better from a long-term view when we consider ecosystem stability in the face of uncertain future conditions. Moreover, multiple ecosystem services tend to continue to increase with biodiversity (Gamfeldt et al. 2013; Mori et al. 2016); however, none of these has as yet accounted for climate change. The economic valuation of biodiversity effects on forest growth and yields under climate change, i.e. monetary valuation (Farley 2008; Barrett et al. 2016; Zhou 2017), will further strengthen the diversity–mitigation concept.

2.8 Conclusions

(1) Biodiversity may mitigate climate change impacts on: (I) biodiversity itself, and (II) ecosystem functioning. This review presents the concept of biodiversity as a solution to mitigate climate change impacts (mitigation type II), as demonstrated by B→EF studies in which biodiversity improved productivity, stability, resistance, and/or resilience under experimental climatic changes and perturbations.

(2) Future combined work on B→EF and climate change impacts using long-term data will help test this concept in natural systems. In terms of socio-ecological perspectives, the biodiversity-mitigation concept should also be integrated with studies of biodiversity–multiple ecosystem services in forest systems in order to make it practicably feasible.

(3) Management strategies based on our concept will enhance the effectiveness of ‘the climate change mitigation role of forests (Canadell & Raupach 2008)’ by mitigating climate change impacts on carbon sequestration.

CHAPTER 3: SPECIES-RICH BOREAL FORESTS GREW MORE AND SUFFERED LESS MORTALITY THAN SPECIES-POOR FORESTS UNDER THE ENVIRONMENTAL CHANGE OF THE PAST HALF-CENTURY

3.1 Abstract

It is certain that climate and other global environmental changes will alter ecosystem functioning and biodiversity. However, the importance of plant diversity in mitigating the responses of functioning of natural ecosystems to long-term environmental change remains unclear. Using inventory data of boreal forests of western Canada from 1958-2011, we found that aboveground biomass growth increased over time in species-rich forests but decreased in species-poor forests, and importantly, aboveground biomass loss after tree mortality was smaller in species-rich than species-poor forests. A further analysis indicated that growth of species-rich (but not species-poor) forests was statistically positively associated with rising CO_2, and that mortality in species-poor forests increased more as climate moisture availability decreased than it did in species-rich forests. In contrast, growth decreased and mortality increased as the climate warmed regardless of species diversity. Our results suggest that promoting high tree diversity may help reduce the vulnerability of boreal forests to climate and other environmental changes.

3.2 Introduction

Climate change has significantly affected global forest ecosystems. Temporal increases in tree growth have been tied to rising atmospheric CO_2 (Pretzsch et al. 2014) through improved water-use efficiency (Ponce Campos et al. 2013) and climate warming induced longer growing seasons (Pretzsch et al. 2014). On the other hand, tree carbon gain and mortality have increased under warming accompanied by more frequent droughts (Choat et al. 2018; Reich et al. 2018) or even without temporally decreasing climate moisture availability (Brienen et al. 2015; Luo & Chen 2015). Recent studies that have simultaneously examined biomass gain from the growth of surviving and newly recruited stems, as well as biomass loss from mortality, suggested that climate change had a negative effect on net forest biomass change in boreal and tropical forests (Brienen et al. 2015; Chen et al. 2016).

Plant diversity has been shown to enhance the positive response of ecosystem productivity to elevated CO_2 (Reich et al. 2001) and buffers ecosystems against climate extremes (Isbell et al. 2015) in controlled experiments. Therefore, plant diversity has been hypothesized to mitigate the influence of long-term environmental change on the biomass dynamics of natural forests, i.e., the biodiversity-mitigation concept (Hisano et al. 2018). The assumption of the biodiversity-mitigation concept is that positive diversity effects on ecosystem functioning are persistent after experiencing climate and other global environmental change-induced modifications, i.e., higher plant diversity systems have persistently higher growth and net biomass change under such change. Experimental studies have demonstrated the persistence of the positive effects of species diversity on ecosystem functioning under short-term manipulated warming, drought, and elevated

CO_2 in controlled systems (Reich et al. 2001; Isbell et al. 2015; O'Brien et al. 2017). Viewed from another perspective, CO_2 enrichment can increase productivity more in systems with higher species diversity than lower diversity due to the sampling effect (i.e., selection probability effect), niche complementarity, and positive species interactions (Reich et al. 2001). While support for the persistence of positive diversity effects on growth in natural forests under climate change is equivocal (Grossiord et al. 2014; Paquette et al. 2018), how tree species diversity affects the response of tree mortality to climate change remains unexplored.

Here we addressed the general hypothesis that boreal forests in western Canada with higher tree species diversity would be better able to take advantage of improved conditions and better able to withstand unfavorable ones as over time CO_2 levels rose, climate warmed, and moisture availability changed. Specifically, we hypothesized that under negative climate change impacts such as a long-term decrease in climate moisture availability, forests with higher tree species diversity would experience less net biomass change declines due to less reduction in growth with less mortality (Fig. 3-1) since (i) species diversity enhances ecosystem resistance to climate extremes as a result of differential responses among species to environmental changes (Isbell et al. 2015; O'Brien et al. 2017); and (ii) positive diversity effects (particularly niche complementarity including resource partitioning and facilitation, leading to reduced competition) tend to be stronger in environmental conditions unfavorable for growth (Grossiord et al. 2014). To examine the hypothesis, we used 871 permanent sampling plots (naturally regenerated after wildfire and unmanaged) with a range of stand ages (17–210 years old) and tree species richness (1–7 species), monitored between 1958 and

2011 in the western boreal forests of Canada (Table S3-1 and Fig. S3-1). We modelled biomass changes with calendar year (van Mantgem et al. 2009; Brienen et al. 2015), which represented forest response over time as atmospheric CO_2 concentration, temperature and climate moisture availability all changed concurrently in the boreal region, while simultaneously accounting for the strong influences of stand age (Chen et al. 2016) and site quality (Chen et al. 2002). We also examined the temporal trends of atmospheric CO_2 concentration, mean annual temperature, and climate moisture index and performed a further analysis to further examine to the extent possible the relationship between biomass dynamics and these climate change drivers.

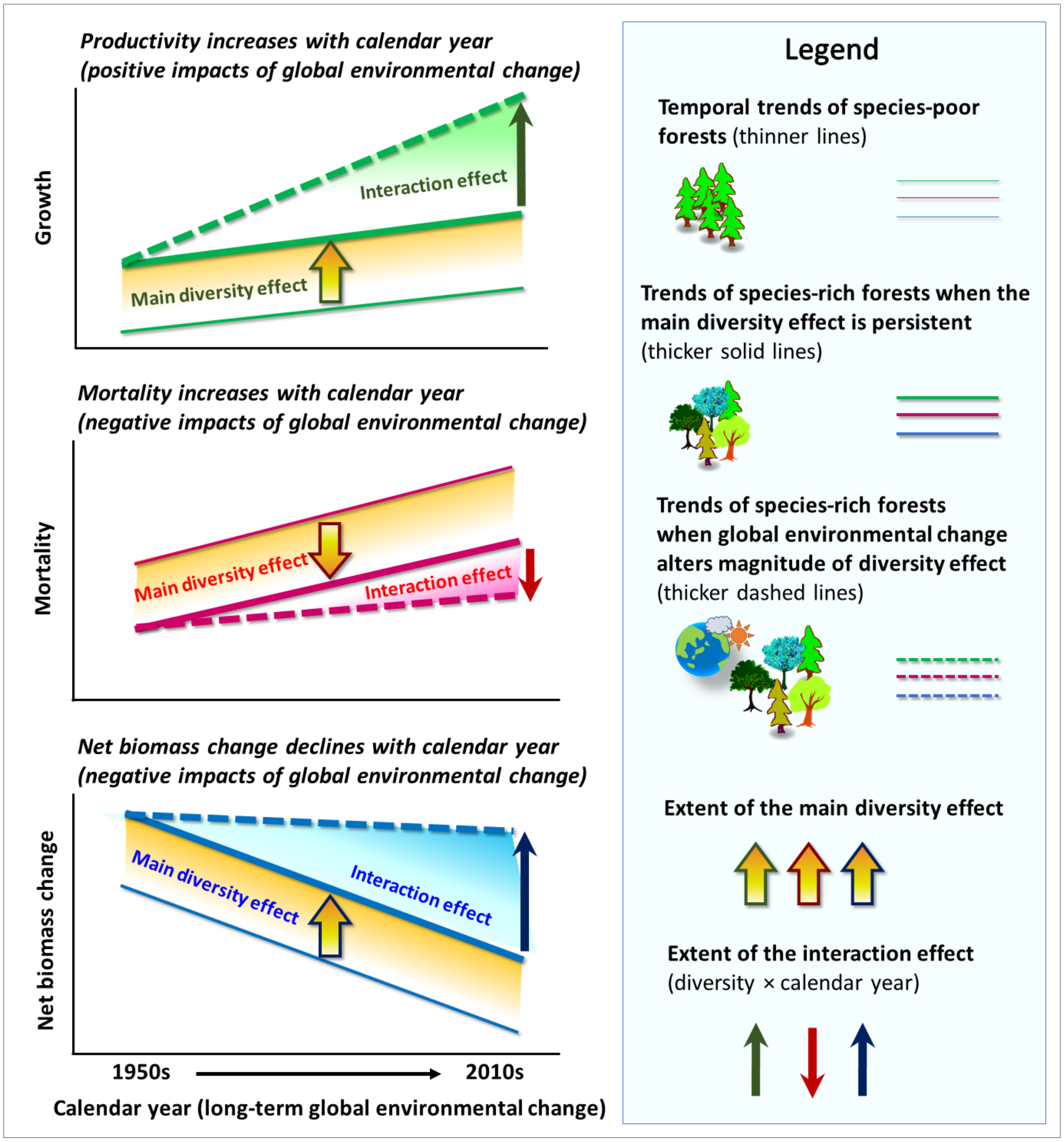

Figure 3-1: Hypothesized effects of tree species richness on growth, mortality and net biomass change with main (average) effect of richness and different responses to calendar year with richness (slopes). The thicker yellow arrow shown in the middle represents the extent of average species richness effect. The thinner green (growth), red (mortality), and blue (net biomass change) arrows indicate the extent of the interaction effect (species richness × calendar year). Thinner lines are temporal responses of net biomass change and its components in species-poor forests, while thicker solid lines (parallel) are those in species-rich forests with the main richness effect being significant but the interaction effect being insignificant. Dashed lines are those in species-rich forests when both the main richness and interaction effects are significant, i.e., the magnitude of richness effect on ecosystem functioning is altered with elapse of long time period.

3.3 Materials and Methods

3.3.1 Study area and forest inventory data

Permanent sampling plots (PSP) were established and monitored by the provincial governments of Alberta and Saskatchewan during the 1960s and 1970s. These plots were located in stands (>1 ha in area) of visually homogenous structure and composition and at least 100 m from any openings to minimize edge influences. Until 2011, the plots were re-measured at varying intervals (Table S3-1). We selected the PSPs following criteria; plots must: (i) be originated from wildfire and unmanaged, with known stand age (year); (ii) have at least three censuses with monitoring period ≥10 years; (iii) have all trees marked with their diameter at breast height (DBH) measured; and (iv) have ≥30 trees at initial measurement to ensure that the plot represented the sample forest (Chen et al. 2016). A total of 871 unmanaged natural forest plots (170.6 ha; 49°01'–59°44'N; 101°44'–119°40'W) were selected for analyses with 208,961 trees measured during the monitoring period from1958 to 2011. Average measurement interval was 9.20 years with 3.91 times of census; the initial and final census years varied from 1958–1993 and 1972–2011, respectively. The plot sizes ranged between 600 m^2 and 8,092 m^2 (Table S3-1). Annual mean temperature and annual mean precipitation in the area varied between -2.38 °C and 4.08 °C, and 365 mm and 1,184 mm (1950–2009), respectively. Elevation ranged between 260 m and 2,073 m above sea level. The dominant species made up >1% of tree biomass across all censuses and plots were *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera*, *Pinus banksiana*, *Pinus contorta*, *Picea mariana*, *Abies balsamea*, and *Picea glauca*. The dominant stand-replacing disturbance in the area is wildfire (return interval: 15–90 years) (Weir et al. 2000). The compiled data was comprised with deciduous broadleaves (262 plots), early-successional coniferous forests (210 plots), late-successional coniferous forests (260 plots), and mixed forests (139 plots) (see Chen and Luo 2015).

Tree size criteria for monitoring were different between the provinces (Alberta: DBH ≥7.3 cm, Saskatchewan: DBH ≥9.7 cm); therefore, we standardized the data by excluding trees with DBH <10 cm to avoid the biased biomass estimation from the different sampling efforts (Searle & Chen 2017b). Trees that reached 10 cm DBH between two successive censuses were defined as recruits. In the case DBH for a given tree decreased from the previous measurement, we corrected those by interpolating DBH values from the previous and the next measurements (Phillips et al. 1998).

3.3.2 Annual net aboveground biomass change and its components

Plot-level aboveground biomass was calculated by summing the biomass of all trees in each plot for each measurement. Aboveground biomass of individual trees was estimated based on allometric equations specific to each tree species of Canada (for the stem, bark, leaves, and branches, respectively) (Lambert et al. 2005). As recommended (Chave et al. 2004), the equations were developed using a large number of samples (207 to 1,534 trees per species with a wide range of sizes) across the Canadian boreal forest. We used the equations of softwood or hardwood (Lambert et al. 2005) to estimate biomass for less frequently occurring species: *Pseudotsuga menziesii* (437 trees), *Picea engelmannii* (42 trees), and *Pinus flexilis* (five trees).

We calculated annual net aboveground biomass change (ΔAGB, Mg ha^{-1} yr^{-1}) as the difference in aboveground biomass between two consecutive censuses divided by the census length in years (Brienen et al. 2015). The ΔAGB comprised biomass gain by the growth of surviving trees (ΔAGB_G), ingrowth by new recruitment trees (ΔAGB_I), and loss from tree mortality (ΔAGB_M). Biomass change over long census intervals could be underestimated due to the unrecorded growth of trees that were recruited and died during a single interval (Lewis et al. 2004; Brienen et al. 2015). Therefore, we calculated biomass of the unobserved recruitment and mortality (defined as trees with DBH 10–15 cm) as described previously (Chen et al. 2016) although adding the additional calculation had negligible effects on net aboveground biomass change estimates.

3.3.3 Climate and other environmental change drivers

Similar to the previous studies (van Mantgem et al. 2009; Brienen et al. 2015), we used the middle calendar year (Year) of a census period represent climate change as a whole on ΔAGB and its components. We derived CO_2 measurements from the Mauna Loa Earth System Research Laboratory in Hawaii (http://www.esrl.noaa.gov/gmd/ccgg/trends/co2_data_mlo.html), and annual mean temperature and climate moisture index (CMI) by *BioSIM* 10 software (Régnière et al. 2014). CMI accounts for both temperature and precipitation effects on available moisture by taking the difference between precipitation and evapotranspiration (Hogg et al. 2017). It has been reliably used to quantify water availability in western Canada (Ma et al. 2012; Hogg et al. 2017). Negative values of CMI indicate evapotranspiration exceeding precipitation, while positive values denote precipitation exceeding evapotranspiration. Following previous studies (e.g., Ma et al. 2012), we calculated anomalies of both annual mean temperature (ATA) and climate moisture index (ACMIA), defined as a departure from their long-term climate means between 1958 and 2011 (Clark et al. 2011). We used the following equation to calculate these climate anomalies:

$$(\text{Climate Anomaly})_{ij} = \overline{(\text{Annual Climate})}_{ij} - \overline{(\text{Annual Climate})}_{1958\text{-}2011j} \qquad \text{(eqn. 1)}$$

where i and j were ith census period and jth plot; Climate Anomaly was ATA or ACMIA for the ith census period and jth plot; $\overline{(\text{Annual Climate})}_{ij}$ was mean annual temperature or annual CMI; $\overline{(\text{Annual Climate})}_{1958\text{-}2011j}$ was the long-term average (between 1958 and 2011) of mean annual temperature or annual CMI (Clark et al. 2011).

3.3.4 Tree species diversity

We derived species richness as the number of tree species for each census in each plot (S_{org}). To factor out the influence of stand density in our study, we calculated rarefied species richness based on the stem number in a plot (S) (Poorter et al. 2015), using the *vegan* package (Oksanen et al. 2018). Alternatively, we accounted for variation in plot size by deriving expected species richness at the mean size of all sample plots (rarefied richness by plot size, S_{area}) (Avery & Burkhart 2002) based on the species-area relationship curve (Connor & Mccoy 1979). Plot size and stem number within a plot were positively correlated ($r = 0.76$), and the two metrics of rarefied richness produced qualitatively similar results (Fig. S3-2). We employed rarefied richness based on stem number because it directly removes the confounding effect of stem density on richness (Poorter et al. 2015; Oksanen et al. 2018). Acknowledging that richness alone does not explain abundance-based diversity (Zhang et al. 2012), we also calculated the middle value of Shannon's diversity index (H') to account for both species richness and evenness, and results were qualitatively similar.

Since species richness varied during the census period (Fig. S3-3a), we used their middle value of two consecutive censuses, similar to the middle calendar year.

Alternatively, we replaced the middle value of the census with the value of the first census period or the second census period of two consecutive surveys, which showed similar results (Fig. S3-2).

3.3.5 Estimation of stand age

Because of the strong influences of endogenous processes associated with stand age on biomass dynamics in boreal forests (Chen & Luo 2015; Chen et al. 2016), we determined stand age by a known stand-replacing fire, or by coring at least three dominant/codominant trees of each tree species inside or outside of the plot at the plot establishment. Among the 871 selected plots, the stand ages of 176 plots were determined by a known fire, whereas 695 plots were determined from coring. We used the middle stand age (SA) of a census period (i.e., the period between two successive censuses) to account for effects of forest development processes on ΔAGB and its components.

3.3.6 Site quality

Across large forest landscapes, biomass dynamics are strongly associated with local site quality (inherent productive capacity of a given location usually dependent on temperature, light, water, and nutrients availability) (Chen et al. 2002). We quantified site quality of each plot by site index (total height (m) of the dominant trees at stand age of 100 years; estimated by the species-specific growth curves) (Wang 1998). *P. glauca* was the dominant species for 302 of the 871 plots. For plots dominated by other species, we standardized their site indices to *P. glauca* by converting the site indices of the other species using a published site index conversion equation for tree species in western Canada (Wang 1998).

3.3.7 Statistical analysis

To disentangle effects of SA, Year, and S on temporal trends of $\Delta\mathrm{AGB}$, $\Delta\mathrm{AGB}_{\mathrm{GI}}$ and $\Delta\mathrm{AGB}_{\mathrm{M}}$, and to test whether the temporal trends of $\Delta\mathrm{AGB}$ and its components were dependent on S, we used the following univariate linear mixed effects model:

$$
\begin{aligned}
(\Delta\mathrm{AGB})_{ijk}, (\Delta\mathrm{AGB}_{\mathrm{GI}})_{ijk}, \text{ or } (\Delta\mathrm{AGB}_{\mathrm{M}})_{ijk} = {} & \beta_0 + \beta_1 \times \ln(\mathrm{SA})_{ij} + \beta_2 \times \mathrm{Year}_{ij} + \beta_3 \times f(S)_{ij} \\
& + \beta_4 \times \ln(\mathrm{SI})_j + \beta_5 \times \ln(\mathrm{SA})_{ij} \times \mathrm{Year}_{ij} \\
& + \beta_6 \times \ln(\mathrm{SA})_{ij} \times f(S)_{ij} + \beta_7 \times \mathrm{Year}_{ij} \times f(S)_{ij} \\
& + \pi_j + \varepsilon_{k(ij)} \qquad \text{(eqn. 2)}
\end{aligned}
$$

where i and j were ith census period and jth plot; β_i were coefficients to be estimated; SA was the middle stand age and was log-transformed to properly model the stand age-dependent trends of $\Delta\mathrm{AGB}$, $\Delta\mathrm{AGB}_{\mathrm{GI}}$, and $\Delta\mathrm{AGB}_{\mathrm{M}}$, based on Akaike Information Criterion (AIC) (Chen et al. 2016). Year and S were the middle calendar year and rarefied species richness of a census period, respectively; SI is *Picea glauca* site index; π_j was a random plot effect accounting for site-specific climates and disturbance history; $\varepsilon_{k(ij)}$ is random error. The interaction term '$f(S)$ × Year' specifically tests whether the effects of Year on $\Delta\mathrm{AGB}$, $\Delta\mathrm{AGB}_{\mathrm{GI}}$ or $\Delta\mathrm{AGB}_{\mathrm{M}}$ are dependent on S, or *vice versa*. To assess potential nonlinear responses of $\Delta\mathrm{AGB}$ and its components to S and SI, we compared linear models with logarithmic ones using AIC, and we employed natural log-transformed S to $\Delta\mathrm{AGB}_{\mathrm{GI}}$ and $\Delta\mathrm{AGB}_{\mathrm{M}}$ models and natural log-transformed SI to all models (Table 3-1) as they had lowest AIC values. Each observation was weighted by the square root of plot size (ha) × the total plot census length (years) to remove the influence of variations in plot sizes and census lengths (Brienen et al. 2015; Chen et al. 2016). Alternatively, we also weighted observations by plot size × length, and the results were qualitatively similar. We reported only the results using the square root of plot size × length as weightings for simplicity. To facilitate coefficient interpretation, all explanatory variables were centered prior to analysis.

Although there was temporal autocorrelation in the residuals of eqn. 2 (examined by autocorrelation function estimation using *acf* function in *R*), it did not influence our results. Models with a continuous autoregressive structure using the *nlme* package (Pinheiro et al. 2018) produced qualitatively similar coefficient estimates of Year × $f(S)$ to the original model (Fig. S3-6). Moreover, we replaced the response variables in eqn. 2 with relative growth, mortality, and net biomass change (%, the absolute values divided by the mean standing biomass between the two consecutive censuses × 100, similar to the previous study (Searle & Chen 2017c); i.e., changes in the absolute values within each plot), and this approach also yielded similar results (Fig. S3-4).

Similar to previous studies (van Mantgem et al. 2009), we investigated spatial dependency of the residuals of our models using Moran's I since spatially autocorrelated data violates the assumption of independence of statistical models. We found that Moran's I statistic decreased with the neighborhood range (lag), and spatial autocorrelation mattered until range >2,000 km (Fig. S3-7). To deal with this issue, we fitted a spatial autoregressive structure (with latitude and longitude) (Dormann et al. 2007), using a Matern correlation, to the linear mixed effects model using *fitme* function in the *spaMM* package (Rousset et al. 2018). As the spatial autoregressive structure effectively accounted for the spatial autocorrelation in our dataset (Moran's I tests: P = 1.000 (ΔAGB_{GI}), P = 0.998 (ΔAGB_{M}), P = 0.999 (ΔAGB); based on the distance at which 95% of the plots had at least one neighbor (Portier et al. 2017), i.e., 17 km, defined by *dnearneigh* function in the *spdep* package (Bivand et al. 2018), we relied on this approach for subsequent analyses.

To graphically show how Year effects on stand-level biomass dynamics are associated with S, we calculated temporal trends of biomass dynamics as $\beta_0 + \beta_2 \times \text{Year} + \beta_3 \times f(S) + \beta_7 \times \text{Year} \times f(S)$ for the lowest, highest and three evenly divided levels between the lowest and highest S (Fig. 3-2b).

To explore the underlying mechanism of temporal changes in biomass associated with species richness, we calculated species-level growth, mortality, and ΔAGB by sub-setting aboveground biomass by main species (defined as those accounted for >10% of the total biomass across all the plots during the whole census: *Populus tremuloides* 30.9%, *Picea glauca* 30.8%, *Pinus contorta* 22.9%; Fig. S3-4). We then replaced the response variable in eqn. 2 with relative values of species-level growth, mortality, or ΔAGB, allowing comparison among species, as well as with their stand-level relative values.

To investigate influences of climate change drivers on observed temporal biomass changes, we included climate change drivers instead of Year in eqn. 2:

$$
\begin{aligned}
(\Delta\text{AGB})_{ij},\ (\Delta\text{AGB}_{\text{GI}})_{ij},\text{ or }(\Delta\text{AGB}_{\text{M}})_{ij} = {} & \beta_0 + \beta_1 \times \ln(\text{SA})_{ij} + \beta_2 \times \text{CO}_{2ij} + \beta_3 \times \text{ATA}_{ij} \\
& + \beta_4 \times \text{CMI}_{ij} + \beta_5 \times \ln(S)_{ij} + \beta_6 \times \ln(\text{SI})_j \\
& + \beta_7 \times \ln(\text{SA})_{ij} \times \text{CO}_{2ij} + \beta_8 \times \ln(\text{SA})_{ij} \times \text{ATA}_{ij} \\
& + \beta_9 \times \ln(\text{SA})_{ij} \times \text{CMI}_{ij} + \beta_{10} \times \ln(\text{SA})_{ij} \times \ln(S)_{ij} \\
& + \beta_{11} \times \text{CO}_{2ij} \times \ln(S)_{ij} + \beta_{12} \times \text{ATA}_{ij} \times \ln(S)_{ij} \\
& + \beta_{13} \times \text{CMI}_{ij} \times \ln(S)_{ij} + \pi_j + \varepsilon_{k(ij)} \qquad \text{(eqn. 3)}
\end{aligned}
$$

where CO_{2ij}, ATA_{ij}, and CMI_{ij} are atmospheric CO_2 concentration, ATA, and ACMIA at ith census period in jth plot (Table S3-4). All analysis was performed in R 3.5.2 (R Development Core Team 2018).

Table 3-1: Growth, mortality, and net biomass change associated with stand age, calendar year, species richness, and site quality (site index).

Fixed effects[a]	Coefficients (mean ± s.e.m.)	*df*	*t*	*P*
Growth (Mg ha^{-1} yr^{-1})				
(Intercept)	2.696 ± 0.24	-	11.214	<0.001
ln(SA)	-0.920 ± 0.086	1, 984	-10.691	<0.001
Year	-0.004 ± 0.002	1, 984	-2.633	0.009
ln(*S*)	0.290 ± 0.065	1, 984	4.484	<0.001
ln(SI)	0.531 ± 0.147	1, 984	3.609	<0.001
ln(SA) × Year	-0.003 ± 0.004	1, 984	-0.857	0.391
ln(SA) × ln(*S*)	0.271 ± 0.154	1, 984	1.767	0.078
ln(*S*) × Year	0.021 ± 0.004	1, 984	5.922	<0.001
Mortality (Mg ha^{-1} yr^{-1})				
(Intercept)	1.567 ± 0.147	-	10.654	<0.001
ln(SA)	2.100 ± 0.135	1, 984	15.609	<0.001
Year	0.018 ± 0.003	1, 984	5.962	<0.001
S	-0.175 ± 0.048	1, 984	-3.623	<0.001
ln(SI)	2.773 ± 0.233	1, 984	11.885	<0.001
ln(SA) × Year	0.014 ± 0.008	1, 984	1.842	0.066
ln(SA) × *S*	0.140 ± 0.121	1, 984	1.158	0.247
S × Year	-0.006 ± 0.003	1, 984	-2.214	0.027
Net biomass change (Mg ha^{-1} yr^{-1})				
(Intercept)	1.079 ± 0.14	-	7.683	<0.001
ln(SA)	-2.942 ± 0.151	1, 984	-19.458	<0.001
Year	-0.021 ± 0.003	1, 984	-6.192	<0.001
ln(*S*)	0.593 ± 0.122	1, 984	4.866	<0.001
ln(SI)	-2.134 ± 0.262	1, 984	-8.147	<0.001
ln(SA) × Year	-0.020 ± 0.009	1, 984	-2.276	0.023
ln(SA) × ln(*S*)	0.048 ± 0.291	1, 984	0.164	0.869
ln(*S*) × Year	0.029 ± 0.008	1, 984	3.655	<0.001

[a] SA: middle stand age; Year: middle calendar year; *S*: middle rarefied species richness; SI: site index. *S* (except for mortality) and SA were transformed by natural-logarithm (see *Methods*).

3.4 Results and Discussion

During the study period (1958–2011), the average ΔAGB was 1.08 ± 0.14 (mean ± s.e.m.) Mg ha^{-1} yr^{-1}, which was comprised of 2.70 ± 0.24 Mg ha^{-1} yr^{-1} in growth and 1.57 ± 0.15 Mg ha^{-1} yr^{-1} in mortality (Table 3-1). After controlling for the effects of stand age and site index, we found that growth on average increased logarithmically with species richness (Table 3-1 and Fig. 3-2a). This result is consistent with other studies in boreal forests (Zhang et al. 2012). However, despite increased biomass growth, biomass loss from mortality decreased with increasing richness. The simultaneous benefits in increased growth and reduced mortality associated with increasing richness led to a significant positive effect of species richness on ΔAGB (Table 3-1 and Fig. 3-2a).

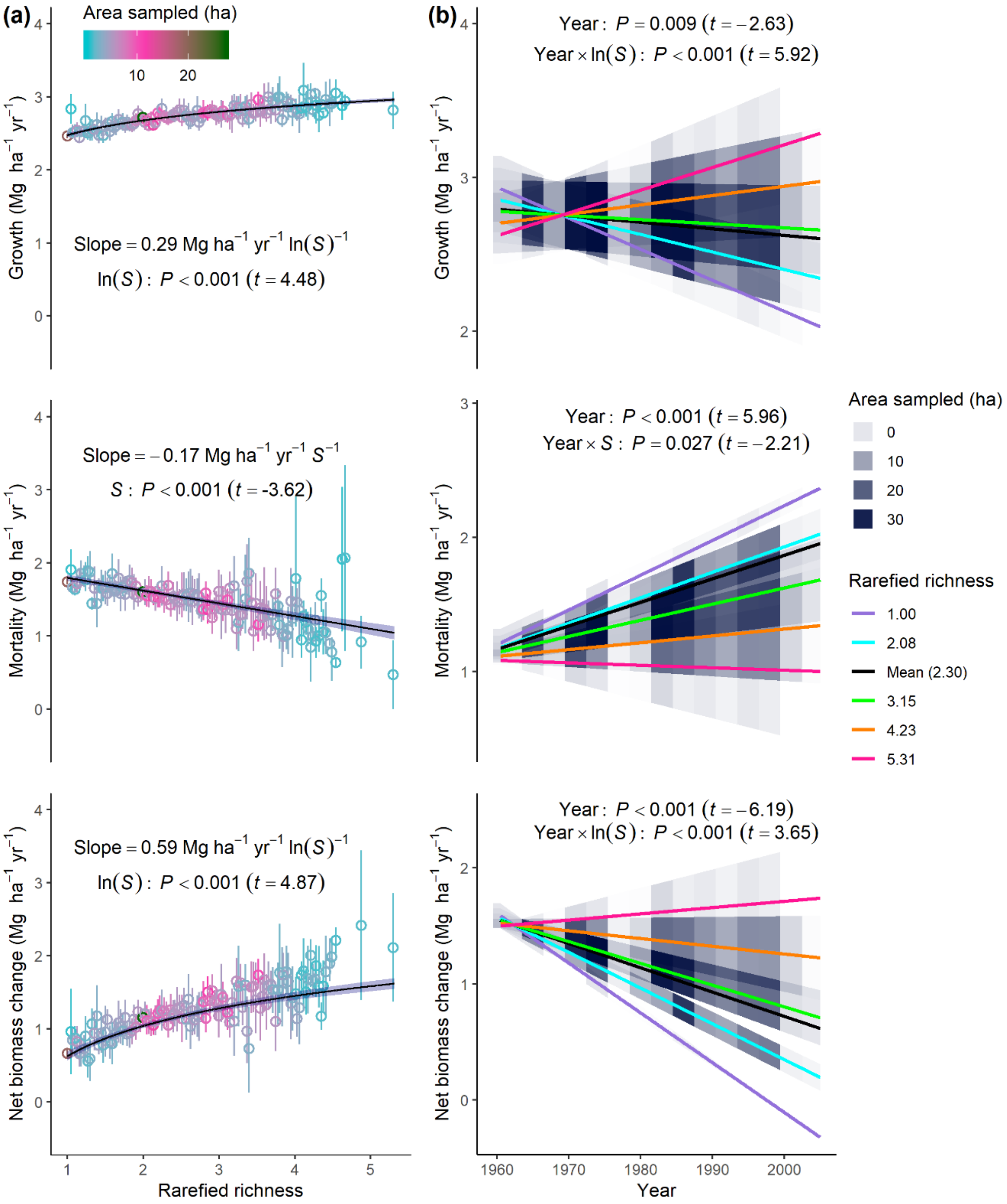

Figure 3-2: Trends associated with rarefied species richness and calendar year after accounting for the effect of stand age, and site quality (site index). (a), Average effect of species richness. Dots and error bars show mean and their 95% confidence intervals, with colour scheme showing yearly sampling efforts (sampled area in ha). The black line and shades are the mean and 95% confidence intervals. (b), Species richness-dependent temporal trends of aboveground biomass dynamics. The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. Shading gradients show sampling efforts (sampled area in ha) with three-year interval. Black lines show the main Year effect. Rarefied richness was analysed as a continuous variable but

here illustrated based on the meaningful five levels of breakpoints. P values for effects of main richness ($f(S)$) and the interaction term (Year × $f(S)$) obtained from the linear mixed effect model for each component are shown in each panel of (a) and (b), respectively.

Consistent with previous findings (Chen et al. 2016), mortality increased on average with calendar year, with a concurrent decrease in growth, resulting in a temporal decline in ΔAGB (Table 3-1 and Fig. 3-2b). However, the temporal trends of biomass dynamics were significantly dependent on species richness (Table 3-1 and Fig. 3-2b). Growth was not only higher on average (Fig. 3-2a) but also increased significantly over time in species-rich plots (rarefied species richness >3), while growth decreased in species-poor plots (rarefied species richness ≤2) (Fig. 3-2b). Simultaneously, mortality increased less in species-rich plots than in species-poor plots (Fig. 3-2b). The species richness-dependent responses in growth and mortality led to significantly slower temporal declines of ΔAGB in species-rich plots than species-poor plots (Fig. 3-2b).

In our study, the physical environment, particularly local soil condition, accounted for 9.8% of the variation in species richness (Table S3-2; see *Supplementary Methods*), while the remaining variation in species richness could have resulted from random dispersion and historical disturbance regimes (Chen et al. 2009). However, our estimates of the effects of species richness on biomass dynamics are independent of the inherent difference in local site quality, since our models have accounted for the positive effects of site index on growth and mortality (Table 3-1). Similarly, the model substituting site index by latitude and elevation (which accounted for 8.8% and 2.8% of the variation in richness, respectively; Table S3-2) yielded similar species richness effects on biomass dynamics (Table S3-3; see *Supplementary Methods*). Although there was a slight decrease in species richness during the study period (-0.008 species yr^{-1}; Fig. S3-3a), alternative models using the first or second census period value of richness produced similar results (Fig. S3-2). Moreover, structural equation models accounting for the temporal change in species richness (Fig. S3-3b, c, d) showed consistently similar outcomes to the original models. Our choice of diversity metrics did not influence the results because alternative models with original richness, plot size based-rarefied richness, and Shannon's diversity index (accounting for species evenness) all resulted in qualitatively similar coefficient estimates (Fig. S3-2).

To explore the underlying mechanism of the species richness effects, we calculated species-level biomass change for three dominant species (see *Methods*). We found that relative growth of *Populus tremuloides* and *Pinus contorta*, relative mortality of *Populus tremuloides* and *Picea glauca*, as well as relative ΔAGB of all three species, were dependent on plot level species richness (Fig. S3-4a). Moreover, the effects of species richness remained similar for both stand-level and species-level analyses after the inclusion of functional identity of shade-tolerance (Zhang et al. 2018) as a predictor (Fig. S3-4b). After factoring out the effect of composition (i.e., selection effect), the remaining richness effect could have resulted from multiple mechanisms of niche complementarity (given that the total effect of species diversity is an additive product of these mechanisms (Loreau & Hector 2001)) such as increased canopy packing (Williams et al. 2017), hydraulic lift by deep-rooting species (Pretzsch et al. 2013), and reduced damage from pathogens and pests (Chen et al. 2018) in species-rich forests. Thus, our study suggests that both the selection effect and positive species interactions likely explain the species richness-dependent temporal trends in biomass dynamics in the boreal forest.

We assessed temporal trends of atmospheric CO_2 concentration, temperature, and climate moisture availability during the study period with the latter two quantified as annual temperature anomaly (ATA; hereafter temperature) and annual climate moisture index anomaly (ACMIA; hereafter water availability), respectively. During the 50 years, atmospheric CO_2 concentration and temperature increased persistently (but not completely in parallel; $R^2 = 0.99$ and 0.57 with Year, respectively), while water availability decreased over the period ($R^2 = 0.038$), again not in close synchrony with either CO_2 or temperature (Fig. 3-3a). We then tested whether the association of growth, mortality, and ΔAGB with these climate change drivers would be dependent on species richness. We used four alternative approaches (one driver at a time and all three drivers at the same time using linear mixed effect model, ridge regression and nonparametric regression, respectively; see *Supplementary Methods*) to model the main and interaction effects of individual divers and species richness on growth, mortality, and ΔAGB, while accounting for stand age and site quality effects. These approaches yielded similar parameter estimates (Fig. S3-5). Interpreting from the results of linear mixed effect models with all three drivers modelled simultaneously, we found that among these drivers, increasing temperature had the greatest association with growth, mortality, and ΔAGB (indicated by the standardized coefficients, estimated with all the explanatory variables scaled (mean = 0, SD = 1) allowing comparison of the strength of each effect to the response variable; Table S3-4). The partial R^2 of each predictor also showed that temperature had the largest relative importance in explaining the variation in ΔAGB and its components (Table S3-4).

The association of growth with CO_2 mirrored that of calendar year (Fig. 3-3b) due to their high correlation (Fig. 3-3a), although the CO_2 effects from the model persist after removing effects of other climate drivers, suggesting that CO_2 likely contributes to the temporal trend. Similar to previous findings (Chen et al. 2016), growth and mortality were on average positively associated with rising CO_2 while ΔAGB was negatively related to this driver due to a higher sensitivity of mortality than growth (Fig. 3-3b). However, new to this study, we found that the growth slope of species-rich forests to rising CO_2 was higher than species-poor forests (Fig. 3-3b). This result suggests that the enhancement of rising CO_2 effects on productivity by higher species richness may not only occur in controlled grassland experiments (Reich et al. 2001), but also in natural forests. The mortality slope to CO_2 was independent of species richness (Fig. 3-3b); while the mechanism is unclear, this trend may be due to accelerated tree life cycles (Brienen et al. 2015; Searle & Chen 2018) and increased tree-to-tree competition (Luo & Chen 2015), yielding higher biomass turnover rates. Along with rising CO_2, other factors such as nitrogen deposition could also affect forest biomass dynamics and it is difficult to explicitly discern the effect of CO_2 from such coupled drivers by field observations alone (Brienen et al. 2015). However, nitrogen deposition in western Canada occurs at low levels (Reay et al. 2008) that are unlikely to drive big shifts in biomass. Nonetheless, although it is likely that rising CO_2 is at least partially responsible for the diversity-related biomass responses over time, other factors may have also contributed.

On the other hand, growth decreased with increasing temperature despite potentially extended growing seasons, while mortality increased regardless of species richness (Fig. 3-3c). This resulted in decreased ΔAGB with climate warming (Fig. 3-3c).

The changes in growth, mortality, and ΔAGB with reduced water availability were relatively slower than those with temperature (see standardized coefficients in Table S3-4), but they were dependent on species richness (Figs. 3-3c, d). With decreasing water availability, growth decreased and mortality increased in species-poor forests, but they did not change in species-rich forests. This resulted in a significant decrease of ΔAGB in species-poor forests with decreasing water availability but an increase in species-rich forests (Fig. 3-3d). The lack of correlation between growth and reduced climate moisture availability in species-rich forests could have resulted from increased soil water access via enhancing horizontal and vertical soil volume utilization by fine roots (Ma & Chen 2017). In the meantime, reduced mortality in species-rich forests under decreased water availability could have benefited from reduced aboveground tree-to-tree competition due to weaker interspecific than intraspecific competition strength (Luo & Chen 2015) in this climate condition, as well as from the ability to access more soil water by greater numbers of fine roots, which increase water uptake vertically and horizontally (Ma & Chen 2017). It should be noted that the observed trends could be attributed to a combination of long-term effects associated with climate change and acute effects, including heat pulse or drought events in the region (Chen et al. 2018).

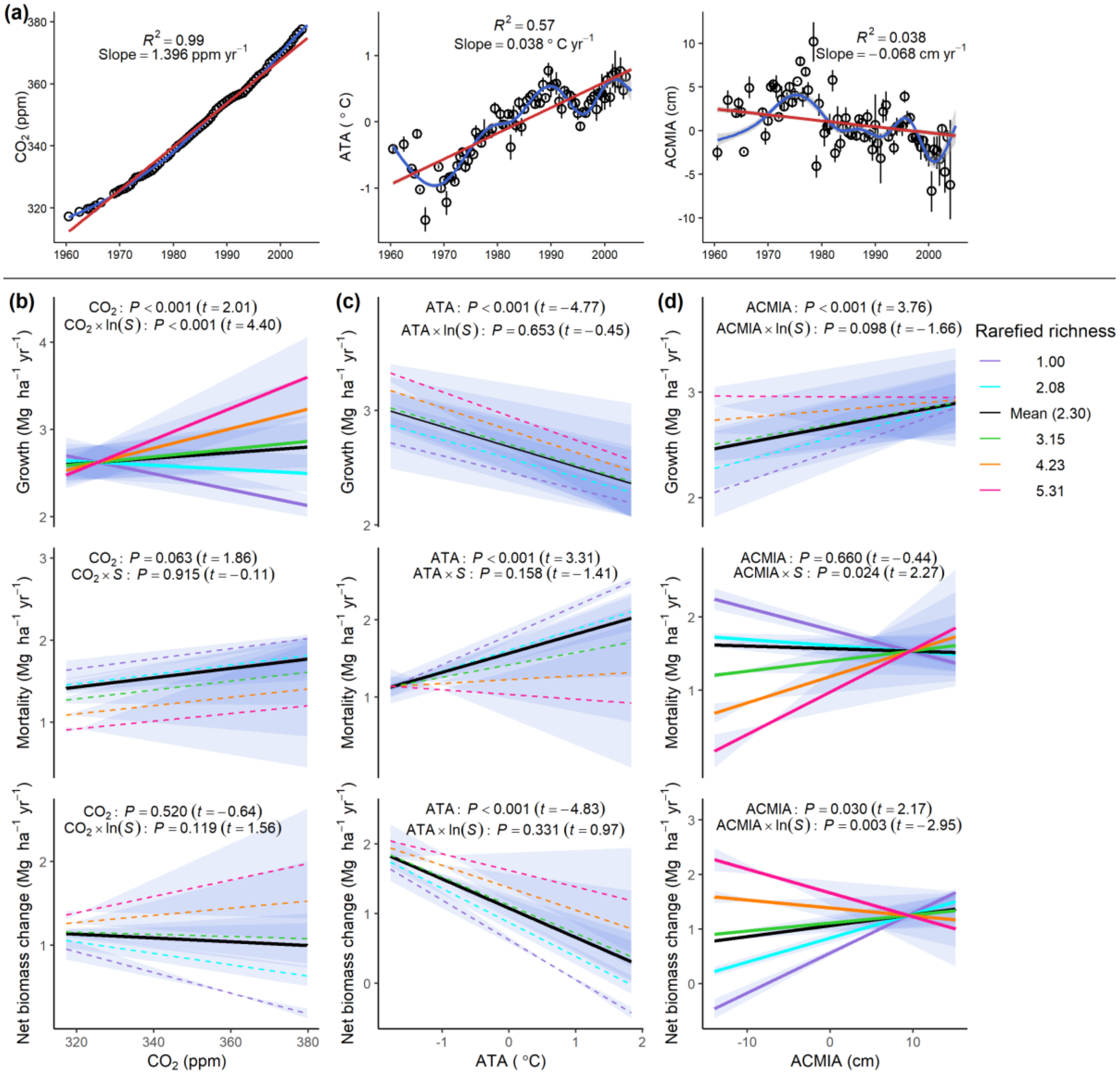

Figure 3-3: Temporal trends in climate change drivers and the responses of growth, mortality and net biomass change to these drivers. (a) Atmospheric CO$_2$ concentration, mean annual temperature anomaly (ATA), and annual climate moisture index anomaly (ACMIA) through calendar year. Dots and error bars are yearly mean and their 95% confidence intervals. The lines of fitted linear effect are shown in red, and LOESS smooth lines are shown in blue. Grey shades represent 95% confidence intervals. (b), (c), (d) Species richness-dependent responses of biomass dynamics to CO$_2$, ATA, and ACMIA, respectively. The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. *P* values for effects of main climate change drivers (CO$_2$, ATA, ACMIA) and the interaction term (CO$_2$ × $f(S)$, ATA × $f(S)$, ACMIA × $f(S)$) obtained from the linear mixed effect model for each component are shown in each panel. Solid black lines show the main effect of each climate change driver. Dashed lines indicate that the interaction effects were insignificant at α = 0.05.

Previous studies have shown that mortality has increased and net biomass change has on average decreased temporally, with inconsistent temporal growth trends in the western boreal forests of Canada (Ma et al. 2012; Chen et al. 2016; Hogg et al. 2017). We examined whether the over 50-yr temporal trends in growth, mortality and ΔAGB, and their associations with atmospheric CO_2, temperature, and water availability were dependent on species richness. We found that: (i) growth of species-rich forests increased more with rising atmospheric CO_2 concentration (and/or other temporally co-varying factors) and decreased less with reducing water availability than those of species-poor forests; and (ii) tree mortality increased with rising atmospheric CO_2 and warming independent of richness, whereas mortality in species-poor forests increased with decreasing water availability but not in species-rich forests. Our study scales up the results from small spatial and short-term experiments (Reich et al. 2001; Isbell et al. 2015; O'Brien et al. 2017) to large spatial and long-term observational networks of natural forests and suggests that the role of species diversity to mitigate impacts of climate change (Hisano et al. 2018) is not tentative or momentary, but rather persistent and even enhanced with long-term directional changes in climate. This may not be true for other forest types or biomes because the existence or magnitude of plant diversity and its relationships with ecosystem function can be abiotic context-dependent (Grossiord et al. 2014; Paquette et al. 2018).

In the western boreal forests of Canada, atmospheric CO_2 and temperature are expected to further increase and climate moisture availability to decrease in the 21st century (IPCC 2018), and decreasing moisture availability may regulate forest responses to rising temperatures (Reich et al. 2018). Our study suggests that promoting high tree species diversity is critically important to enhance the long-term resistance (experiencing less negative change in biomass over decades) of aboveground biomass in these forests to on-going climate change. Moreover, improved growth in diverse forests could contribute to climate change mitigation by increasing the amount of CO_2 uptake (IPCC 2014). Since species diversity is affected not only by disturbance (Chen et al. 2009), but also by local site conditions in these forests (Table S2), promoting high tree species diversity would require a simultaneous effort in maintaining or enhancing site productivity.

CHAPTER 4: SPATIAL VARIATIONS IN CLIMATE MODIFY EFFECTS OF FUNCTIONAL DIVERSITY ON BIOMASS DYNAMICS IN NATURAL FORESTS ACROSS CANADA

4.1 Abstract

Forest net biomass change (ΔAGB, the difference between biomass gain from growth and loss through mortality) determines how forests function in the global carbon cycle. Understanding how plant diversity affects ΔAGB under diverse abiotic conditions is critical in the face of anthropogenic global environmental change. Recent studies have advanced our understanding of the effects of plant diversity on growth, but we know little about how diversity influences biomass loss after tree mortality, preventing us from knowing how diversity affects ΔAGB under diverse abiotic conditions. Here we examined how the effects of tree functional diversity on growth, mortality, and ΔAGB are dependent on the abiotic gradients in natural forests. We used a large spatial inventory network of temperate and boreal forests across Canada (17,107 plots with 1,470,904 trees) with a range of water availability and temperature. Growth and mortality on average increased with functional diversity, but the magnitude of growth increase was greater than that of mortality, resulting in an increase of ΔAGB. The positive effect of functional diversity on growth was more prominent in humid sites than drier sites. Mortality increased with functional diversity in drier sites but decreased in wetter sites. Consequently, the positive effect of functional diversity on ΔAGB increased with water availability. Although the positive effect of functional diversity on growth increased with temperature, the positive diversity effects on mortality and ΔAGB were consistent across the gradient of temperature. Our results suggest that higher functional diversity leads to

an increase in forest biomass accumulation as the result of a greater positive effect of functional diversity on productivity than mortality. However, in contrast to the stress gradient hypothesis, our finding shows that the positive effect of functional diversity is more pronounced in the environment favourable for growth.

4.2 Introduction

Forests play a critical role in the global carbon cycle (Pan et al. 2011). Net aboveground biomass change (ΔAGB, the difference between biomass gain from growth and biomass loss due to mortality) is a direct measure of biomass accumulation in forests (Brienen et al. 2015; Chen & Luo 2015). In the face of the anthropogenic environmental changes that have affected global ecosystem function and biodiversity (Isbell et al. 2017), it is important to address how the effects of diversity on ΔAGB may be dependent on the environment (Hisano et al. 2018).

Tree diversity can increase productivity (i.e., biomass growth) in forest ecosystems (biodiversity-ecosystem functioning, B-EF) primarily through ‘niche complementarity’ and ‘selective processes’. The former involves interspecific niche partitioning and facilitative interactions, while the latter results from inherent performances of individual species/traits (Isbell et al. 2017; Huang et al. 2018). The positive diversity effects on productivity are thought to be strengthened in environments unfavourable for growth in both experimental and natural systems (Garcia-Palacios et al. 2018; Kardol et al. 2018). The environmental dependency of the B-EF relationship could be explained by how the extent of niche complementarity among species changes with environmental stress (Maestre et al. 2009). Previous B-EF studies in forest ecosystems showed that the positive diversity effects on productivity were stronger in drier (Jucker et al. 2016; Ratcliffe et al. 2016; Ratcliffe et al. 2017) or colder (Paquette & Messier 2011; Jucker et al. 2016; Mori 2018) regions (i.e., conditions unfavourable for growth) than warmer or more humid regions. Such information is useful for developing forest management strategies among various regions experiencing different abiotic conditions and environmental changes (Forrester 2014).

The effect of tree diversity on mortality has been largely neglected. This lack of knowledge prevents us from formulating the relationship between diversity and forest carbon dynamics because mortality is a critical determinant of forest biomass dynamics by affecting stem density and standing biomass (Brienen et al. 2015; Chen et al. 2016). Species-rich forests may have less mortality due to a lower intensity of competition with niche partitioning among species. However, the limited studies available have reported that mortality either increases (Poorter et al. 2017) or decreases (Hisano et al. 2019) with increasing tree diversity. This discrepancy could be attributed to potentially different responses of tree mortality to diversity associated with the abiotic environment, as it has been suggested for tree growth (Paquette & Messier 2011; Ratcliffe et al. 2017; Mori 2018). However, it is unknown how spatial gradients in abiotic conditions may explain variation in the effects of diversity on mortality and thus on ΔAGB.

Here we examined how the effects of tree functional diversity on growth, mortality, and ΔAGB were dependent on the abiotic gradients in natural forests. We used a large spatial inventory network of temperate and boreal forests across Canada (17,107 plots with 1,470,904 trees) with a range of water availability and temperature (Fig. S4-1). We expected that higher water availability and temperature would increase growth due to resource enrichment and a longer growing season, and increase mortality due to intensified competition with enhanced growth (i.e., higher biomass turnover rate (Keeling & Phillips 2007)). By explicitly partitioning the effects of abiotic drivers and functional identity (community-weighted mean of resource acquisition traits), we tested the following hypotheses: (i) the effects of functional diversity on growth would be greater in drier/colder sites than humid/warmer sites; and (ii) mortality would decrease with functional diversity due to reduced competition, and its magnitude of decrease would be greater in drier/colder sites than humid/warmer sites. We modelled biomass changes with functional diversity, which represented niche complementarity (Laliberte & Legendre 2010), while simultaneously accounting for the influence of functional identity, which represented the selection effect based on the mass-ratio hypothesis (Grime 1998) (Ratcliffe et al. 2016) and stand ageing (Hisano et al. 2019).

4.3 Materials and Methods

4.3.1 Study area and forest inventory data

To examine the temporal dynamics in aboveground biomass after accounting for endogenous factors, we used a network of permanent sampling plots (PSP) established by the provincial governments of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Nova Scotia, and Newfoundland and Labrador between the 1950s and 1980s (Fig. S4-1). We selected the PSPs using the following criteria; plots must: (i) be unmanaged, with known stand age (year); (ii) have all trees tagged and repeatedly measured; (iii) have all trees marked with their diameter at breast height (DBH). A total of 17,107 plots (914.21 ha; 43°47’–60°00’ N, 52°81’–133°71’ W) were selected for analyses with 1,470,904 trees measured during the monitoring period from 1951 to 2016 (Fig. S4-1). Average measurement interval was 9.47 years with 4.70 census times; the initial and final census years varied from 1951–2011 and 1956–2016, respectively. The plot sizes ranged between 20 m^2 and 2,023 m^2 (Table S4-1). Mean annual temperature and mean annual precipitation in the area varied between -3.91 °C and 12.26 °C, and 291 mm and 3,884 mm (1951–2016), respectively. Elevation ranged between 0.1 m and 2,355 m above sea level (Table S4-1).

4.3.2 Annual net aboveground biomass change and its components

Plot-level aboveground biomass was calculated by summing the biomass of all trees in each plot for each measurement. Aboveground biomass of individual trees was estimated based on allometric equations specific to each tree species of Canada (for the stem, bark, leaves, and branches, respectively) (Lambert et al. 2005; Ung et al. 2008). We used the equations of hardwood and softwood, respectively, to estimate biomass for less frequently occurring species (hardwood: *Carpinus caroliniana* (eight trees), *Amelanchier* spp. (105 trees), *Acer macrophyllum* (1,427 trees), *A. negundo* (34 trees), *A. glabrum* (3,234 trees), *A. spicatum* (384 trees), *A. pensylvanicum* (2,364 trees), *A. circinatum* (3,079 trees) *Rhamnus* spp. (one tree), *Rhamnus purshiana* (202 trees), *Crataegus* spp. (five trees), *Sorbus americana* (1,891 trees), *S. decora* (209 trees), *Malus* spp. (112 trees), *M. fusca* (25 trees), *Cornus nuttallii* (18 trees), *C. rugosa* (two trees), *Salix* spp. (20,978 trees), *S. scoleriana* (84,235 trees), *Alnus incana* (2,721 trees), unidentified hard woods (468 species); softwood: *Abies grandis* (331 trees), *Pinus nigra* (three trees), *P. flexilis* (26 trees), *P. ponderosa* (4,704 trees), *P. sylvestris* (126 trees), *P. albicaulis* (two trees), *Juniperus scopulorum* (225 trees), *Taxus brevifolia* (402 trees), *Picea abies* (324 trees), unidentified softwoods (three trees)). We then calculated annual net aboveground biomass change (ΔAGB, Mg ha^{-1} yr^{-1}) as the difference of aboveground biomass between censuses divided by the census length in years (Brienen et al. 2015). The ΔAGB was comprised of biomass gain by the growth of surviving trees (ΔAGB_G), ingrowth by new recruitment trees (ΔAGB_I), and loss from tree mortality (ΔAGB_M).

4.3.3 Stand age

Stand age for each plot was determined by dendrochronological ageing based on the average age of the oldest species in the stand. We used the middle stand age (SA) of a census period (i.e., the period between two successive censuses) to account for effects of forest development processes (representing changes in stem density and composition (Hisano et al. 2019)) on growth, mortality, and ΔAGB.

4.3.4 Climate variables

We used the long-term average (between 1951 and 2016) of annual climate moisture availability index (CMI_{ave}) (Luo et al. 2019) as a resource-driven abiotic driver and mean annual temperature (MAT_{ave}) as a non-resource-based driver (Table S4-1; Fig. S4-1). For each study plot, we derived monthly mean temperature, precipitation (PPT) and potential evapotranspiration (PET) by BioSIM 11 software (Régnière et al. 2014) and then calculated annual CMI (annual PPT minus annual PET) (Hogg et al. 2017). Alternative to CMI_{ave}, the long-term average of annual aridity index (AI_{ave}) was also calculated in the same way for each plot, where AI is defined as annual PPT divided by annual PET (UNEP 1997). Smaller values of CMI and AI denote drier conditions, while their greater values indicate wetter conditions.

4.3.5 Functional diversity and identity

Functional traits have been suggested to explain ecosystem functioning better than species diversity alone and thus used to disentangle the underlying mechanisms of B-EF

(Anderegg et al. 2018). Following previous studies (Ratcliffe et al. 2016), we took trait-based approaches with functional diversity (FD) representing ‘niche complementarity’ and functional identity (community-weighted mean of traits (Ratcliffe et al. 2016), hereafter CWM) quantifying ‘selection effect based on the mass ratio hypothesis (Grime 1998)’. Greater dissimilarity in traits should be associated with greater complementarity in resource use and reduced competition because functional traits can be regarded as a species’ resource-based niche in a community (Laliberte & Legendre 2010).

To calculate FD, we used eight key functional traits that should be related with growing and competitive abilities under the gradient of water availability and temperature based on previous studies (Niinemets & Valladares 2006; Reich 2014; Anderegg et al. 2018): ‘leaf nitrogen content per leaf dry mass’ (N_{mass}, mg g^{-1}), ‘leaf phosphorus content per leaf dry mass’ P_{mass}, mg g^{-1}), ‘specific leaf area’ (SLA, mm^2 mg^{-1}; i.e., leaf area per leaf dry mass), ‘wood density’ (WD, g cm^{-3}), ‘shade tolerance’ (ST, categorical class 1–5 (Niinemets & Valladares 2006)), ‘drought tolerance’ (DT, categorical class 1–5 (Niinemets & Valladares 2006), leaf habit (‘deciduous’ = ‘1’ vs ‘evergreen’ = ‘0’), and leaf structure (‘broadleaves’ = ‘1’ vs ‘coniferous’ = ‘0’). These trait values were extracted from the TRY database (Kattge et al. 2011) and other published sources (Reich & Oleksyn 2004; Wright et al. 2004; Niinemets & Valladares 2006; Chave et al. 2009; Berner & Law 2016).

FD was calculated as functional dispersion with the eight traits, which can account for species abundance as well as the distance of species to the centre of multi-trait functional space (Laliberte & Legendre 2010). Functional identity was measured as the CWM of the continuous trait values (Ratcliffe et al. 2016). Similar to previous studies

(Ruiz-Benito et al. 2017b), we performed a principal component analysis (PCA) with CWMs of the eight traits to obtain a comprehensive functional identity to represent them because these values were highly correlated with each other (e.g., $\mathrm{CWM_{Nmass}}$ with $\mathrm{CWM_{Pmass}}$ ($r = 0.88$), $\mathrm{CWM_{SLA}}$ ($r = 0.88$), $\mathrm{CWM_{Habit}}$ ($r = 0.88$), $\mathrm{CWM_{Struct}}$ ($r = 0.88$), $\mathrm{CWM_{WD}}$ ($r = 0.53$); $\mathrm{CWM_{DT}}$ with $\mathrm{CWM_{ST}}$ ($r = 0.62$)) (Fig. S4-2). We employed the first axis ($\mathrm{CWM_{PC1}}$, explained 53% of the variation) of the PCA as a variable of functional identity because it collectively represents traits associated with resource acquisition (Wright et al. 2004; Niinemets & Valladares 2006; Chave et al. 2009; Reich 2014), being strongly related with higher $\mathrm{CWM_{Nmass}}$, $\mathrm{CWM_{Pmass}}$, $\mathrm{CWM_{SLA}}$, $\mathrm{CWM_{Habit}}$ (i.e., deciduous), $\mathrm{CWM_{Struct}}$ (i.e., broadleaves), and $\mathrm{CWM_{WD}}$ and relatively associated with lower $\mathrm{CWM_{ST}}$ (Fig. S4-2). Plot-level FD and $\mathrm{CWM_{PC1}}$ varied during the census period, and thus we used the mean FD and $\mathrm{CWM_{PC1}}$ of the two consective measurements of a census period (Hisano et al. 2019), similar to the middle stand age.

4.3.6 Statistical analysis

To test whether the effects of FD on ΔAGB and its components are dependent on the spatial gradient of $\mathrm{CMI_{ave}}$ and $\mathrm{MAT_{ave}}$, we used the following univariate linear mixed effects model:

$$
\begin{aligned}
(\Delta\mathrm{AGB})_{ijk}, (\Delta\mathrm{AGB_{GI}})_{ijk}, \text{ or } (\Delta\mathrm{AGB_{M}})_{ijk} = {} & \beta_0 + \beta_1 \times \ln(\mathrm{SA})_{ij} + \beta_2 \times (\mathrm{CMI_{ave}})_j \\
& + \beta_3 \times (\mathrm{MAT_{ave}})_j + \beta_4 \times f(\mathrm{FD})_{ij} + \beta_5 \times f(\mathrm{CWM_{PC1}})_{ij} \\
& + \beta_6 \times (\mathrm{CMI_{ave}})_j \times (\mathrm{MAT_{ave}})_j \\
& + \beta_7 \times (\mathrm{CMI_{ave}})_j \times f(\mathrm{FD})_{ij} \\
& + \beta_8 \times (\mathrm{MAT_{ave}})_j \times f(\mathrm{FD})_{ij} \\
& + \beta_9 \times (\mathrm{CMI_{ave}})_j \times f(\mathrm{CWM_{PC1}})_{ij}
\end{aligned}
$$

$$+ \beta_{10} \times (\mathrm{MAT}_{\mathrm{ave}})_j \times f(\mathrm{CWM}_{\mathrm{PC1}})_{ij}$$

$$+ \beta_{11} \times f(\mathrm{FD})_{ij} \times f(\mathrm{CWM}_{\mathrm{PC1}})_{ij}$$

$$+ \pi_j + \rho_k + \varepsilon \qquad (1)$$

where i, j, k, and l were ith census, jth plot, and kth province. β_i were coefficients to be estimated. SA, Year, FD, and $\mathrm{CWM}_{\mathrm{PC1}}$ were the middle values of stand age, functional diversity, and CWM of resource acquisition traits between two consecutive censuses. $\mathrm{CMI}_{\mathrm{ave}}$ and $\mathrm{MAT}_{\mathrm{ave}}$ were the long-term average of annual climate moisture index and mean annual temperature during the study period (1951–2016). π_j was a random plot effect accounting for site-specific conditions such as site-specific disturbance history and ρ_k was a random province effect accounting for differences in sampling methods (e.g., DBH threshold (Searle & Chen 2017b)) among provinces. ε was a random error. The two-way interactions of $\mathrm{CMI}_{\mathrm{ave}}$, $\mathrm{MAT}_{\mathrm{ave}}$, FD, and $\mathrm{CWM}_{\mathrm{PC1}}$ were included based on the model selection by the Akaike Information Criterion (AIC). Based on AIC, SA, FD, and $\mathrm{CWM}_{\mathrm{PC1}}$ were transformed by logarithmic or square root functions (Ratcliffe et al. 2016; Hisano et al. 2019). All the explanatory variables were centred and scaled (mean = 0, SD = 1) before analysis to allow coefficient comparison. We modelled the effects of these variables on biomass dynamics using the *lme4* package with the restricted maximum likelihood estimation (Bates et al. 2014).

Similar to the previous study (Phillips et al. 2009), we assessed whether plot size (ha) and census length (year) affect biomass dynamics but found their influences negligible (assessed by correlations between residuals of eqn. 1 and plot size: $r = -0.016$ for growth, $r = 0.009$ for mortality, $r = -0.019$ for ΔAGB; and those between residuals of eqn. 1 and census length: $r = -0.005$ for growth, $r = 0.006$ for mortality, $r = -0.005$ for

ΔAGB). We also examined biomass dynamics trends with AI, by replacing CMI_{ave} in eqn. 1 with AI_{ave} to ensure that our choice of water availability variable did not influence outcomes. This analysis assumes normally distributed data, but in our data, the distributions of growth and mortality were right-skewed, while that of ΔAGB was left-skewed. We thus bootstrapped the fitted coefficients using 1,000 iterations. We further employed a rank-based estimator for linear models (nonparametric regression) using the *Rfit* package (Kloke & McKean 2012).

Although the maximum variance inflation factors (VIF) among the explanatory variables were 2.76 for growth, 2.77 for mortality, and 2.80 for ΔAGB, there was a positive correlation between CMI_{ave} and MAT_{ave} ($r = 0.44$). To ensure that multicollinearity did not influence coefficient estimates, we compared outcomes from eqn. 1 (accounting for both CMI_{ave} and MAT_{ave} simultaneously) with those from alternative models accounting for either CMI_{ave} and MAT_{ave} individually (individual models) (Fig. S4-3), similar to the previous study (Hisano et al. 2019). Moreover, we also refitted eqn. 1 by ridge regression (penalised parameter estimates) (Dormann et al. 2013) using the *glmnet* package (Friedman et al. 2017). Values of λ (that controls the amount of shrinkage) at which the mean cross-validation errors were the largest within 1 standard error of the minimum (*lambda.1se*), and they were selected through 100-fold cross-validation by the *cv.glmnet* function (Friedman et al. 2017). We then bootstrapped coefficients estimated by ridge regression with a range of *lambda.1se* 1,000 times to compare them with the bootstrapped coefficients estimated by the linear mixed effect model (Hisano et al. 2019). Before fitting the ridge regression and nonparametric regression, we removed the random effects from ΔAGB and its components by using the estimated effects of the plot and province from eqn. 1. Explanatory variables were scaled for the ridge regression, bootstrapped linear mixed effect models, and nonparametric regression to allow coefficient comparison. All alternative methods yielded qualitatively similar results (Fig. S4-3).

4.4 Results

The growth model accounted for 34.7% of the variation in growth from the fixed effects alone, increasing to 80.2% when including the random effects, while those for mortality model accounted for 6.1% and 13.6% of the variation in mortality, respectively, from the fixed effects and both the fixed and random effects (Table 4-1). Among the fixed effects, temperature was a major driver for growth, while stand age was a major driver for ΔAGB and mortality (Fig. 4-1). Water availability explained 11.4%, 0.2%, and 12.1% of the total variation in growth, mortality, and ΔAGB, respectively, and temperature explained 48.3%, 6.9%, and 18.8% (Fig. 4-1). The standardised coefficients (allowing comparison of the strength of each effect to the response variable) also showed that temperature had a greater statistical effect on growth and mortality than water availability, but their effects on ΔAGB were similar (Table 4-1). Functional diversity accounted for 26.6% of the variation of growth, with CWM of resource acquisition traits ($\mathrm{CWM}_{\mathrm{PC1}}$) accounting for 2.3%. Mortality was more explained by $\mathrm{CWM}_{\mathrm{PC1}}$ (32.9%) than functional diversity (3.6%) (Table 4-1). Functional diversity accounted for 4.0% and $\mathrm{CWM}_{\mathrm{PC1}}$ explained 1.0% of the variation in ΔAGB. The two-way interactions collectively accounted for 8.7, 6.0, and 5.7%, respectively for growth, mortality and ΔAGB.

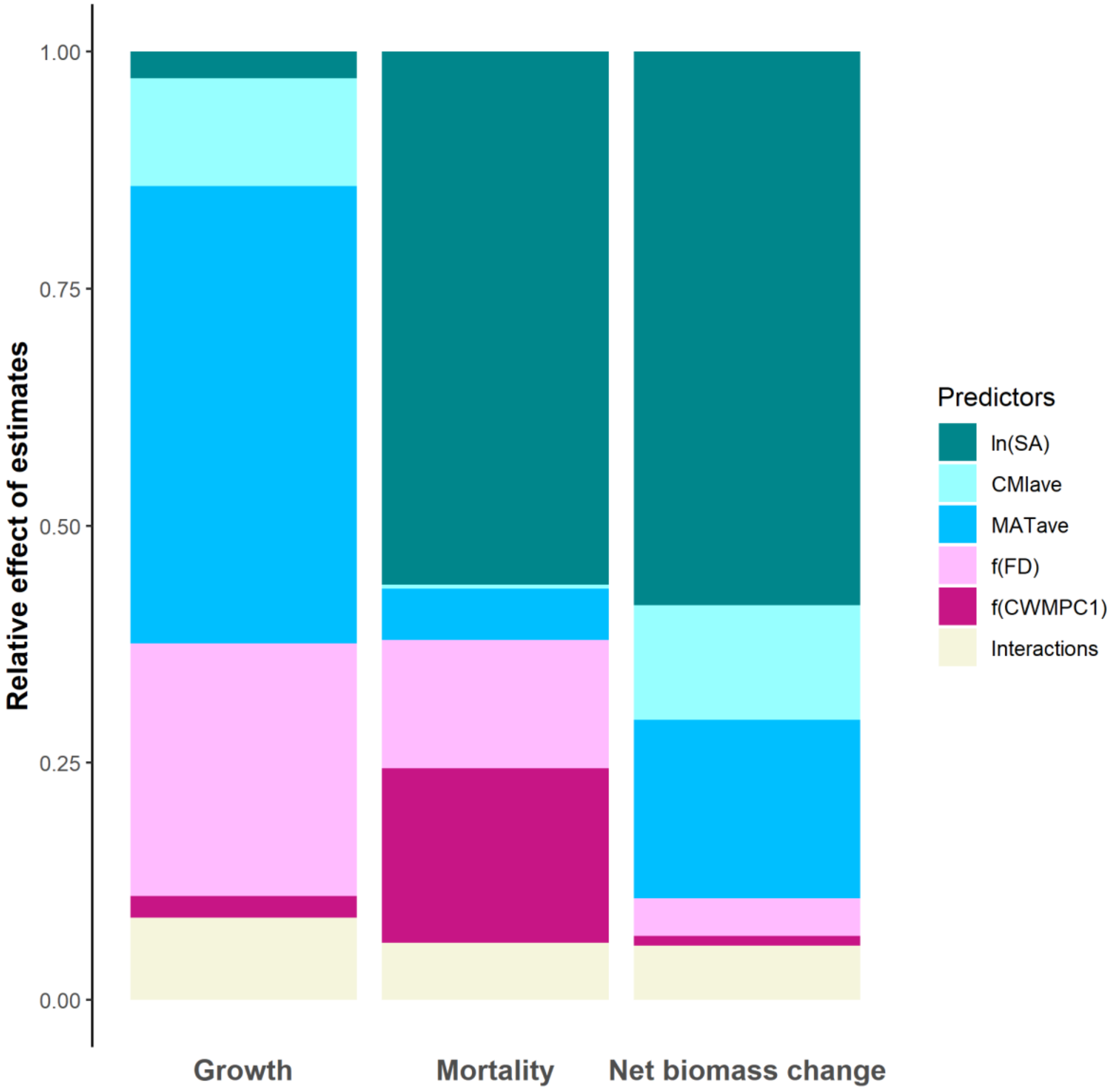

Figure 4-1: Variance components showing the proportion of total variation (% sum of squares) in growth, mortality, and ΔAGB explained by the fitted model (fixed effects in Equation 1). ln(SA) = stand age, CMI_{ave} = the long-term average of climate moisture index (for each plot), MAT_{ave} = the long-term average of mean annual temperature (for each plot), *f*(FD) = functional diversity, *f*(CWM_{PC1}) = community-weighted mean of resource acquisition traits (CWM_{PC1}; see *Methods*). Interactions are the sum of all interactions described in Equation 1.

Table 4-1: Growth (biomass gain), mortality (biomass loss), and net biomass change associated with stand age, climates, functional diversity, and identity.

Fixed effects	Coefficients (mean ± s.e.m.)	*df*	*F*	*P*
Growth (Mg ha^{-1} yr^{-1})				
(Intercept)	2.996 ± 0.340	-	-	<0.001
ln(SA)	-0.108 ± 0.009	1, 38658.3	135.6	<0.001
$\mathrm{CMI}_{\mathrm{ave}}$	0.475 ± 0.020	1, 15556.6	550.9	<0.001
$\mathrm{MAT}_{\mathrm{ave}}$	0.724 ± 0.015	1, 16035.4	2342.1	<0.001
$f(\mathrm{FD})$	0.342 ± 0.010	1, 29246.9	1292.1	<0.001
$f(\mathrm{CWM}_{\mathrm{PC1}})$	0.115 ± 0.011	1, 23891.2	111.0	<0.001
$\mathrm{CMI}_{\mathrm{ave}} \times \mathrm{MAT}_{\mathrm{ave}}$	0.104 ± 0.013	1, 15558.7	66.5	<0.001
$\mathrm{CMI}_{\mathrm{ave}} \times f(\mathrm{FD})$	0.070 ± 0.012	1, 23844.8	36.3	<0.001
$\mathrm{MAT}_{\mathrm{ave}} \times f(\mathrm{FD})$	0.032 ± 0.012	1, 28952.5	7.2	0.007
$\mathrm{CMI}_{\mathrm{ave}} \times f(\mathrm{CWM}_{\mathrm{PC1}})$	-0.242 ± 0.015	1, 20618.5	264.7	<0.001
$\mathrm{MAT}_{\mathrm{ave}} \times f(\mathrm{CWM}_{\mathrm{PC1}})$	0.054 ± 0.013	1, 23011.0	17.4	<0.001
$f(\mathrm{FD}) \times f(\mathrm{CWM}_{\mathrm{PC1}})$	-0.048 ± 0.009	1, 35462.8	28.2	<0.001
Mortality (Mg ha^{-1} yr^{-1})				
(Intercept)	1.914 ± 0.155	-	-	<0.001
ln(SA)	0.374 ± 0.016	1, 44970.9	570.2	<0.001
$\mathrm{CMI}_{\mathrm{ave}}$	0.041 ± 0.029	1, 12970.1	2.1	0.149
$\mathrm{MAT}_{\mathrm{ave}}$	0.196 ± 0.021	1, 38446.2	83.7	<0.001
$f(\mathrm{FD})$	0.097 ± 0.015	1, 47664.5	43.6	<0.001
$f(\mathrm{CWM}_{\mathrm{PC1}})$	0.323 ± 0.016	1, 47571.9	396.2	<0.001

CMI$_{ave}$ × MAT$_{ave}$	0.056 ± 0.018	1, 14273.4	9.8	0.002
CMI$_{ave}$ × f(FD)	-0.057 ± 0.018	1, 47898.5	10.0	0.002
MAT$_{ave}$ × f(FD)	0.051 ± 0.019	1, 47800.5	7.2	0.007
CMI$_{ave}$ × f(CWM$_{PC1}$)	-0.045 ± 0.022	1, 47902.0	4.1	0.044
MAT$_{ave}$ × f(CWM$_{PC1}$)	-0.089 ± 0.020	1, 47829.0	20.5	<0.001
f(FD) × f(CWM$_{PC1}$)	-0.112 ± 0.015	1, 47414.9	57.0	<0.001
Net biomass change (Mg ha^{-1} yr^{-1})				
(Intercept)	1.113 ± 0.369	-	-	0.014
ln(SA)	-0.577 ± 0.018	1, 20213.9	1004.0	<0.001
CMI$_{ave}$	0.485 ± 0.034	1, 17076.7	207.9	<0.001
MAT$_{ave}$	0.452 ± 0.025	1, 18425.5	324.1	<0.001
f(FD)	0.151 ± 0.018	1, 17865.9	68.0	<0.001
f(CWM$_{PC1}$)	-0.083 ± 0.020	1, 16658.4	17.6	<0.001
CMI$_{ave}$ × MAT$_{ave}$	0.011 ± 0.021	1, 17974.9	0.3	0.592
CMI$_{ave}$ × f(FD)	0.084 ± 0.023	1, 20819.9	13.5	<0.001
MAT$_{ave}$ × f(FD)	-0.032 ± 0.023	1, 18969.7	1.9	0.165
CMI$_{ave}$ × f(CWM$_{PC1}$)	-0.142 ± 0.027	1, 18966.8	28.2	<0.001
MAT$_{ave}$ × f(CWM$_{PC1}$)	0.161 ± 0.023	1, 17850.6	48.4	<0.001
f(FD) × f(CWM$_{PC1}$)	0.048 ± 0.020	1, 21135.8	5.6	0.018

SA: stand age; CMI$_{ave}$: average of climate moisture index during the study period for each plot; MAT$_{ave}$: mean annual temperature during the study period; FD: functional diversity (functional dispersion (Laliberte & Legendre 2010)); FD was transformed by square root for growth and mortality, and CWM$_{PC1}$ was transformed by natural-logarithm for growth and net biomass change and by square root for mortality (see *Methods*).

Growth on average decreased with stand age and increased with water availability and temperature, and mortality increased with stand age and temperature (Table 4-1; Fig. 4-2). The positive effects of water availability on growth and mortality were stronger in warmer sites (Table 4-1; Fig. S4-4a). Growth, mortality, and ΔAGB on average, increased with functional diversity (Table 4-1; see also the mean lines in Fig. 4-3). The more prominent response of growth to functional diversity than that of mortality led to increased ΔAGB on average with functional diversity (Table 4-1; Fig. 4-3). Both growth and mortality also increased with $\mathrm{CWM}_{\mathrm{PC1}}$ on average, while ΔAGB decreased due to a higher $\mathrm{CWM}_{\mathrm{PC1}}$ effect on mortality than growth (Table 4-1; see also the mean lines in Fig. 4-4). Moreover, the functional diversity effect on both growth and mortality decreased with $\mathrm{CWM}_{\mathrm{PC1}}$, with a more pronounced effect on mortality, resulting in a stronger effect of functional diversity on ΔAGB with increasing $\mathrm{CWM}_{\mathrm{PC1}}$ (Table 4-1; Fig. S4-4b).

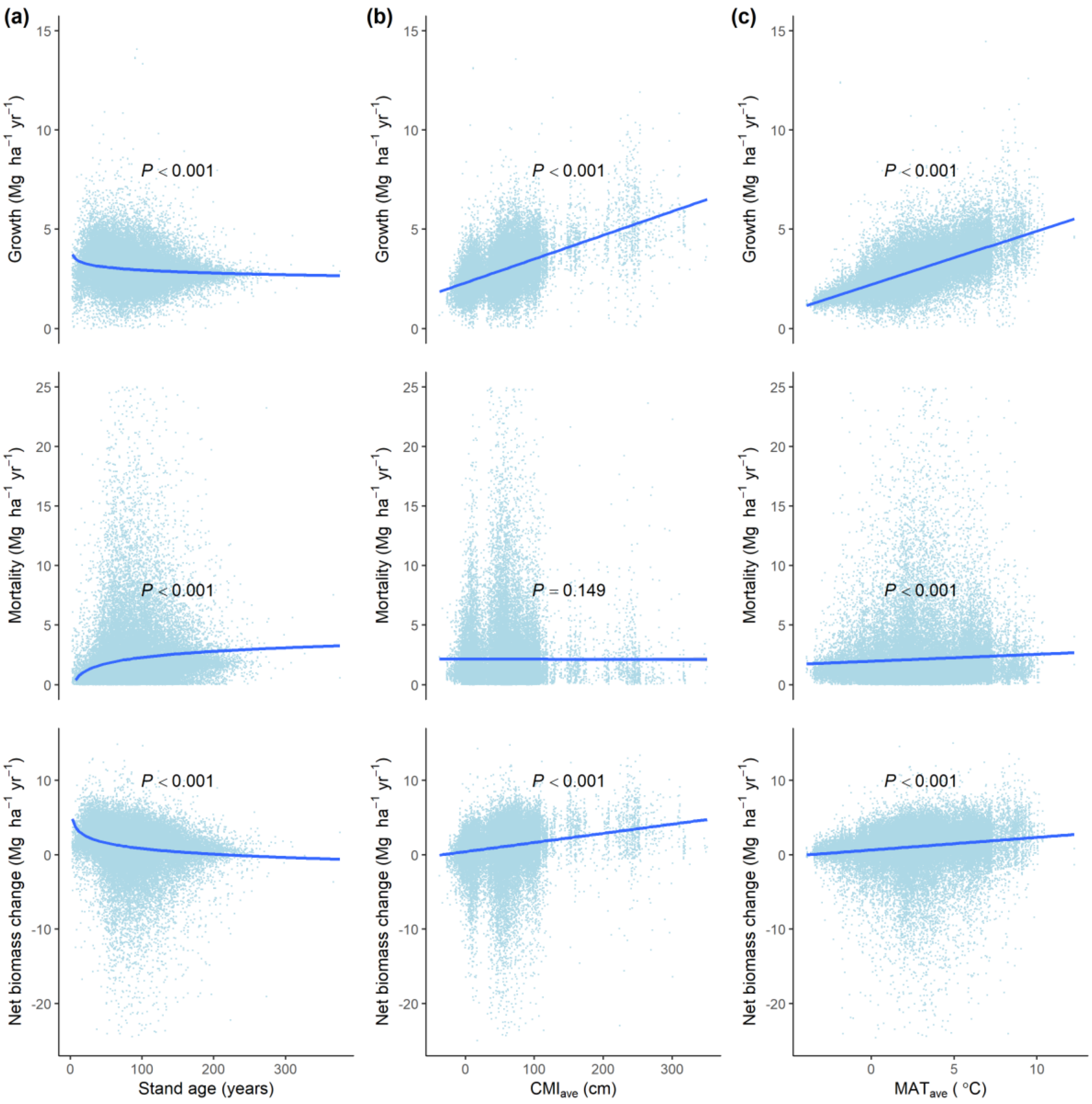

Figure 4-2: The relationship between biomass dynamics (growth, mortality and net biomass change) and (a) stand age, (b) the long-term average of climate moisture index (CMI$_{ave}$), and (c) the long-term average of mean annual temperature (MAT$_{ave}$). Dots are the values predicted by partial regressions with each explanatory variable. The shaded areas are 95% confidence intervals of the estimated regressions.

Importantly, the responses of biomass dynamics to functional diversity and CWM_{PC1} were dependent on abiotic condition (CMI_{ave} and MAT_{ave}) (Table 4-1; Figs. 4-3, 4-4). The positive effect of functional diversity on growth was more prominent in humid sites than drier sites (Fig. 4-3a). Mortality increased with functional diversity in drier sites but did not in wetter sites (Fig. 4-3a). Consequently, the positive effect of functional diversity on ΔAGB increased with increasing water availability (Fig. 4-3a). With changes in temperature, the positive effect of functional diversity on growth and ΔAGB were consistent across the gradient of temperature, but its effect on mortality increased with temperature (Fig 3b). Growth increased with CWM_{PC1} in drier sites but decreased in wetter sites (Fig. 4-4a), while the positive effect of CWM_{PC1} on mortality was strengthened with decreasing water availability, resulting in positive trends in ΔAGB with CWM_{PC1} in drier sites and negative trends in wetter sites (Fig. 4-4a). Increasing temperature, on the other hand, promoted the positive effect of CWM_{PC1} on growth, while it reduced its positive effect on mortality, leading to a shift from a negative effect of CWM_{PC1} on ΔAGB in colder sites to a positive one in warmer sites (Fig. 4-4b).

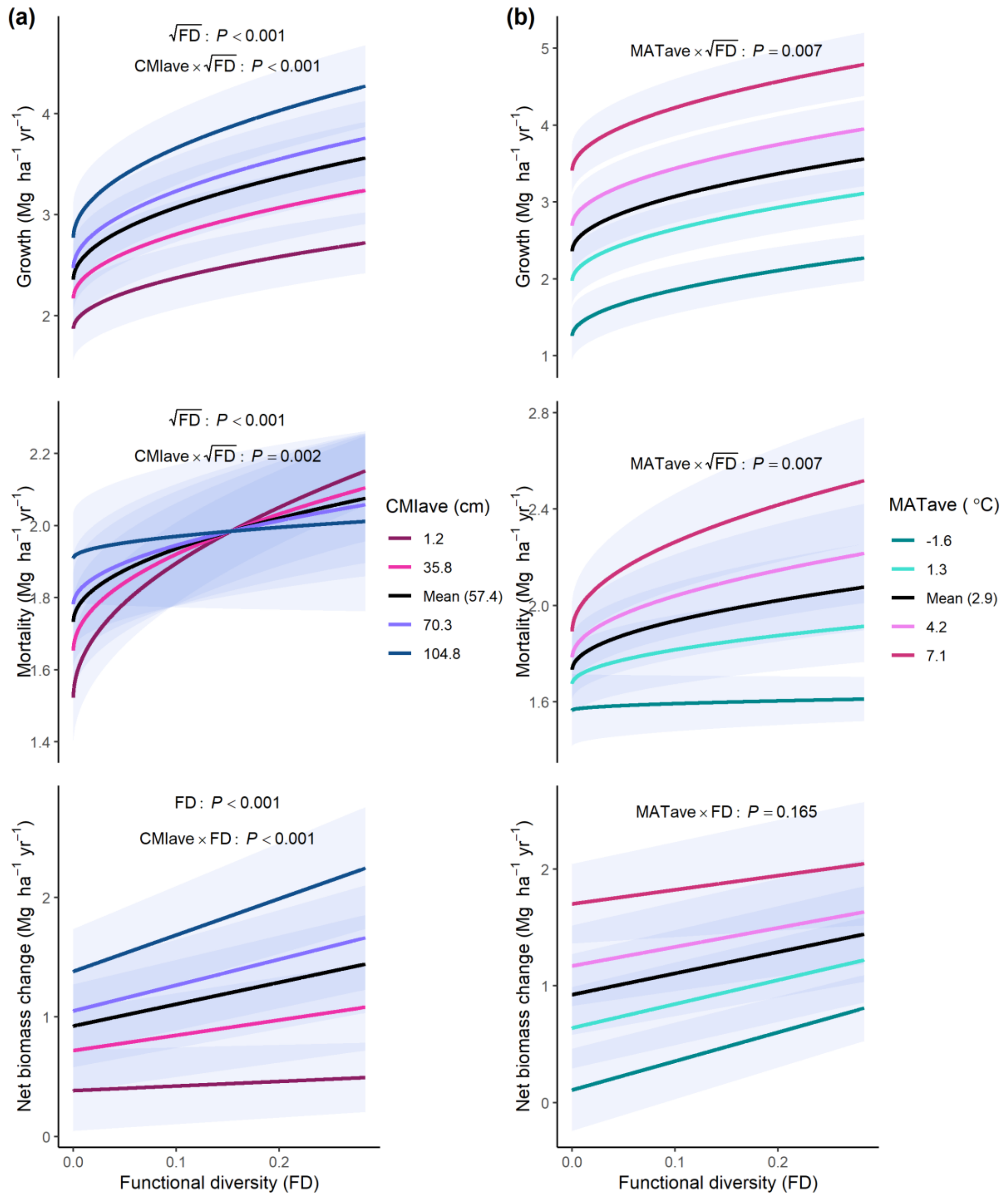

Figure 4-3: Abiotic context-dependent response of aboveground biomass dynamics to functional diversity (functional dispersion; FD). (a) Trends with the long-term average of climate moisture index (CMI_{ave}) and (b) trends with the long-term average of mean annual temperature (MAT_{ave}). The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. CMI_{ave} and MAT_{ave} were binned from 1.2 to 104.8 (cm) and from -1.6 to 7.1 (°C) (their 5% and 95% percentiles) for four levels. Mean values are also shown as black lines.

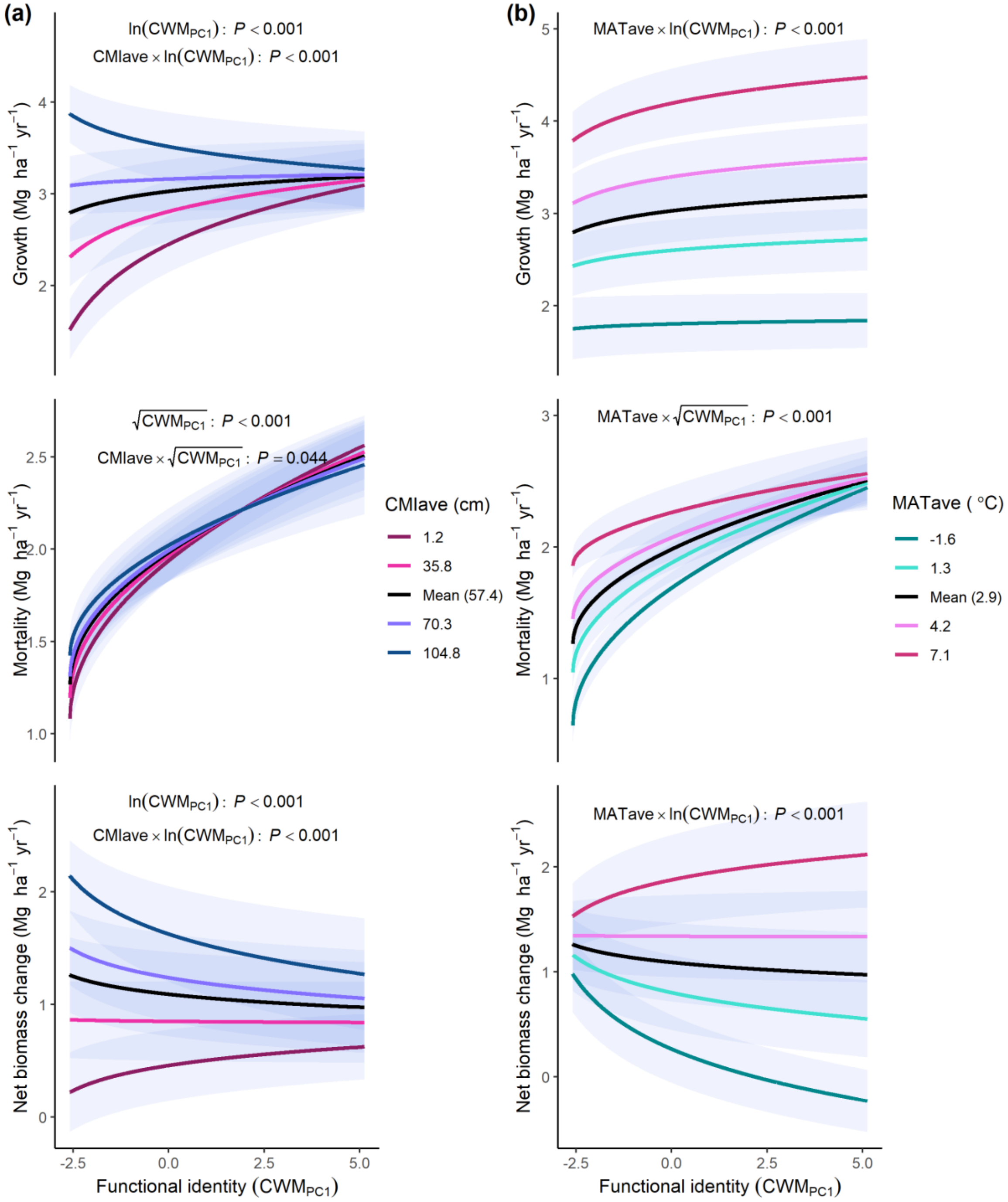

Figure 4-4: Abiotic context-dependent response of aboveground biomass dynamics to functional identity (community-weighted mean of resource acquisition traits; CWM_{PC1}). (a) Trends with the long-term average of climate moisture index (CMI_{ave}) and (b) trends with the long-term average of mean annual temperature (MAT_{ave}). The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. CMI_{ave} and MAT_{ave} were binned from 1.2 to 104.8 (cm) and from -1.6 to 7.1 (°C) (their 5% and 95% percentiles) for four levels. Mean values are also shown as black lines.

Our results were robust because the alternative models accounting for water availability and temperature individually, ridge regression, and non-parametric regression yielded qualitatively similar coefficient estimates for the terms of our interest to those produced by the original simultaneous model (Fig. S4-3). Moreover, our choice of water availability metrics did not influence the outcomes as alternative models with AI_{ave} resulted in qualitatively similar coefficient estimates (Figs. S4-5 and S4-6).

4.5 Discussion

This study shows abiotic context-associated relationships between tree diversity and forest net biomass change by simultaneously examining growth and mortality. On average, functional diversity enhanced growth, but in contrast to previous studies with species diversity (Jucker et al. 2016; Ratcliffe et al. 2017), decreasing water availability reduced positive effects of functional diversity on growth. Functional diversity also increased mortality on average. However, the positive effects of functional diversity on mortality decreased with increasing water availability. If we consider lower water availability and temperature should be a higher level of stresses, these results are in contrast to the stress gradient hypothesis (Maestre et al. 2009). While the mechanisms are unclear, one plausible explanation would be that hydrological niche breadths in drier sites are limited so that functional diversity effects to improve facilitation or reduce competition might not have been realised, while in more humid sites, niche partitioning for water could be more effective to enhance growth or reduce mortality (Hooper et al. 2005; Silvertown et al. 2015). Moreover, changes in water availability could be associated with changes in the availability of other resources such as soil nutrients (Silvertown et al. 2015; Wright et al. 2015).

Decreasing temperature reduced the positive effects of functional diversity on growth. This result was similar to those in the study in Europe, where functional diversity effects, with identity effects being accounted for, were reduced with increasing latitude (i.e., decreasing temperature) (Ratcliffe et al. 2016). The warmer environment should have longer growing seasons (i.e., greater availability of energy for photosynthesis), which might have accelerated and promoted the positive interactions among trees differentiating resource acquisition traits, similar to rising CO_2 enhancing positive species diversity effects on productivity (Reich et al. 2001; Hisano et al. 2019). Our analysis also shows that the positive effect of functional diversity on mortality was enhanced by temperature. Nevertheless, functional diversity had consistently positive effects on ΔAGB because of its greater effects on growth than mortality. This suggests the importance of promoting tree functional dissimilarity to maintain aboveground live carbon stocks in these forests across Canada. However, our results tend to be in contrast with those reported in Japan, where the responses of productivity to species diversity decreased with temperature with the study plots established between 26ºN and 45ºN (from temperate to transition between temperate and boreal) (Mori 2018). It is possible that these differences could be a result of a concave pattern with the strongest diversity effect on productivity occurring in the transition zone between boreal and temperate climates.

The effects of functional diversity on mortality responded to water availability and temperature in contrasting manners. The reduced mortality in functionally diverse forests or the lack of diversity effects on mortality in wetter sites could also be associated with resource-rich conditions, which might have provided greater capacity for trees to survive. This has led to the greater sensitivity of ΔAGB to functional diversity in wetter sites, indicating even more significance of enhancing functional diversity in such sites to increase biomass stock. On the other hand, trees in warmer sites could have shorter longevity being associated with faster growth (Keeling & Phillips 2007), and functional diversity may have accelerated mortality by increasing growth (Poorter et al. 2017) especially in such warmer sites. Although this detrimental trend in mortality with functional diversity and temperature cancelled out the beneficial trends in growth, it resulted in the persistence of functional diversity effects on ΔAGB throughout the temperature gradient. Our study revealed that increasing functional diversity is promising to maintain or enhance aboveground biomass stock, regardless of abiotic contexts.

We also found that the positive effects of functional diversity on growth and mortality decreased with CWM_{PC1} (representing resource acquisition traits). Sites with higher CWM_{PC1} showed greater growth and mortality than those with lower CWM_{PC1} (Table 4-1; Fig. 4-4), regardless of functional diversity (Fig. S4-4b). Stands of high CWM_{PC1} are inherently productive but may compete for resources more intensively, leading to less overyielding (Toigo et al. 2015), accompanied by less mortality. These trends in growth and mortality translated into strengthened positive effects of functional diversity on ΔAGB with CWM_{PC1}, suggesting that communities with lower resource acquisition species (e.g., late-successional conifers; see Fig. S4-2) can maximise the role of diversity not only in increasing productivity (Toigo et al. 2015), but also in maintaining aboveground biomass stock. Moreover, the functional identity effects on biomass dynamics were also dependent on environmental conditions. The positive effects of CWM_{PC1} on growth were more prominent in drier sites, while its effects were detrimental in wetter sites. This suggests the importance of resource acquisition identity in the sites with limited resources (Drobyshev et al. 2013). The more positive effect of $\mathrm{CWM}_{\mathrm{PC1}}$ on mortality in dry sites than humid sites also suggests that the water resource was more intensively exhausted in the communities with high competition for resources (Reich 2014). On the other hand, the positive effects of $\mathrm{CWM}_{\mathrm{PC1}}$ on growth were more prominent in warmer sites, where the resource acquisition rate could have been improved by higher temperatures (Drobyshev et al. 2013), or its amount might have been enhanced by longer growing seasons.

Our study provides insights into the effects of diversity on forest net biomass change including both growth and mortality. We found that functional diversity does not only increase growth but also mortality. However, the stronger diversity effect on growth than on mortality leads to increased net biomass change with functional diversity on average across all study sites. More importantly, these functional diversity effects were pronounced in the environment favourable for growth. Promoting high functional diversity is important to increase stand-level biomass growth and stock, especially in humid and warmer sites in boreal and temperate forests. Our finding of the abiotic context-dependent relationship between ΔAGB and diversity can guide forest management across different environmental conditions (Forrester 2014), and can help meet international standards for carbon sequestration (Pan et al. 2011).

CHAPTER 5: FUNCTIONAL SHIFTS OF NATURAL FORESTS UNDER THE ENVIRONMENTAL CHANGE OF THE PAST 65 YEARS ARE DEPENDENT ON BASELINE CLIMATE

5.1 Abstract

Global environmental changes that persist over many decades have significantly impacted terrestrial plant diversity and composition. Changes in diversity and composition have critical consequences for ecosystem functioning and related services, and by extension, humanity. While there is mounting evidence that environmental changes have modified plant species diversity and functional composition in forest ecosystems, our knowledge of spatial variations in the mode of compositional shifts is limited. Thus, it remains unclear whether temporal shifts in functional composition are dependent on baseline climatic conditions. Utilizing extensive spatial and long-term forest inventory data (17,109 plots with 1,471,165 trees monitored between 1951 and 2016) across Canada, we found that functional composition shifted toward fast-growing deciduous broadleaved trees and higher drought tolerance over time; however, this shifting rate was faster in colder regions. Further analysis revealed that the functional composition of colder plots shifted toward deciduous broadleaved trees and drought tolerance more rapidly with rising CO_2 than warmer plots, whereas the functional composition of wetter and colder plots shifted toward conifers and drought intolerance more quickly with warming. Our study suggests vulnerability of functional composition of colder and wetter plots against global environmental changes. To ensure the sustainable functioning of forest ecosystems, future forest management practices should consider spatial differences in functional responses to global environmental change, with

particular efforts aimed at enhancing the compositional stability of colder and wetter plots.

5.2 Introduction

Global environmental change lasting over the century is altering terrestrial plant diversity and composition worldwide (Dornelas et al. 2014). Rising atmospheric CO_2 favours fast-growing species (Laurance et al. 2004; Esquivel-Muelbert et al. 2019), and increasing temperatures have caused directional shifts in plant species composition toward thermophilic (Fadrique et al. 2018) and resource acquisitive traits (Bjorkman et al. 2018). Additionally, more frequent droughts have increased the abundance of dry-affiliated plant taxa (Aguirre-Gutiérrez et al. 2019; Esquivel-Muelbert et al. 2019) by favouring drought-tolerant strategies (Bartlett et al. 2019). As these compositional changes can critically influence changes in forest biomass (Zhang et al. 2018), which is an important measure of terrestrial carbon dynamics, understanding the long-term responses of functional composition can provide insights into the sustainability of global forest ecosystem functioning (Hisano et al. 2018) and related services (Isbell et al. 2017). However, forests may not necessarily respond to global environmental change in the same manner, and our knowledge on spatial variations in the mode of compositional shifts is limited. To aid in the development of globally applicable strategies for ‘climate action’ (Overpeck & Conde 2019), it is imperative to quantify how rapidly compositional shifts occur on larger scales across biomes.

Canada has a wide variation in its baseline climate (i.e., local historic climate), as both mean annual temperatures and precipitation can vary substantially (Figs. 5-1A, B). Eastern Canada possesses higher water availability than the central and western regions of the country as it receives a greater amount of the mean annual precipitation, which satisfies the mean annual evapotranspiration demand (Fig. 5-1A). Moreover, Canada experiences spatially diverse temporal climate driving trends. For example, temporal changes in water availability varied significantly between regions (Fig. 5-1C), although both atmospheric CO_2 concentrations and temperatures consistently rose across Canada, with higher warming rates at higher latitudes (Fig. 5-1D). At regional scales, spatial differences in the baseline climate have been shown to affect the temporal trends of biomass changes in boreal forests. For example, the growth of boreal forests in colder regions that experienced lower, or no changes in water availability, were less negatively affected by long-term climate change compared to boreal forests in warmer regions of eastern Canada (D'Orangeville et al. 2016). Moreover, boreal forests in more humid regions suffered a lower extent of biomass loss under long-term changes in climate in western Canada (Luo et al. 2019). If long-term global environmental change favours tree species with traits that are better adapted to the new climate reality (while causing higher mortality for species with unfavoured traits), these spatial differences in demographic changes may induce spatially divergent shifts in functional composition. However, exactly how temporal shifts in functional traits are associated with spatial gradients of the baseline climate have rarely been tested, with insights limited only to a water availability gradient in tropical forests (Aguirre-Gutiérrez et al. 2019). Yet, we are not cognizant of how the rate and directionality of compositional shifts are dependent on larger scale environmental contexts across regions and biomes, particularly with baseline temperature. Moreover, no study has yet determined the relative contributions of these regionally dependent environmental change drivers to shifts in functional composition.

In this chapter, we explore how the directionality and rate of temporal functional shifts in response to persistent long-term global environmental change over 65 years in Canada have been spatially dependent on baseline climatic conditions across multiple biomes. We hypothesised that, overall, the compositions of forests across Canada would shift toward resource acquisitive deciduous broadleaved trees in response to rising CO_2 and temperatures (Laurance et al. 2004; Searle & Chen 2017a). Further, that the functional composition of forests in drier plots would respond more quickly to long-term global environmental change than humid plots, by increasing community-level drought tolerance due to their greater susceptibility to decreasing water availability (Luo et al. 2019).

Moreover, the functional shifts of colder plots would be more prominent than warmer plots due to the higher propensity for increased temperatures at higher latitudes (Huang et al. 2017) (Fig. 5-1). To test these hypotheses, we surveyed the data for 17,109 permanent sampling plots (with 1,471,165 trees naturally regenerated after wildfire and unmanaged) of temperate and boreal forests monitored between 1951 and 2016 across Canada (Fig. 5-1). We quantified functional composition as the community-weighted mean (CWM) of trait values of the first and second axes of principle component analysis (PCA), using eight traits associated with competitive and tolerative abilities. These included leaf nitrogen and phosphorus content per leaf dry mass, specific leaf area, wood density, shade tolerance, drought tolerance (Niinemets & Valladares 2006), leaf habit, and leaf structure (Fig. 5-2). The first axis was correlated with deciduous broadleaved trees vs conifers (CWM_{PC1}, positively associated with leaf nitrogen and phosphorus content, specific leaf area, and wood density), whereas the second axis was negatively correlated with drought tolerance (CWM_{PC2} × -1; converted to make it positively associated with drought tolerance; Fig. 5-2). Subsequently, we modelled temporal trends in these functional composition metrics over 65 years (representing changes in atmospheric CO_2 concentration, temperature, and water availability), while simultaneously accounting for the influences of stand development (Hisano et al. 2019) and spatial variations in the baseline climate (i.e., long-term averages of mean annual temperature (MAT_{ave}) and climate moisture index (CMI_{ave}) (D'Orangeville et al. 2016; Luo et al. 2019). We also examined temporal trends in atmospheric CO_2 concentrations, anomalies of mean annual temperature (ATA), and the climate moisture index (ACMIA), to examine the relationships between functional shifts and these environmental change drivers. Moreover, we investigated the correlations between global environmental change drivers and the relative abundance of the primary tree genera (see *Methods*) to understand functional shift processes.

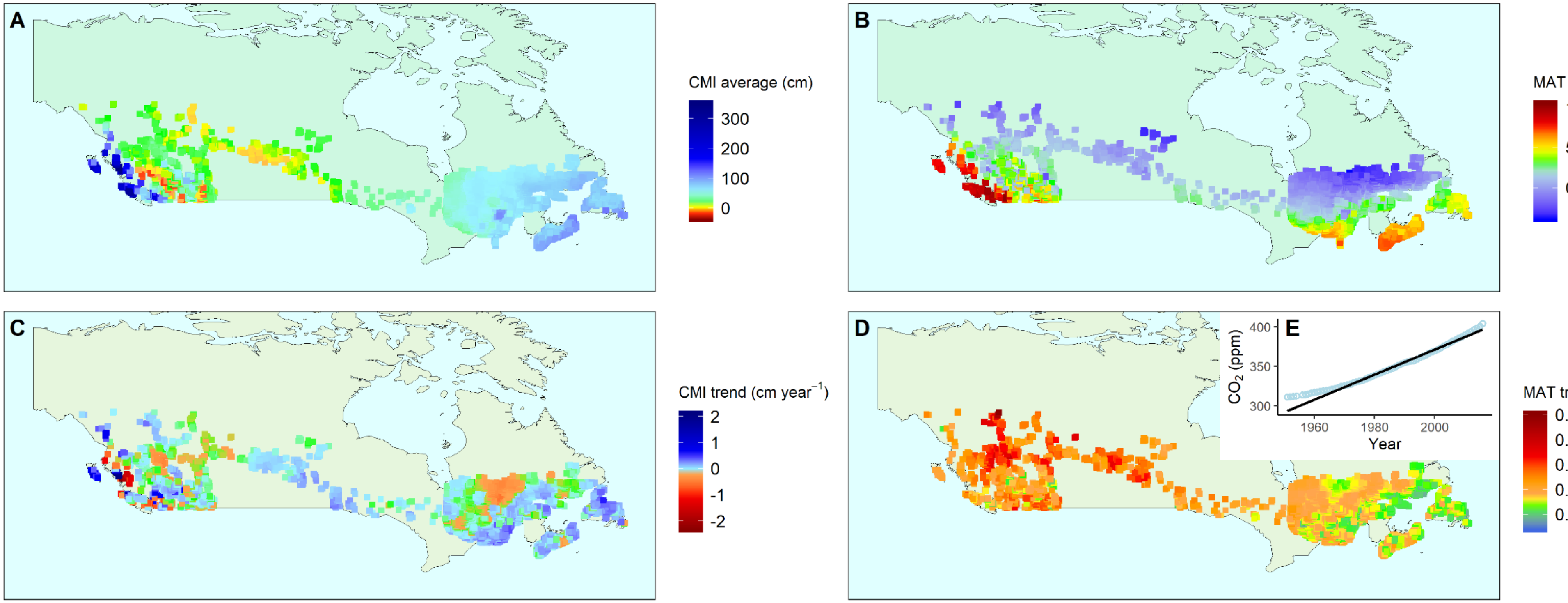

Figure 5-1: Permanent sampling plot locations across Canada and spatiotemporal patterns of global environmental change drivers. Spatial variations in climate defined as long-term averages of climate moisture index (CMIave, A) and mean annual temperature (MATave, B) between 1951 and 2016. Temporal trends of annual CMI and MAT between 1951 and 2016. (E) Temporal trend in atmospheric CO_2 concentrations.

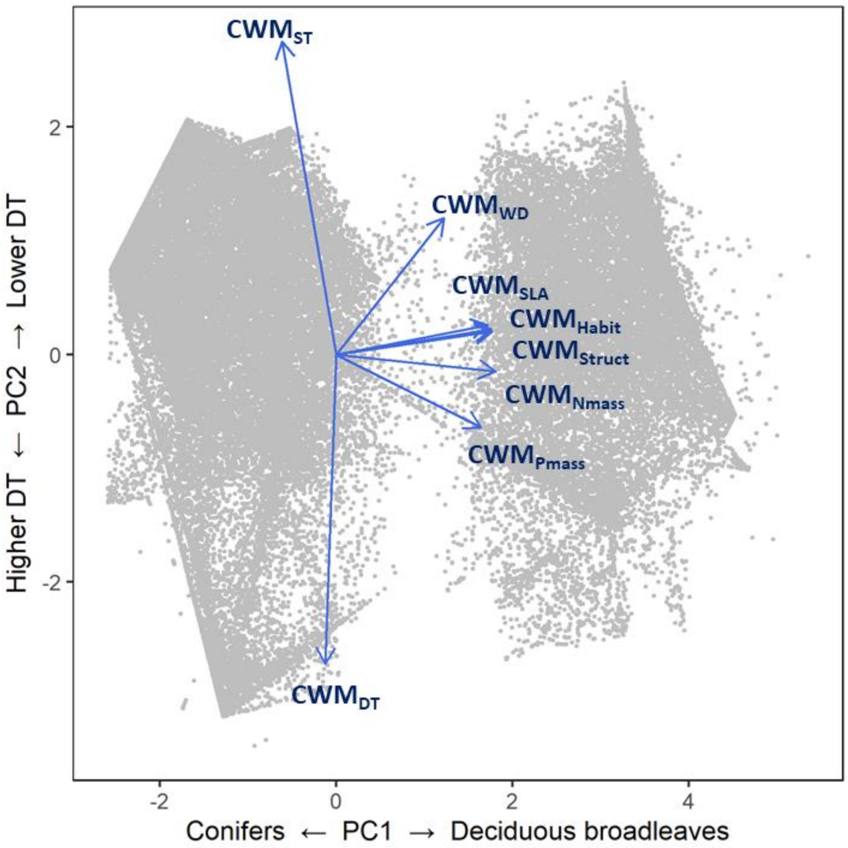

Figure 5-2: Results of principal component analysis (PCA) showing permanent sampling plots and each functional identity (community-weighted mean of trait value, CWM). CWM$_{Nmass}$ = CWM of nitrogen content per leaf mass, CWM$_{Pmass}$ = CWM of phosphorus content per leaf mass, CWM$_{SLA}$ = CWM of specific leaf area, CWM$_{Struct}$ = CWM of leaf structure, CWM$_{Habit}$ = CWM of leaf habit, CWM$_{WD}$ = CWM of wood density, CWM$_{ST}$ = CWM of shade tolerance, CWM$_{DT}$ = CWM of drought tolerance. The first axis (PC1) represents traits associated with deciduous broadleaved trees *vs* conifers, while the second axis (PC2) refers to traits associated with environmental tolerance.

5.3 Methods

5.3.1 Study area and forest inventory data

To examine the temporal compositional shifts after accounting for endogenous factors, we used a large network of permanent sampling plots (PSP) established by the provincial governments of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Nova Scotia, Newfoundland, and Labrador between the 1950s and 1980s (Fig. 5-1). We selected the PSPs using the following criteria. The plots must: (i) be unmanaged, with a known stand age (year); (ii) have all trees tagged and repeatedly measured; (iii) have all trees marked with their diameter at breast height (DBH). A total of 17,109 plots (914.21 ha; 43°47’–60°00’ N, 52°81’–133°71’ W) were selected for our analyses, with 1,471,165 trees measured during the monitoring period of from 1951 to 2016. The average measurement interval was 9.47 years with 4.70 census times, where the initial and final census years varied from 1951-2011 and 1956-2016, respectively. The plot sizes ranged from between 20 m^2 and 2,023 m^2 (Table S5-1). The mean annual temperature and precipitation in the area varied from between -3.91 °C and 12.26 °C, and 291 mm and 3,884 mm (1951-2016), respectively. The elevation ranged between 0.1 m and 2,355 m above sea level (Table S5-1).

5.3.2 Functional composition

To quantify functional composition, we employed eight key functional traits related to growing and competitive abilities, as well as environmental tolerance capacities, based on previous studies (Niinemets & Valladares 2006; Reich 2014; Anderegg et al. 2018): ‘leaf nitrogen content per leaf dry mass’ (N_{mass}, mg g^{-1}), ‘leaf phosphorus content per leaf dry mass’ (P_{mass}, mg g^{-1}), ‘specific leaf area’ (SLA, mm^2 mg^{-1}; i.e., leaf area per leaf dry mass), ‘wood density’ (WD, g cm^{-3}), ‘shade tolerance’ (ST, categorical class 1–5 (Niinemets & Valladares 2006)), ‘drought tolerance’ (DT, categorical class 1–5 (Niinemets & Valladares 2006), ‘leaf habit’ (‘deciduous’ = ‘1’ *vs* ‘evergreen’ = ‘0’), and ‘leaf structure’ (‘broadleaves’ = ‘1’ *vs* ‘coniferous’ = ‘0’). These trait values were extracted from the TRY database (Kattge et al. 2011) and other published sources (Reich & Oleksyn 2004; Wright et al. 2004; Niinemets & Valladares 2006; Chave et al. 2009; Berner & Law 2016).

The functional composition was quantified as the CWM. Similar to previous studies (Ruiz-Benito et al. 2017b), we performed a principal component analysis (PCA) with CWMs of the eight traits to obtain a comprehensive functional identity to represent them, as these values were highly correlated with each other (Fig. 5-2). We employed the first and (CWM$_{\mathrm{PC1}}$, explained 60% of the variation) and second axes (CWM$_{\mathrm{PC2}}$, explained 22% of the variation) of the PCA as a variable of the functional composition. The CWM$_{\mathrm{PC1}}$ collectively represented traits associated with deciduous broadleaved trees and higher resource acquisition (Wright et al. 2004; Niinemets & Valladares 2006; Chave et al. 2009; Reich 2014), being positively related with CWM$_{\mathrm{Nmass}}$, CWM$_{\mathrm{Pmass}}$, CWM$_{\mathrm{SLA}}$, CWM$_{\mathrm{Habit}}$ (i.e., deciduous), CWM$_{\mathrm{Struct}}$ (i.e., broadleaves), and CWM$_{\mathrm{WD}}$, while CWM$_{\mathrm{PC2}}$ represented those associated with environmental tolerance, being negatively associated with CWM$_{\mathrm{DT}}$ and positively related with CWM$_{\mathrm{ST}}$ (Fig. 5-2).

5.3.3 Stand age

The stand age of each plot was determined by dendrochronological aging based on the average age of the oldest species in the stand. We used stand age (SA) to account for the effects of forest development (representing changes in stem density and composition associated with forest succession (Searle & Chen 2017a; Hisano et al. 2019)).

5.3.4 Climate change drivers

Similar to previous studies (Searle & Chen 2017a; Esquivel-Muelbert et al. 2019), we used the calendar year (Year), which represented the effect of climate change overall on functional composition. For climate change drivers, we derived CO_2 measurements from the Mauna Loa Earth System Research Laboratory in Hawaii (http://www.esrl.noaa.gov/gmd/ccgg/trends/co2_data_mlo.html), and calculated annual mean temperature, annual mean precipitation and potential evapotranspiration, using *BioSIM* 11 software (Régnière et al. 2014). Subsequently, we calculated an annual climate moisture index (CMI; mean annual precipitation minus potential evapotranspiration (Hogg et al. 2017)). Following a previous study (Searle & Chen 2017a; Hisano et al. 2019), we calculated the anomalies of annual mean temperature (ATA) and climate moisture index (ACMIA), which were defined as annual departures from their long-term climate means (Clark et al. 2011). CMI is widely employed as an indicator of drought conditions in Canada, which accurately reflects global environmental change-induced changes in water availability (Hogg et al. 2017; Searle & Chen 2017a; Hisano et al. 2019), of which negative values indicate drier conditions, while positive values denote wetter conditions.

5.3.5 Baseline climate

Following previous studies (D'Orangeville et al. 2016; Luo et al. 2019), we calculated the long-term average (between 1951 and 2016) of annual CMI (CMI_{ave}) and MAT (MAT_{ave})

for each plot, as variables of site-specific baseline climate (i.e., local historic climate; Table S5-1; Fig. S5-1).

5.3.6 Statistical analysis

To examine the temporal trends in functional shifts associated with spatial variations in baseline climate, we employed the following mixed effect linear models:

$$
\begin{aligned}
(\mathrm{CWM}_{\mathrm{PC1}})_{ijkl} \text{ or } (\mathrm{CWM}_{\mathrm{PC2}})_{ijkl} = {} & \beta_0 + \beta_1 \times f(\mathrm{SA})_{ij} + \beta_2 \times (\mathrm{Year})_i + \beta_3 \times (\mathrm{CMI}_{\mathrm{ave}})_j + \\
& \beta_4 \times (\mathrm{MAT}_{\mathrm{ave}})_j + \beta_5 \times f(\mathrm{SA})_{ij} \times (\mathrm{Year})_i + \\
& \beta_6 \times f(\mathrm{SA})_{ij} \times (\mathrm{CMI}_{\mathrm{ave}})_j + \beta_7 \times f(\mathrm{SA})_{ij} \times (\mathrm{MAT}_{\mathrm{ave}})_j + \\
& \beta_8 \times (\mathrm{Year})_{ij} \times (\mathrm{CMI}_{\mathrm{ave}})_j + \beta_9 \times (\mathrm{Year})_{ij} \times (\mathrm{MAT}_{\mathrm{ave}})_j + \\
& \beta_{10} \times (\mathrm{CMI}_{\mathrm{ave}})_j \times (\mathrm{MAT}_{\mathrm{ave}})_j + \\
& \pi_j + \rho_k + \varepsilon \qquad (1)
\end{aligned}
$$

where i, j, and k were ith census, jth plot, and kth province; $\mathrm{CWM}_{\mathrm{PC1}}$ and $\mathrm{CWM}_{\mathrm{PC2}}$ were community-weighted means of ‘angiosperm- *vs* conifers traits’ (Ruiz-Benito et al. 2017b) and ‘stress-tolerance traits’ (Niinemets & Valladares 2006), respectively; β_i were the coefficients to be estimated; SA was the stand age being transformed by a square root based on Akaike Information Criterion (AIC); Year was the calendar year representing long-term climate change effect (Searle & Chen 2017a; Hisano et al. 2019); π_j was a random plot effect accounting for site-specific conditions such as (e.g., site-specific disturbance history); and ρ_k was a random province effect accounting for differences in sampling methods (e.g., DBH threshold (Searle & Chen 2017b)) among provinces. ε was a random error. All of the two-way interaction terms were included, as the model that included these showed a consistently lower AIC. The maximum variance inflation factor (VIF) was 2.1. As the measurement interval (years) varied between censuses, we fitted a continuous first-order autoregressive strucure using the *nlme* package, following the previous study (Searle & Chen 2017a). All explanatory variables were centred and scaled (mean = 0, SD = 1) prior to analysis to allow a coefficient comparison. We used weight by plot size (ha) to account for the influences of its variation (Searle & Chen 2017a). Model residuals for $\mathrm{CWM}_{\mathrm{PC1}}$ were right-skewed, whereas those for $\mathrm{CWM}_{\mathrm{PC1}}$ were left-skewed. We thus bootstrapped the fitted coefficients through 1000 interations to generate 95% confidence intervals.

We also examined temporal trends in atmospheric $\mathrm{CO_2}$ concentrations, ATA, and ACMIA, and how they were associated with $\mathrm{CMI_{ave}}$ and $\mathrm{MAT_{ave}}$ via linear fixed effects models. To further explore the roles of climate change drivers on CWMs, we then used the following model (simultaneous modelling with three climate change drivers rather than the Year term in eqn. 1):

$$
\begin{aligned}
(\mathrm{CWM_{PC1}})_{ijkl} \text{ or } (\mathrm{CWM_{PC2}})_{ijkl} = {} & \beta_0 + \beta_1 \times f(\mathrm{SA})_{ij} + \beta_2 \times (\mathrm{CO_2})_i + \beta_3 \times (\mathrm{ATA})_i + {} \\
& \beta_4 \times (\mathrm{ACMIA})_i + \beta_5 \times (\mathrm{CMI_{ave}})_j + \beta_6 \times (\mathrm{MAT_{ave}})_j + {} \\
& \beta_7 \times f(\mathrm{SA})_{ij} \times (\mathrm{CO_2})_i + \beta_8 \times f(\mathrm{SA})_{ij} \times (\mathrm{ATA})_{ij} + {} \\
& \beta_9 \times f(\mathrm{SA})_{ij} \times (\mathrm{ACMIA})_{ij} + \beta_{10} \times f(\mathrm{SA})_{ij} \times (\mathrm{CMI_{ave}})_j + {} \\
& \beta_{11} \times f(\mathrm{SA})_{ij} \times (\mathrm{MAT_{ave}})_j + \beta_{12} \times (\mathrm{CO_2})_i \times f(\mathrm{CMI_{ave}})_j + {} \\
& \beta_{13} \times f(\mathrm{ATA})_{ij} \times (\mathrm{CMI_{ave}})_j + {} \\
& \beta_{14} \times f(\mathrm{ACMIA})_{ij} \times (\mathrm{CMI_{ave}})_j + {} \\
& \beta_{15} \times (\mathrm{CO_2})_i \times f(\mathrm{MAT_{ave}})_j + \beta_{16} \times f(\mathrm{ATA})_{ij} \times (\mathrm{MAT_{ave}})_j + {} \\
& \beta_{17} \times f(\mathrm{ACMIA})_{ij} \times (\mathrm{MAT_{ave}})_j + {} \\
& \beta_{18} \times f(\mathrm{CMI_{ave}})_j \times (\mathrm{MAT_{ave}})_j + \pi_j + \rho_k + \varepsilon \qquad (2)
\end{aligned}
$$

where CO_2, ATA, and ACMIA were atmospheric CO_2 concentration, anomalies of mean annual temperature and climate moisture index, where CO_2 and ATA in our data was positively correlated ($r^2 = 0.19$). As the maximum VIF in this model was = 4.3, we also modelled CWMs with individual climate drivers. The coefficient estimates did not qualitatively differ between those produced by the individual models and eqn. 2 (simultaneously modelled the three climate drivers (Fig. S5-2). Therefore, similar to the previous study (Hisano et al. 2019), therefore, we focused on outcomes from the simultaneous model.

To understand the functional response processes to the calendar year, and global environmental change drivers, we calculated genus-level relative abundance (%) by subsetting basal area (m^2/ha) by major tree genus. Similar to a previous study (Hisano et al. 2019), major tree genus (or a species when a genus is comprised of only one species) was defined as those that accounted for >5% of the total basal area across all of the plots during the entire census: *Picea* spp. (26.7%); *Abies* spp. (11.8%); *Pseudotsuga menziesii* (6.9%); *Tsuga* spp. (6.2%); *Populus* spp. (8.5%); *Acer* spp. (7.9%); and *Pinus* spp. (15.4%) (Figs. S5-4, S5-6). The basal areas of individual stems were summed to obtain total basal area by major tree genus. The relative abundance of each major genus was calculated as the proportion of its basal area to the total basal area of the stand at each census for each plot, multiplied by 100 to obtain a percentage abundance (Searle & Chen 2017a). Similar to a previous study (Searle & Chen 2017a), we then examined the responses of the relative abundance of each genus to the calendar year, as well as the three global environmental change drivers with the following linear mixed effects models:

$$\begin{aligned}(\mathrm{RA})_{ijkl} = {} & \beta_0 + \beta_1 \times f(\mathrm{SA})_{ij} + \beta_2 \times (\mathrm{Year})_i + \beta_3 \times (\mathrm{CMI}_{\mathrm{ave}})_j + \beta_4 \times (\mathrm{MAT}_{\mathrm{ave}})_j + \\ & \beta_5 \times f(\mathrm{SA})_{ij} \times (\mathrm{Year})_i + \beta_6 \times f(\mathrm{SA})_{ij} \times (\mathrm{CMI}_{\mathrm{ave}})_j + \beta_7 \times f(\mathrm{SA})_{ij} \times (\mathrm{MAT}_{\mathrm{ave}})_j + \\ & \beta_8 \times (\mathrm{Year})_{ij} \times (\mathrm{CMI}_{\mathrm{ave}})_j + \beta_9 \times (\mathrm{Year})_{ij} \times (\mathrm{MAT}_{\mathrm{ave}})_j + \\ & \beta_{10} \times (\mathrm{CMI}_{\mathrm{ave}})_j \times (\mathrm{MAT}_{\mathrm{ave}})_j + \pi_j + \rho_k + \varepsilon \qquad (3)\end{aligned}$$

and

$$\begin{aligned}(\mathrm{RA})_{ijkl} = {} & \beta_0 + \beta_1 \times f(\mathrm{SA})_{ij} + \beta_2 \times (\mathrm{CO_2})_i + \beta_3 \times (\mathrm{ATA})_i + \beta_4 \times (\mathrm{ACMIA})_i + \\ & \beta_5 \times (\mathrm{CMI}_{\mathrm{ave}})_j + \beta_6 \times (\mathrm{MAT}_{\mathrm{ave}})_j + \beta_7 \times f(\mathrm{SA})_{ij} \times (\mathrm{CO_2})_i + \\ & \beta_8 \times f(\mathrm{SA})_{ij} \times (\mathrm{ATA})_{ij} + \beta_9 \times f(\mathrm{SA})_{ij} \times (\mathrm{ACMIA})_{ij} + \beta_{10} \times f(\mathrm{SA})_{ij} \times (\mathrm{CMI}_{\mathrm{ave}})_j + \\ & \beta_{11} \times f(\mathrm{SA})_{ij} \times (\mathrm{MAT}_{\mathrm{ave}})_j + \beta_{12} \times (\mathrm{CO_2})_i \times f(\mathrm{CMI}_{\mathrm{ave}})_j + \\ & \beta_{13} \times f(\mathrm{ATA})_{ij} \times (\mathrm{CMI}_{\mathrm{ave}})_j + \beta_{14} \times f(\mathrm{ACMIA})_{ij} \times (\mathrm{CMI}_{\mathrm{ave}})_j + \\ & \beta_{15} \times (\mathrm{CO_2})_i \times f(\mathrm{MAT}_{\mathrm{ave}})_j + \beta_{16} \times f(\mathrm{ATA})_{ij} \times (\mathrm{MAT}_{\mathrm{ave}})_j + \\ & \beta_{17} \times f(\mathrm{ACMIA})_{ij} \times (\mathrm{MAT}_{\mathrm{ave}})_j + \beta_{18} \times f(\mathrm{CMI}_{\mathrm{ave}})_j \times (\mathrm{MAT}_{\mathrm{ave}})_j + \pi_j + \rho_k + \varepsilon \qquad (4)\end{aligned}$$

where RA was the relative abundance of each genus, and all the other terms were identical to eqns. 1 and 2.

5.4 Results and Discussion

Across the study area, plots were dominated by conifers ($\mathrm{CWM}_{\mathrm{PC1}} = -0.85 \pm 0.02$, mean ± s.e.m.). Across all study plots and temporally repeated measurements, stand age (0.2 to 379 years) accounted for more variation in functional composition metrics and had stronger statistical effects than temporal changes (calendar year) over 65 years (indicated by the sums of squares and standardized coefficients; Table 5-1). Overall, functional composition shifted toward conifers and lower drought tolerance (or higher shade tolerance; see Fig. 5-2) with stand age (Fig. 5-3A). Increased baseline water availability ($\mathrm{CMI}_{\mathrm{ave}}$) was also associated with conifers and lower drought tolerance (Fig. 5-3C), while baseline temperature (MAT_{ave}) was associated with deciduous broadleaved trees and lower drought tolerance (Fig. 5-3D).

Table 5-1: Fixed effects of stand age (SA), calendar year (Year), long-term averages of climate moisture index ($\mathrm{CMI}_{\mathrm{ave}}$), and mean annual temperature ($\mathrm{MAT}_{\mathrm{ave}}$) on the community-weighted mean of trait values (see footnote).

Fixed effects	Coefficients (mean ± s.e.m.)	SS[c]	*df*	*F*	*P*
Angiosperm- vs Conifers ($\mathrm{CWM}_{\mathrm{PC1}}$)[a]					
(Intercept)	-0.846 ± 0.016	-	-	-	<0.001
f(SA)	-0.419 ± 0.015	67.8	1, 47913	752.8	<0.001
Year	0.096 ± 0.007	17.3	1, 47913	192.1	<0.001
$\mathrm{CMI}_{\mathrm{ave}}$	-0.872 ± 0.018	219.8	1, 17105	2439.3	<0.001
$\mathrm{MAT}_{\mathrm{ave}}$	0.991 ± 0.017	323.7	1, 17105	3592.0	<0.001
f(SA) × Year	-0.061 ± 0.005	14.5	1, 47913	160.6	<0.001
f(SA) × $\mathrm{CMI}_{\mathrm{ave}}$	-0.021 ± 0.014	0.2	1, 47913	2.2	0.134
f(SA) × $\mathrm{MAT}_{\mathrm{ave}}$	0.128 ± 0.014	7.2	1, 47913	79.7	<0.001
Year × $\mathrm{CMI}_{\mathrm{ave}}$	0.009 ± 0.006	0.2	1, 47913	2.2	0.135
Year × $\mathrm{MAT}_{\mathrm{ave}}$	-0.019 ± 0.007	0.6	1, 47913	7.0	0.008
$\mathrm{CMI}_{\mathrm{ave}}$ × $\mathrm{MAT}_{\mathrm{ave}}$	0.339 ± 0.011	80.1	1, 17105	889.0	<0.001
Drought tolerance ($-\mathrm{CWM}_{\mathrm{PC2}}$)[b]					
(Intercept)	0.017 ± 0.008	-	-	-	0.039
f(SA)	-0.327 ± 0.008	28.2	1, 47913	1806.3	<0.001
Year	0.057 ± 0.003	4.8	1, 47913	305.9	<0.001
$\mathrm{CMI}_{\mathrm{ave}}$	-0.544 ± 0.009	56.2	1, 17105	3598.5	<0.001
$\mathrm{MAT}_{\mathrm{ave}}$	-0.164 ± 0.008	5.9	1, 17105	376.6	<0.001
f(SA) × Year	-0.037 ± 0.002	6	1, 47913	382.0	<0.001
f(SA) × $\mathrm{CMI}_{\mathrm{ave}}$	0.060 ± 0.007	1.1	1, 47913	69.7	<0.001
f(SA) × $\mathrm{MAT}_{\mathrm{ave}}$	0.081 ± 0.007	2	1, 47913	130.3	<0.001

Year × CMI_{ave}	0.006 ± 0.003	0.1	1, 47913	3.7	0.053
Year × MAT_{ave}	-0.039 ± 0.003	2.4	1, 47913	152.7	<0.001
CMI_{ave} × MAT_{ave}	0.088 ± 0.006	3.5	1, 17105	225.5	<0.001

Fixed effects were scaled to allow a comparison of the strength of each effect to the response variable.

Stand age was transformed by a squared root function based on AIC.

[a] Higher value indicates traits associated with deciduous broadleaved trees, while lower value indicates conifers (as represented by CWM_{PC1}; see *Methods*; Fig. 5-2).

[b] Higher value indicates traits associated with higher drought tolerance (CWM_{PC2} being multiplied by -1 to facilitate interpretation; see *Methods*; Fig. 5-2).

[c] Sum of squares.

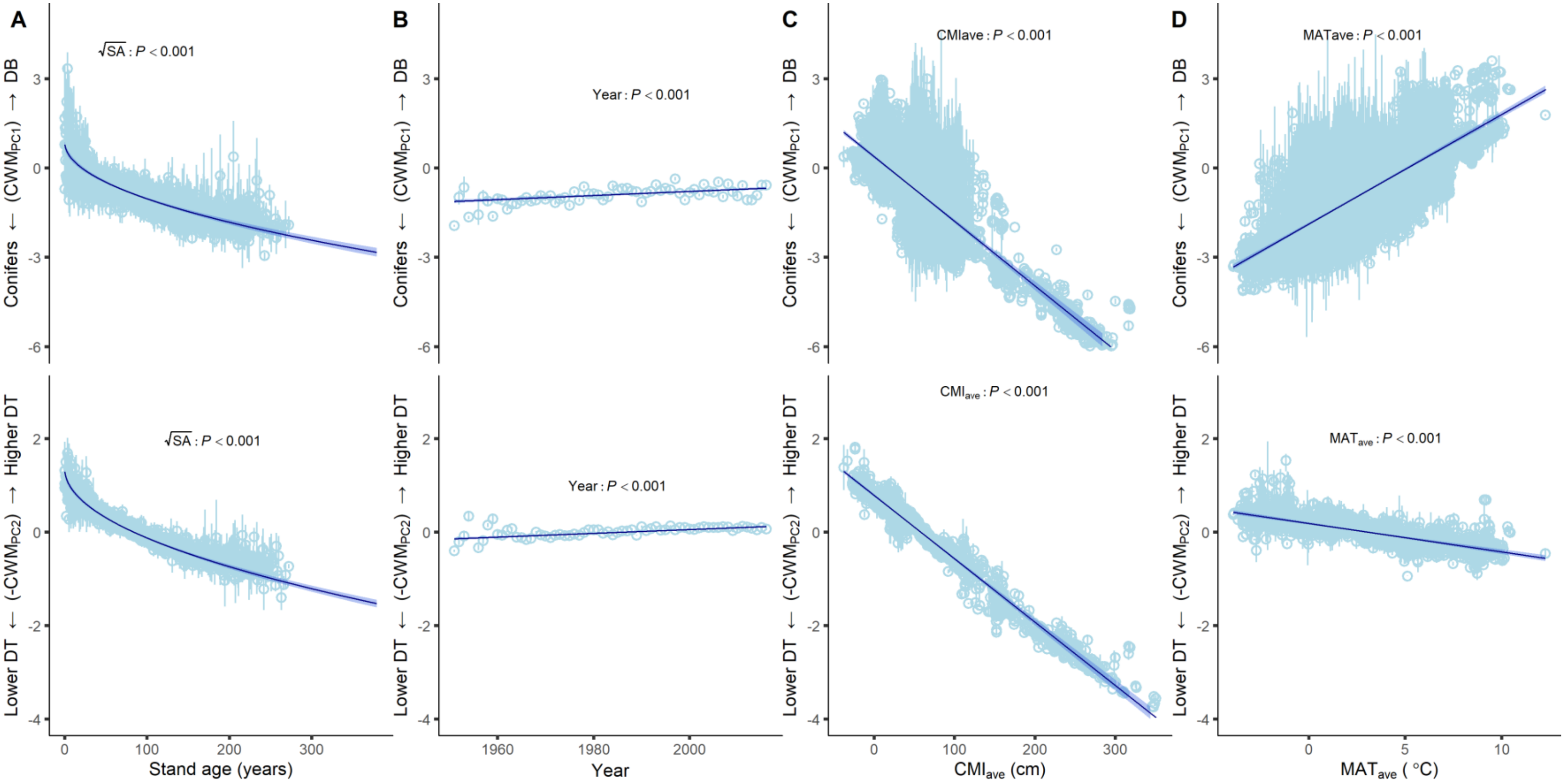

Figure 5-3:Temporal and spatial trends in functional composition. The main effects of stand age (A), calendar year (B), the long-term average of climate moisture index (CMI_{ave}, C), and the long-term average of mean annual temperature (MAT_{ave}, D) on community-weighted mean of trait values (CWM_{PC1} and $-CWM_{PC2}$). CWM_{PC1} is a functional composition associated with deciduous broadleaved trees (higher value) vs conifers (lower value), while CWM_{PC2} is related to environmental tolerance (higher value = higher drought tolerance (DT); see *Methods*). Dots and error bars reflect mean and their bootstrapped 95% confidence intervals. Blue lines are fitted main effects with their bootstrapped 95% confidence intervals shown as shaded areas. Based on AIC, stand age was transformed by the squared root.

After factoring out the strong influences of stand age and baseline climate, we found that functional composition shifted toward deciduous broadleaved trees and higher drought tolerance over time (Fig. 5-3B). This was consistent with the results in other studies, of the western boreal and temperate forests of western Canada (Searle & Chen 2017a), eastern USA (Zhang et al. 2018), and Europe (Ruiz-Benito et al. 2017b). However, our analysis revealed that the functional composition responses over time were dependent on baseline temperature, although it was consistent across the spatial gradient of water availability (Table 5-1; Fig. 5-2). Specifically, the temporal shift toward deciduous broadleaved trees was more prominent in colder plots than warmer plots (Fig. 5-4B), and drought tolerance increased over time more rapidly in colder plots than warmer plots (Fig. 5-4B). The observed trends in functional composition, as related to the base-line temperature, were due to greater temporal increases in the relative abundance of deciduous broadleaved trees and early-successional conifers (particularly *Betula* and *Pinus*) with a reduction in drought intolerant conifers (*Picea* and *Abies*; see Table S5-2 for genus-level trait values) in colder plots (Fig. 5-5B). This suggested lower compositional stability in boreal forests at higher latitudes (Fig. 5-1B) under long-term global environmental change.

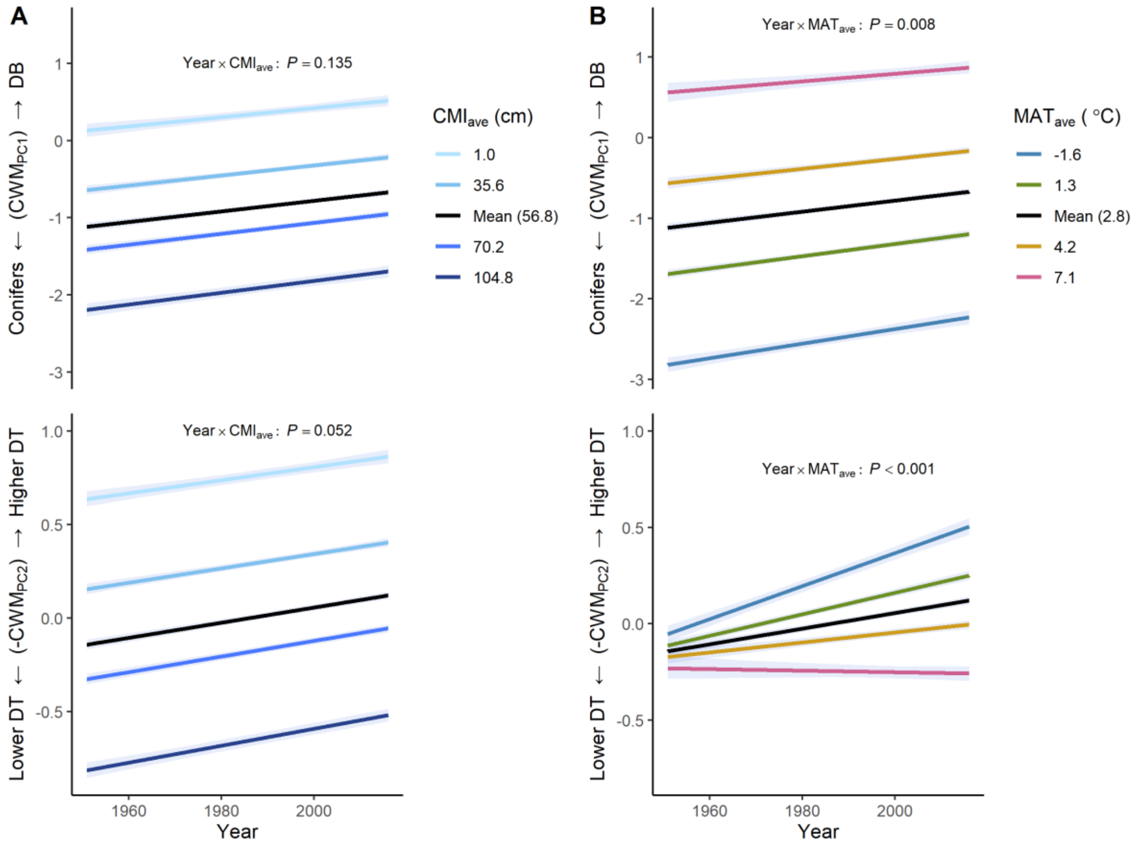

Figure 5-4: Temporal trends in community weighted-mean of traits associated with deciduous broadleaved trees vs conifers (CWM_{PC1}) and drought tolerance ($-CWM_{PC2}$). Trends dependent on the long-term average of the climate moisture index (CMI_{ave}, A) and the long-term average of mean annual temperature (MAT_{ave}, B). Values are means and their bootstrapped 95% confidence intervals. CMI_{ave} and MAT_{ave} were binned from 1.0 to 104.8 (cm) and from -1.6 to 7.1 (°C) (their 5th and 95th percentiles) for four levels.

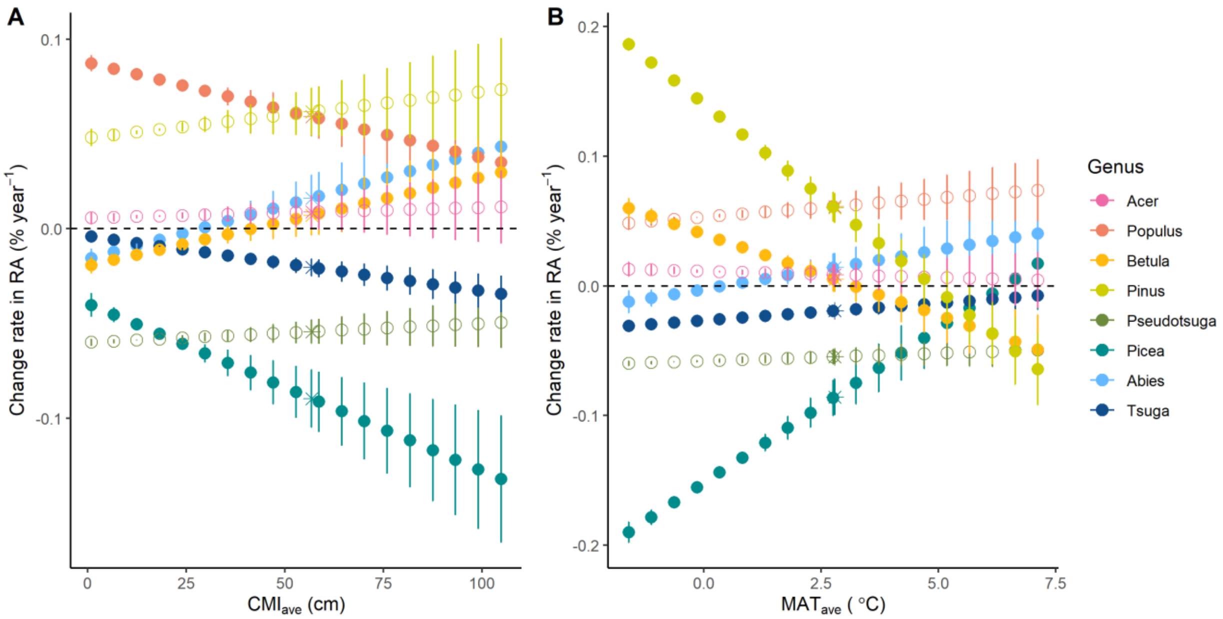

Figure 5-5: Response slopes of the relative abundance (RA) of major tree genus (>5% of the total basal area across all the plots during the whole census; see Table S5-2 for genus-level trait values) to the calendar year in relation to baseline climate. (A) Slopes associated with the long-term average of climate moisture index (CMI_{ave}). (B) Slopes associated with the long-term average of mean annual temperature (MAT_{ave}).

Over the 65 years surveyed for this study, atmospheric CO_2 concentrations (Fig. 5-1E) and temperature (ATA) increased across the study area (Fig. 5-1D; Fig. S5-1). However, the temperature rose more quickly in wetter and colder sites, in contrast to drier and warmer sites (Fig. S5-1). Across the study area, water availability (ACMIA) showed a convex curve, which increased and then decreased over the calendar year (Fig. S5-1). However, drier sites experienced more substantial temporal changes in water availability, although the most humid sites showed a gradual concave curve, which decreased and then increased over the calendar year (Fig. S5-1A). The temporal trend in water availability was consistently concaved with the baseline temperature (Fig. S5-1B).

We then tested whether the association of functional composition with these global environmental change drivers would be dependent on the baseline climate. We employed two alternative approaches (one driver at a time, and all three drivers simultaneously, using a linear mixed effect model, respectively) to model the primary and interaction effects of individual drivers and baseline climate on functional composition. These approaches yielded similar coefficient estimates (Fig. S5-2). As interpreted from the results of the linear mixed effect models with all three drivers modelled simultaneously, CO_2 had the greatest explanatory power for both types of functional composition, while the temporal increases in temperature had minimal effects (see standardized coefficients and sum of squares in Table S5-3). The association of functional composition with rising CO_2 levels largely mirrored that of the calendar year (Fig. 5-6), due to their high correlation ($r^2 = 0.99$; Fig. 5-6A). Similar to previous studies (Laurance et al. 2004; Searle & Chen 2017a), rising CO_2 was associated with deciduous broadleaved trees and higher drought tolerance across the study area (see black average lines in Fig. 5-6A, D). However, our new finding was that although the response slope of angiosperm- vs conifers to rising CO_2 was consistent across the spatial gradient of baseline water availability (Fig. 5-6A), rising CO_2 was more strongly associated with deciduous broadleaved trees in colder plots than warmer plots (Fig. 5-6D). Moreover, the positive relationship between rising CO_2 levels and the functional shift toward drought tolerance was more prominent in wetter and colder plots (Figs. 5-6A, D). This was attributable to the negative relationship between rising CO_2 levels and the relative abundance of drought intolerant species such as *Picea* spp. and *Tsuga* spp. (Table S5-2), particularly in humid plots (Fig. 5-7A). In colder plots, rising CO_2 levels were also related to the reduced relative abundance of *Picea* spp., *Pseudotsuga menziesii*, *Tsuga* spp., and increased abundance of *Pinus* spp. and *Betula* spp. (Fig. 5-7B). Specifically, our study added to previous findings by showing that drought-tolerant and early-successional (resource acquisitive or fast-growing species (Laurance et al. 2004; Reich 2014)) might have benefitted more from rising CO_2 levels in wetter and colder plots.

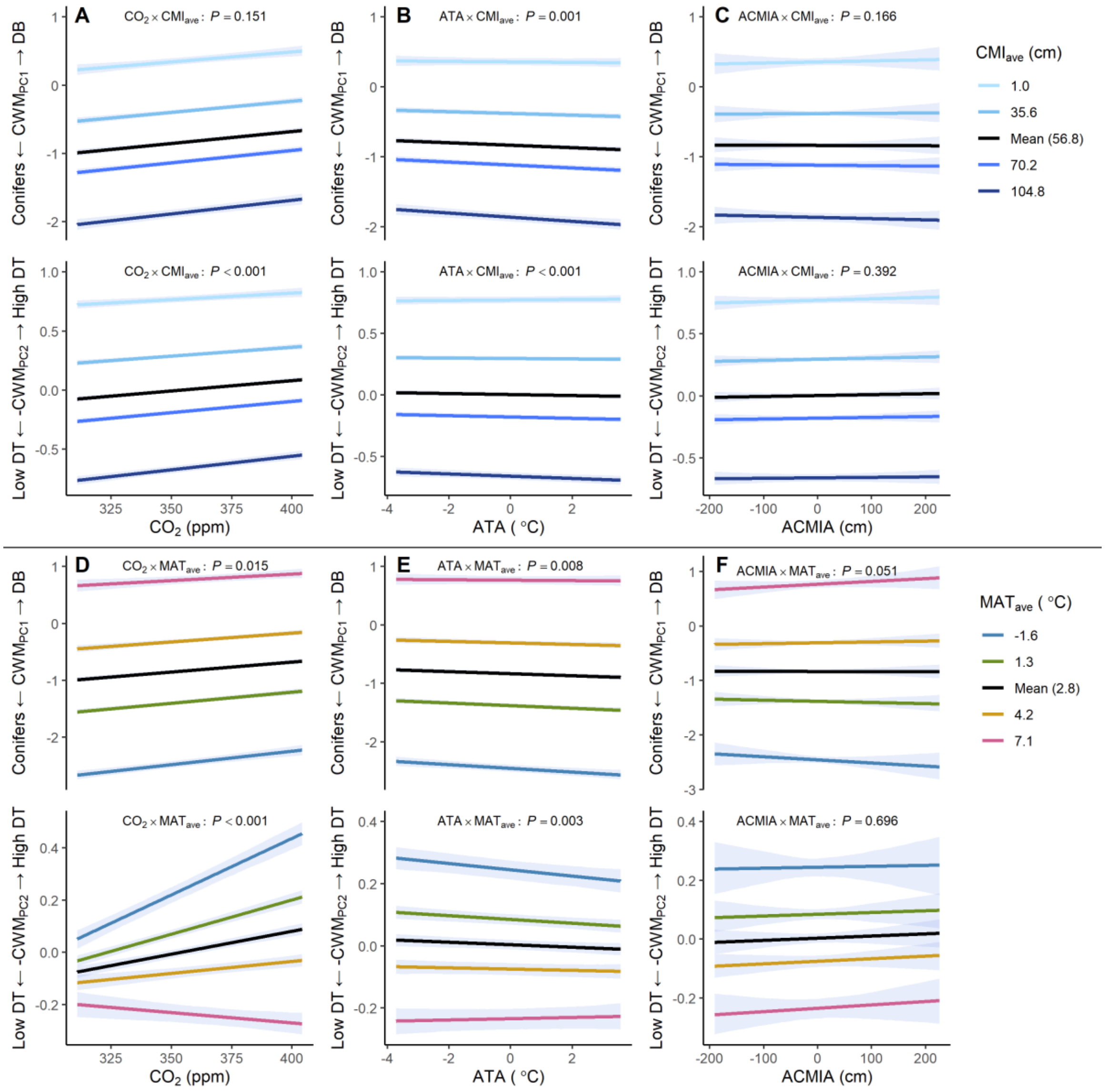

Figure 5-6: Responses of community weighted-mean of traits associated with deciduous broadleaved trees vs conifers (CWM$_{PC1}$) and drought tolerance (DT, -CWM$_{PC2}$) to global environmental change drivers [atmospheric CO$_2$ concentration, anomaly of mean annual temperature (ATA), and anomaly of climate moisture index (ACMIA)]. Response slopes in relation to the long-term averages of climate moisture index (CMI$_{ave}$, A, B, C) and mean annual temperature (MAT$_{ave}$, D, E, F) (shown as their 5th and 95th percentiles). Values are means and their bootstrapped 95% confidence intervals. Solid circles reflect a significant difference (*P* <0.05) in response slopes. T Values are means and their bootstrapped 95% confidence intervals. CMI$_{ave}$ and MAT$_{ave}$ were binned from 1.0 to 104.8 (cm) and from -1.6 to 7.1 (°C) (their 5th and 95th percentiles) for four levels.

Across the study areas, functional shifts toward conifers and lower drought tolerance occurred with a temporal increase in temperature (Table S5-3; average effects are shown as black lines in Figs. 5-6B, E). Warming had no association with both types of functional composition in drier and warmer plots; however, it was significantly associated with shifts toward conifers and lower drought tolerance in wetter and colder plots (Figs. 5-6B, E). This was because temporal increases in temperature were associated with the higher relative abundance of drought intolerant *Abies* spp., albeit also with decreased *Betula* spp. (Table S5-2; Fig. 5-7A). With warming, the relative abundance of *Populus* spp. and *Pseudotsuga menziesii* (relatively drought intolerant; Table S5-2) was increased in warmer plots, whereas that of *Betula* spp. was reduced in colder plots (Fig. 5-7B). The more remarkable responses of functional composition and the relative abundance of these species in colder plots would be partly due to their higher rates of increasing temperatures (Fig. 5-1). A previous study revealed that warming had positive effects on the growth of *Picea mariana*, particularly at higher latitudes (i.e., colder areas) in Eastern Canada (D'Orangeville et al. 2016). Although our genus-level analysis did not detect significant interaction effects of warming and baseline temperature, the greater functional shifts toward conifers and drought intolerance in colder plots might have been partly due to the positive relationships between warming and the relative abundance of *Picea* spp. and *Abies* spp. (D'Orangeville et al. 2016), increasing or at least maintaining their abundance under such baseline conditions (Fig. 5-7B). It should be noted, however, that these baseline climate-dependent responses of functional composition to rising CO_2 and warming could be of little ecological importance, considering their apparently similar slopes (except for the drought tolerance response to CO_2 in relation to baseline temperature; Fig. 5-6D), even though they were statistically different due to their large sample sizes.

Temporal changes in water availability had no relationship with both types of functional composition throughout the baseline climate gradient (Fig. 5-6C, F). Although a decrease in the relative abundance of *Picea* spp. with the temporal reduction in water availability was more prominent in historically drier plots (Fig. 5-7A), and an increase in the relative abundance of *Pinus* spp. was greater in colder plots, these changes were not translated to shifts in functional composition. The previous study in the western boreal forests of Canada also showed no significant influence of temporal variations in water availability to life history-based composition (Searle & Chen 2017a).

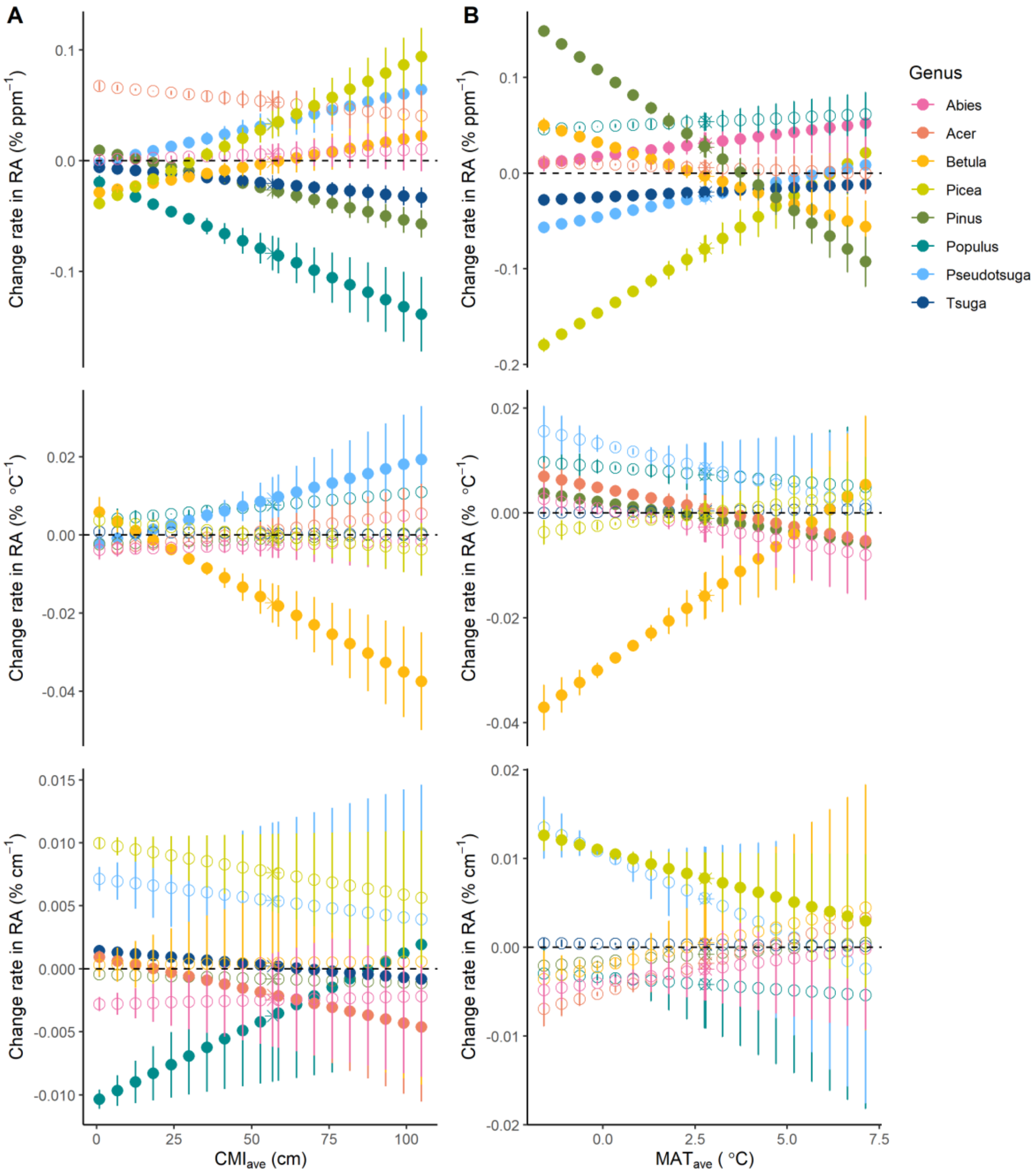

Figure 5-7: Response slopes of the relative abundance (RA) of major tree genus (>5% of the total basal area across all plots during the entire census; see Table S5-2 for genus-level trait values) to global environmental change drivers (atmospheric CO_2 concentration and anomalies of mean annual temperature (ATA) and climate moisture index (ACMIA)) in relation to baseline climate. (A) Slopes associated with the long-term average of climate moisture index (CMI_{ave}). (B) Slopes associated with the long-term average of mean annual temperature (MAT_{ave}).

Previous studies in temperate and boreal forests have shown that the functional composition of forests shifted toward fast-growing and drought-tolerant identity (or early-successional and deciduous traits) with rising CO_2 levels, increased temperatures, or decreased water availability (Ruiz-Benito et al. 2017b; Searle & Chen 2017a; Zhang et al. 2018). However, we found clear patterns in functional composition in relation to the baseline climate: (i) colder plots experienced more rapid functional shifts toward deciduous broadleaved trees and drought tolerance under rising CO_2 levels than in warmer plots. (ii) wetter and colder plots showed quicker functional shifts toward conifers and drought intolerance with warming. Thereby, our study scaled up the findings from regional observations (Searle & Chen 2017a; Zhang et al. 2018; Aguirre-Gutiérrez et al. 2019; Esquivel-Muelbert et al. 2019) to larger spatial networks across multiple biomes (e.g., boreal forest, temperate broadleaf and mixed forests, temperate coniferous forests (Olson et al. 2001)) in North America, by incorporating baseline water availability and temperature.

While global environmental change is anticipated to intensify, our study suggests the vulnerability of the composition (or lower compositional stability) of colder and wetter plots as the result of these changes. As these compositional shifts are likely to influence the functioning of forest ecosystems (e.g., net changes in biomass through growth and mortality) (Zhang et al. 2018) by altering functional identity (Grime 1998) or temporal β-diversity (Mori et al. 2018; Zhang et al. 2018), our findings of baseline-dependent functional shifts may be considered as part of the process that induces spatial variation in global environmental change impacts on forest ecosystem functions (D'Orangeville et al. 2016; Huang et al. 2017; Luo et al. 2019). Specifically, greater increases in the capacity for resource acquisition might consequently be translated to increased productivity and mortality (Chen & Luo 2015), while increases in drought-tolerant abilities could result in reduced productivity and mortality in the face of changes brought about by global warming (Greenwood et al. 2017; Zhang et al. 2018). Future forest management should consider spatial differences in the response of forest composition to global environmental change, with a particular effort toward enhancing the compositional stability of colder and wetter plots.

CHAPTER 6: GENERAL CONCLUSION

Understanding the modes of global environmental change impacts on plant diversity and ecosystem functioning and related services is critical to the sustainability of human welfare (Isbell et al. 2017) because ecosystem functioning focused here (i.e., biomass dynamics contributing to carbon sequestration) can benefit our life and society by, for example, providing timber supplies, food production, and reducing carbon emission. In this dissertation, I showed how temporal environmental change impacted terrestrial ecosystem functioning and plant diversity by reviewing existing literature and analysing the data of permanent sample plot networks of natural forests of Canada. I revealed patterns of both spatial and temporal environmental drivers modifying the relationship between plant diversity and ecosystem functioning in natural forest systems. I also found that spatial variations in climate mediate the effect of temporal environmental change on plant compositional shifts. Our long-term (over decades) and large spatial (continental) scale studies extend findings from previous studies on biodiversity→ecosystem functioning in experimental systems (Reich et al. 2001; Isbell et al. 2015; Cowles et al. 2016), as well as those in relation to short-term climate events (Grossiord et al. 2014; Gazol & Camarero 2016; O'Brien et al. 2017). A summary of the key outcomes of each chapter of this dissertation are as follows:

1. By reviewing studies on biodiversity→ecosystem functioning (B→EF), in which diversity improved productivity, stability, resistance, and/or resilience under experimental climatic changes and perturbations, I presented the concept of plant diversity as a solution to mitigate global environmental change impacts (biodiversity-mitigation concept). The key assumption of this concept is the persistence of the

positive effects of diversity on ecosystem functioning under environmental change-induced stresses. I suggest that this concept can be empirically tested by combined work on B→EF and environmental change impacts on natural systems. The biodiversity-mitigation concept should also be integrated with studies of biodiversity–multiple ecosystem services in forest systems in order to make it practicably feasible. Management strategies based on this concept will enhance the effectiveness of 'the climate change mitigation role of forests' by mitigating climate change impacts on carbon sequestration.

2. By analysing the responses of natural forests in Canada to long-term global change, I revealed that tree species diversity promotes the positive impacts, and reduces the negative impacts, of global change on forest biomass dynamics that contribute to the terrestrial carbon cycle. This is the first comprehensive evidence of a positive biodiversity effect that can mitigate negative chronic global change effects on natural forest systems.
3. My examination of a large-spatial inventory network of natural forests across Canada found that the effects of tree functional diversity on growth, mortality, and net biomass change were dependent on the spatial gradient of water availability and temperature. This is the first study to show that abiotic context can alter tree diversity effects on biomass dynamics, including both growth and mortality.
4. By analysing the responses of natural forests in Canada to long-term environmental change, I showed that temporal shifts in the functional composition were dependent on baseline (local historic) climatic conditions across biomes. Specifically, I found that functional composition shifted toward fast-growing deciduous broadleaved trees

and higher drought tolerance over time; however, this shifting rate was faster in colder regions. This is the first evidence of a baseline climate effect that can mediate or enhance the impacts of long-term global change on the functional composition of forests across biomes.

The findings of this dissertation will aid national and regional governmental agencies and the private sector in developing effective forest management and conservation strategies that can cope with global environmental change and meet international standards for carbon sequestration by conserving or promoting diverse forests. Moreover, the findings emphasise the importance of baseline climate effects that can modify the strength of B→EF relationship in forest ecosystems and the rate of global environmental impacts on functional composition. This dissertation enhanced ecologists’ and policy makers’ knowledge of the relationship between spatial and temporal environmental conditions, plant diversity, and ecosystem functioning, which is critical to the sustainability of humanity.

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APPENDIX I: SUPPLEMENTARY INFORMATION FOR CHAPTER 3

Supplementary Methods

Assessing possible methodological problems

We conducted several additional analyses to verify our models.

(i) In natural systems where species richness varies among sites, it is possible that species richness-dependent biomass dynamics reflected the effects of environmental covariates on productivity. To understand the spatial variation in species richness, we examined the association between the rarefied species richness and physical environmental covariates. We firstly constructed a full model predicting rarefied richness as a function of latitude (°), longitude (°), elevation (m), and site index; and then selected the following linear fixed effect model, based on AIC:

$$S_{ij} = \beta_0 + \beta_1 \times \ln(\mathrm{SI})_j + \beta_2 \times \mathrm{ELE}_j + \beta_3 \times \mathrm{LAT}_j + \varepsilon_{k(ij)} \qquad \text{(eqn. S1)}$$

where ELE_j and LAT_j are elevation and latitude of *j*th plot. All the predictors were centered and scaled. We found that species richness increased with site index (P <0.001), elevation (P <0.001), and latitude (P <0.001; Table S3-2). To distinguish the effects of species richness from the physical environment covariates, the original analysis included site index. Site index represents site quality, measuring the effects of climate, local topography, soil texture and nutrients on tree productivity and species richness. Alternatively, we replaced site index in eqn. 2 with elevation and latitude, and we found that the models with elevation and latitude showed qualitatively similar results (Table S3-3). As the original models had a lower AIC (Growth: 5423.2, Mortality: 8927.1, Net biomass change:

9672.1) than those with latitude and elevation (Growth: 5427.1, Mortality: 8994.2, Net biomass change: 9710.8), we present the results from the original analysis.

(ii) To investigate a temporal change in plot-level rarefied species richness (Fig. S3-3a), we used following linear mixed effects model, based on AIC:

$S_{ij} = \beta_0 + \beta_1 \times \ln(\mathrm{SI})_j + \beta_2 \times \ln(\mathrm{SA})_{ij} + \beta_3 \times \mathrm{Year}_{ij} + \beta_4 \times \ln(\mathrm{SA})_{ij} \times \mathrm{Year}_{ij} + \varepsilon_{k(ij)}$ (eqn. S2)

We then evaluated the relationship between the temporal change in species richness and biomass dynamics, using structural equation modeling (SEM). First, we developed a conceptual SEM model by considering all the explanatory variables of eqn. 2 and eqn. S2., and we assessed the conceptual model (full model) vs. reduced models by the goodness-of-fit statistics and AIC selection, following ref. (Grace 2006). We used the *piecewiseSEM* package (Lefcheck 2016) in *R* to account for the plot random effects. The SEMs confirmed that the temporal change in species richness did not influence our results (Fig. S3-3b, c, d).

(iii) Stand age in the eqn. 2 was assumed to partly represent the effects of stand packing (Pretzsch et al. 2014; Jucker et al. 2016) and overstory composition (Chen & Luo 2015; Zhang et al. 2018) on biomass change (see refs. (Chen & Popadiouk 2002; Chen et al. 2016)). To account for these effects explicitly, we modified the eqn. 2 by replacing SA with standing biomass (SB) and community-weighted mean of shade tolerance ($\mathrm{CWM_{ST}}$):

$$(\Delta\mathrm{AGB})_{ijk},\ (\Delta\mathrm{AGB_{GI}})_{ijk},\ \text{or}\ (\Delta\mathrm{AGB_M})_{ijk} = \beta_0 + \beta_1 \times f(\mathrm{CWM_{ST}})_{ij} + \beta_2 \times \ln(\mathrm{SB})_{ij}$$
$$+ \beta_3 \times \mathrm{Year}_{ij} + \beta_4 \times f(S)_{ij} + \beta_5 \times \ln(\mathrm{SI})_j$$

$$\begin{aligned}&+\beta_6\times f(\mathrm{SB})_{ij}\times \mathrm{Year}_{ij}+\beta_7\times f(\mathrm{SB})_{ij}\times f(S)_{ij}\\&+\beta_8\times f(\mathrm{CWM}_{\mathrm{ST}})_{ij}\times \mathrm{Y}_{ij}\\&+\beta_9\times \mathrm{Year}_{ij}\times f(S)_{ij}+\pi_j+\varepsilon_{k(ij)}\qquad \text{(eqn. S3)}\end{aligned}$$

where $\mathrm{CWM}_{\mathrm{ST}}$ and SB were middle values of $\mathrm{CWM}_{\mathrm{ST}}$ (transformed by quadratic function for $\Delta\mathrm{AGB}_{\mathrm{GI}}$ and natural logarithm for ΔAGB, based on AIC) and SB (log-transformed for $\Delta\mathrm{AGB}_{\mathrm{GI}}$, $\Delta\mathrm{AGB}_{\mathrm{M}}$, and ΔAGB) between the consecutive censuses. An interaction term '$\mathrm{SB}\times f(S)$' was included because competition intensity can affect species diversity and ecosystem functioning relationship (Forrester & Bauhus 2016). Shade tolerance here was defined as growing capability in the shade (Niinemets & Valladares 2006; Zhang et al. 2018), and $\mathrm{CWM}_{\mathrm{ST}}$ was employed as a functional component of species composition, which should mirror species' competitive trade-offs (early-successional (fast growing/shade intolerant) vs late-successional (slow growing/shade tolerant)) in boreal forests, where stand-replacing fire governs the compositional/structural development (Weir et al. 2000; Chen & Popadiouk 2002). We used the shade tolerance scale following (Niinemets & Valladares 2006): "1" (very intolerant) – "5" (very tolerant) (Table S1). The coefficient estimates for $f(S)$ and $\mathrm{Year}\times f(S)$ from the above equation (Fig. S3-4a) were also comparable to those of eqn. 2. This analysis accounted for species' functional identity effects, with shade tolerance representing growing and competitive abilities (Niinemets & Valladares 2006). As results from this approach were qualitatively similar to the original one (Fig. S3-4), we were confident that stand age in the eqn. 2 well represented the effects of stand packing and species composition. We also replaced the response variable in eqn. S3 with the species-level relative change in growth, mortality, or ΔAGB for each species (see above), which also showed similar trends (Fig. S3-4b).

(iv) There was a positive correlation between ln(SA) and Year ($r = 0.15$) and ln(S) and ln(SI) ($r = 0.58$) although the maximum variance inflation factors (VIF) among the explanatory variables was 1.57 (for ln(SA)). To ensure multicollinearity was not an issue in our modelling framework, we used residual and sequential regressions by assigning the priority to ln(SA) and ln(SI) to model the effects of Year, $f(S)$, and their interaction (Dormann et al. 2013; Chen et al. 2016). Moreover, we also conducted penalized parameter estimates by ridge regression (Dormann et al. 2013). Prior to fitting the ridge regression, we removed effects of random plot and spatial autocorrelation from ΔAGB and its components by using the estimated effects of these from eqn. 2. We used the *glmnet* package (Friedman et al. 2017) in *R* to refit eqn. 2. Values of λ (controlling the amount of shrinkage) at which the mean cross-validation errors were the largest within 1 standard error of the minimum (*lambda.1se*) were selected through 100-fold cross-validation by the *cv.glmnet* function (Friedman et al. 2017). We then bootstrapped coefficients estimated by ridge regression with a range of *lambda.1se* 1,000 times to compare them with the bootstrapped coefficients estimated by the linear mixed effect model (independent variables were standardized for both ridge regression and linear mixed effect models). Second, residuals from models of ΔAGB_M and ΔAGB were left-skewed, while those of ΔAGB_{GI} were right-skewed. To address potential issues from departure in normality and to improve the robustness of coefficient estimation, we employed a nonparametric rank-based estimator for linear models using the *Rfit* package (Kloke & McKean 2012). The four approaches (*fitme*, sequential model, ridge regression, and *Rfit*) yielded qualitatively similar coefficient estimates for $f(S)$ and Year × $f(S)$ (Fig. S6). In addition, we modelled the effect of species diversity, quantified by S_{area}, S_{org} and H' instead of S, the results from the three diversity indices were similar (Fig. S6). We modelled the eqn. 3 using three alternative approaches (*fitme*, ridge regression, and nonparametric estimation). Moreover, we replaced Year in eqn. 2 with each climate change driver (one driver at a time). Parameters estimated from the four methods were qualitatively similar (Fig. S3-5; the maximum VIF in the simultaneous model (eqn. 3) was 3.29 for $CO_2 \times \ln(S)$). For simplicity, we focused on interpreting results from the spatial linear mixed effect models.

(v) Because of uncertainties associated with biomass allometric equations, we assessed temporal trends in stand basal area (m^2 ha^{-1} $year^{-1}$) and annual demographic change (stem number ha^{-1} $year^{-1}$). We found that the trends of annual net stand basal area change and its growth/mortality components (Fig. S3-8a), as well as annual demographic change (stem number ha^{-1} $year^{-1}$) and its recruitment/mortality components (Fig. S3-8b) were consistently similar to those of aboveground biomass.

Table S3-1: Summary statistics (mean, SD, and range) of the permanent sample plots from Alberta and Saskatchewan.

Attribute	Mean	SD	Range
Plot size (m^2)	1959.5	2107.45	600–8092
Number of census	3.91	0.89	3–8
Measurement interval (years)	9.2	4.27	1–29
Length of monitoring (years)	26.72	10.01	10–48
Number of alive trees per plot[*]	205.79	171.03	33–948
Stand basal area (m^2/ha)[*]	34.40	10.50	4.3–90.7
Stand aboveground biomass (Mg/ha)[*]	153.25	53.16	15.12–569.82
Site index (m)	27.37	4.32	8.92–37.80
Annual net aboveground biomass change (Mg ha^{-1} yr^{-1})	1.07	1.96	-16.98–6.47
Annual aboveground biomass growth (Mg ha^{-1} yr^{-1})	2.76	1.03	0.39–9.94
Annual aboveground biomass mortality (Mg ha^{-1} yr^{-1})	1.66	1.66	0–17.5
Forest age (years)[‡]	87.36	32.07	19.5–205.5
Year (mid calendar year)[‡]	1982.78	10.88	1960.5–2005
Atmospheric CO$_2$ concentration (ppm)[‡]	343.78	15.40	317.28–379.80
Annual temperature anomaly (ATA) (°C)[‡]	0.06	0.86	-1.83–1.78
Annual climate moisture index anomaly (ACMIA) (cm)[‡]	0.93	3.81	-13.91–15.12
Rarefied species richness by stem number (S)[‡]	2.30	1.07	1.00–5.31
Rarefied species richness by area (S_{area})[‡]	3.33	1.30	1.00–7.59
Original species richness (before rarefaction; S_{org})[‡]	3.19	1.37	1–7
Shannon's diversity index (H')[‡]	0.54	0.37	0–1.62

[*] The variables were summarized based on the first census.

[**] The variables were defined as the middle point of a census period (see *Methods*).

[‡] Based on the five-level scale for shade tolerance: "1" (very intolerant, >50% light availability of full sunlight required); "2" (intolerant, 25–50%); "3" (moderately tolerant, 10–25%); "4" (tolerant, 5–10%); and "5" (very tolerant, 2–5%) (Niinemets & Valladares 2006) (see *Supplementary Methods*).

Table S3-2: Rarefied species richness in relation to elevation and site index. The model results from AIC selection of the full model (rarefied species richness = latitude + longitude + elevation + site index). All predictors were centered and scaled (mean = 0, SD = 1).

Fixed effects	Sum of squares	Mean squares	Partial R^2	Coefficients (mean ± s.e.m.)	*df*	*F*	*P*
(Intercept)	-	-	-	2.299 ± 0.016	-	-	-
Site index	129.1	129.6	0.098	0.265 ± 0.016	1	208.7	<0.001
Elevation	117.2	117.2	0.088	0.262 ± 0.017	1	189.5	<0.001
Latitude	45.5	45.5	0.028	0.141 ± 0.016	1	73.6	<0.001

Table S3-3: Growth, mortality, and net biomass change associated with calendar year, diversity, latitude, and elevation.

Fixed effects[a]	Coefficients (mean ± s.e.m.)	*t*	*P*
Growth (Mg ha^{-1} yr^{-1})			
(Intercept)	2.738 ± 0.263	10.421	<0.001
ln(SA)	-1.022 ± 0.080	-12.792	<0.001
Year	-0.003 ± 0.002	-2.064	0.039
ln(*S*)	0.353 ± 0.063	5.639	<0.001
Elevation	$-3.8\times10^{-5} \pm 2.2\times10^{-5}$	-1.725	0.085
Latitude	-0.169 ± 0.073	-2.301	0.022
ln(SA) × Year	-0.004 ± 0.004	-0.986	0.324
ln(SA) × ln(*S*)	0.315 ± 0.153	2.060	0.040
ln(*S*) × Year	0.021 ± 0.004	5.872	<0.001
Mortality (Mg ha^{-1} yr^{-1})			
(Intercept)	1.570 ± 0.120	13.082	<0.001
ln(SA)	1.526 ± 0.137	11.175	<0.001
Year	0.024 ± 0.003	7.995	<0.001
S	-0.033 ± 0.050	-0.657	0.511
Elevation	$-6.3\times10^{-5} \pm 2.9\times10^{-5}$	-2.148	0.032
Latitude	-0.089 ± 0.063	-1.415	0.157
ln(SA) × Year	0.010 ± 0.008	1.337	0.182
ln(SA) × *S*	0.149 ± 0.131	1.139	0.255
S × Year	-0.006 ± 0.003	-2.167	0.030
Net biomass change (Mg ha^{-1} yr^{-1})			
(Intercept)	1.076 ± 0.081	13.284	<0.001
ln(SA)	-2.501 ± 0.145	-17.309	<0.001
Year	-0.025 ± 0.003	-7.581	<0.001
ln(*S*)	0.330 ± 0.120	2.759	0.006
Elevation	$5.9\times10^{-5} \pm 2.4\times10^{-5}$	2.478	0.013
Latitude	0.027 ± 0.047	0.571	0.568
ln(SA) × Year	-0.019 ± 0.009	-2.177	0.030
ln(SA) × ln(*S*)	-0.117 ± 0.300	-0.391	0.696
ln(*S*) × Year	0.028 ± 0.008	3.563	<0.001

[a] Year: middle calendar year; *S*: middle rarefied species richness.

S (except for mortality) and SA were transformed by natural-logarithm based on AIC (see *Methods*).

Table S3-4: Growth, mortality, and net biomass change associated with stand age, diversity, and individual climate change drivers.

Fixed effects[a]	Coefficients (mean ± s.e.m.)	Standardized coefficients[b] (mean ± s.e.m.)	Partial R^2	*df*	*t*	*P*
Growth (Mg ha^{-1} yr^{-1})						
(Intercept)	2.673 ± 0.219	2.673 ± 0.219	-	-	12.231	<0.001
SI	0.379 ± 0.113	0.106 ± 0.031	0.095	1, 978	3.364	0.001
ln(SA)	-1.142 ± 0.082	-0.437 ± 0.031	0.606	1, 978	-13.954	<0.001
CO$_2$	0.005 ± 0.002	0.077 ± 0.024	0.018	1, 978	3.144	0.002
ATA	-0.018 ± 0.004	-0.099 ± 0.021	0.124	1, 978	-4.836	<0.001
ACMIA	0.015 ± 0.004	0.057 ± 0.015	0.043	1, 978	3.806	<0.001
ln(*S*)	0.282 ± 0.066	0.110 ± 0.026	0.136	1, 978	4.301	<0.001
ln(SA)*CO$_2$	-0.012 ± 0.004	-0.070 ± 0.024	0.043	1, 978	-2.934	0.003
ln(SA)*ATA	0.041 ± 0.010	0.089 ± 0.021	0.079	1, 978	4.133	<0.001
ln(SA)*ACMIA	0.035 ± 0.011	0.050 ± 0.016	0.033	1, 978	3.219	0.001
ln(SA)*ln(*S*)	0.302 ± 0.152	0.045 ± 0.023	0.024	1, 978	1.983	0.048
CO$_2$*ln(*S*)	0.016 ± 0.004	0.099 ± 0.022	0.014	1, 978	4.442	<0.001
ATA*ln(*S*)	-0.004 ± 0.009	-0.009 ± 0.019	0.009	1, 978	-0.446	0.656
ACMIA*ln(*S*)	-0.017 ± 0.010	-0.026 ± 0.015	0.006	1, 978	-1.684	0.092
Mortality (Mg ha^{-1} yr^{-1})						
(Intercept)	1.525 ± 0.147	1.525 ± 0.147	-	-	10.349	<0.001
SI	1.439 ± 0.189	0.402 ± 0.053	0.396	1, 978	7.629	<0.001
ln(SA)	1.213 ± 0.136	0.464 ± 0.052	0.626	1, 978	8.932	<0.001
CO$_2$	0.014 ± 0.003	0.209 ± 0.048	0.024	1, 978	4.391	<0.001
ATA	0.024 ± 0.008	0.133 ± 0.042	0.048	1, 978	3.157	0.002
ACMIA	-0.002 ± 0.008	-0.009 ± 0.031	0.001	1, 978	-0.301	0.763

S	-0.174 ± 0.052	-0.149 ± 0.044	0.051	1, 978	-3.379	0.001
ln(SA)*CO_2	-0.002 ± 0.008	-0.010 ± 0.048	0.006	1, 978	-0.220	0.826
ln(SA)*ATA	0.001 ± 0.020	0.001 ± 0.043	6.0×10^{-5}	1, 978	0.030	0.976
ln(SA)*ACMIA	-0.017 ± 0.022	-0.024 ± 0.032	0.002	1, 978	-0.774	0.439
ln(SA)**S*	0.150 ± 0.126	0.049 ± 0.041	0.004	1, 978	1.194	0.233
CO_2**S*	0.000 ± 0.003	0.001 ± 0.042	0.002	1, 978	0.029	0.977
ATA**S*	-0.011 ± 0.007	-0.051 ± 0.035	1.4×10^{-4}	1, 978	-1.469	0.142
ACMIA**S*	0.020 ± 0.009	0.066 ± 0.030	0.001	1, 978	2.240	0.025
Net biomass change (Mg ha^{-1} yr^{-1})						
(Intercept)	1.104 ± 0.130	1.104 ± 0.130	-	-	8.465	<0.001
ln(SI)	-0.896 ± 0.207	-0.250 ± 0.058	0.222	1, 978	-4.330	<0.001
ln(SA)	-2.324 ± 0.149	-0.890 ± 0.057	0.709	1, 978	-15.554	<0.001
CO_2	-0.008 ± 0.004	-0.121 ± 0.054	0.005	1, 978	-2.231	0.026
ATA	-0.041 ± 0.009	-0.229 ± 0.049	0.103	1, 978	-4.723	<0.001
ACMIA	0.019 ± 0.009	0.072 ± 0.035	0.015	1, 978	2.043	0.041
ln(*S*)	0.532 ± 0.128	0.208 ± 0.050	0.088	1, 978	4.155	<0.001
ln(SA)*CO_2	-0.013 ± 0.009	-0.077 ± 0.055	0.028	1, 978	-1.384	0.167
ln(SA)*ATA	0.043 ± 0.024	0.091 ± 0.051	0.015	1, 978	1.809	0.071
ln(SA)*ACMIA	0.052 ± 0.025	0.076 ± 0.037	0.012	1, 978	2.081	0.038
ln(SA)*ln(*S*)	0.057 ± 0.297	0.009 ± 0.045	4.4×10^{-4}	1, 978	0.193	0.847
CO_2*ln(*S*)	0.013 ± 0.009	0.077 ± 0.052	0.009	1, 978	1.489	0.137
ATA*ln(*S*)	0.020 ± 0.021	0.044 ± 0.045	0.001	1, 978	0.965	0.335
ACMIA*ln(*S*)	-0.068 ± 0.024	-0.102 ± 0.036	0.003	1, 978	-2.866	0.004

[a] *S*: middle rarefied species richness (log-transformed, except for mortality); SA: middle stand age (long-transformed); Year: middle calendar year; SI: site index.

[b] Coefficient estimates produced by models with all the fixed effects scaled (mean = 0, SD = 1), allowing comparison of the strength of each effect to the response variable.

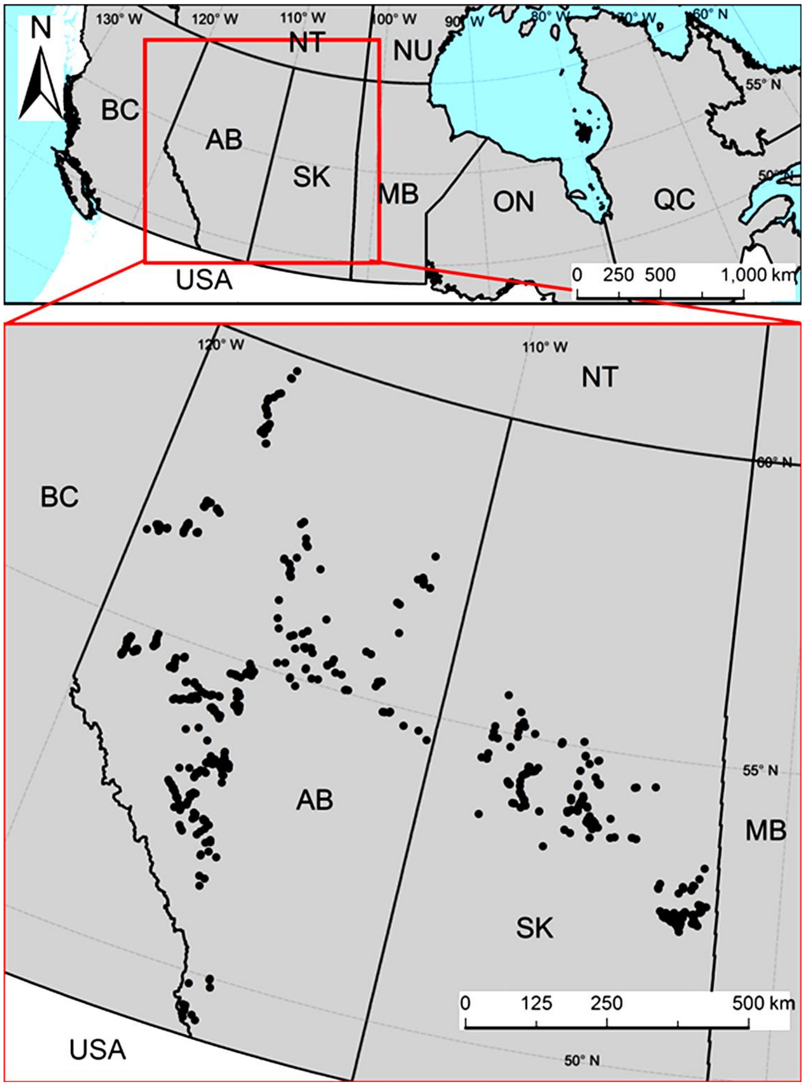


Figure S3-1: Plot locations of 871 plots of western boreal forests of Canada.

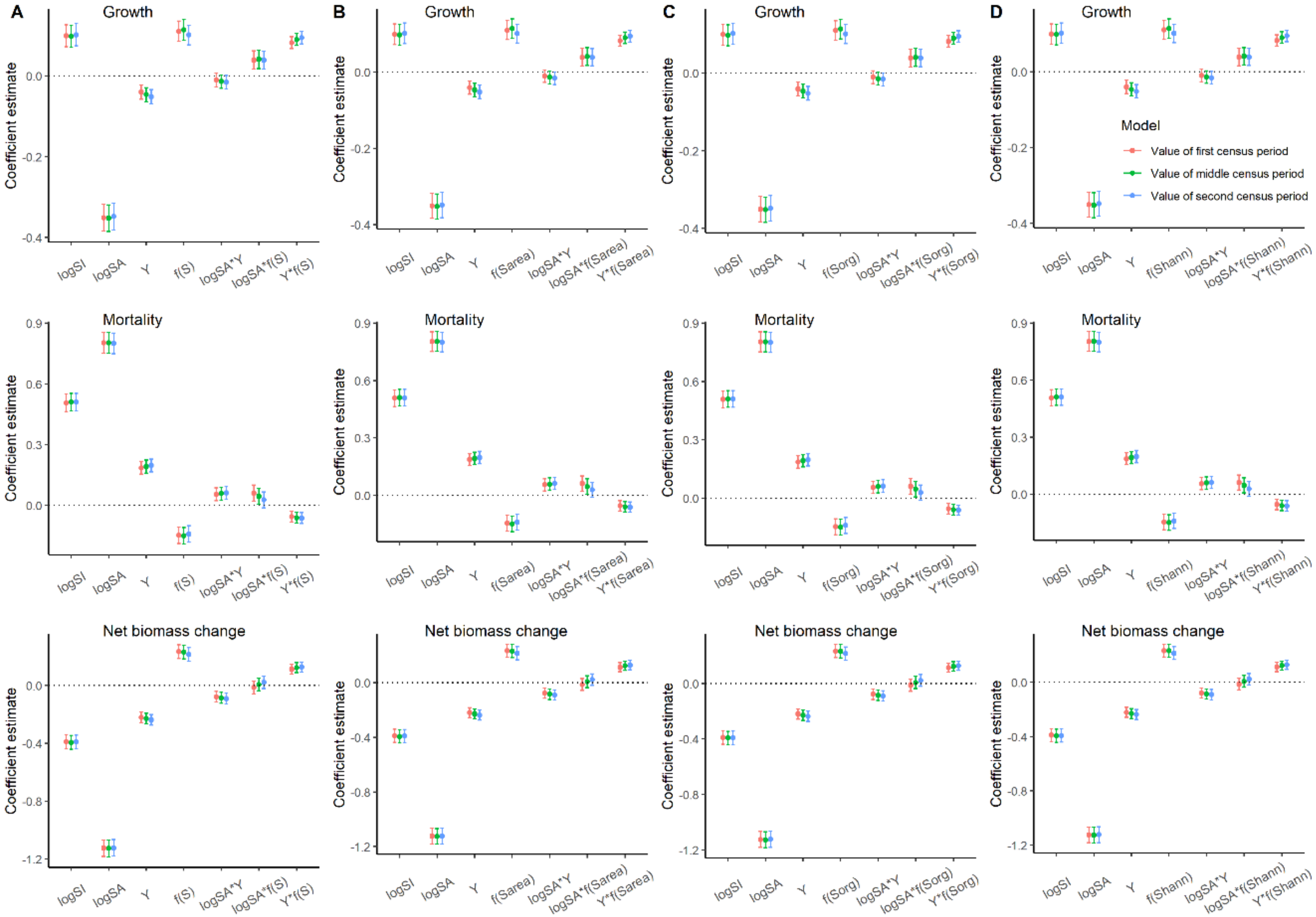

A
B
C
D
Growth
Mortality
Net biomass change
Coefficient estimate
0.0
-0.2
-0.4
0.9
0.6
0.3
-0.8
-1.2
logSI
logSA
Y
f(S)
logSA*Y
logSA*f(S)
Y*f(S)
f(Sarea)
logSA*f(Sarea)
Y*f(Sarea)
f(Sorg)
logSA*f(Sorg)
Y*f(Sorg)
f(Shann)
logSA*f(Shann)
Y*f(Shann)
Model
Value of first census period
Value of middle census period
Value of second census period

Figure S3-2: Coefficient estimates (scaled) for growth, mortality, and net biomass change associated with site index (SI), stand age (SA), calendar year (Y), rarefied richness by stem number (*S*) (a), rarefied richness by plot size (S_{area}) (b), original richness (S_{org}) (c), or Shannon's diversity index (*Shann*) (d). Values are means with 95% confidence intervals. SI, SA and the diversity metrics were transformed by natural logarithm based on AIC. Diversity metrics are the first (red), middle (green), or second (blue) census value of two consecutive surveys.

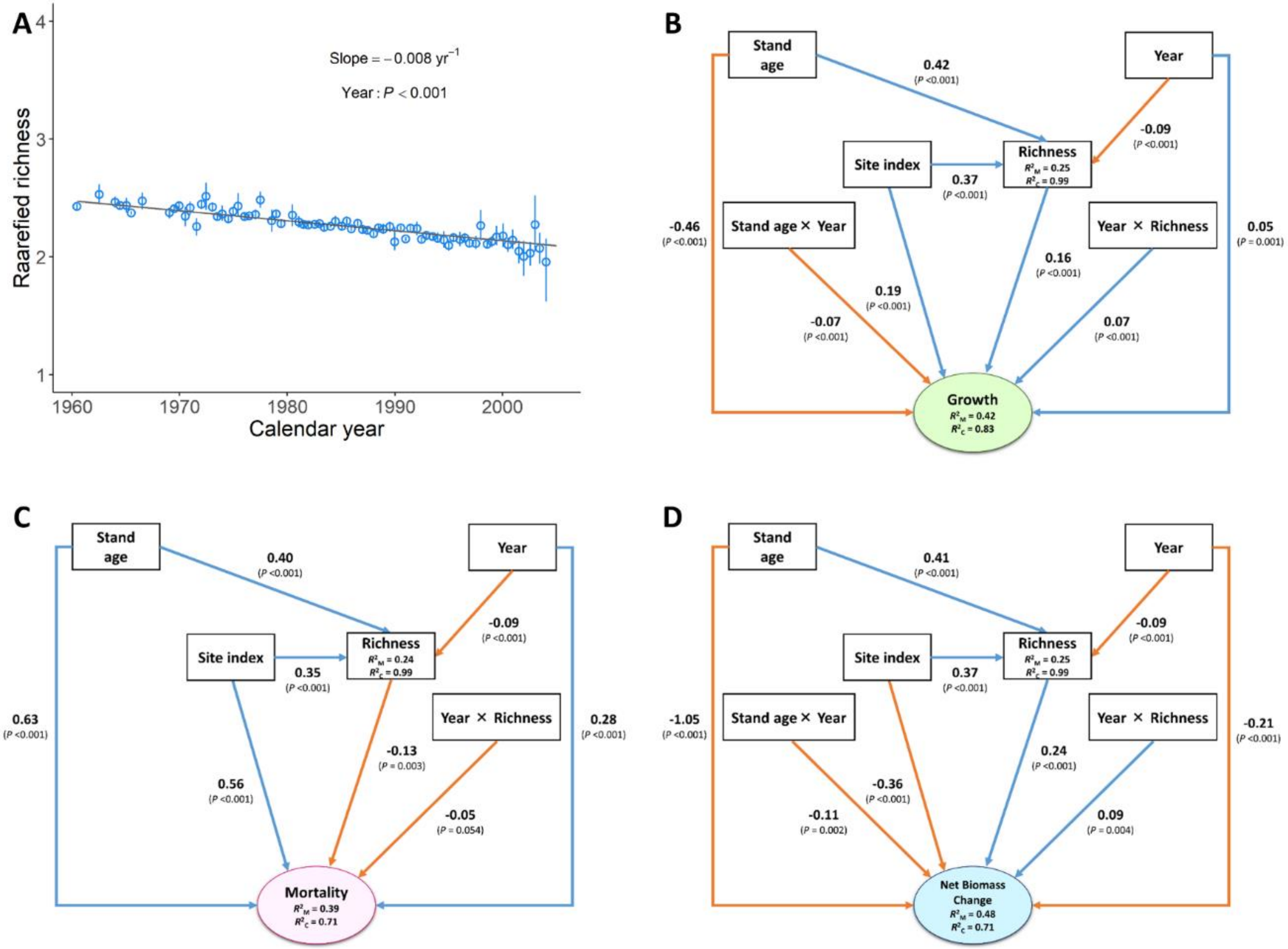

A
Slope = – 0.008 yr^{-1}
Year : P < 0.001
Raarefied richness
1
2
3
4
1960
1970
1980
1990
2000
Calendar year
B
Stand age
Year
0.42 (P <0.001)
-0.09 (P <0.001)
Site index
Richness R^2_M = 0.25 R^2_C = 0.99
0.37 (P <0.001)
Stand age × Year
Year × Richness
-0.46 (P <0.001)
0.05 (P = 0.001)
0.16 (P <0.001)
0.19 (P <0.001)
-0.07 (P <0.001)
0.07 (P <0.001)
Growth R^2_M = 0.42 R^2_C = 0.83
C
Stand age
Year
0.40 (P <0.001)
-0.09 (P <0.001)
Site index
Richness R^2_M = 0.24 R^2_C = 0.99
0.35 (P <0.001)
Year × Richness
0.63 (P <0.001)
0.28 (P <0.001)
-0.13 (P = 0.003)
0.56 (P <0.001)
-0.05 (P = 0.054)
Mortality R^2_M = 0.39 R^2_C = 0.71
D
Stand age
Year
0.41 (P <0.001)
-0.09 (P <0.001)
Site index
Richness R^2_M = 0.25 R^2_C = 0.99
0.37 (P <0.001)
Stand age × Year
Year × Richness
-1.05 (P <0.001)
-0.21 (P <0.001)
0.24 (P <0.001)
-0.36 (P <0.001)
-0.11 (P = 0.002)
0.09 (P = 0.004)
Net Biomass Change R^2_M = 0.48 R^2_C = 0.71

Figure S3-3: a, Changes in rarefied richness associated with calendar after accounting for the effects of stand age and site index (all the explanatory variables were centered, but not scaled). b, c, d, Structural equation models depicting the effects of stand age, calendar year (Year), and site index on rarefied richness (Richness), and the effects of stand age, Year, Richness, and site index on growth, mortality, and net biomass change, respectively. All the explanatory variables were centered and scaled (mean = 0, SD = 1) to allow comparison of the strength of each effect to the response variables. Blue arrows indicate positive paths, while orange lines show negative paths. Coefficient estimates and *P* values are expressed beside the arrows. R^2_M and R^2_C stand for marginal R^2 and conditional R^2, the amount of variation of the variable explained by all paths from the fixed effects and both the fixed effects and plot random effects.

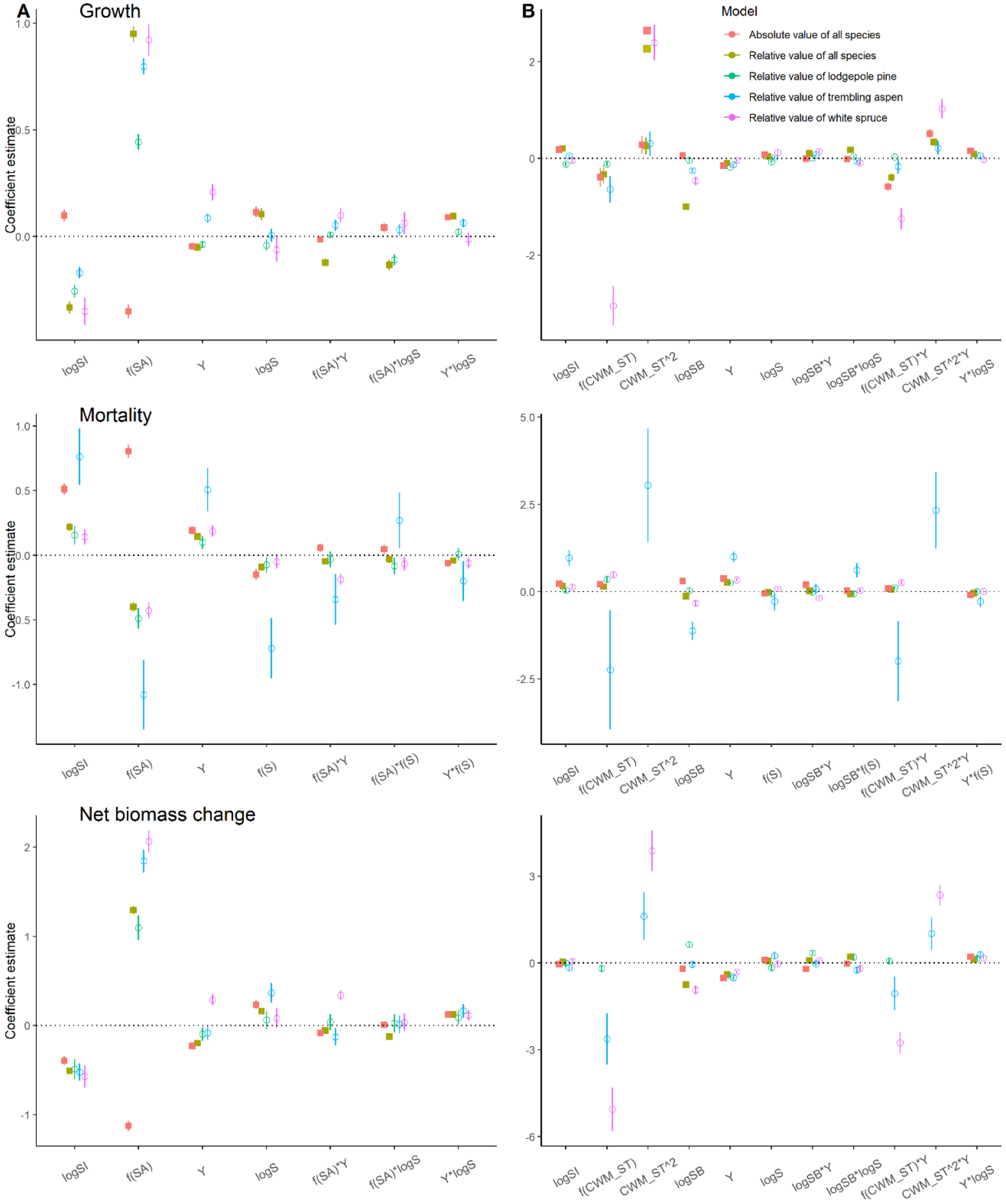

A
Growth
B
Model
Absolute value of all species
Relative value of all species
Relative value of lodgepole pine
Relative value of trembling aspen
Relative value of white spruce
Coefficient estimate
1.0
0.5
0.0
2
0
-2
logSI
f(SA)
Y
logS
f(SA)*Y
f(SA)*logS
Y*logS
f(CWM_ST)
CWM_ST^2
logSB
logSB*Y
logSB*logS
f(CWM_ST)*Y
CWM_ST^2*Y
Mortality
1.0
0.5
0.0
-0.5
-1.0
5.0
2.5
0.0
-2.5
f(S)
f(SA)*f(S)
Y*f(S)
logSB*f(S)
Net biomass change
2
1
0
-1
3
0
-3
-6

Figure S3-4: Coefficient estimates (scaled) for stand-level (all species; filled squared symbols) and species-level (*Populus tremuloides*, *Picea glauca*, *Pinus contorta*; blank circle symbols) growth, mortality, and net biomass change associated with site index (SI), stand age (SA), calendar year (Y), rarefied richness (*S*) (eqn. 2; a), and those of which stand age being replaced with standing biomass (SB) and community-weighted mean of shade tolerance (Niinemets & Valladares 2006) (CWM_ST) (eqn. S3; b). Values are means with 95% confidence intervals. The response variables for each species are relative values (absolute values divided by standing biomass (Searle & Chen 2017c)) allowing comparison among species, as well as with those of stand-level relative values. SI, *S* (when necessary) and SB were transformed by natural logarithm, and CWM_ST was transformed by quadratic function or natural logarithm, when necessary, based on AIC. *f*(SA) is the logarithmically transformed age for the absolute value models and the inverse of logarithmically transformed age for the relative value models (Searle & Chen 2017c).

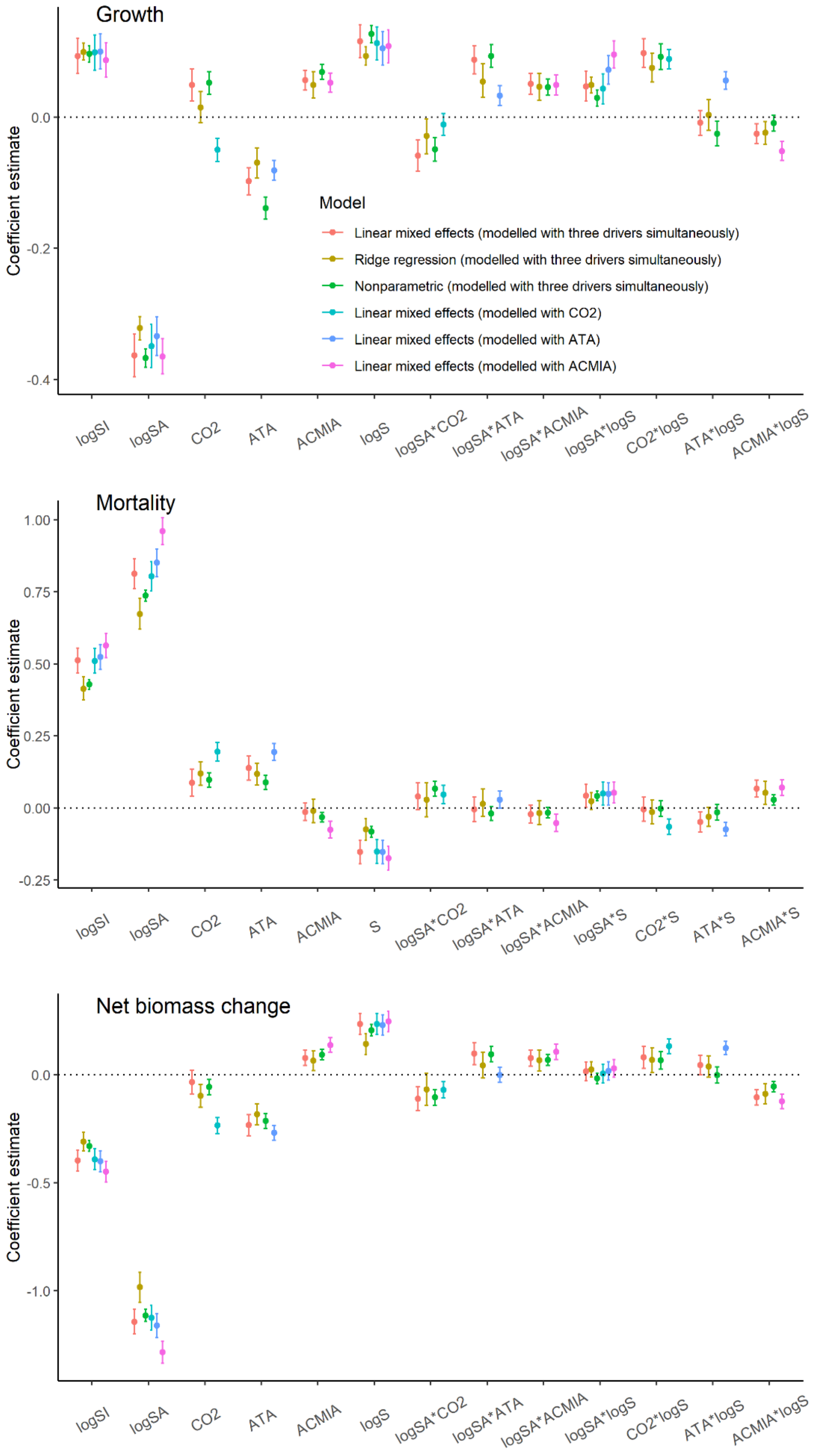

Growth
Coefficient estimate
0.0
-0.2
-0.4
Model
Linear mixed effects (modelled with three drivers simultaneously)
Ridge regression (modelled with three drivers simultaneously)
Nonparametric (modelled with three drivers simultaneously)
Linear mixed effects (modelled with CO2)
Linear mixed effects (modelled with ATA)
Linear mixed effects (modelled with ACMIA)
logSI
logSA
CO2
ATA
ACMIA
logS
logSA*CO2
logSA*ATA
logSA*ACMIA
logSA*logS
CO2*logS
ATA*logS
ACMIA*logS
Mortality
Coefficient estimate
1.00
0.75
0.50
0.25
0.00
-0.25
logSI
logSA
CO2
ATA
ACMIA
S
logSA*CO2
logSA*ATA
logSA*ACMIA
logSA*S
CO2*S
ATA*S
ACMIA*S
Net biomass change
Coefficient estimate
0.0
-0.5
-1.0
logSI
logSA
CO2
ATA
ACMIA
logS
logSA*CO2
logSA*ATA
logSA*ACMIA
logSA*logS
CO2*logS
ATA*logS
ACMIA*logS

Figure S3-5: Coefficient estimates (scaled) from linear mixed effect models (eqn. 3), ridge regressions, and nonparametric methods (see *Supplementary Methods*) with climate change drivers (CO_2 = atmospheric CO_2 concentration, ATA = annual mean temperature anomaly, ACMIA = annual climate moisture index (Hogg et al. 2017) anomaly). The linear mixed effect models were modelled with three climate change drivers simultaneously and with one driver at a time, respectively. Ridge regression was conducted with a range of *lambda.1se* (see *Supplementary Methods*). Values are means with 95% confidence intervals.

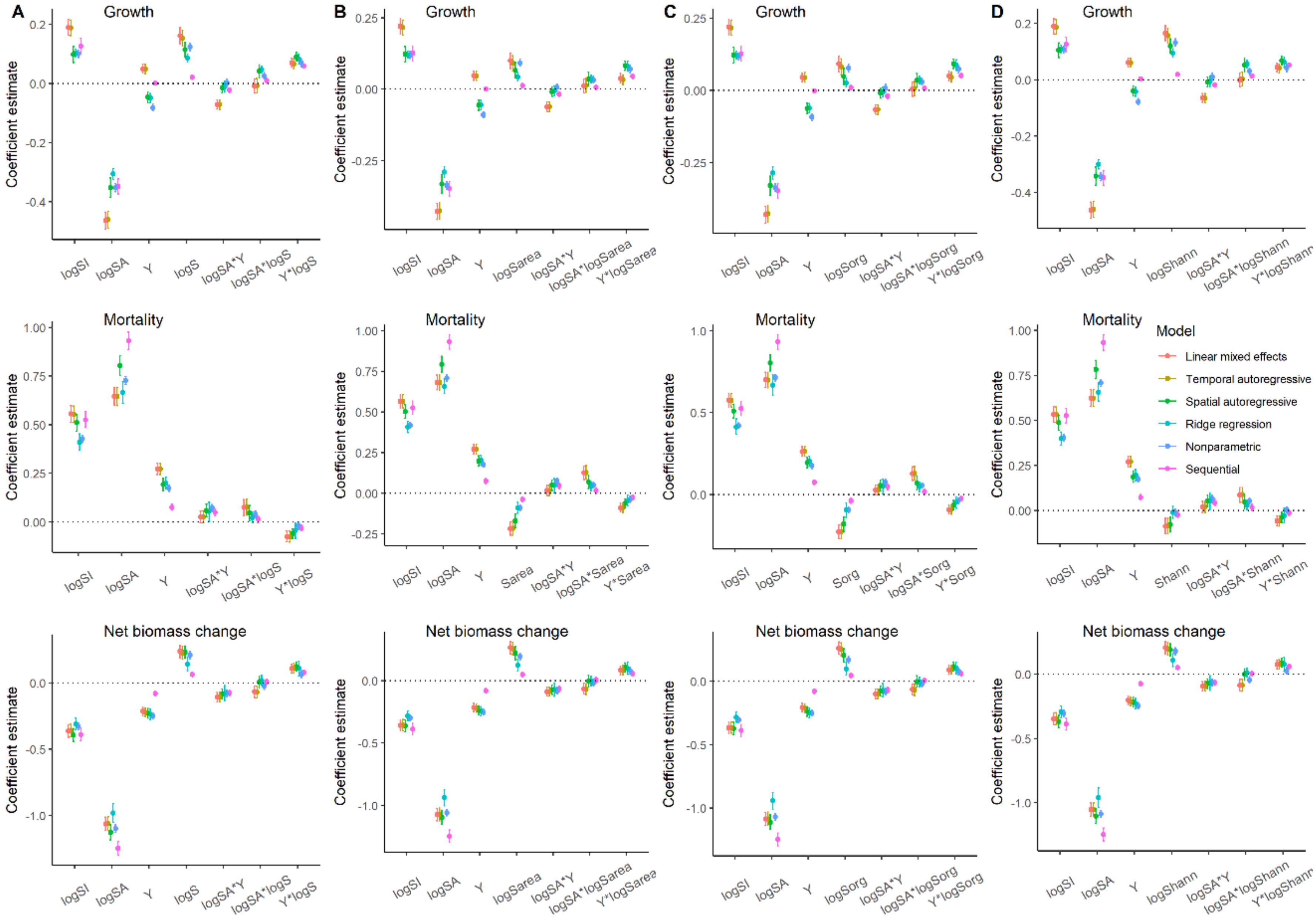
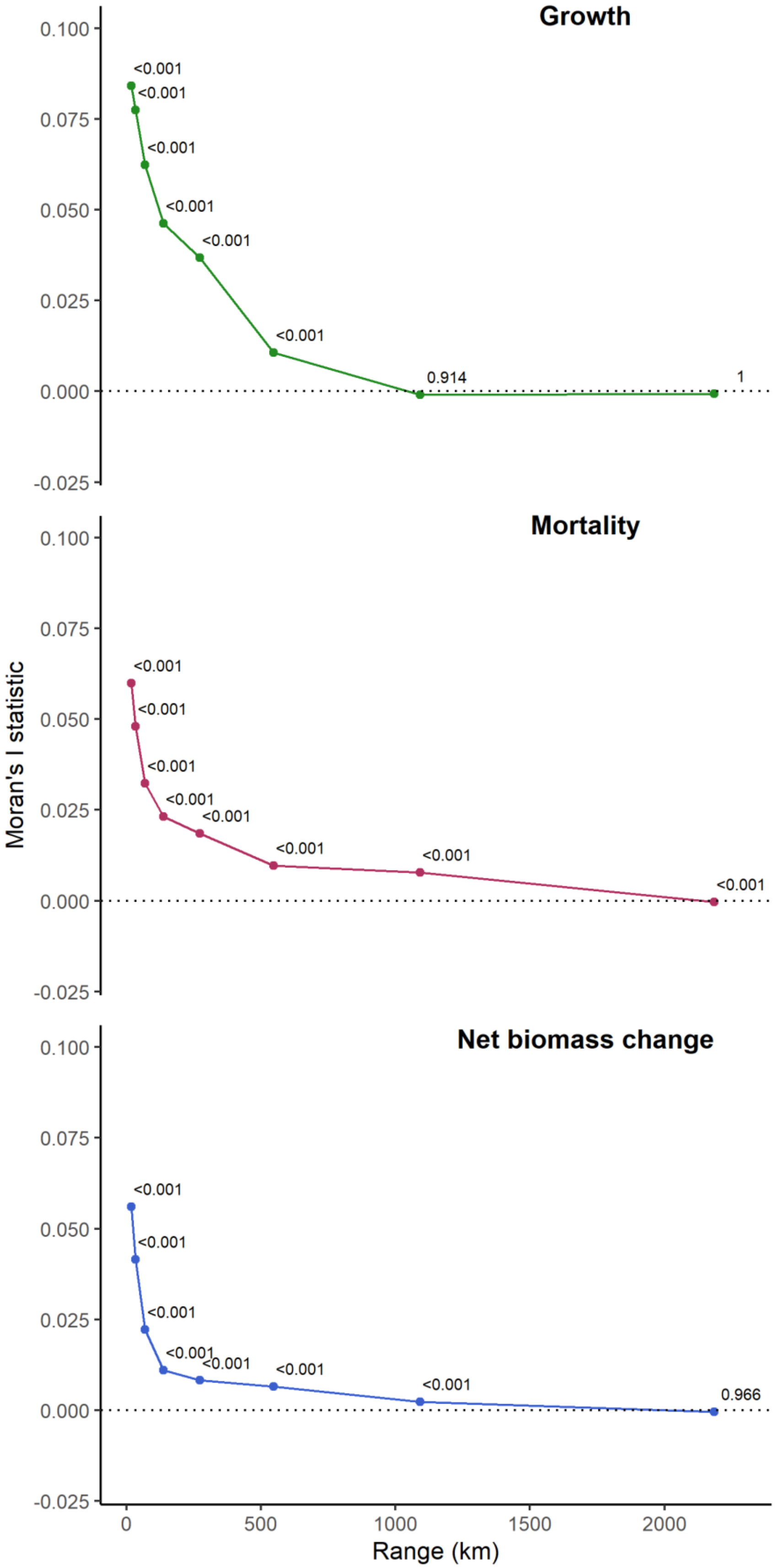

A
B
C
D
Growth
Mortality
Net biomass change
Coefficient estimate
logSI
logSA
Y
logS
logSA*Y
logSA*logS
Y*logS
logSarea
logSA*logSarea
Y*logSarea
Sarea
logSA*Sarea
Y*Sarea
logSorg
logSA*logSorg
Y*logSorg
Sorg
logSA*Sorg
Y*Sorg
logShann
logSA*logShann
Y*logShann
Shann
logSA*Shann
Y*Shann
0.2
0.0
-0.2
-0.4
0.25
0.00
-0.25
1.00
0.75
0.50
1.0
0.5
-0.5
-1.0
Model
Linear mixed effects
Temporal autoregressive
Spatial autoregressive
Ridge regression
Nonparametric
Sequential

Figure S3-6: Coefficient estimates (scaled) from liner mixed effects models without any autoregressive structure (Linear mixed effect models), those with temporal autoregressive structure (Temporal autoregressive), those with spatial autoregressive structure (Spatial autoregressive; employed as the main model), ridge regressions, nonparametric methods, and residual sequential models for the eqn. 2 in *Methods*. Coefficients estimated by the linear mixed effect model are shown in pink. Ridge regression was conducted with a range of *lambda.1se* (in blue). a, Rarefied richness based on stem number (*S*). b, Rarefied richness based on plot size. c, Original species richness (S_{org}). d, Shannon's diversity index (*H'*). Values are means with 95% confidence intervals.



Growth
Mortality
Net biomass change
Moran's I statistic
Range (km)
0.100
0.075
0.050
0.025
0.000
-0.025
0
500
1000
1500
2000
<0.001
0.914
1
0.966

Figure S3-7: Spatial correlogram calculated on the residuals of the eqn. 2, showing Moran's I associated with each range. Values shown in the correlogram are *P* values for Moran's I tests for each range.

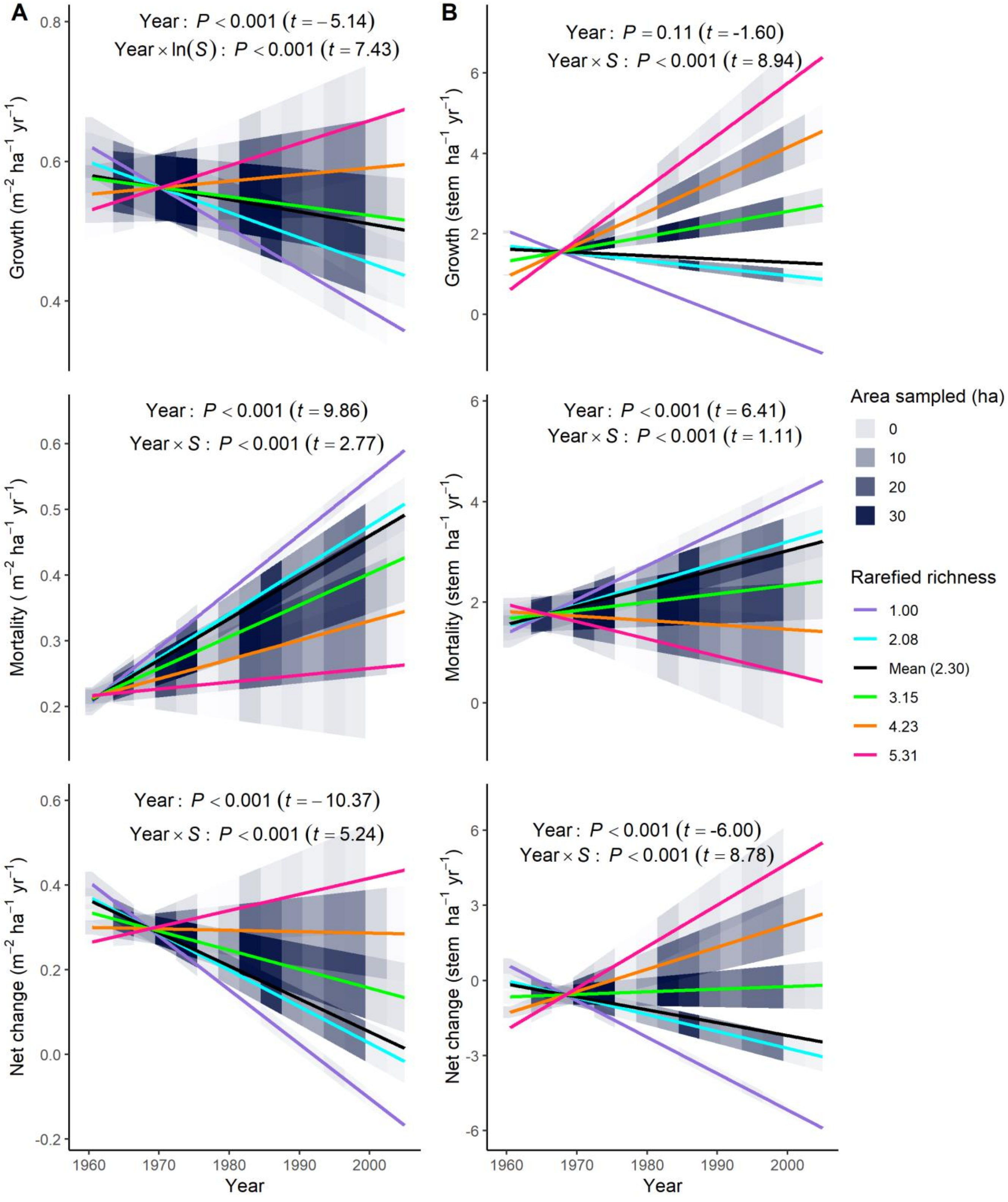

A
Year : P < 0.001 (t = −5.14)
Year × ln(S) : P < 0.001 (t = 7.43)
Growth (m−2 ha−1 yr−1)
0.8
0.6
0.4
B
Year : P = 0.11 (t = -1.60)
Year × S : P < 0.001 (t = 8.94)
Growth (stem ha−1 yr−1)
6
4
2
0
Year : P < 0.001 (t = 9.86)
Year × S : P < 0.001 (t = 2.77)
Mortality (m−2 ha−1 yr−1)
0.6
0.5
0.4
0.3
0.2
Year : P < 0.001 (t = 6.41)
Year × S : P < 0.001 (t = 1.11)
Mortality (stem ha−1 yr−1)
6
4
2
0
Area sampled (ha)
0
10
20
30
Rarefied richness
1.00
2.08
Mean (2.30)
3.15
4.23
5.31
Year : P < 0.001 (t = − 10.37)
Year × S : P < 0.001 (t = 5.24)
Net change (m−2 ha−1 yr−1)
0.6
0.4
0.2
0.0
-0.2
Year : P < 0.001 (t = -6.00)
Year × S : P < 0.001 (t = 8.78)
Net change (stem ha−1 yr−1)
6
3
0
-3
-6
1960
1970
1980
1990
2000
Year
1960
1970
1980
1990
2000
Year

Figure S3-8: Diversity-dependent temporal trends of (a) basal area and (b) tree population dynamics (stem number per ha). The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. Shading gradients show sampling efforts (sampled area in ha) with three-year interval. *P* values for effects of main diversity ($f(S)$) and the interaction term (Year × $f(S)$) obtained from the linear mixed effect model for each component are shown in each panel of *A* and *B*, respectively.

APPENDIX II: SUPPLEMENTARY INFORMATION FOR CHAPTER 4

Table S4-1: Summary statistics (mean ± SD with the range in brackets) of the permanent sample plots across Canada.

Attribute	Mean	SD	Range
Plot size (m^2)	536.61	309.03	20.00 - 2023.00
Number of census	4.7	1.86	2.00 - 9.00
Measurement interval (years)	9.47	3.97	1.00 - 44.00
Length of monitoring (years)	31.81	10.57	2.00 - 52.00
Number of alive trees per plot*	56.1	68.8	1.00-1684.00
Stand basal area (m^2/ha)*	22.72	17.17	0.03 - 223.68
Stand aboveground biomass (Mg/ha)*	104.11	97.06	0.05 - 3270
Annual net aboveground biomass change (Mg ha^{-1} yr^{-1})	1.04	3.24	-53.62 - 29.14
Annual aboveground biomass growth (Mg ha^{-1} yr^{-1})	2.68	1.83	-3.25 - 32.34
Annual aboveground biomass mortality (Mg ha^{-1} yr^{-1})	1.63	2.78	0.00 - 60.8
Forest age (years)‡	86.29	40.21	2.70 - 376.00
Year (mid calendar year)‡	1989.72	11.67	1953.50 - 2013.50
Long-term average of climate moisture index (CMI_{ave}; cm)‡	57.37	39.68	-37.63 - 350.51
Long-term average of aridity index (AI_{ave}; unitless)‡	1.08	0.39	-0.27 - 3.74
Long-term average of mean annual temperature (MAT; °C)‡	2.88	2.69	-3.91 - 12.26
Species richness‡	3.49	1.65	1.00 - 12.00
Functional diversity (functional dispersion, FDis)‡	0.1	0.08	0.00 - 0.28
Community weighted mean of leaf nitrogen content per leaf dry mass (CWM_{Nmass}; mg/g)‡	14.3	3.74	9.35 - 27.44
Community weighted mean of leaf phosphorus content per leaf dry mass (CWM_{Pmass}; mg/g)‡	1.41	0.34	0.83 - 3.2

Community weighted mean of specific leaf area (CWM_{SLA}; mm^2/mg)‡	9.33	4.52	3.30 - 32.85
Community weighted mean of wood density (CWM_{WD}; g/cm^3)‡	0.45	0.05	0.29 - 0.61
Community weighted mean of drought tolerance (CWM_{DT})‡, †	2.25	0.69	0.83 - 4.32
Community weighted mean of shade tolerance (CWM_{ST})‡, †	3.35	1.04	0.98 - 5.01
Community weighted mean of resource acquisition traits (CWM_{PC1})‡, #	0.05	2.18	-2.59 – 5.13

[*] The variables were summarised based on the first census.

[‡] The variables were defined as the middle point of a census period (see *Methods*). A census period was defined as the period between two successive censuses.

[†] The five-level scale for shade tolerance and drought tolerance: "1" (very intolerant) – "5" (very tolerant) (Niinemets & Valladares 2006).

[#] Community weighted mean of the first axis of principal component analysis (PCA) with the six functional traits above.
Larger value indicates faster-growing ability (higher N_{mass}, P_{mass}, SLA; i.e., greater resource acquisition ability) while smaller value indicates slower growing ability (see *Methods*; Fig S2).

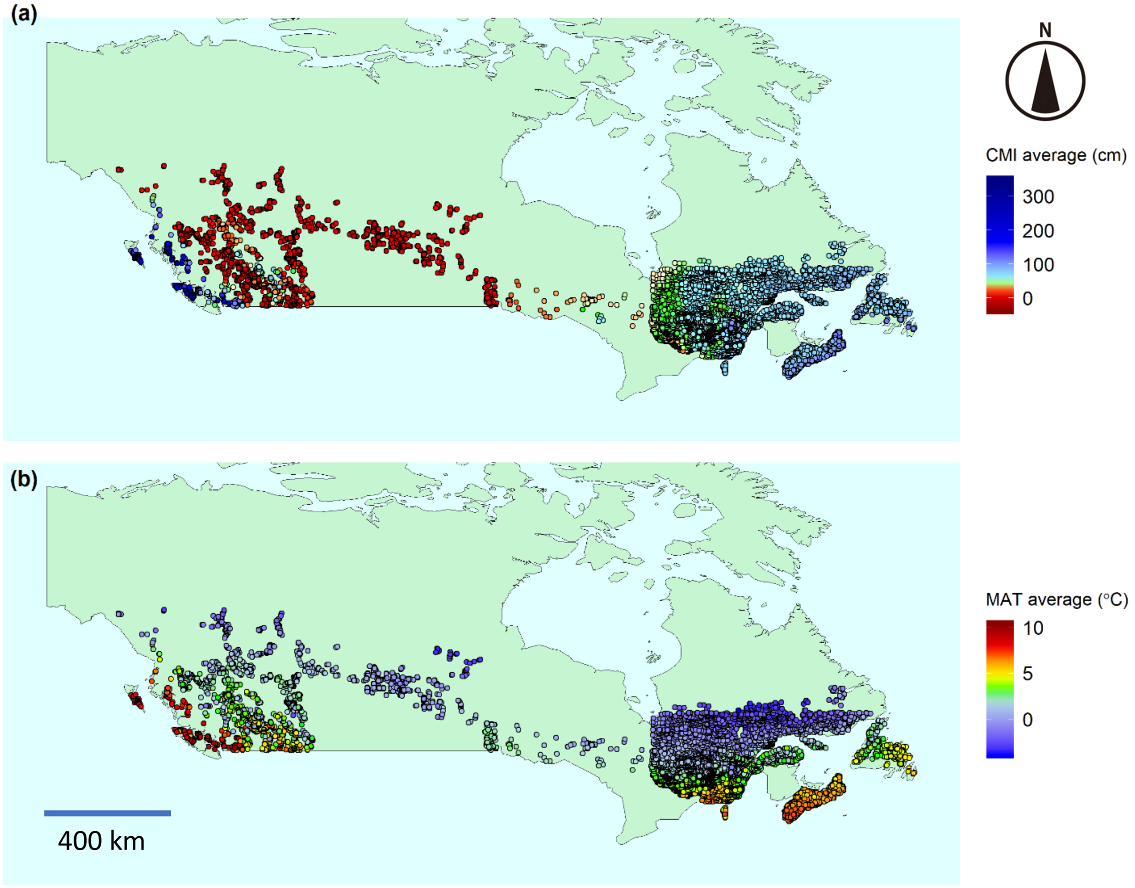


Figure S4-1: Permanent sampling plot location across Canada with information on long-term averages of climate moisture index (CMI_{ave}) and mean annual temperature (MAT_{ave}) between 1951 and 2016.

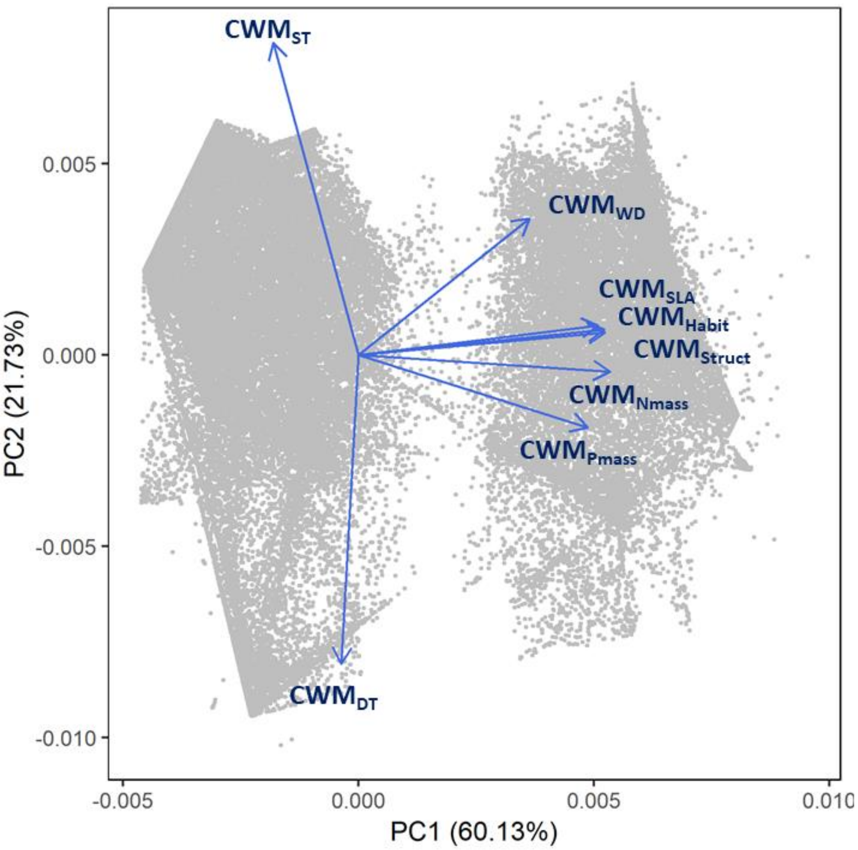


Figure S4-2: A result of the principal component analysis (PCA) showing permanent sampling plots and each functional identity (community-weighted mean of trait value, CWM). CWM$_{Nmass}$ = CWM of nitrogen content per leaf mass, CWM$_{Pmass}$ = CWM of phosphorus content per leaf mass, CWM$_{SLA}$ = CWM of specific leaf area, CWM$_{Struct}$ = CWM of leaf structure, CWM$_{Habit}$ = CWM of leaf habit, CWM$_{WD}$ = CWM of wood density, CWM$_{ST}$ = CWM of shade tolerance, CWM$_{DT}$ = CWM of drought tolerance. The first axis (PC1) represents traits associated with resource acquisitions, while the second axis (PC2) stands for traits associated with tolerance. Values of PC1 and PC2 axes were scaled for the graphical purpose.

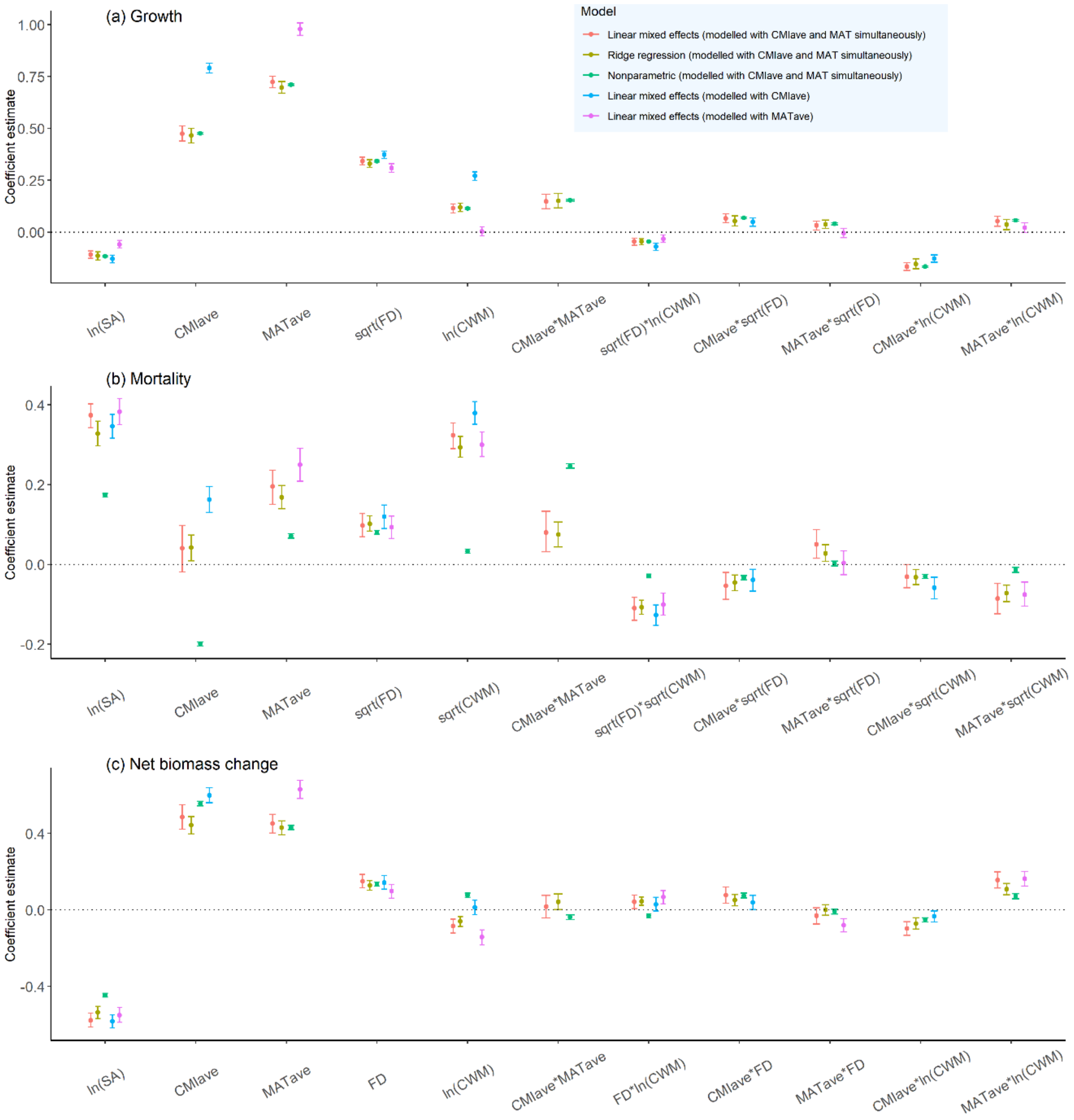


Figure S4-3: Coefficient estimates (scaled) from linear mixed effect models (eqn. 1), ridge regressions, and nonparametric methods (see *Methods*). The linear mixed effect models were modelled with two spatial variations in climate (long-term averages of climate moisture index (CMI_{ave}) and mean annual temperature (MAT_{ave})) simultaneously (red) and with one driver at a time (blue and purple, respectively). Ridge regression was conducted with a range of *lambda.1se* (see *Methods*). Values are means with 95% confidence intervals. Coefficient estimates of ecoregion and province are not shown for convenience.

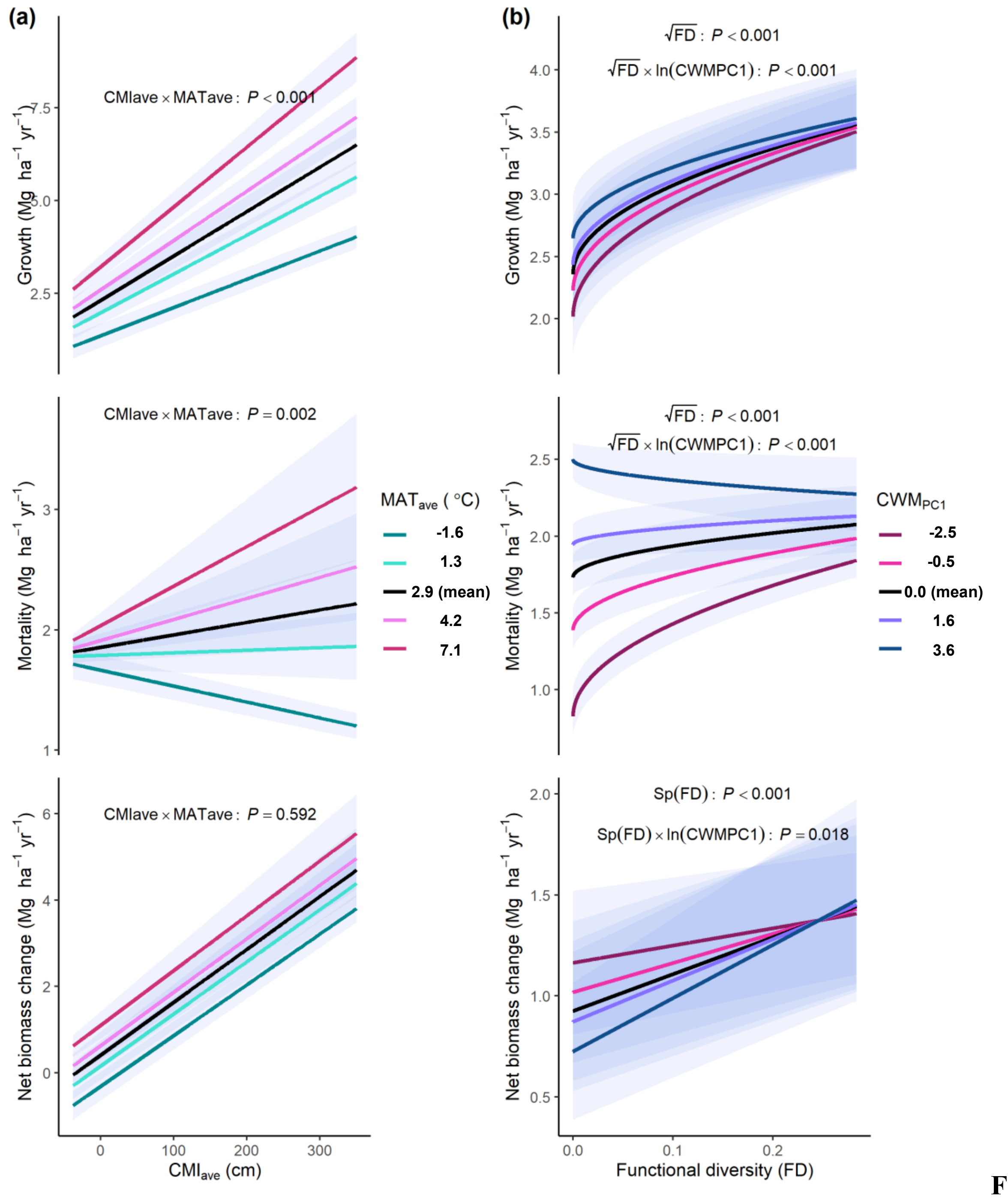


Figure S4-4: (a) Biomass dynamics responses to the long-term average of climate moisture index (CMI$_{ave}$) are dependent on that of mean annual temperature (MAT$_{ave}$). (b) Biomass dynamics responses to functional diversity (functional dispersion; FD) are dependent on community-weighted mean of resource acquisition trait value (CWM$_{PC1}$). The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. MAT$_{ave}$ and CWM$_{PC1}$ were binned from -1.6 to 7.1 (°C) and from -2.5 to 3.6 (unitless) (their 5% and 95% percentiles) for four levels. Mean values are also shown as black lines.

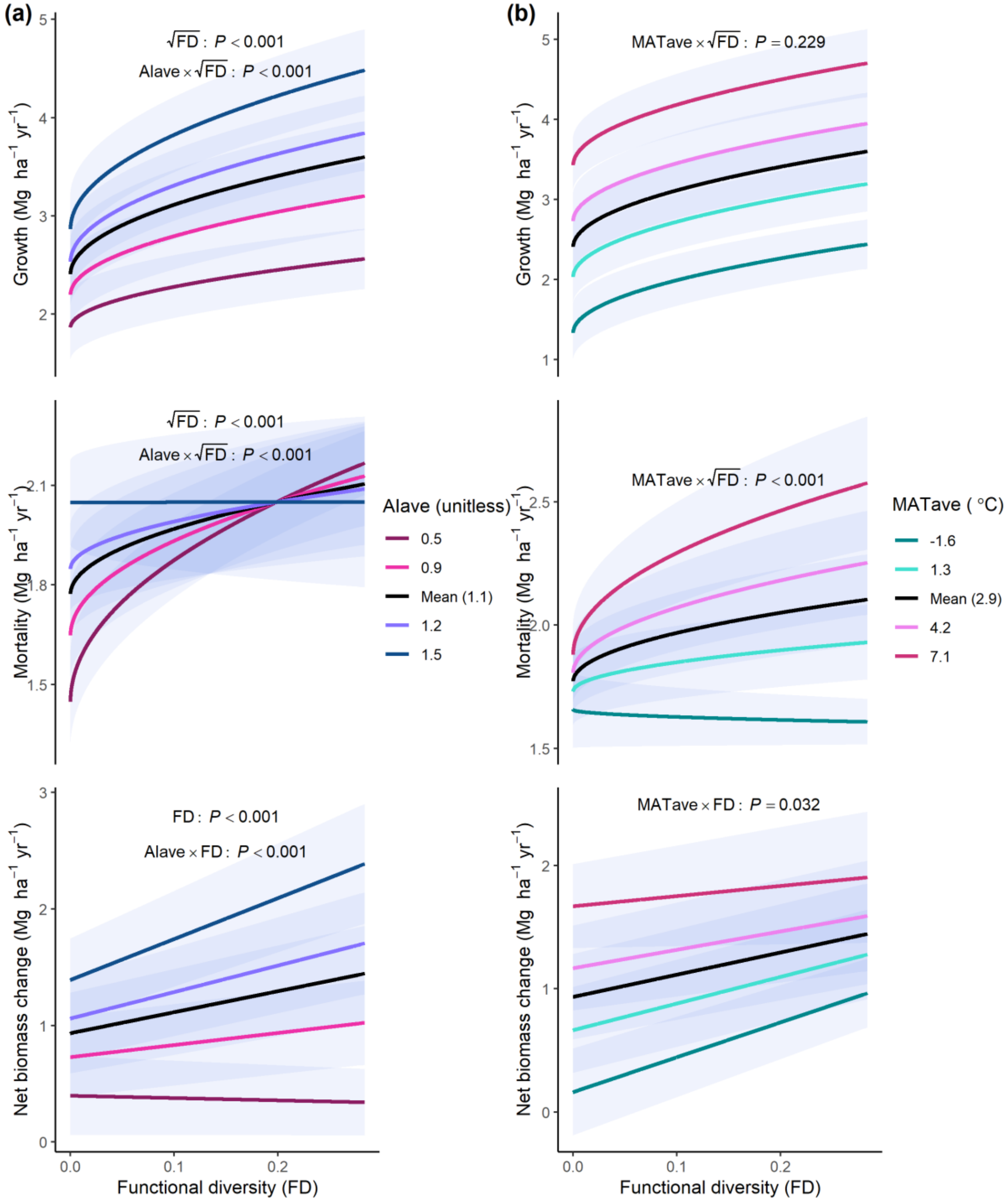

(a)
(b)
√FD : P < 0.001
Alave × √FD : P < 0.001
MATave × √FD : P = 0.229
Growth (Mg ha⁻¹ yr⁻¹)
√FD : P < 0.001
Alave × √FD : P < 0.001
MATave × √FD : P < 0.001
Mortality (Mg ha⁻¹ yr⁻¹)
Alave (unitless)
0.5
0.9
Mean (1.1)
1.2
1.5
MATave (°C)
-1.6
1.3
Mean (2.9)
4.2
7.1
FD : P < 0.001
Alave × FD : P < 0.001
MATave × FD : P = 0.032
Net biomass change (Mg ha⁻¹ yr⁻¹)
Functional diversity (FD)
Functional diversity (FD)
0.0
0.1
0.2

Figure S4-5: Abiotic context-dependent response of aboveground biomass dynamics to functional diversity (functional dispersion; FD). (a) Trends with the long-term average of aridity index (AI_{ave}) and (b) trends with the long-term average of mean annual temperature (MAT_{ave}). The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. AI_{ave} and MAT_{ave} were binned from 0.5 to 1.5 (unitless) and from -1.6 to 7.1 (°C) (their 5% and 95% percentiles) for four levels. Mean values are also shown as black lines.

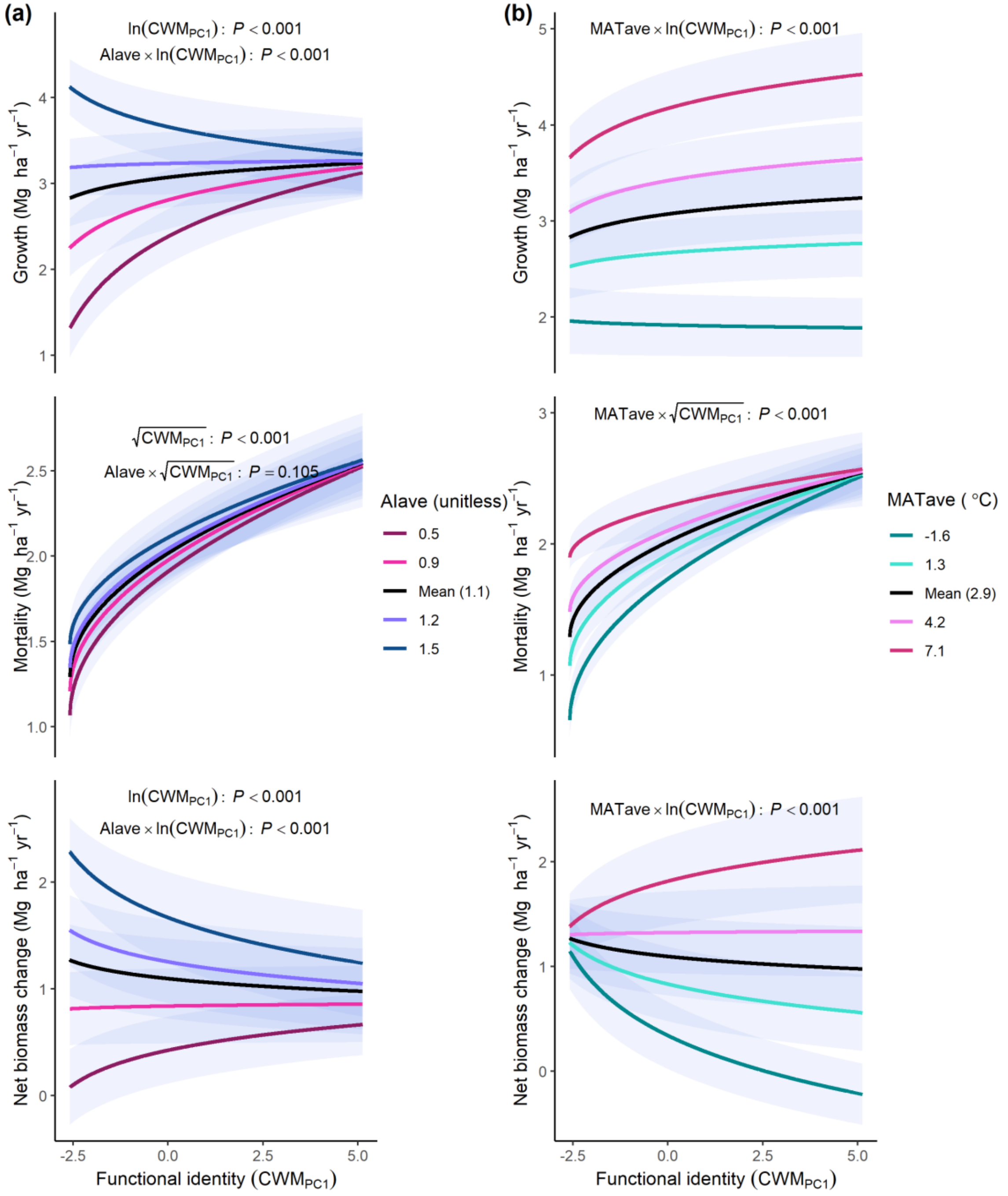


Figure S4-6: Abiotic context-dependent response of aboveground biomass dynamics to functional identity (community-weighted mean of resource acquisition traits; CWM_{PC1}). (a) Trends with the long-term average of aridity index (AI_{ave}) and (b) trends with the long-term average of mean annual temperature (MAT_{ave}). The lines and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models. AI_{ave} and MAT_{ave} were binned from 0.5 to 1.5 (unitless) and from -1.6 to 7.1 (°C) (their 5% and 95% percentiles) for four levels. Mean values are also shown as black lines.

APPENDIX III: SUPPLEMENTARY INFORMATION FOR CHAPTER 5

Table S5-1: Summary statistics (mean ± SD with the range in brackets) of the permanent sample plots across Canada.

Attribute	Mean	SD	Range
Plot size (m^2)	536.0	303.0	20.0 - 2023.0
Number of census	4.5	1.8	2.0 - 9.0
Measurement interval (years)	9.5	4.0	1.0 - 44.0
Length of monitoring (years)	30.5	11.3	2.0 - 52.0
Number of alive trees per plot*	56.1	68.8	1.0-1684.0
Stand basal area (m^2/ha)*	22.7	17.2	0.03 - 223.7
Stand age (years)*	86.7	41.1	0.2 - 379
Year (mid calendar year)*	1990.3	14.0	1951 - 2016
Atmospheric CO_2 concentration	355.9	22.3	311.1 - 404.2
Anomaly of mean annual temperature (ATA, °C)	0.0	1.0	-3.7 - 3.6
Anomaly of climate moisture index (ACMIA, cm)	2.0	18.4	-190.7 - 225.8
Long-term average of climate moisture index (CMI_{ave}, cm)	56.8	40.2	-37.6 - 350.5
Long-term average of mean annual temperature (MAT_{ave}, °C)	2.8	2.7	-3.9 - 12.3
Community weighted mean of leaf nitrogen content per leaf dry mass (CWM_{Nmass}; mg/g)*	14.3	3.8	9.4 - 27.4
Community weighted mean of leaf phosphorus content per leaf dry mass (CWM_{Pmass}; mg/g)*	1.4	0.3	0.8 - 3.2
Community weighted mean of specific leaf area (CWM_{SLA}; mm^2/mg)*	9.4	4.6	3.3 - 32.6
Community weighted mean of wood density (CWM_{WD}; g/cm^3)*	0.4	0.1	0.3 - 0.6
Community weighted mean of leaf habit (1 = deciduous, 0 = evergreen)*	0.3	0.5	0 - 1
Community weighted mean of leaf structure (1 = broadleaf, 0 = coniferous)*	0.3	0.5	0 - 1
Community weighted mean of drought tolerance (CWM_{DT})*, †	2.3	0.7	0.8 - 4.3
Community weighted mean of shade tolerance (CWM_{ST})‡, †	3.3	1.1	1 - 5

Community weighted mean of resource acquisition traits ($\mathrm{CWM}_{\mathrm{PC1}}$)[*, #]	0.0	2.2	-2.6 - 5.4
Community weighted mean of resource acquisition traits ($\mathrm{CWM}_{\mathrm{PC2}}$)[*, ‡]	0.0	1.3	-3.4 - 2.4

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[*] The variables were summarised based on the first census.

[†] The five-level scale for shade tolerance and drought tolerance: “1” (very intolerant) – “5” (very tolerant; (Niinemets & Valladares 2006)).

[#] Community weighted mean of the first axis of principal component analysis (PCA) with the six functional traits above. A larger value indicates angiosperm-like strategies (higher N_{mass}, P_{mass}, SLA; broadleaf, deciduous) while smaller value indicates gymnosperm-like strategies (see *Methods*; Fig S2).

[‡] Community weighted mean of the second axis of principal component analysis (PCA) with the six functional traits above. A larger value indicates higher shade tolerance and lower drought tolerance, while a smaller value indicates lower shade tolerance and higher drought tolerance ((Niinemets & Valladares 2006); see *Methods*; Fig S2).

Table S5-2: Functional trait values of major tree genus (>5% of the total basal area across all plots during the entire census; see Supplementary Methods). Values of each species were averaged to obtain genus-level values to aid our interpretation of the results (see Results and Discussion; Figs. S5-3, S5-6). Pseudotsuga was comprised only of P. menziesii, and thus the values for this species are shown. Note that species-level trait values are used for the analysis (see Methods) but not those of the genus-level.

Genus/Species	N_{mass}	P_{mass}	SLA	WD	DT	ST	Habit	Struct
Abies	11.08	1.35	7.17	0.40	1.60	4.48	0	0
Acer	22.03	2.01	30.99	0.53	2.35	3.80	1	1
Betula	21.86	1.75	17.15	0.54	2.21	2.00	1	1
Picea	11.15	1.25	5.54	0.39	2.21	4.22	1	1
Pinus	11.99	1.24	5.77	0.41	3.85	1.89	0	0
Populus	21.75	2.14	13.99	0.38	1.90	1.36	1	1
Pseudotsuga menziesii	11.40	1.59	9.20	0.45	2.62	2.78	0	0
Tsuga	11.00	1.37	13.83	0.44	1.18	4.73	0	0

Trait values were compiled based on the TRY database (Kattge et al. 2011) and other published sources (Reich & Oleksyn 2004; Wright et al. 2004; Niinemets & Valladares 2006; Chave et al. 2009; Berner & Law 2016).

N_{mass} = leaf nitrogen content per leaf dry mass (mg g^{-1})

P_{mass} = leaf phosphorus content per leaf dry mass' (mg g^{-1})

SLA = specific leaf area (mm^2 mg^{-1}; i.e., leaf area per leaf dry mass)

WD = wood density (g cm^{-3})

ST = shade tolerance (categorical class 1–5 (Niinemets & Valladares 2006))

DT = drought tolerance' (categorical class 1–5 (Niinemets & Valladares 2006))

Habit = leaf habit' ('deciduous' = '1' *vs* 'evergreen' = '0')

Struct = leaf structure' ('broadleaves' = '1' *vs* 'coniferous' = '0')

Table S5-3: The fixed effects of stand age (SA), climate change drivers (atmospheric CO$_2$ concentration and anomalies of mean annual temperature (ATA) and climate moisture index (ACMIA)), long-term averages of climate moisture index (CMI$_{ave}$) and mean annual temperature (MAT$_{ave}$) on community-weighted mean of trait values (CWM$_{PC1}$ and -CWM$_{PC2}$; see *Methods* and footnote).

Fixed effects	Coefficients (mean ± s.e.m.)	SS[c]	*df*	*F*	*P*
Angiosperm- vs Gymnosperm-like strategies (CWM$_{PC1}$)[a]					
(Intercept)	-0.833 ± 0.016	-	-	-	<0.001
f(SA)	-0.370 ± 0.015	53.3	1, 47905	596.800	<0.001
CO$_2$	0.078 ± 0.007	10.8	1, 47905	120.800	<0.001
ATA	-0.017 ± 0.003	3.7	1, 47905	41.700	<0.001
ACMIA	$-4.5 \times 10^{-4} \pm 0.003$	<0.1	1, 47905	<0.1	0.89
CMI$_{ave}$	-0.858 ± 0.018	210.9	1, 17105	2361.900	<0.001
MAT$_{ave}$	0.995 ± 0.017	323.1	1, 17105	3618.200	<0.001
f(SA) × CO$_2$	-0.057 ± 0.005	11.7	1, 47905	131.100	<0.001
f(SA) × ATA	-0.004 ± 0.003	0.2	1, 47905	2.600	0.108
f(SA) × ACMIA	0.006 ± 0.003	0.4	1, 47905	4.700	0.03
f(SA) × CMI$_{ave}$	-0.025 ± 0.014	0.3	1, 47905	3.300	0.069
f(SA) × MAT$_{ave}$	0.127 ± 0.014	7.3	1, 47905	81.300	<0.001
CO$_2$× CMI$_{ave}$	0.009 ± 0.006	0.2	1, 47905	2.100	0.151
ATA × CMI$_{ave}$	-0.010 ± 0.003	1	1, 47905	10.800	0.001
ACMIA × CMI$_{ave}$	-0.002 ± 0.002	0.2	1, 47905	1.900	0.166
CO$_2$ × MAT$_{ave}$	-0.017 ± 0.007	0.5	1, 47905	5.900	0.015
ATA × MAT$_{ave}$	0.009 ± 0.003	0.6	1, 47905	7.000	0.008
ACMIA × MAT$_{ave}$	0.006 ± 0.003	0.3	1, 47905	3.800	0.051
CMI$_{ave}$ × MAT$_{ave}$	0.330 ± 0.011	74.5	1, 17105	834.000	<0.001

Drought tolerance (-CWM_{PC2})[b]					
(Intercept)	0.004 ± 0.008	-	-	-	0.633
f(SA)	-0.285 ± 0.008	22.1	1, 47905	1414.400	<0.001
CO_2	0.039 ± 0.003	2.2	1, 47905	140.700	<0.001
ATA	-0.004 ± 0.001	0.2	1, 47905	15.100	<0.001
ACMIA	0.001 ± 0.001	<0.1	1, 47905	1.200	0.275
CMI_{ave}	-0.553 ± 0.009	58.2	1, 17105	3728.000	<0.001
MAT_{ave}	-0.148 ± 0.008	4.8	1, 17105	307.400	<0.001
f(SA) × CO_2	-0.036 ± 0.002	5.2	1, 47905	330.100	<0.001
f(SA) × ATA	0.002 ± 0.001	0.1	1, 47905	3.900	0.048
f(SA) × ACMIA	0.001 ± 0.001	<0.1	1, 47905	0.800	0.367
f(SA) × CMI_{ave}	0.047 ± 0.007	0.7	1, 47905	45.600	<0.001
f(SA) × MAT_{ave}	0.076 ± 0.007	1.9	1, 47905	122.400	<0.001
CO_2 × CMI_{ave}	0.010 ± 0.003	0.2	1, 47905	12.500	<0.001
ATA × CMI_{ave}	-0.004 ± 0.001	0.2	1, 47905	13.3	<0.001
ACMIA × CMI_{ave}	-0.001 ± 0.001	<0.1	1, 47905	0.7	0.392
CO_2 × MAT_{ave}	-0.035 ± 0.003	2.1	1, 47905	136.7	<0.001
ATA × MAT_{ave}	0.004 ± 0.001	0.1	1, 47905	9	0.003
ACMIA × MAT_{ave}	4.7×10^{-4} ± 0.001	<0.1	1, 47905	0.2	0.696
CMI_{ave} × MAT_{ave}	0.093 ± 0.006	3.8	1, 17105	246.5	<0.001

Fixed effects were scaled to allow a comparison of the strength of each effect to the response variable. Stand age was transformed by squared root function based on AIC.

[a] Higher values indicate traits associated with angiosperm-like strategies, while lower values indicate gymnosperm-like strategies (as represented by CWM_{PC1}; see *Methods*; Fig. S2).

[b] Higher values indicate traits associated with higher drought tolerance (CWM_{PC2} being multiplied by -1 to facilitate interpretation; see *Methods*; Fig. S2).

[c] Sum of squares.

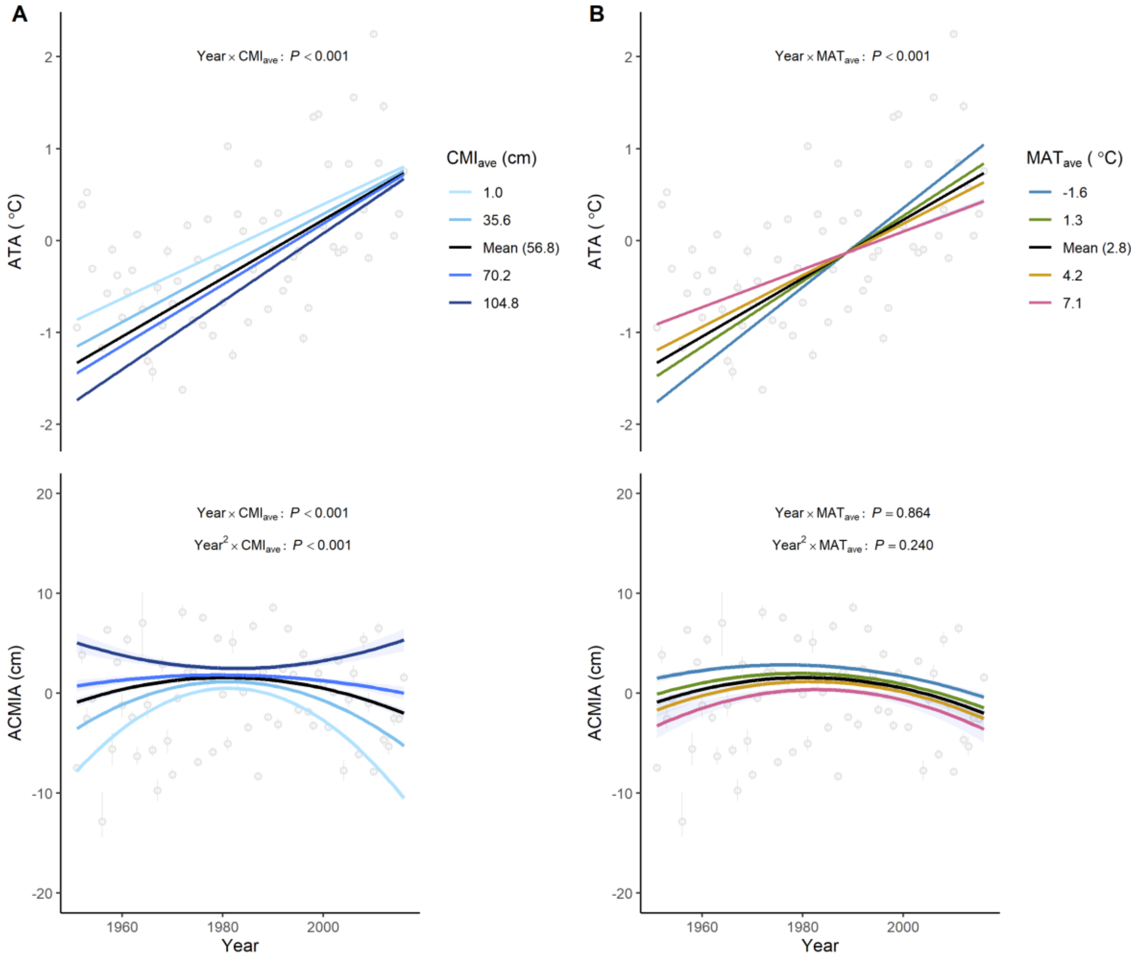

Figure S5-1: Temporal trends in environmental change drivers. Anomalies of mean annual temperature (ATA) and climate moisture index (ACMIA) in relation to the long-term averages of climate moisture index (CMI_{ave}, A) and mean annual temperature (MAT_{ave}, B), with ranges of their 5th and 95th percentiles. Grey dots and error bars show yearly mean and their 95% confidence intervals. Lines are mean values with their 95% confidence intervals.

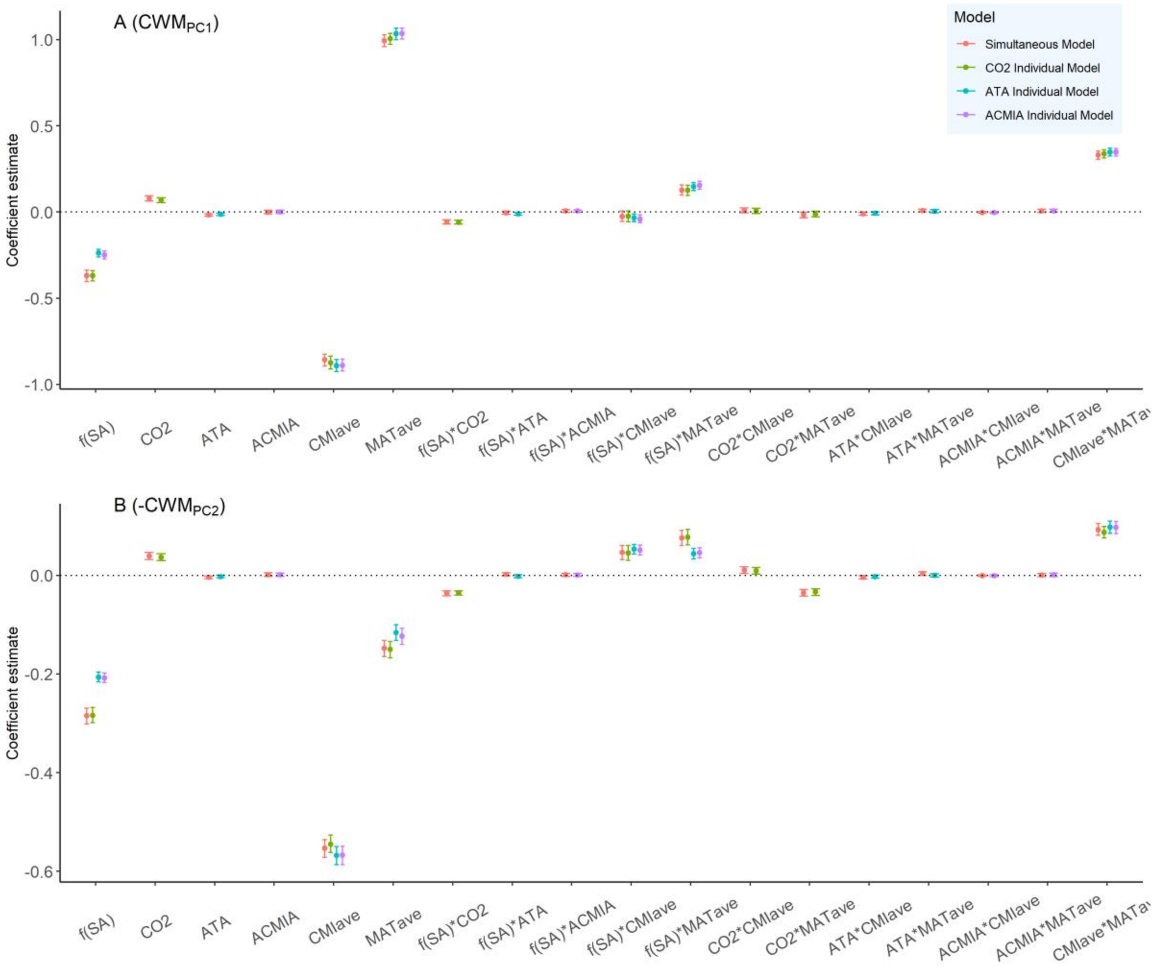

Figure S5-2: Coefficient estimates (scaled) from linear mixed effect models with climate change drivers (eqn. 2; see *Methods*). (A) Community weighted-mean of traits associated with angiosperm- vs gymnosperm-like strategies (CWM_{PC1}) and (B) drought tolerance (-CWM_{PC2}). These were modelled with three climate variables (atmospheric CO_2 concentrations, the anomaly of mean annual temperature (ATA), and the anomaly of climate moisture index (ACMIA)) simultaneously (red), and with one driver at a time (green, blue, and purple, respectively). Values are means with 95% bootstrapped confidence intervals.