A Macrosystems Approach Towards Improved Understanding of Interactions Between Forest Management, Structure, Function and Climate Change, and Implications for the Terrestrial Carbon Cycle

By

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Abstract

A Macrosystems Approach Towards Improved Understanding of Interactions Between Forest Management, Structure, Function and Climate Change, and Implications for the Terrestrial Carbon Cycle

By Bailey A. Murphy

Forests constitute a significant global carbon sink that continues to expand in size, in addition to supporting a range of environmental, economic, and social co-benefits. Forests interact with the overlying atmosphere through exchanges of carbon, water, and energy, and because of the climatic relevance of these fluxes, processes related to terrestrial ecology and land use have a considerable impact on global climate. The comparatively large size of the forest carbon sink in combination with the complimentary climate feedbacks it provides give it significant potential as an avenue for climate mitigation through management practices designed to enhance carbon sequestration.

However, anthropogenic management and shifting environmental conditions due to climate change modify forest structure and function, which fundamentally alters land-atmosphere exchanges and the resultant feedbacks with climate. Gaps remain in our understanding of how forest management, structure, function, and climate change interact across long timescales, and whether relationships are spatially dependent, particularly with regards to vulnerabilities of forest function to climate change. These knowledge gaps manifest as substantial uncertainty surrounding the future of the terrestrial carbon sink and other ecosystem services, and the viability of improved forest management as a climate mitigation strategy hinges on addressing these uncertainties.

Here, we sought to address three overarching questions: **1)** What is the mechanistic relationship between forest structure and function? **2)** What is the primary driver of future shifts in forest function? And **3)** How does management impact the stability of forest function in the face of climate change? Observational data from the Chequamegon Heterogeneous Ecosystem Energy-balance Study Enabled by a High-density Extensive Array of Detectors 2019 (CHEESEHEAD19) field campaign was used to construct simplified models of the mechanistic relationships between forest structure and function and evaluate spatial dependence. We found that the mechanistic relationship between forest structure and function is mediated by resource use efficiency, is dependent upon the spatial resolution used to calculate structural complexity metrics, and that structural metrics representing the degree of vertical heterogeneity are the most influential productivity drivers for heterogeneous temperate forests.

Next, a process-based model was employed to simulate multi-decadal projections of vegetation demographics in response to management, using data from National Ecological Observatory Network (NEON) core terrestrial sites in two U.S. regions. Additionally, downscaled global climate model (GCM) output under two future radiative forcing scenarios (RCP4.5 and RCP8.5) was used to drive model meteorology, allowing for the approximation of vegetation responses to shifting climatic conditions, and facilitating understanding of how management might moderate those responses. With this approach, we showed that management is the strongest driver of future variability in forest function at the regional scale, but that at broader spatial scales gradients in future climate become critical. The narrow precedence of climate over management as a driver of forest function at the sub–continental scale suggests that their effects are likely not independent of one another. We also found that temporal stability is driven primarily by climate, while resilience is shaped by management, but that the impact of management on forest functional stability is regionally dependent and varies by management intensity and severity.

These findings allow us to improve representation in ecosystem models of how structural complexity impacts light and water-sensitive processes, and ultimately productivity. Improved models enhance our capacity to accurately simulate forest responses to management, furthering our ability to assess climate mitigation strategies. Additionally, these findings highlight the regional dependency of the response of forest function to management and climate change, and caution that the same management approach is not necessarily viable everywhere, meaning that the durability of management related Nature-based Climate Solutions have to be assessed at the regional scale. This information can help forest managers evaluate trade offs between ecosystem goods and services, assess climate risks of applying management practices in different regions, and potentially identify specific components of ecosystem function to bolster through targeted management practices.

Acknowledgements

This work would not have been possible without the support of my advisor Ankur. I've learned so much over the past five years doing both my masters and PhD in the Ecometeorology Lab at UW-Madison, and have grown exponentially as a scientist, writer, and person, more so than I could have imagined when Claire Phillips first mentioned your name to me some 7 (?) years ago. I appreciate your freakishly expansive knowledge of all things, skill at recentering and strategizing when projects feel incoherent, but mostly, your unwavering ability to support and lift up those around you. I'm thankful to my Ecometeorology lab members and AOS cohort for all of their support and companionship as we waded through the weird world of grad school, especially Sreenath and Juliet for always being willing to talk through ruminating ideas and concepts. I'm thankful to my committee members Paul Stoy, Chris Kucharick, Jack Williams, and Erika Marin-Spiotta for their insights, feedback, and for taking the time out of their busy schedules to be a part of this process.

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greatest gift to be given the opportunity to spend the past few years pursuing my curiosity about the natural world, asking big questions, and learning how to answer them as well as how to share that information with others.

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"The very facts of the world are a poem. Light is turned into sugar. Salamanders find their way to ancestral ponds following magnetic lines radiating from the earth. The saliva of grazing buffalo causes the grass to grow taller. Tobacco seeds germinate when they smell smoke. Microbes in industrial waste can destroy mercury.

Aren't these stories we should all know? Who is it that holds them?

In long-ago times, it was the elders who carried them. In the twenty-first century, it is often scientists who first hear them. The stories of buffalo and salamander belong to the land, but scientists are one of their translators, and carry a large responsibility for conveying their stories to the world."

Robin Wall Kimmerer, Braiding Sweetgrass

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Chapter 1

Introduction and motivation

Covering approximately 30% of the land surface and taking up roughly 19% of the total carbon released through fossil fuel emissions and land use change each year (Pugh et al., 2019, Friedlingstein et al., 2022, Harris et al., 2021), forests constitute a significant global carbon sink that continues to expand in size (Bonan 2008, Keenan and Williams, 2018). Additionally, forests support a range of environmental, economic, and social co-benefits, including cleaner air and water, enhanced biodiversity, wood products, and improved ecosystem quality for recreational and cultural purposes (Becknell et al., 2015, Baskent 2020, Brockerhoff et al., 2017).

1.1 Historical context of land-atmosphere interactions

Forests interact with the overlying atmosphere through exchanges of carbon, water, and energy to produce climatic responses including cloud formation, temperature regulation, precipitation, and shifts in the surface energy budget (Laguë 2019, Zhang et al., 2020). Exchanges of energy, water, and carbon between the atmosphere and the land surface are regulated by a suite of biogeochemical and biogeophysical processes such as photosynthesis, evapotranspiration, and albedo (Keenan and Williams 2018, Turner and Gardner 2015). Because of the climatic relevance of these fluxes, processes related to terrestrial ecology and land use have a significant impact on global climate (Poulter et al., 2015, Fisher et al., 2018, Foley et al., 2005, Albani et al., 2006). For example, tropical forests maintain high rates of evapotranspiration, which increases cloud cover and has the effect of both decreasing surface air temperature and supporting higher levels of precipitation and moisture in the boundary layer (Bonan 2008). The impact of terrestrial processes can be observed both directly and indirectly through amplifying or stabilizing existing feedbacks within the earth system (Bonan 2008, Anderegg et al., 2020). For example, early work by Charney (1975) demonstrated the existence of biogeophysical feedbacks between deserts and the overlying atmosphere, and drew connections to the global climate implications of reduced vegetative cover in the Sahara. Charney showed that deserts enhanced their own dryness through high albedo contributing to a net loss of radiative heat, inducing a circulation to maintain thermal equilibrium that ultimately increased aridity.

As stated by Schimel (2013), “One of the oldest observations of ecology is that climate and vegetation have corresponding patterns”. The first observational link between climate and the geographic distribution of vegetation was published by von Humboldt (von Humboldt 1849), and was expanded upon 23 years later by Grisebach’s detailed account of global vegetation and comparison to climate (Grisebach 1872), which inspired Köppen’s climate classification system (Köppen 1884) to categorize global climate zones based on local vegetation, a system that is frequently used to this day. A famous study by Merriam and Steineger (1890) in the San Francisco Mountain Plateau of Arizona found that the distribution of flora and fauna further organized along gradients in elevation within the same ecological zone, corresponding to differences in microclimate. However, while the conclusion that climate influenced the geographic distribution, structure, and function of vegetation was solidified early on, the consensus that vegetation also influenced climate took considerably longer to arrive at.

The widespread conversion of forests to agricultural land in Europe was thought to have warmed the regional climate (Fleming 1998), and throughout the 1600s and 1700s this viewpoint was used in part to support deforestation in the American colonies (Bonan 2016), with the idea that it would result in less severe winters as well as a more ‘civilized’ habitat (Adams 1756, Thompson 1980). The proposed mechanism was that cutting trees exposed the ground to incoming solar radiation, increasing air temperatures (Hume and Miller 1987) and melting snow cover in the winter (Franklin 1966). A Harvard professor named Samuel Williamson got close in 1771 when he proposed that differences in albedo between forests and grasslands might be responsible for the observed climate impacts, although his conclusion was that the higher proportion of reflected radiation from fields warmed the air (Williamson 1771). However, the idea that forests could influence climate was largely dismissed by meteorologists at the time as anecdotal, and the idea of forest impacts on climate went dormant until its revival in the 1970s (Bonan 2016). William Ferrel, of the atmospheric Ferrel cell fame, argued in 1889 that large-scale atmospheric circulations controlled precipitation, and there was no evidence to support the claim that forests played any role in precipitation patterns (Ferrel 1889). However, in a bit of foreshadowing, it's worth noting that there were fundamental differences in the scale at which meteorologists and ecologists were operating in their endeavors to understand the Earth system.

In the early 1970s energy balance research by scientists such as Mikhail Budyko of the Soviet Union and William D. Sellers of the United States began to point to the role of humans in shaping climate (Oldfield 2016), particularly the impact of large scale deforestation (Budyko 1971), and introduced the possibility of a ‘runaway positive feedback’ between the land surface and climate (Sellers 1969). Key observational datasets such as Keeling’s atmospheric CO_2

measurements on Mauna Loa in Hawaii (Keeling 1998) provided evidence that significant amounts of carbon were being absorbed by the Earth system, either on land or by the oceans, and that the potential existed for carbon-climate feedbacks (Woodwell et al., 1995). Landmark work by Tans, Fung, and Takahasi (1990) traced a large portion of that carbon uptake to the midlatitudes of the Northern Hemisphere, identifying the land surface as the ‘missing sink’.

1.2 Management and forest structure

The comparatively large size of the forest carbon sink in combination with the complimentary climate feedbacks it provides give it significant potential as an avenue for climate mitigation (Fargione et al., 2018, Canadell and Schulze, 2014). Nature-based climate solutions (NbCS) manipulate natural systems through management and design to increase carbon sequestration and decrease greenhouse gas emissions (Novick et al., 2022), which when paired with emissions reductions can help mitigate the effects of climate change. NbCS have the potential to sequester up to 1.2 Pg CO_2e year-1 in the United States (Figure 1.1), which is approximately 21% of net annual emissions (Fargione et al., 2018), while also supporting a range of environmental and social co-benefits (Becknell et al., 2015, Novick et al., 2022). Furthermore, NbCS such as forest management could potentially be designed to increase resilience to future climate change impacts, whether that be rising temperatures, increased storm severity, or enhanced vulnerability to pest and pathogen infestation.

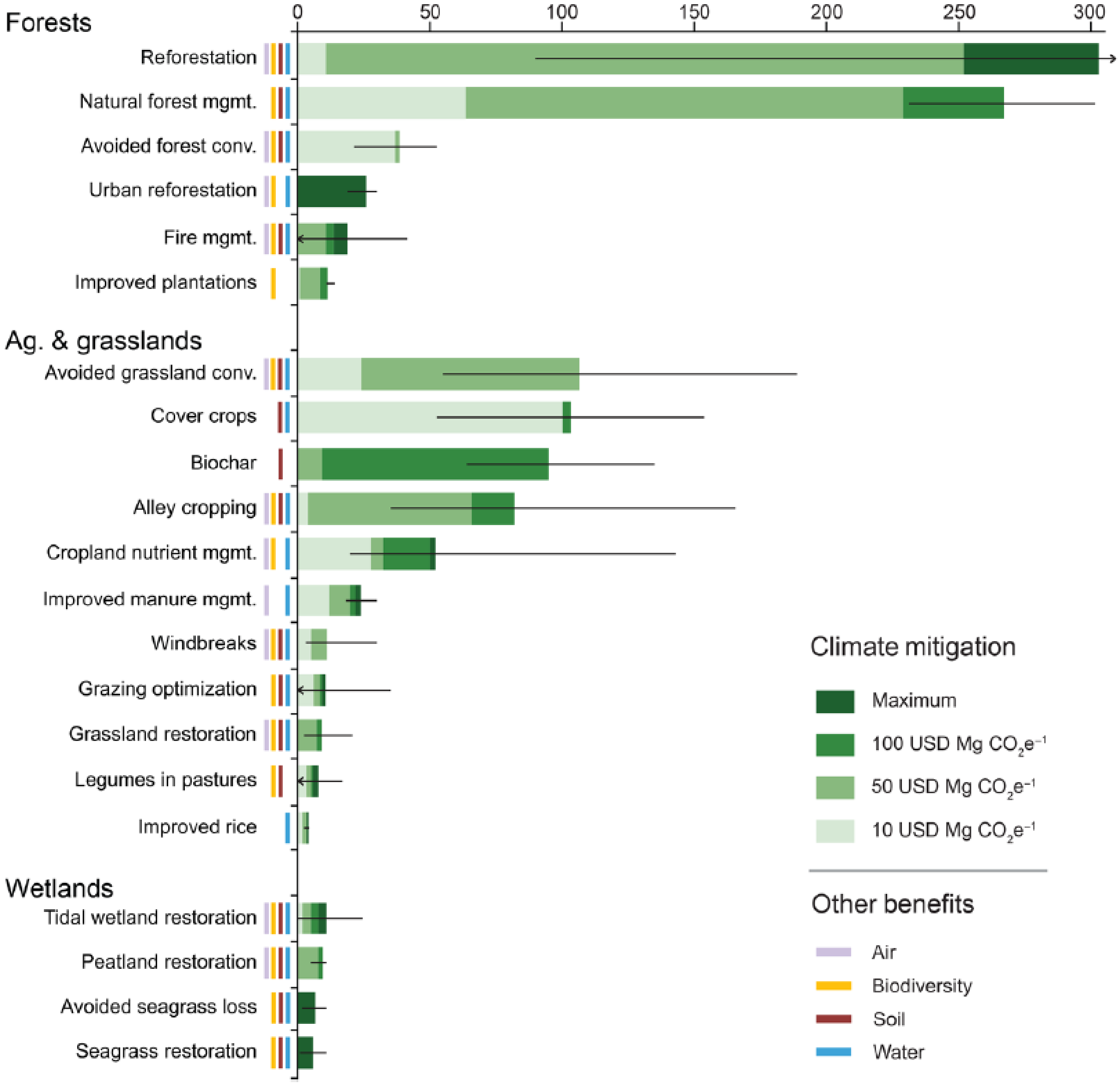

Figure 1.1: 2025 projected climate mitigation potential (in Tg CO$_2$e year^{-1}) of Nature-based Climate Solutions (NbCS) in the United States from Fargione et al. (2018). Black lines represent 95% confidence intervals or reported ranges, and colored bars indicate additional ecosystem benefits such as air quality, biodiversity enhancement, soil enrichment, and water filtration and flood control.

However, anthropogenic management and disturbance modify forest structure and thus forest function, which fundamentally alters land-atmosphere exchanges and the resultant interactions with global climate (Fisher and Koven 2020). But how does forest structure connect to forest function? Forest structure broadly describes the three dimensional arrangement of vegetation, spatial patterns in arrangement, composition and diversity, and the efficiency of how canopy space is utilized; the degree of heterogeneity in that arrangement is the structural complexity (Ehbrecht et al., 2021). The structure of a forest determines its ability to intercept incoming light resources (Atkins et al., 2018b), the extent of competition for available water and nutrients (Anten 2016,), and shapes the forest microclimate (Ehbrecht et al., 2017, Parker et al., 2004), all of which have consequences for carbon and water cycling (Atkins et al., 2018a, Atkins et al., 2018b, Dănescu et al., 2016).

The study of forest structure and composition became popularized as a way to describe vegetation development and succession in response to disturbance (Clements 1916), and to relate habitat heterogeneity to animal biodiversity (MacArthur and MacArthur 1954). Odum’s famous 1969 paper "The Structure and Function of Ecosystems" emphasized the importance of understanding the arrangement of components within an ecosystem, and how structural attributes influence the functioning and productivity of the system. Forest structure was soon recognized as both a key product and driver of ecosystem processes (Franklin et al., 1981), and connections were drawn between management-induced changes in forest structure and impacts on forest function (Spies 1998). Soon a plethora of indices and metrics were developed to facilitate stand based assessment of forest structure (Pommerening 2002, McElhinny et al., 2005), but attempts to scale relationships between forest structure and function beyond the stand didn’t take off until the advent of terrestrial LiDAR and remote sensing approaches, although significant knowledge gaps persist regarding the scale dependence of relationships, controls on relationships, and the utility of various structural complexity metrics.

Because of the enduring unknowns surrounding how forest management, structure, function, and climate change interact, substantial uncertainty persists surrounding the future of the terrestrial carbon sink and other ecosystem services. Particularly with regards to vulnerabilities of forest function to climate change, how management will interact with climate change across long timescales, and how specific management strategies will impact forest structure and function across broad spatial scales. The successful implementation of improved forest management as an NbCS hinges on addressing these uncertainties (Giebink et al., 2022).

1.3 Interaction of management and climate change

It remains unknown whether the impacts of management on carbon dynamics that we observe at the site scale, where many observational studies take place, will persist at the regional to continental scales, where many of the decisions about managing for a climate resilient future are made (Novick et al., 2022). The reason for this knowledge gap is the vast range of spatial and temporal scales that processes related to disturbance, biotic response, and vegetation patterns occur at (Turner and Gardner, 2015, Delcourt et al., 1983, Figure 1.2).

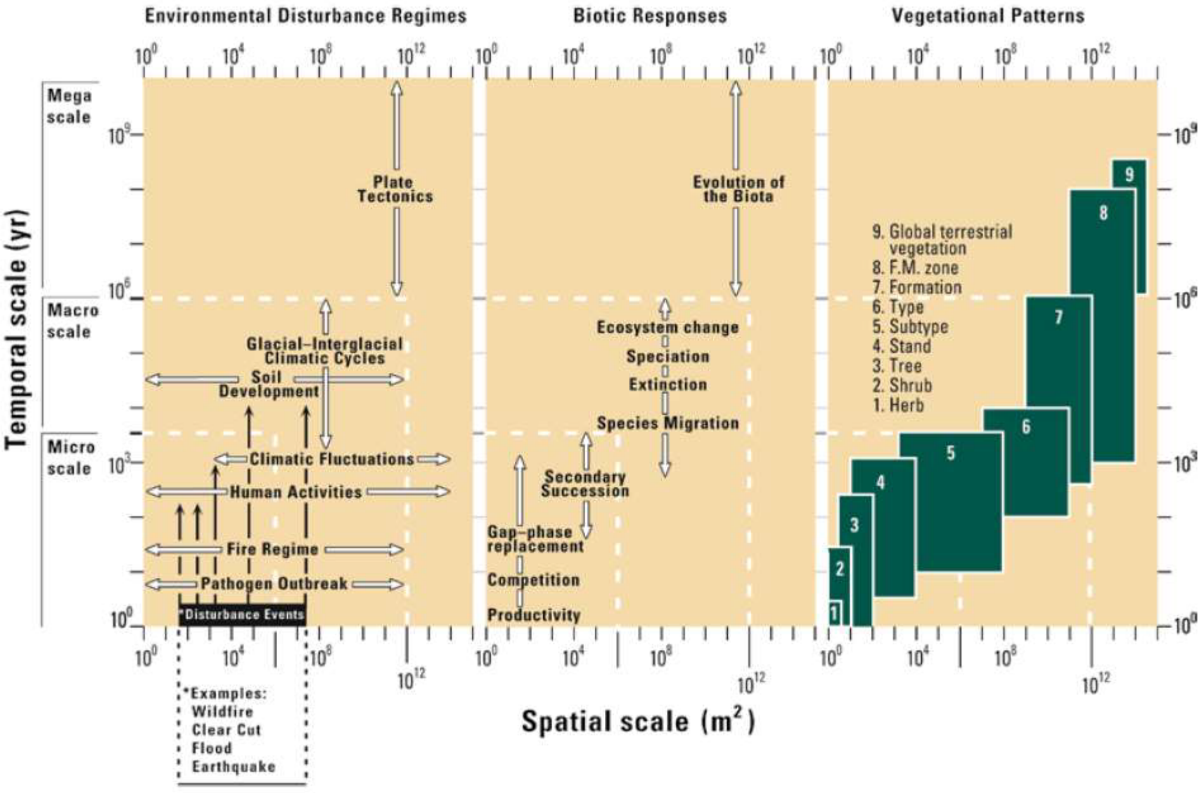

Figure 1.2: Conceptual diagram relating the hierarchy of spatial and temporal scales of environmental disturbance regimes, biotic responses, and vegetation patterns. The figure was modified by Turner and Gardner (2015), originally created by Delcourt et al. (1983).

Furthermore, interactions between management, structure, and climate are controlled by different biophysical processes, involve scale-dependent emergent properties that affect those processes (Turner and Gardner, 2015), and are regulated by different earth system feedbacks operating at different spatial scales (Bonan 2008). As stated by ecologist Simon Levin during his 1992 MacArthur Award speech to the Ecological Society of America, “The problem of relating phenomena across scales is the central problem in biology and in all of science” (Turner and Gardner, 2015). All of these additional dimensions change how resources are spatially distributed, forest resilience to disturbance (Hillebrand et al., 2018), the net exchange of carbon and water (Wang et al., 2006), and overall carbon storage estimates.

The future of forest function will also be affected by climate change-induced shifts in forest structure (McDowell et al., 2020, Grimm et al., 2013), growth (Zhu et al., 2018), mortality (Wu et al., 2023, Dietze and Moorcroft, 2011, Allen et al., 2010), resource competition, reproduction (Qiu et al., 2022, Sharma et al., 2022), and intensifying disturbance regimes (Seidl et al., 2017), contributing to significant uncertainty in future forest carbon biomass and carbon exchanges (Zhu et al., 2018). It has been established that forests can be managed to help mitigate the effects of climate change (Canadell and Raupach, 2008, Anderegg et al., 2020, Fargione et al., 2018, Canadell and Schulze, 2014), and that active management can even reduce the predictive uncertainty of carbon storage at the landscape level (Andrews et al., 2018), but given that the impact of management varies depending on management type and intensity, substantial uncertainty exists surrounding the utility of specific management strategies, or how managing for increased carbon sequestration might impact other ecosystem services (Duncker et al., 2012, Gutsch et al., 2018). Climatic conditions affect how forests respond to disturbance (Seidl et al., 2017, Anderson-Teixeira et al., 2013, Dorheim et al., 2022), and rapidly changing environmental conditions could decrease ecological stability (Bauman et al., 2022, Reich et al., 2022), hindering an ecosystem's ability to recover from disturbance events (Seidl et al., 2017). Feedbacks between decreased ecosystem stability and climate change have also been demonstrated, increases in forest mortality across the globe have been linked to climate-induced acceleration of environmental change (Liu et al., 2019, Anderegg et al., 2020).

1.4 Ecological stability and resilience

Broadly speaking, ecological stability refers to the ability of an ecosystem to withstand and recover from perturbation. Specific definitions of ecological stability have evolved over time; it has been characterized by time alone, where persistence over time of some ecosystem property defines how stable the property is (i.e, temporal stability) (Preston 1969), and the more stable system is simply the one that has existed in a state of constancy relative to its mean for longer (Margalef 1969). It has been defined as the ability of a system to return to its equilibrium state following perturbation (i.e., resilience) (Lewontin 1969, May 1973, Thornton and Mulholland 1974, Pimm 1984), and it has been described as the degree to which a system is able to resist changing despite facing perturbations of varying magnitudes (i.e., resistance) (Rutledge 1976). Recently it has been argued that quantifying stability using a single measure is an oversimplification (Hillebrand et al., 2018), and definitions have shifted towards representing ecosystem stability through a multidimensional framework (Pimm 1984, Donohue et al., 2013, Mathes et al., 2021) that includes temporal stability, resistance, resilience, and recovery time as factors (Hillebrand et al., 2018) (Figure 1.3).

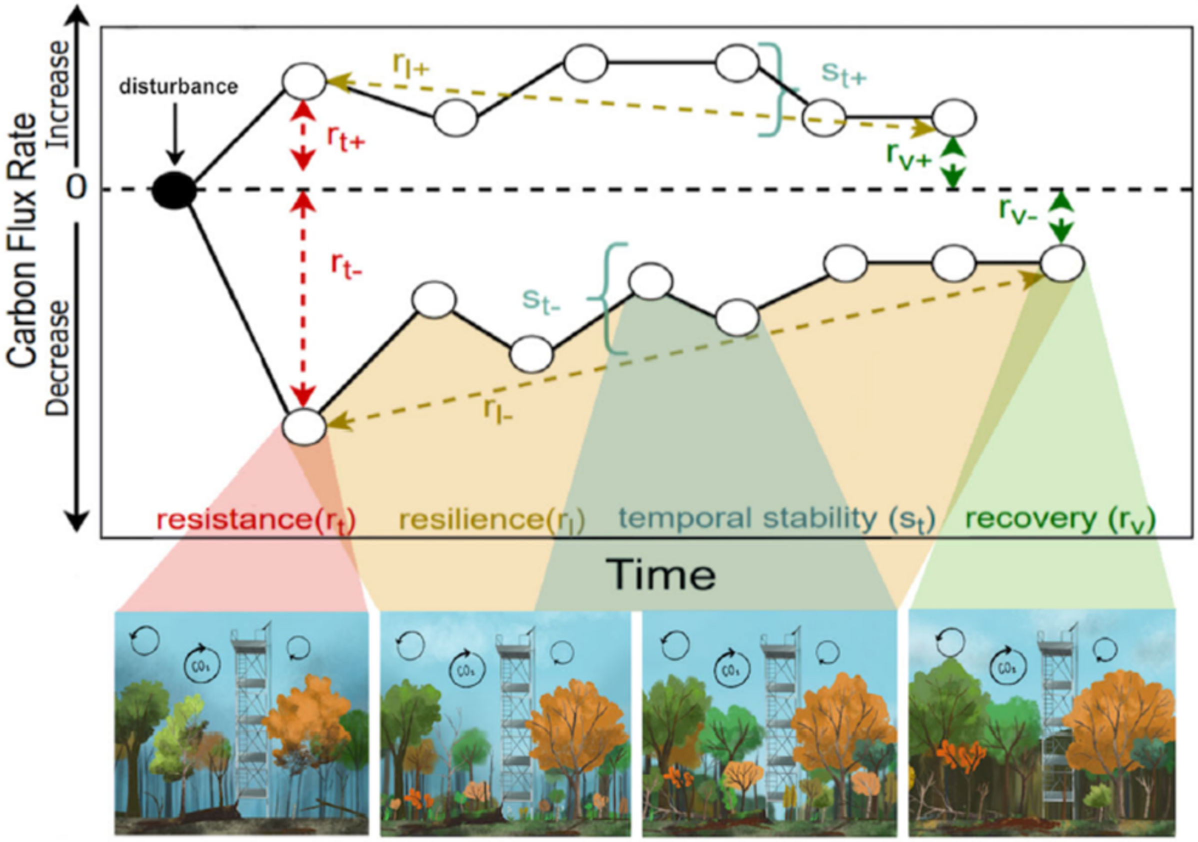

Figure 1.3: A multidimensional stability framework characterized by resistance, resilience, temporal stability, and recovery following perturbation, applied to capture carbon cycle responses to disturbance (Mathes et al., 2021).

As applied to ecosystems, the concept of stability is often segregated into compositional and functional stability (Hillebrand et al., 2018), where compositional stability relates to community composition and diversity, and functional stability is associated with the suite of functions performed by an ecosystem, such as carbon and water cycling. Shifts in composition are inevitable as ecosystems adjust to changes in climate and environmental conditions in the coming decades (Falk et al., 2022). For example, Esquivel-Muelbert et al. (2018) showed that Amazonian forests are transitioning towards larger stature trees in response to escalated atmospheric CO_2 concentrations, and an increasing abundance of genera that are capable of tolerating enhanced moisture stress. In higher latitudes, Dial et al. (2022) showed that migration of tree species is taking place across broader ecoclimatic ranges than originally expected, reporting populations of boreal white spruce establishing in the Arctic tundra.

Climate driven changes in disturbance regimes (Seidl et al., 2017, Seidl et al., 2011) are also expected to have profound impacts on forest composition and function (Thom and Seidl, 2016, Johnstone et al., 2016), and may cause large-scale land cover transitions if the ecological resilience thresholds of forests are exceeded (Reyer et al., 2015). With regards to the durability of forest management as an NbCS, the functional stability of forests in response to climate change is the more exigent dimension of stability, as enhancing the uptake and storage of carbon is a central goal of NbCS (Novick et al., 2022, Hemes et al., 2021, Fargione et al., 2018). A recent study by Wu et al. (2023) showed that 71% of forest types in the U.S. are projected to lose stored carbon by the end of the century in response to increased climate stress and fire mortality. These findings have significant implications for NbCS as well as market-based carbon offset projects (Figure 1.4), particularly projects on the West Coast, such as those affiliated with California's Cap-and-Trade Program. Ultimately, our limited understanding of variability in feedbacks, ecosystem processes, and anthropogenic impacts all manifest as uncertainty in our understanding of the future realities of climate change (Keenan and Williams, 2018, Fisher et al., 2018).

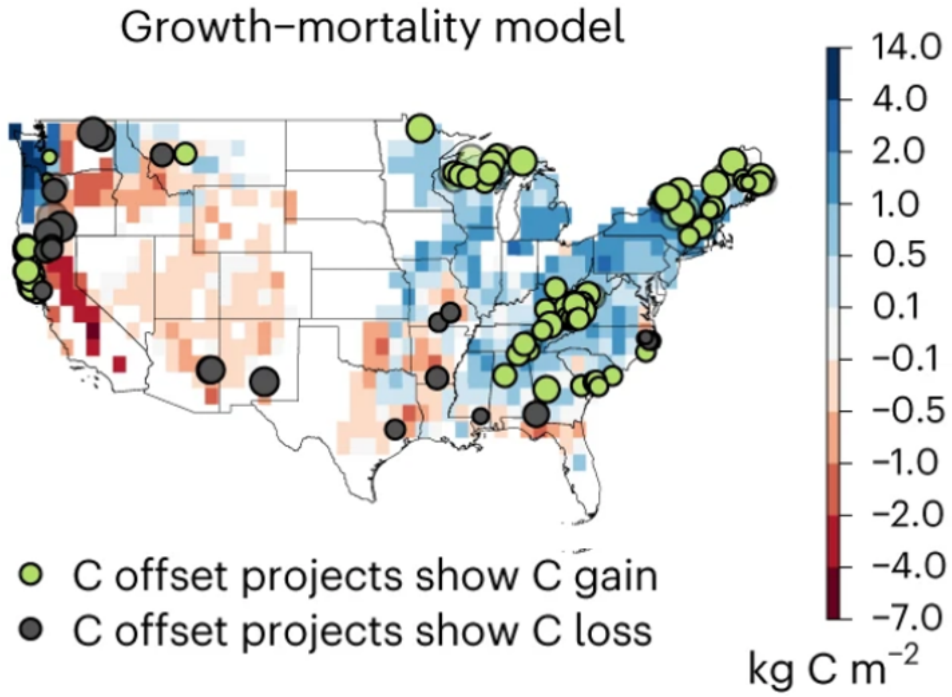

Figure 1.4: Projected carbon gain or loss of 139 carbon offset projects in the continental U.S., adapted from Wu et al. (2023). Green points indicate net carbon gains by the end of the century and gray points indicate net carbon losses. The size of the points correspond to the log-transformed project area, and the colorbar represents the magnitude of carbon gains and losses. Predictions are derived from a growth mortality model that does not include CO_2 fertilization effects, but does represent fire-vegetation feedbacks.

1.5 Modeling the terrestrial biosphere

Process-based models are one tool that can be used to facilitate understanding of what modulates spatial and temporal shifts in forest structure and function, and how structure and function respond to variations in management and climate. Models offer an opportunity to capitalize on the information gained from site-level observational studies and not only expand to larger spatiotemporal scales, but also provide a chance to explore previously intractable research questions that allow us to test and subsequently advance our theoretical understanding of the processes driving ecosystem responses to climate change.

The model utilized in chapters four and five of this dissertation, the Ecosystem Demography model version 2.1 (ED2; Moorcroft et al., 2001, Hurtt et al., 2002, Albani et al., 2006, Medvigy et al., 2009, Longo et al., 2019) is a type of vegetation dynamics model, similar to what's known as a forest gap model, which simulates population dynamics, demography, and community composition of individual trees, but ED2 simulates cohorts rather than individual trees, making it less computationally expensive than traditional forest gap models (Fisher and Koven 2020). Vegetation dynamics models are one class of terrestrial ecosystem models, other classes include biogeography models, biogeochemistry models, canopy models, hydrology models, biophysics or land surface models, and dynamic global vegetation models (DGVMs; Bonan 2019). Biogeography, biogeochemistry, biophysics, and vegetation dynamics models formed the foundation for the field of terrestrial ecosystem modeling as it exists today, with DGVMs representing more recent advancements.

The science of modeling the terrestrial biosphere was initiated with biogeography models, the work of von Humboldt, Grisebach, and Köppen described earlier, and was expanded upon by Holdridge's life zones system, which classifies global biomes into 38 types based on temperature, precipitation, and potential evapotranspiration (Holdridge 1947). Plant biogeography models predict the spatial distribution of vegetation based on climate, but they're simplistic in that they don't account for any sort of carbon, water, or nutrient cycling, there are no exchanges of heat or energy, and they assume a state of climate equilibrium (Fisher et al., 2014). Biogeochemical models, originally known as compartment or box models (Schimel 2013), do represent fluxes, and utilize a system of first-order linear differential equations to represent flows of carbon, nitrogen, etc. between ecosystem 'compartments' (Bonan 2019), as shown in Figure 1.5.

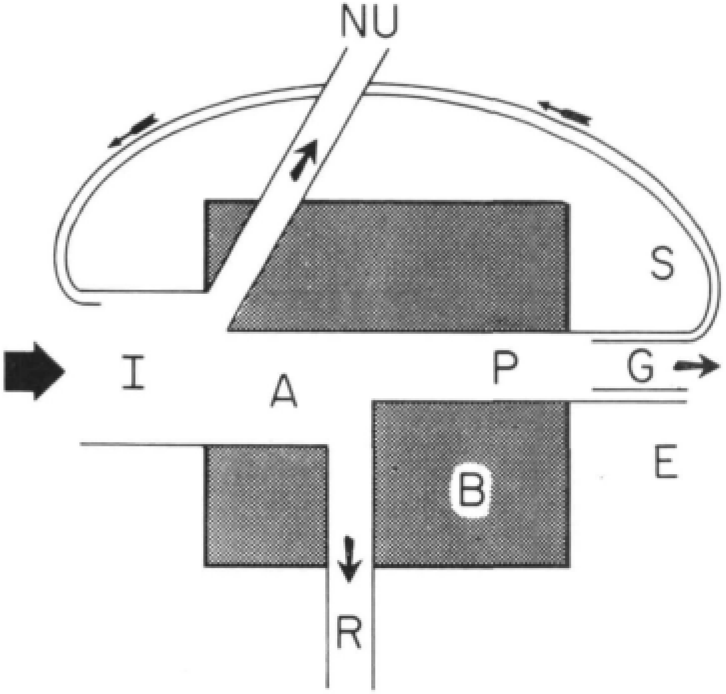

Figure 1.5: Visualization of a compartmental model of ecological energy flow from Odum (1968). The shaded box labeled 'B' represents the living biomass component, 'I' is the total energy input, and 'NU' is the non-utilized energy component. 'A' is the assimilated energy or gross production when considering vegetation (efficiency of the system would be the ratio A/NU), 'R' is the portion of the assimilated energy lost via respiration, and 'P' is the portion of the assimilated energy that is transformed into a different form of organic matter. 'G', 'S', and 'E' represent the fate of what gets produced by the energy assimilation. 'G' refers to growth, or additions in biomass, 'S' is the reserve or maintenance energy, and 'E' is the leakage of assimilated organic matter, such as through urea or simple sugars.

The conceptualization of an ecosystem as a system of compartments and flows of energy or material between compartments was a popular framework for analyzing ecosystem scale interactions, as illustrated by the work of Odum demonstrating energy flows through trophic levels (Odum 1957), and relationships between energy budgets and primary productivity in limnology (Juday 1940). An early example of a biogeochemical model is Olson's 1965 model simulating the transport of radioactive cesium in a forest (Olson 1965), and a more recent example is CENTURY, an agroecosystem model (Parton and Rasmussen, 1994). Biogeochemical models tend to operate on a daily to monthly time step, and focus on carbon and nutrient flows while simplifying the rest of the physical environment (Bonan 2019).

Vegetation dynamics models are rooted in population dynamics and directly represent demographic processes such as establishment, competition for resources, and mortality, where carbon storage and allocation is an emergent property. Vegetation dynamics models emerged in the 1970s (Botkin et al., 1972, Shugart and West 1977), with dynamics originally driven by canopy light availability, but were later expanded to include nutrient and soil water availability as controls and were generalized to broader spatial areas (Pastor and Post 1986, Bonan and Shugart 1989). Ecosystem demography models later reduced the computational demand of traditional vegetation demography models by simulating cohorts of similar age and size rather than individual trees (Hurtt et al., 1998, Moorcroft et al., 2001, Medvigy et al., 2009, Fisher et al., 2010). In the late 1970s the basic equations required to relate the biophysics of energy and water fluxes from vegetation and soil to the atmosphere were outlined (Deardorff 1978), and began to be included in climate models. Biophysics models originated to provide global scale boundary conditions for land-atmosphere exchange in general circulation models, and operated on sub-daily time steps (Fisher et al., 2014). Biophysics models emphasized processes relevant for atmospheric coupling, such as hydrological interactions with plant canopies and soil (Bonan 2019). These early models of land-atmosphere interactions were essential in highlighting the climatic relevance of vegetation, and the ability of plant processes to influence climate, as demonstrated by Sellers et al. (1996).

Development of these various terrestrial models occurred separately for the most part until the 1980s when scientists decided to combine efforts and form DGVMs, which were capable of representing biogeography, plant demography, and biogeochemistry, and opened doors for global scale ecology (Fisher and Koven, 2020). DGVMs are capable of simulating productivity, nutrient cycling, and community composition at the global scale, through the utilization of plant functional types (PFTs) rather than individual species (Bonan 2002, Sitch et al., 2003). Atmospheric models were soon adapted to facilitate pairing with DGVMs and include exchanges between the atmosphere and the terrestrial carbon cycle, as demonstrated by Foley et al. (1996) and Kucharik et al. (2000) with the Integrated Biosphere Simulator (IBIS), which consisted of four component models each running on a common grid but operating on different time steps (Figure 1.6). The eventual coupling of DGVMs with general circulation models (GCMs) to include the carbon cycle in climate models led to prolific discoveries such as the attribution of climate change amplification to carbon cycle feedbacks (Cox et al., 2000).

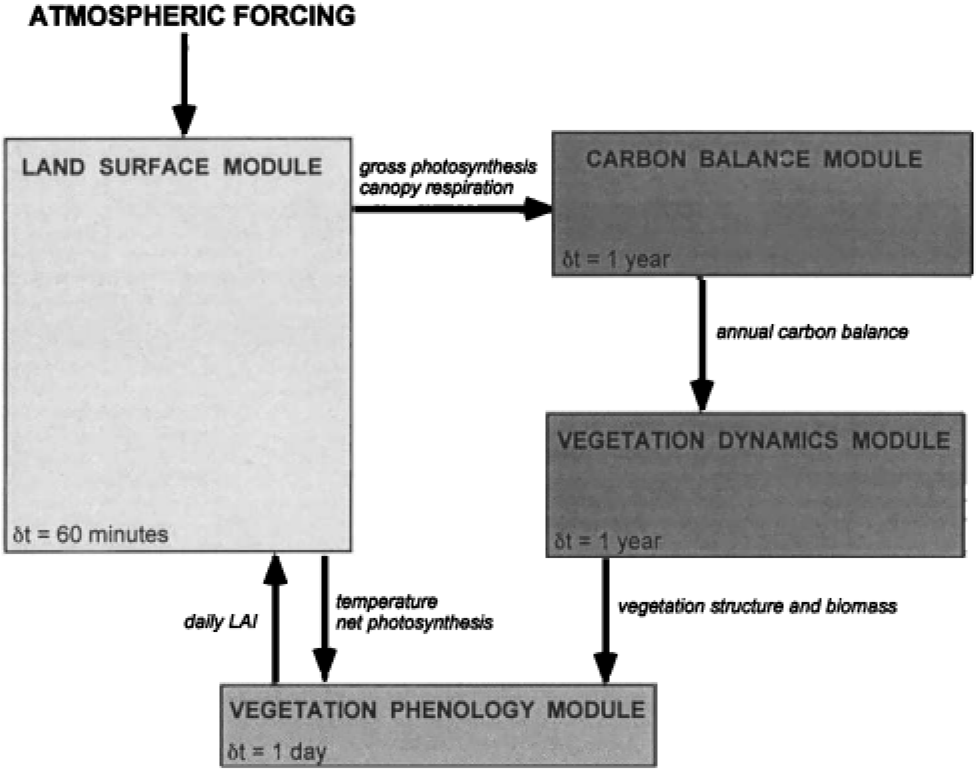

Figure 1.6: Representation of the IBIS model organization from Foley et al. (1996). The model consists of four component modules, shown as rectangles (**δ**t denotes the time step of each module), with arrows indicating the flow of information between modules.

The field of terrestrial ecosystem modeling continues to advance, expanding the detail of process representation and interaction, and providing vital information about the future of natural ecosystems as well as societal risks. However, despite their central role in shaping land-atmosphere interactions, management and disturbance are underrepresented in many models. This is not due to a lack of importance, but rather because of the difficulty of accurately characterizing the impact of management and disturbance on ecosystem structure and function, and addressing uncertainties about scaling those relationships. One strategy for representing the connection between forest management and function could be through the use of structural complexity metrics, which are directly altered by management and have been shown to exert strong controls over forest resource use efficiency and productivity (Atkins et al., 2018, Hardiman et al., 2011, Anten et al., 2016, Gough et al., 2016). Unfortunately, the mechanisms underlying these links remain unclear, thus mapping these links is a fundamental aspect of scaling measurements from the leaf to the landscape level and beyond.

1.6 Overview of dissertation research

Here, this dissertation seeks to expand the existing knowledge base surrounding interactions between forest structure and function, and how these factors respond to changes in human management and climate across spatiotemporal scales.

In pursuit of this, three overarching questions are asked:

Question 1: **What is the mechanistic relationship between forest structure and function?**

Question 2: **What is the primary driver of future variability in forest function?**

Question 3: **How does management impact the stability of forest function in the face of climate change?**

Like any sound scientific investigation, addressing these questions requires both breadth and depth. This is accomplished here by incorporating a short duration spatially intensive observational perspective with a temporally intensive process-based modeling perspective.

Observational forest structure and land-atmosphere exchange data from the spatially intensive CHEESEHEAD19 field campaign was used to construct simplified models of the mechanistic relationships between forest structure and function at a range of scales. While this approach fails to capture the full spectrum of ecosystem dynamics, condensing complexity to a few key principles helps guide understanding and illuminate patterns of change. Complex models that employ size structured representations to simulate vegetation demographics and response to disturbance were then used for a more realistic look at how forests might respond to management across long time scales. Additionally, by using downscaled GCM output to drive model meteorology, we were able to approximate vegetation responses to shifting climatic conditions, and how management might moderate those responses.

This dissertation is divided into three core chapters that address each of the overarching questions presented above, one additional chapter detailing the modeling experimental design, and a conclusion chapter summarizing the key findings as well as presenting study limitations and directions for future work. Chapter two establishes the theoretical basis behind forest structure and function dynamics. Mechanistic relationships between structural complexity, resource use efficiency, and productivity are explored at the site scale where gradients in climate, forest type, and edaphic factors are minimal. A simple regression-based structural equation model is used as a proof-of-concept experiment before expanding to larger spatiotemporal scales in chapters four and five. While the mechanistic relationships described above including scale dependence and mediation effects are quantitative, the influence of management and disturbance legacies on productivity explored in this chapter are largely qualitative. Chapter two seeks to isolate the important structural complexity metrics for predicting gross primary productivity (GPP) in a temperate mixed forest with a high degree of heterogeneity and management, establish the scale dependence of forest structural metric calculation resolution, and qualitatively explore the impact of management on forest structure and function using observational data.

Chapter three does not constitute a stand-alone analysis, but instead provides a brief overview of the vegetation demography model that generated the data used in chapters four and five. Chapter three includes the modeling experimental design, and site and model driver data descriptions. Chapters four and five expand in scale through a comparison of multi-decadal model simulations of forest dynamics in response to management in two regions, the Great Lakes and Southeastern U.S. Simulations were conducted across gradients in forest type, edaphic factors, and climate under two alternate radiative forcing scenarios (RCP4.5 and RCP8.5). Management is represented by four distinct scenarios constituting a range of intensities: preservation, passive, ecological, and production forestry. This approach allowed us to characterize the impacts of both management and climate change on forest function across broad spatiotemporal scales.

Chapter four focuses on understanding future variability in forest function in response to human management and shifting climatic conditions. This chapter outlines the dominant axes of future functional variability using principal component analysis, then applies a combination of generalized additive modeling and random forests to determine whether management or climate change is the dominant driver of the observed functional variability, and whether conclusions are dependent on spatial scale. Chapter five outlines the response of forest structure to variations in management and climate intensity, and relates structural changes to shifts in ecosystem functional stability over time. This chapter utilizes a multidimensional framework to characterize functional stability, both resilience (S_R, speed of functional recovery following perturbation) and temporal stability (S_T, persistence over time of ecosystem function) are calculated to quantify stability shifts in response to climate change, and compare regional differences in forest response across a spectrum of management intensities. This chapter seeks to improve understanding of how forest resilience to perturbations will shift in response to climate change, and the implications of these shifts for the durability of forest management as a NbCS. The specific research questions and hypotheses associated with each chapter are presented in Table 1.1.

The contents of Chapter 2 were published in May 2022 in the Journal of Geophysical Research–Biogeosciences. Chapter 3 is in the process of being prepared for submission with co-authors from the Management and Disturbance in Forest Ecosystems (MANDIFORE) research team, and Chapter 4 will be shared with the same group of co-authors shortly thereafter.

Table 1.1: Research questions and hypotheses for each of the dissertation chapters described above, organized by the broad question (BQ) and sub-question (SQ) that they address.

Chap.	BQ	SQ	Research Question	Hypothesis
2	1	1	Which canopy structural complexity (CSC) metrics are most influential for the prediction of stand primary productivity in mixed temperate forests with a high degree of heterogeneity and a long history of management?	Structural metrics related to vertical complexity will be the most influential in predicting productivity, as they are best suited to capture the impact of vertical heterogeneity in light environments
		2	How do forest management legacies impact CSC metrics, and ultimately stand productivity?	Sites with a record of more intensive disturbance will have reduced CSC and thus reduced productivity
		3	Is the mechanistic relationship between forest structure and function direct, or is it mediated by other factors such as resource use efficiency?	The relationship is not direct, but is mediated by light and water use efficiency, with light use efficiency being the stronger driver of productivity
		4	Is the mechanistic relationship between forest structure and function dependent upon the scale of structural metric calculation?	The relationship is not dependent upon metric calculation resolution
4	2	1	How do variations in climate and management intensity and severity impact forest function (defined as carbon and water cycling), and are relationships regionally dependent?	Active management strategies that promote uneven-aged stands and a multi-layered structure through periodic harvest of individual large trees (such as ecological forestry) will have higher resource use efficiency and be less susceptible to reductions in ecosystem function in response to climate variability, whereas more passive management strategies (such as passive and preservation forestry) will have greater sensitivity to climate change and lower levels of resource use efficiency. We also expect that both the impact of management on forest function and interactions between climate and management will vary in relative strength by geographic region, due to the pace and pattern of climate change by region and differences in treatments (harvest rates, rotation, species) applied to managed forests.

		2	What are the dominant axes of future variability in ecosystem function in managed forests?	Forest productivity and resource use efficiency will be key axes of future functional variability in managed forests, as these encapsulate the mechanistic basis of how management and climate change influence forest carbon exchanges.
		3	What is the relative importance of management versus climate change as drivers of variability in forest function over multi-decadal timescales, and is driver importance scale dependent?	Management will be a stronger overall driver of changes in forest function than climate change, as forest structure is largely determined by management, and forest structure and composition are important factors that shape forest function. However, we expect driver importance to vary spatially, with climate change importance increasing at higher latitudes.
5	3	1	How does forest management across a range of intensities impact forest structure on multi-decadal timescales, and do impacts vary regionally or by climate change scenario?	Management intensity and severity is a stronger driver of shifts in forest structure than climate change, but structural responses to management will diverge regionally over time due to differences in regional climate change impacts.
		2	How do the ensuing structural changes alter ecosystem functional resilience and temporal stability in the face of a changing climate, and are impacts regionally dependent?	Management is the most important factor shaping functional resilience, but regional interactions between management and climate change will alter stability outcomes over time, and more intensive management practices (e.g. production forestry) will decrease functional stability. We also expect to see a positive correlation between functional stability and structural complexity and diversity.

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Chapter 2

Unraveling Forest Complexity: Resource Use Efficiency, Disturbance, and the Structure-Function Relationship

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Abstract

Structurally complex forests optimize resources to assimilate carbon more effectively, leading to higher productivity. Information obtained from Light Detection and Ranging (LiDAR)-derived canopy structural complexity (CSC) metrics across spatial scales serves as a powerful indicator of ecosystem-scale functions such as gross primary productivity (GPP). However, our understanding of mechanistic links between forest structure and function, and the impact of disturbance on the relationship, is limited.

Here, we paired eddy covariance measurements of carbon and water fluxes from nine forested sites within the 10 × 10 km CHEESEHEAD19 study domain in Northern Wisconsin, USA with drone LiDAR measurements of CSC to establish which CSC metrics were strong drivers of GPP, and tested potential mediators of the relationship. Mechanistic relationships were inspected at five resolutions (0.25, 2, 10, 25, and 50 m) to determine whether relationships

persisted with scale. Vertical heterogeneity metrics were the most influential in predicting productivity for forests with a significant degree of heterogeneity in management, forest type, and species composition. CSC metrics included in the structure-function relationship as well as driver strength was dependent on metric calculation resolution. The relationship was mediated by light use efficiency (LUE) and water use efficiency (WUE), with WUE being a stronger mediator and driver of GPP. These findings allow us to improve representation in ecosystem models of how CSC impacts light and water-sensitive processes, and ultimately GPP. Improved models enhance our capacity to accurately simulate forest responses to management, furthering our ability to assess climate mitigation strategies.

2.1 Introduction

Recent studies have indicated strong links between forest canopy structural complexity (CSC) and key ecosystem functions such as carbon and water cycling (Atkins et al., 2018a, Atkins et al., 2018b, Dănescu et al., 2016, Gough et al., 2019, Hardiman et al., 2011, Zhang et al., 2012). Mapping these links is a fundamental aspect of scaling measurements from the leaf to the landscape level and beyond, a preeminent challenge in the field of ecosystem ecology (Bonan 2008, Fahey et al., 2019), yet the mechanisms underlying these links remain unclear. One approach to addressing this knowledge gap is through the pairing of high-frequency measurements of land-atmosphere exchange with high resolution measurements of CSC taken within the same spatial domain, to isolate mechanistic connections between forest structure and function. Forest CSC characterizes the three-dimensional arrangement of vegetation in a forest and includes variables such as rugosity, vertical complexity index, and mean canopy height (Atkins et al., 2018a, Atkins et al., 2018b, McElhinny et al., 2005). Taken together, these variables constrain the ability of the forest to assimilate available resources, and thus the capacity for photosynthesis (Ehbrecht et al., 2021). The prevailing theory is that structurally complex forests are better able to optimize incoming light and water resources to assimilate carbon more effectively (Anten 2016, Atkins et al., 2018a, Atkins et al., 2018b, Gough et al., 2016, Hardiman et al., 2011). It has been suggested that heterogeneous mixed forests with higher levels of CSC are tied to a heightened ability to capitalize on available resources, in part due to functional trait variability and niche differentiation (Dănescu et al., 2016, Hillebrand et al., 2018, Williams et al., 2016, Zhang et al., 2012).

Studies have shown that integrating information obtained from CSC metrics across spatial scales to describe overall CSC can serve as a powerful indicator of ecosystem-scale functions such as gross primary productivity (GPP), augmenting other commonly measured characteristics including species composition and diversity (Atkins et al., 2018a, Atkins et al., 2018b, Eitel et al., 2016, Fahey et al., 2019, Gough et al., 2019, Hardiman et al., 2011, Silva Pedro et al., 2017). Identifying not only which CSC variables have the greatest potential to predict GPP, but what potential controls or influential factors of the structure-function relationship might exist is a vital aspect of this effort. As well, relationships between productivity and CSC could provide mechanistic evidence for using these CSC metrics as predictors of forest carbon storage capacity and functionality.

To understand the relationship between forest structure and ecosystem functions such as carbon and water cycling, structural complexity must be characterized in a reproducible way that can be easily incorporated into modeling and statistical analysis. Light Detection and Ranging (LiDAR) offers a way to robustly quantify aspects of structural complexity, and helps address critical knowledge gaps regarding our mechanistic understanding of how structure determines function (Atkins et al., 2018a, Atkins et al., 2018b, Camarretta et al., 2020) by enabling scientists to look at the relationship between forest structure and function through a more quantitative lens. This enhanced understanding results in improved process representation in ecosystem models, advancing our ability to predict ecosystem responses to human management and disturbance, as well as how that response interacts with other components of the earth system. However, as a community we are now faced with the challenge of deciphering which CSC metrics provide novel and relevant information related to ecosystem function, and how those metrics are impacted by spatial scale. Previous work has addressed pertinent issues related to classification and standardization of CSC metrics (Atkins et al., 2018a, Atkins et al., 2018b, Hardiman et al., 2013a, Hardiman et al., 2013b, Parker et al., 2004, van Ewijk et al., 2011), but relatively fewer studies have explored the issue of spatial scale in calculating and representing CSC metrics, especially when using aerial-based LiDAR systems.

Multiple LiDAR formats exist, including portable canopy, terrestrial laser scanning, spaceborne, and aerial LiDAR systems, and systems can be discrete-return or continuous-return recording. Each system is subject to different constraints, e.g., terrestrial laser scanning and aerial systems often encounter issues of canopy occlusion (Donager et al., 2021, Hardiman et al., 2018), and differences in how data are collected and used to calculate CSC metrics can impact CSC metric values. Synthesizing data from multiple LiDAR forms is one potential avenue to overcome the limitations associated with individual LiDAR formats (Hardiman et al., 2018) and advance scaling efforts. To successfully do this, an enhanced understanding of the impacts of scale on CSC data collected via different LiDAR formats is required. This study seeks to contribute to this effort by evaluating the mechanistic relationship between forest structure and function at multiple spatial resolutions ranging from 0.25 to 50 m, using Unoccupied Aerial

System (UAS) LiDAR-derived CSC metrics to characterize forest structure, and high-frequency eddy covariance (EC) flux data of land-atmosphere CO2 exchange to quantify ecosystem function.

Fine spatial resolutions such as 0.25 and 2 m pixel sizes are included in this study to investigate the relationship between ecosystem function and fine-scale heterogeneity in CSC, which is closely tied to the determination of site microclimates (Ehbrecht et al., 2017), canopy light environments (Tang and Dubayah, 2017), and ultimately patterns of ecosystem functional response to changes in CSC (Smith et al., 2019). The ability of UAS LiDAR systems to capture three-dimensional profiles of stand structure is particularly useful in the mixed temperate forests of the upper Midwest USA, where once even-aged forests are undergoing a transition to more complex systems as they approach advanced stages of successional development following a long history of intensive disturbance (Bogdanovich et al., 2021, Frelich 1995, Hardiman et al., 2011). In addition, three-dimensional profiles from LiDAR provide important information about the distribution of foliar traits that drive photosynthesis at the leaf level (Chlus et al., 2020, Kamoske et al., 2021).

The impact of human management and disturbance on structure-function relationships varies depending on the severity, frequency, spatial scale, and intensity of the event (Ehbrecht et al., 2021, Ford and Keeton, 2017). Smaller spatial scale and less severe disturbances such as the selective harvest of a given percentage of large trees within a stand tend to increase complexity by creating favorable conditions for understory trees to establish, which results in multilayered canopies. This amplified subcanopy growth occurs because disturbance drives a compensatory physiological response to more readily available light, which can also help sustain overall production even in the face of frequent low severity disturbances (Hardiman et al., 2013a, Hardiman et al., 2013b). In contrast, high intensity and severity disturbances that occur at broad spatial scales such as clearcutting or a high-mortality wildfire event tend to simplify CSC initially, leading to a temporary reduction in productivity (Gough et al., 2007), although stands often recover to predisturbance carbon uptake levels within the 10–20 years following a major disturbance event (Amiro et al., 2010).

Variability in disturbance legacies combined with a primarily mixed broadleaf-conifer forest composition and general landscape heterogeneity result in large variations in both carbon dynamics and stand complexity at the ecosystem scale. As canopy structural complexity (CSC) has been shown to be positively correlated with stand production, characterizing the mechanistic relationship between complexity and productivity will enable better representation of the potential impacts of these transitions in successional stage and complexity on carbon sequestration in Midwestern forests (Forrester et al., 2013). The study design of the 2019 Chequamegon Heterogenous Ecosystem Energy-balance Study Enabled by a High-density Extensive Array of Detectors (CHEESEHEAD19) field experiment provided a unique opportunity to partially control for the influence of variability in climate, edaphic factors, and forest functional types on productivity, allowing for a more representative physiological understanding of the structure- function relationship than has been previously demonstrated.

The objective of this study was to identify mechanistic relationships between forest structure and function, explore potential controls or mediating factors on that relationship, and determine whether or not the structure-function relationship persisted when structural metrics were calculated at a variety of resolutions. **In pursuit of this objective, this chapter addressed four primary research questions:** 1) Which CSC metrics are most influential for the prediction of stand primary productivity in mixed temperate forests with a high degree of heterogeneity and a long history of management? 2) How do management legacies impact these influential CSC metrics, and ultimately stand productivity? 3) Is the mechanistic relationship between forest structure and function direct, or is it mediated by other factors such as resource use efficiency (RUE)? And lastly, 4) Is the mechanistic relationship between forest structure and function dependent upon the scale of structural metric calculation?

We hypothesize that structural metrics related to vertical complexity will be the most influential in predicting productivity, as they are best suited to capture the impact of vertical heterogeneity in light environments. We expect that sites with a record of more intensive disturbance will have reduced CSC and thus reduced productivity. Lastly, we hypothesize that the relationship between forest structure and function is not direct, but is mediated by light and water use efficiency, with light use efficiency being the stronger driver of productivity, and that the relationship is not dependent upon spatial resolution.

2.2 Methods

2.2.1 Experimental design

This chapter utilized land-atmosphere exchange and CSC data collected at nine of the CHEESEHEAD19 field campaign study sites in Northern Wisconsin, USA. The CHEESEHEAD19 field campaign spanned from June to October 2019, during which 17 EC flux towers from the National Science Foundation Lower Atmosphere Observing Facility (LAOF) were deployed across a 10 × 10 km study domain. These 17 towers were in addition to the pre existing landscape-level AmeriFlux tall tower US-PFa situated within the study domain (Davis et al., 2003), and two additional temporary EC flux towers supported by Dr. Paul Stoy, bringing the total number of CHEESEHEAD19 EC towers to 20. The temporary CHEESEHEAD19 EC tower sites included 14 forested (primarily mixed conifer and broadleaf) sites, two tussock locations, one grass, and two lake locations. The primary research interests of CHEESEHEAD19 were to explore potential drivers behind the enduring lack of energy balance closure frequently observed over heterogeneous landscapes, and to address persistent challenges associated with upscaling surface energy fluxes (Butterworth et al., 2021). The study period reflects both the summer season land-atmosphere exchange as well as exchanges during the transition of vegetation into senescence. This observational period was chosen to support the energy balance related research interests of CHEESEHEAD19, as it captures the shift in energy balance from a latent heat flux dominant landscape to a sensible heat flux dominant landscape (Butterworth et al., 2021).

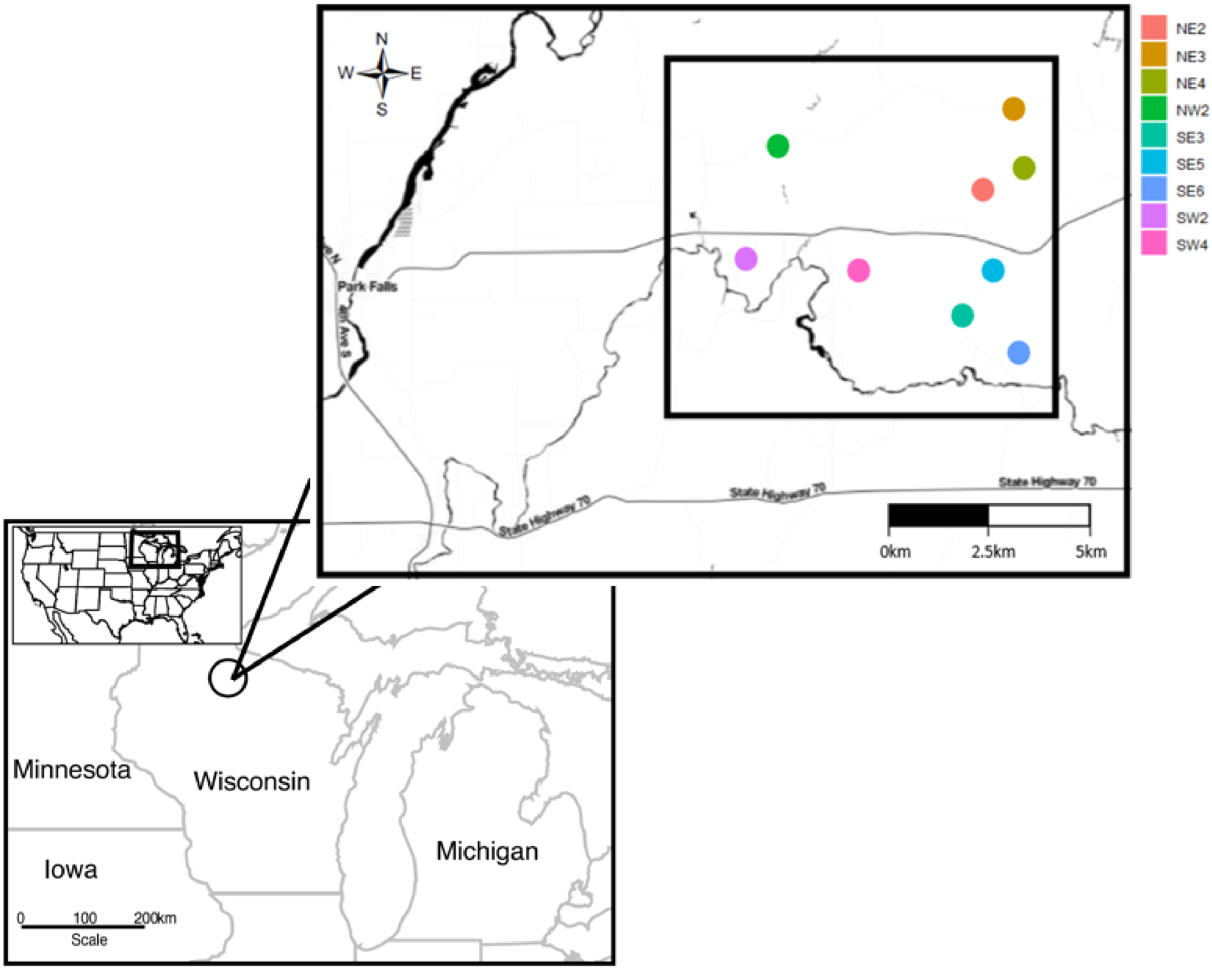


Figure 2.1: Map depicting the location of the study site within a regional and state context. The black circle on the state map depicts a 60-km radius around the location of the Park Falls, Wisconsin WLEF tall tower. Colored dots represent the nine sites within the 10 × 10 km CHEESEHEAD19 study domain (represented by the black square) selected for measurement of forest composition.

Forest CSC was measured at nine of the forested CHEESEHEAD19 study sites using UAS mounted discrete-return LiDAR (Figure 2.1). These nine sites were selected given their forested composition and representative forest type, as well as overlap with flux tower footprints. While climatic conditions and topography are shared across the nine sites, the selected sites span a range of successional stages, dominant vegetation types, management histories, and degrees of heterogeneity. Through pairing EC surface-atmosphere carbon and water fluxes with LiDAR-derived forest CSC metrics, mechanistic relationships between forest structure and function could be directly tested.

Mechanistic relationships were explored using best subsets regression for initial model selection and structural equation modeling (SEM), specifically path analysis. Best subsets regression is a variable selection technique where all possible combinations of predictor variables are explored, and a subset of predictive models are selected based on a suite of model fit and performance criteria (Hocking and Leslie, 1967). The top three models for each metric calculation resolution identified using best subsets regression were then evaluated through SEM to isolate the single best-fit model for each resolution. The application of SEM allows for the establishment not only of which CSC metrics are influential in predicting GPP, but the specific strengths, significance, and variability of their predictive power. In addition, SEM allows for the testing of variables that potentially serve as mediators of the relationship between CSC and GPP, through the comparison of reduced and saturated model designs (Fan et al., 2016). This study explored the viability of resource use efficiency (RUE) as a mediator of the structure-function relationship, as previous studies have demonstrated it to be a strong predictor of forest productivity (Atkins et al., 2018a, Atkins et al., 2018b, Gough et al., 2019). Both water use efficiency (WUE) and light use efficiency (LUE) were used to represent overall stand RUE.

RUE describes how well a forest stand captures and utilizes its available resources to fix carbon dioxide, with greater efficiency typically resulting in higher levels of biomass production (Anderson-Teixeira et al., 2021, Binkley et al., 2004). This paper focuses specifically on light and water as the primary limiting resources controlling the rate of photosynthesis, although other factors including the supply of CO_2, concentration of photosynthetic enzymes such as Rubisco, and availability of catalysts including nitrogen and phosphorous have been explored at length in other studies (Ainsworth and Long, 2005, Hardiman et al., 2013a, Hardiman et al., 2013b, Tang et al., 2018).

In addition, these mechanistic relationships were inspected at different structural metric calculation resolutions to determine whether the relationships persisted with scaling, or if they were simply artifacts of the resolution at which metrics were calculated. Structural metrics were calculated from discrete LiDAR returns (heights) collected at spatial resolutions of 0.25, 2, 10, 25, and 50 m. These five spatial resolutions refer to the size of each pixel contained within the gridded site area, where the gridded area is trimmed to match the average flux footprint of each site. For example, for the majority of the metrics calculated in this study, a metric calculation resolution of 2 m would correspond to a site area broken up into a grid of 2 m × 2 m pixels. CSC metric values are calculated using the LiDAR returns contained within each pixel, and metric values from each pixel are averaged together into a single representative value for each metric at each site. This range of CSC metric calculation resolutions was selected to (a) investigate fine-scale heterogeneity in structural complexity and its impact on ecosystem function, (b) overlap with the resolution of satellite-derived data products from instruments such as the Global Ecosystem Dynamics Investigation (GEDI) full-waveform LiDAR mounted on the International Space Station, and (c) represent a broad enough range in spatial scale to explore the dependency of metric values and derived mechanistic relationships of forest structure and function on spatial scale.

2.2.2 Site description

The study area is a 10 × 10 km domain located in the Chequamegon-Nicolet National Forest in Northern Wisconsin. Most of the region is heavily forested and trees are primarily broadleaf but a significant conifer presence exists as well. There is a high degree of heterogeneity representative of a typical midlatitude forest, displaying a diverse array of wetlands, meadows, streams, and lakes in addition to forest cover. Typical homogenous patches of land cover are generally around 20 ha or less (Desai et al., 2015). Heterogeneity is further accentuated by a long history of nonuniform forest management practices including thinning and clearcuts, resulting in increased variability in stand age and structure.

Forests in Northern Wisconsin typically have an age distribution centered around “middle age,” or 40–90 years (Birdsey et al., 2014, Wisconsin Department of Natural Resources, 2019). This age pattern is reflective of the fact that the majority of the forested land was logged in the mid-19th to early 20th century to clear land for agricultural purposes (Desai et al., 2008, Gough et al., 2007, Rhemtulla et al., 2009), which was followed by subsequent periods of agricultural land abandonment, reforestation, fire suppression, and intensive timber harvest (Birdsey et al., 2006). In addition to human management, the region experiences natural disturbance due to windstorms, insect invasion, and occasionally fire (Gough et al., 2007). Fires were historically influential during times of land clearing and Euro-American settlement (Rhemtulla et al., 2009), but wind damage has had more consistent impacts on stand structure and carbon storage over time (Schulte and Mladenoff, 2005).

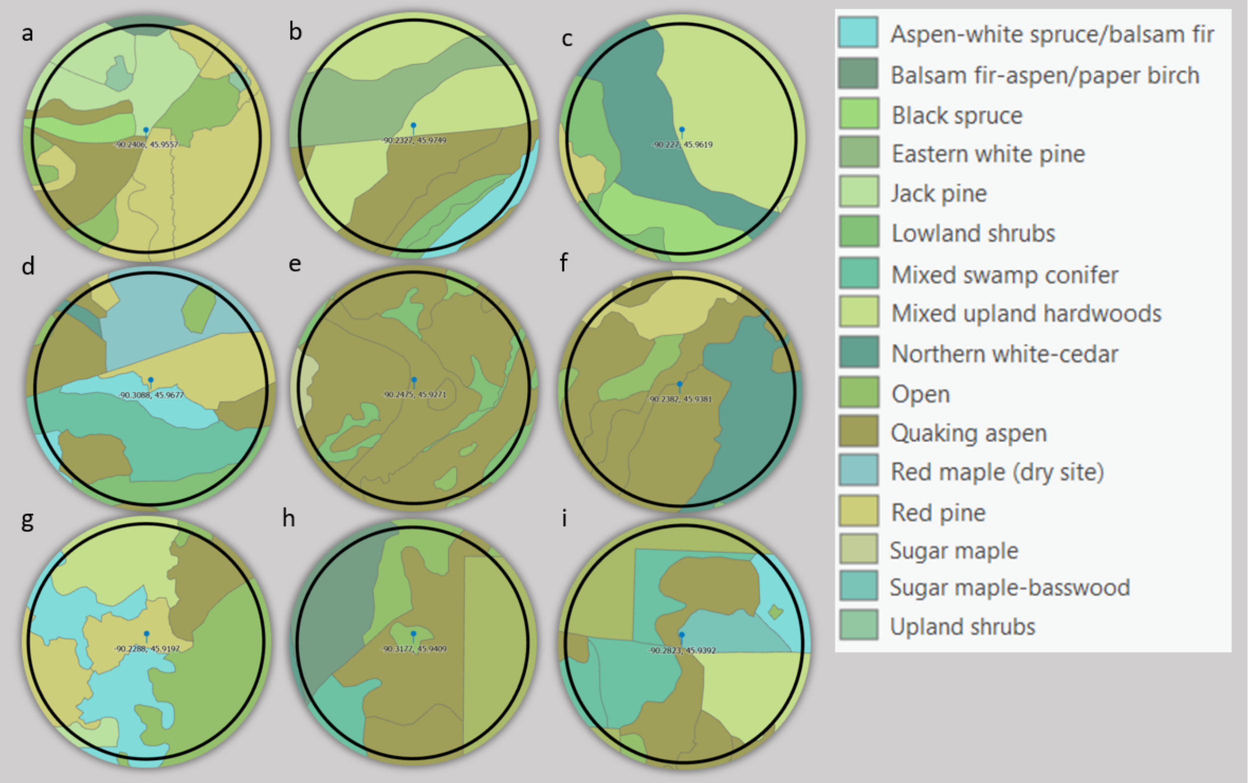


Figure 2.2: Vegetation coverage at each of the nine forested sites: **a)** NE2 **b)** NE3 **c)** NE4 **d)** NW2 **e)** SE3 **f)** SE5 **g)** SE6 **h)** SW2 and **i)** SW4. Coverage is segmented by both vegetation type and stand age.

The study domain is of relatively consistent low-grade elevation and human population is minimal. Slight variations in terrain elevation in combination with significant precipitation in all seasons results in a mix of saturated (wetland) and unsaturated (upland) sandy loam soils (Davis et al., 2003). Upland forests comprise roughly 65% of the landscape (Wisconsin Department of Natural Resources, 2019) and broadleaf deciduous tree types include quaking aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), basswood (*Tilia americana*), beech (*Fagus grandifolia*), and several varieties of oak and birch (Figure 2.2). Coniferous tree varieties include balsam fir (*Abies balsamea*), red, white, and jack pine (*Pinus resinosa, Pinus strobus, Pinus banksiana*), and white spruce (*Picea glauca*). Wetlands are both forested and unforested and account for ~35% of the land cover (Wisconsin Department of Natural Resources, 2019). Wetland tree species include alder (*Alnus incana*), cedar (*Thuja occidentalis*), tamarack (*Larix larcina*), and black spruce (*Picea mariana*; Davis et al., 2003). The area has a Köppen climate classification of Dfb, and experiences a humid continental climate characterized by warm humid summers and cold snowy winters, with no significant difference in precipitation between seasons (Arnfield 2021).

2.2.3 Flux tower data

Exchanges of carbon, water, and energy between the atmosphere and the land surface were collected at a frequency of 20 Hz using an open-path infrared H_2O and CO_2 gas analyzer (Campbell Scientific EC150) and sonic anemometer to measure three-dimensional wind speed (Campbell Scientific CSAT3AW). In addition to flux-specific instrumentation, the nine selected sites were similarly outfitted with meteorological instruments including slow-response air temperature and humidity sensors (NCAR SHT), barometers (Vaisala PTB210), and 4-component radiometers (Hukseflux NR01). Gas analyzers, sonic anemometers, barometers, and radiometers were all mounted at the top of the EC towers above the local forest canopy; mounting heights are presented in Table 2.1. Additional instrumentation included tower-mounted air temperature sensors at two levels within the canopy (2 m and mid canopy, which varied by site), and soil sensors (NCAR 4-level Tsoil, Meter EC-5 Qsoil, REBS HFT Gsoil, and Hukseflux TP01 Csoil) buried near the base of each tower in the upper soil profile (0–5 cm).

Instrument power was supplied via exchangeable batteries, which occasionally resulted in minimal data loss due to limited recharging capacity at the field operations base. NR01 radiometer deployment was delayed for sites NW2, NE3, SW2, and SE5, therefore no data exists for approximately the first 25 days of the study period. Radiometer data was filtered for sensor wetness and cleaning periods. Gas analyzers were cleaned 2–3 times during the study, and data was filtered out for periods of significant nighttime dew formation, which resulted in sensor biases.

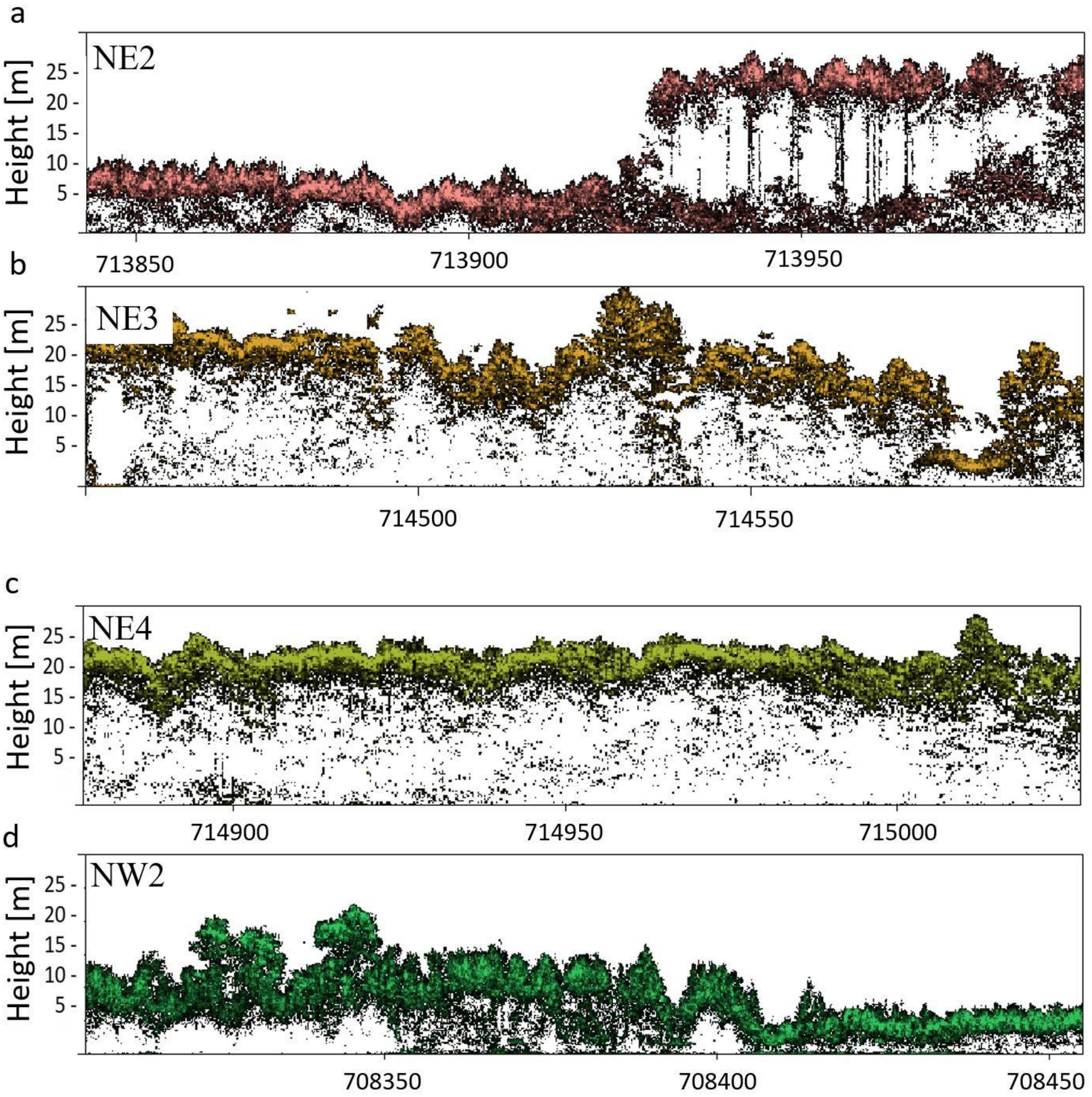
Table 2.1: LiDAR footprint size, instrument installation heights, and tree height metrics for each of the nine selected forest plots

Site	LiDAR footprint (km^2)	EC instrument height (m)	Avg. tree height (m)
NE2	0.48	32.00	14.20
NE3	0.24	32.00	18.10
NE4	0.18	32.00	18.70
NW2	0.23	12.00	8.80
SE3	0.82	32.00	8.10
SE5	0.22	13.00	12.40
SE6	0.23	32.00	10.30
SW2	0.22	30.00	10.90
SW4	0.82	32.00	13.50

Turbulent fluxes of carbon, water, and energy were calculated every 30 minutes from high-frequency (20 Hz) EC measurements. Prior to gap filling, a friction velocity (u*) threshold calculation was performed using the approach outlined in Wutzler et al. (2018), where the u* threshold is estimated with the moving point test. u* is a reference wind velocity that represents the shear stress arising through movement across the land surface. Below the u* threshold, turbulent mixing is weak enough that flux measurements are considered non representative of the actual flux state, and thus net ecosystem exchange (NEE) flux data are filtered out during those time periods. Gap filling and filtering of flux data were performed using the software REddyProc (Wutzler et al., 2018). Prior to gap filling, an average of 37% of NEE values were missing across all nine sites, with individual site missing values ranging from 26% (SW2) to 61% (SE5). A visual representation of EC quality control results for the four checks performed (sonic diagnostic, infrared gas analyzer diagnostic, stationarity, and integral turbulence characteristics) is shown in Figure S2.3. Missing data occurred to some degree at every site, although the reasons for missing data (equipment malfunction or cleaning, temporary power loss, moisture interference, etc.) varied. GPP was approximated from NEE using the flux partitioning method described in Reichstein et al. (2005) and was calculated using both the nighttime and the light response curve methods for respiration (Reichstein et al., 2012).

2.2.4 Drone – based LiDAR

To characterize three-dimensional forest structure, we employed a Routescene © discrete-return LiDAR onboard a UAS hexacopter DJI M600 Pro to collect high-density 3D scans (~600 points m^{-2}; Figure 2.3). Over the span of 25–29 June 2019, we surveyed the footprints of the nine selected flux tower sites and areas ranging between 0.25 and 1 km 2 per site (Table 2.1) with a flight footprint of approximately 500 × 500 m. Autonomous flights (with a duration of ~20 min each) were programmed using Universal ground Control Software (Ug CS) v3.2.113. Flights were performed at a speed of 6 m s^{-1}, 60 m above ground level, and 60 m side distance between parallel flight lines. Raw data were boresight calibrated, filtered and LiDAR heights were *.laz exported using Routescene proprietary software LidarViewer ©. Points within 1 mm radius were filtered and a box range filter centered on the sensor for each scan (scan rate 10 Hz) of 120 m width, 180 m height, and 120 m length was applied, ensuring each flight line would have complete overlap with other flight lines. Random noise was addressed using a statistical outlier removal filter and combined (only for multiple flights per site) in CloudCompare v2.10 (2019).



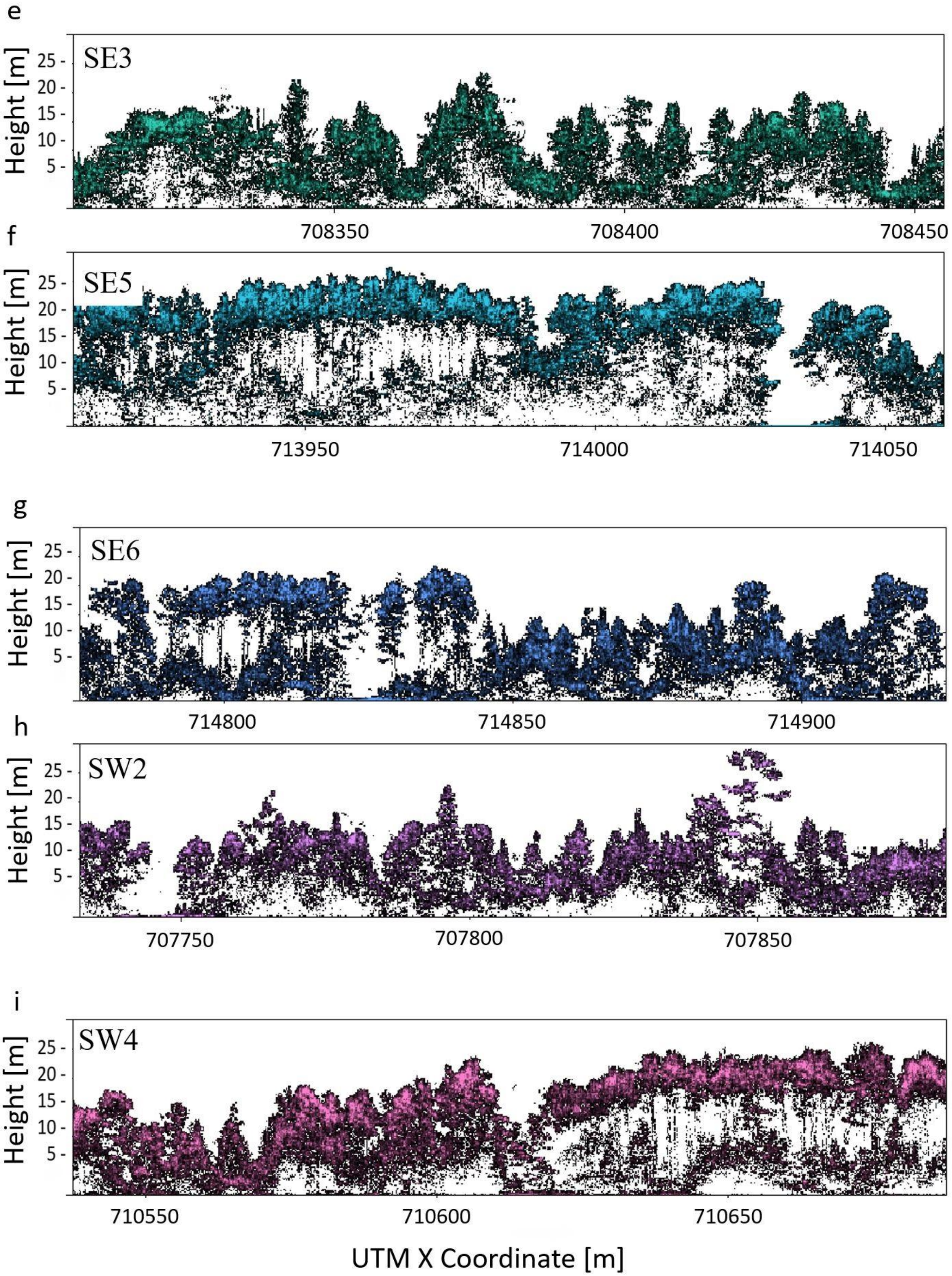

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Figure 2.3: Light Detection and Ranging (LiDAR) point return 150 m transect images for the nine forested sites: **(a)** NE2, **(b)** NE3, **(c)** NE4, **(d)** NW2, **(e)** SE3, **(f)** SE5, **(g)** SE6, **(h)** SW2, and **(i)** SW4. Color saturation represents the relative number of returns at a height interval. The x-axis represents longitudinal coordinates in meters, expressed at 50-m intervals, and the y-axis is height above ground in meters.

2.2.5 Stand age and disturbance

Stand age and disturbance history data were obtained from the publicly available United States Department of Agriculture Forest Service Geodata Clearinghouse. All sites had multiple distinct age classes present, representing a range of successional statuses (Figure S2.1). The majority of the sites were dominated by stands in the young to middle age classes (Table 2.2), although regeneration saplings younger than 5 years were not specifically accounted for. The young age class corresponds to the stand initiation and stem exclusion successional stages (Odum 1969), and the middle age class, defined by Pan et al. (2011) as roughly 40–100 years, corresponds to the understory reinitiation stage. Two sites (NE4 and SW2) contain stands that fall within the old growth successional stage, characterized in the temperate Lake States (Minnesota, Wisconsin, and Michigan) by the presence of long-lived tree species that are at or greater than 120 years of age and exist in an advanced stage of structural development (Frelich 1995). Forest Inventory Analysis data show that the oldest forests sampled in the temperate Lake States region are between 200 and 210 years old (Birdsey et al., 2014).

Table 2.2: Age, disturbance, and management history data for the nine selected forested sites

Site	Average Stand Age	Minimum Stand Age	Maximum Stand Age	Management & Disturbance History
NE2	56.77	92	18	Selective harvest, thinning, clearcut, blowdown, planting
NE3	71.29	108	41	Clearcut
NE4	108.5	150	76	Thinning, harvest
NW2	44.08	111	7	Blowdown, clearcut, thinning, planting, selective harvest
SE3	42	64	22	Hail damage, clearcut
SE5	55.67	106	7	Clearcut, shelterwood harvest, planting, thinning
SE6	49.5	92	19	Hail damage, blowdown, clearcut, thinning, harvest
SW2	63.5	124	26	Clearcut, planting
SW4	76.27	100	39	Blowdown, clearcut, harvest

Several sites have experienced significant disturbance in the form of clearcutting and harvest (Table 2.2), with the most recent harvest taking place in 2016 (SE6), and the most recent clear cut occurring in 2013 at stands in sites SE5 and NW2. Harvest is broadly defined here to include selective and shelterwood cuts as well as any harvest that is not stand replacing, whereas a clear cut specifies a stand replacing harvest occurring within the last 50 years. In addition to anthropogenic disturbance, sites SE6 and SE3 experienced substantial hail damage in the year 2000, and large-scale defoliation resulting from Forest Tent Caterpillar infestation occurred across the domain in 2001 (Wisconsin Department of Natural Resources). Blowdown due to wind stress has also been noted at sites SW4, SE6, NW2, and NE2, with the damage being most substantial at site SE6. Neither wildfire nor prescribed burning management activities have been a significant disturbance factor at any of the study plots. Species-specific planting has occurred at sites SW2, SE5, NW2, and NE2. The sites included in this study incorporate a range of management and disturbance histories that are broadly representative of temperate forests in the regional upper Midwest, but the effects of disturbance on forest structure and function explored here are largely qualitative, as neither stand age nor disturbance are expressly controlled for.

2.2.6 Metric extraction

LiDAR generated data sets were analyzed using the R programming language (R Core Team 2021; Version 4.0.4) package *lidR* (Roussel et al., 2020). The cloth simulation filter was used to identify ground points (Zhang et al., 2016) and triangulation was used to construct a digital terrain model from the ground points, which was then height-normalized. For each plot, 20 LiDAR metrics were calculated to describe tree height, arrangement, and stand complexity using the R programming language package *forestr* (Atkins et al., 2018a, Atkins et al., 2018), a complete list of calculated CSC metrics and references is included in Table S2.1. *forestr* gives a comprehensive formulation of metrics for characterizing forest canopy CSC and arrangement using either portable canopy LiDAR or terrestrial laser scanning ground-based LiDAR platforms. Several metrics described in the *lidR* R library were adapted for an area-based approach with a UAS platform.

With the exception of “Rumple” and “VerticalDistMax,” each of the metrics were calculated by creating a raster of the site with a value for each pixel, then finding the average or standard deviation for all pixels within the site. For example, to find the average tree height, a raster of each site was first created where each pixel in the raster was assigned the average height of all the LiDAR returns within the pixel. For this metric LiDAR returns under 0.5 m were removed to exclude most ground points from the calculation. To summarize the data as a single number, the mean of all the pixels in the raster was used. Each raster-based metric was calculated at a resolution of 0.25, 2, 10, 25, and 50 m per pixel to check for resolution dependencies.

Some metrics require additional explanation. Rumple was computed by creating a canopy height model for each site and dividing its area by the projected ground area. VerticalDistMax was computed by finding the vertical distribution of all the points in a site and determining which height bin contained the most points. Vertical bins of 0.5 m and a lower cutoff of 5 m were used to prevent the ground cover and understory from influencing the result. Both of these metrics were calculated on a per site basis instead of a per pixel basis. Leaf area index (LAI) was also calculated using the formulation provided in the *forestr* library (Atkins et al., 2018a, Atkins et al., 2018b) and compared to LAI field measurements for verification, which showed a high correlation of $R = 0.78$ ($p < 0.05$).

LUE was calculated as the ratio of total daily GPP to total daily incoming photosynthetic photon flux density (PPFD), where PPFD is the incident flux density of photosynthetically active radiation (PAR), or the number of photons incident per unit time on a unit surface (Olson et al., 2004). PPFD is considered a synonym for incident PAR (IPAR; Olson et al., 2004). The exchange of carbon between the forest plots and the atmosphere was measured by the EC towers directly and partitioned into GPP and ecosystem respiration, Reco (Reichstein et al., 2012). The site EC towers were only equipped to measure incoming and outgoing shortwave and longwave radiation as well as net radiation, as opposed to direct measurement of PPFD. Incoming shortwave radiation was converted to PPFD using a fraction of incoming solar irradiance in the photosynthetically active region of 0.50 (Knauer et al., 2018).

WUE describes the amount of carbon fixed per unit of water transpired (De Kauwe et al., 2013), and was calculated here as grams of carbon produced as biomass for every kilogram of water released through evapotranspiration (ET). ET is the sum of evaporation from the land surface and transpiration from vegetation, and is both the key process determining water use in forests (Fisher et al., 2017, Mathias & Thomas, 2021), and the primary process through which the carbon cycle is connected to and maintains the water cycle (Raupach et al., 2005). Since ET was not directly measured by this EC system, it was calculated from measured latent heat flux. Carbon values used in WUE calculations were drawn from EC tower measurements of GPP.

2.2.7 Model determination

A suite of linear regression models was tested to evaluate the relationships between CSC metrics, RUE, and stand productivity. Nonlinear models were not tested, as previous studies exploring multiple nonlinear model representations have shown that although the relationships may in reality be nonlinear, nonlinear representations repeatedly failed to achieve statistical significance (Gough et al., 2019). The combination of CSC and RUE metrics that best predicted stand GPP was assessed using best subsets model selection. Model fit was evaluated using the Schwarz Bayesian Criterion (SBC), mean square error prediction (MSEP), and adjusted R^2 (R^2_{adj}), where the model with the lowest significant SBC ($p < 0.05$), lowest MSEP, and highest R^2_{adj} was selected as optimal. SBC was used as opposed to Akaike information criterion to account for the presence of multiple predictive variables and a relatively small sample size.

High multicollinearity was a significant problem in determining which CSC metrics were the most robust drivers of GPP. Several CSC metrics had intercorrelation values that exceeded 0.98 and thus were not included in the SEM. This included metrics related to the height at which a given quantile of returned energy was reached relative to the ground, such as the mean of the

25th, 50th, 75th, and 95th quantile of point heights. Variance inflation factors (VIF) were calculated for the best-fit models, and models were classified as having severe multicollinearity if the average VIF was greater than 10. Pearson's correlation coefficients were used to determine the strength of pairwise interactions between variables for models where severe multicollinearity was a concern to determine which CSC metric was likely driving the observed multicollinearity, and that variable was subsequently removed and the resulting model was reevaluated. Pairwise correlations between variables selected for the final model formulation at each resolution are shown in Figure S2.2.

A SEM was used to ascertain the mechanistic relationship between stand productivity and the influential CSC metrics determined through best subsets selection, as well as whether or not the relationship was direct or was mediated by RUE. Path analysis, a subset of SEMs where models are created as a series of regressions to specify causal relationships between variables (Fan et al., 2016), was used to determine possible mediation effects of RUE through the comparison of reduced and saturated models. The reduced model allowed CSC metrics to predict WUE and LUE, and WUE and LUE to then predict GPP. The saturated model allowed for the same prediction pipeline, but CSC metrics could also bypass RUE and directly impact GPP (Figure 2.4). The existence of mediation in a relationship was determined by comparison of standardized beta coefficients in the uncontrolled path between predictor and response (the total effect) in bivariate models to beta coefficients representing the controlled path between predictor and response variables (the indirect effect) in multivariate models. The relationship between these controlled and uncontrolled pathway beta coefficients determines not only whether or not mediation exists, but also if it is partial or complete mediation. The strength of mediation is determined by the magnitude of the indirect effect.

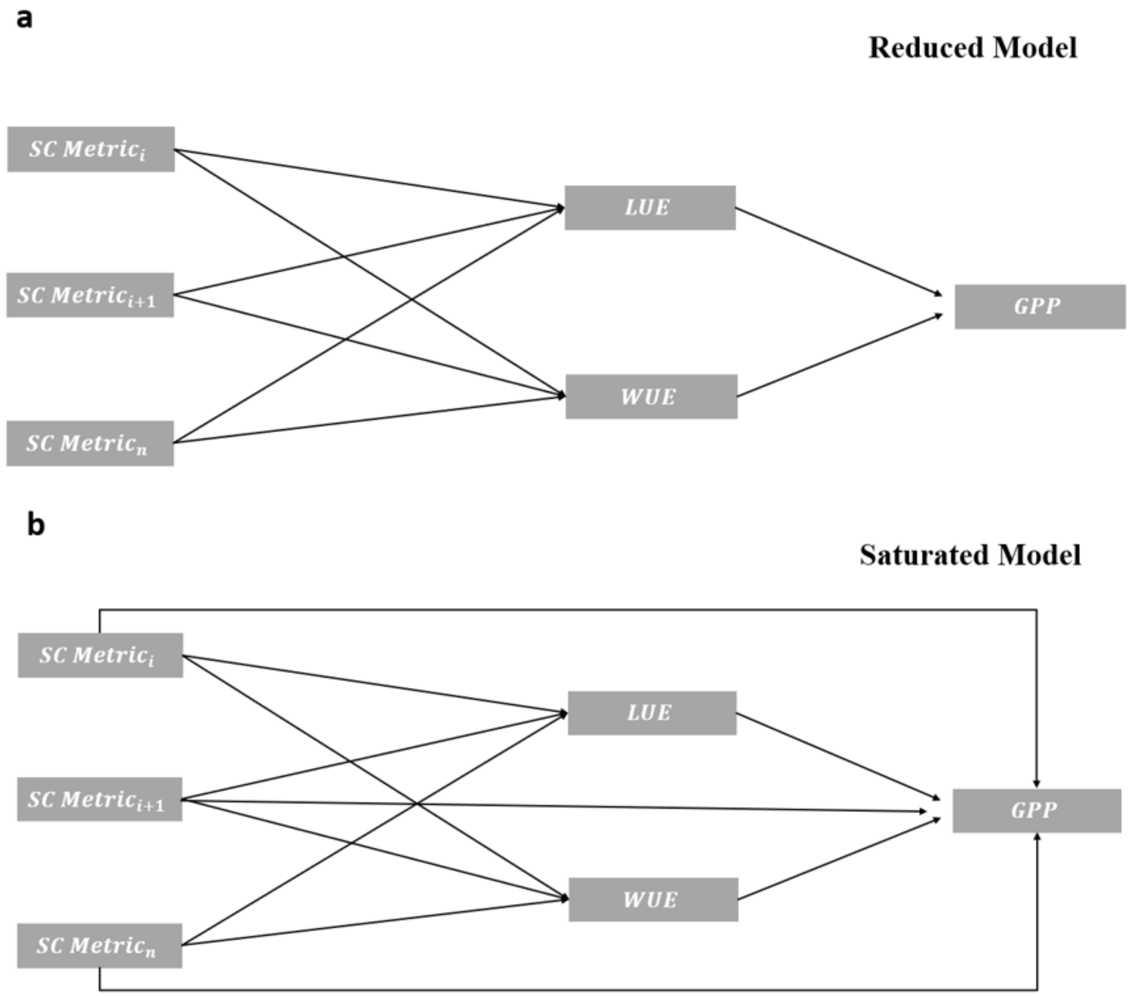


Figure 2.4: Conceptual figure outlining the **(a)** reduced and **(b)** saturated SEM model designs. The reduced model **(a)** restricts CSC metrics to influencing the dependent variable, GPP, indirectly through their effect on LUE and WUE, whereas the saturated model **(b)** allows CSC metrics to affect GPP both directly and indirectly through LUE and WUE. Arrows indicate the direction of influence from one variable to the next.

SEM was performed at each of the five resolutions for LiDAR metric calculation to assess whether or not the mediation effect persisted with resolution changes. Reduced and saturated model fit were assessed using comparative fit index (CFI), standardized root mean square residual (SRMR), and SBC. CFI values closer to one indicate better model fit, so a threshold value of ≥0.80 was applied (Hu et al., 1992). SRMR represents the difference between observed and expected variable correlations, and a threshold value of ≤0.90 was applied, with a lower value indicating a better model fit. Maximum likelihood estimation was used to determine model fit, and parameter estimates were standardized across all observed variables. Bootstrapping was used to test the significance of indirect effects (and thus the significance of mediation) between CSC variables and productivity through LUE and WUE as well as for estimation of standard errors and bootstrap-based confidence intervals. One thousand draws were performed for each indirect effect evaluated. Significance testing of mediation was performed using the R programming language (R Core Team 2021; Version 4.0.4) package *lavaan* (Rosseel 2012).

2.3 Results

2.3.1 Stand productivity and RUE

Of the nine CHEESEHEAD19 sites examined here, eight were classified as net carbon sinks, where a negative flux value indicates a net flux of carbon into the ecosystem from the atmosphere. A single site (NE2) was classified as a net carbon source, albeit a minor one, with a net flux of 35 g C m^{-2} released to the atmosphere over the entire measurement period. In addition, at eight out of the nine sites greater variability in daily fluxes was observed for GPP than NEE, with an average variance of 28 g C m^{-2} for GPP compared to 7.8 g C m^{-2} for NEE. Across all sites average daily GPP ranged from 2.6 g C m^{-2} to 14 g C m^{-2}, and average daily fluxes of NEE ranged between -3.5 g C m^{-2} and 0.30 g C m^{-2}. Substantial variability was observed in daily total ecosystem respiration (R_{eco}), defined as the sum of both heterotrophic and autotrophic respiration, with an average variance of 20 g C m^{-2}.

The highest productivity was observed at sites NE2, SW2, and SW4, with average GPP ranging from 10 – 14 g C m^{-2} day^{-1}. Although NE2 has the highest productivity of the nine sites, it also has the highest average daily R_{eco} (14 g C m^{-2} day^{-1}), resulting in its ultimate classification as a slight net carbon source to the atmosphere, as NEE = R_{eco} – GPP. The three sites with the lowest productivity are NW2, SE5, and NE4. NW2 has a higher number of clear cuts than all other sites, several stands described as wet conifer bogs, and includes stands ranging in age from 7 – 111 years. SE5 includes a mix of aspen, pine, and upland hardwoods ranging in age from 19 – 92 years. NE4 is a considerably older site, with stand age ranging from 76 – 150 years, and consisting of mixed upland hardwoods, pine, and northern white cedar. Over the course of the June-October observational period, productivity peaked in June to mid-July and decreased into fall as leaves began to senesce, with an average change in GPP across all nine sites of 19 g C m^{-2}. Of the sites, NW2 exhibited the least seasonal change in productivity, with a total difference of only 5.9 g C m^{-2} between the start and end of the study period.

Both LUE and WUE varied between sites, with the across-site average LUE equaling 0.70 g C MJ^{-1} and WUE equaling 4.1 g C kg H_2O^{-1}. Average LUE variance was 0.19 g C MJ^{-1} and average WUE variance was 1.4 g C kg H_2O^{-1}. Site NE2 had the highest RUE overall, with a daily LUE of 0.96 g C MJ^{-1} and a WUE of 5.7 g C kg H_2O^{-1}. NE2 also had the highest variability in RUE, although this variability follows a clear pattern indicating the changes in RUE potentially emerge as a response to changes in temperature or other climatic variables. Site NW2 had the lowest overall RUE, with a daily LUE of 0.33 g C MJ^{-1} and a WUE of 2.9 g C kg H_2O^{-1}.

Site NW2 had the lowest variability in LUE (0.11 g C MJ^{-1}), but the fourth highest variability in WUE (1.4 g C kg H_2O^{-1}).

2.3.2 Classification of structural complexity

Of the 20 LiDAR metrics originally calculated, twelve unique metrics related to CSC were shown through best subsets selection to be both influential and statistically significant drivers of stand productivity when combined with RUE variables ($p \leq 0.05$), and thus were included in subsequent SEM testing (Table 2.3). LUE and WUE were present in all of the best-fit models regardless of spatial resolution, but the specific CSC metrics included in each of the five best-fit models varied depending upon resolution, although several overarching trends stood out. CSC metrics describing vertical heterogeneity were the most prevalent and existed in each of the five final model formulations. VCI_mean (van Ewijk et al., 2011) was the most frequently observed CSC metric, and was included in four of the five models. maxZ_sd, a metric associated with outer canopy heterogeneity, was present in three out of five models, and verticalDistMax, a metric associated with vertical heterogeneity, and LAI_sd were present in two out of five models.

The remaining nine CSC metrics each only appeared in a best fit model formulation a single time, and included rumple, meanZ_sd, sdZ_sd, LAI_sd, maxZ_mean, sdZ_mean, gap_fraction, canopy_ratio_mean, and LAI_mean. Of these nine CSC metrics, four are related to vertical heterogeneity (sdZ_sd, sdZ_mean, canopy_ratio_mean, and meanZ_sd), one to outer canopy heterogeneity (rumple), one is a measure of mean outer canopy tree height (maxZ_mean), two describe the area and density of vegetation distribution (LAI_sd and LAI_mean), and one describes the degree of canopy cover and openness (gap_fraction). Of these nine CSC metrics, three are only present in the 25 m resolution model and two are only present in the 50 m resolution model indicating that the larger resolution models have a greater departure from the other best fit models. Fit metric ranges for the single best fit model at each resolution displayed no significant differences by resolution. Average was 0.32 with a range of 0.05, average BIC was 4418 with a range of 51, and average MSE was 16.40 g C m¯2 day¯1 with a range of 1.20 g C m¯2 day¯1. This suggests that CSC metric's viability as a driver of GPP isn't restricted to fine or coarse resolutions.

Table 2.3: Canopy structural complexity metrics included in SEM, isolated as highly influential through best subsets selection for their strength as drivers of GPP.

Resolution (m)	Metric	Symbol	Units	Complexity Category
0.25				
	rumple	rumple	ratio	canopy heterogeneity
	verticalDistMax	$VAI_{maxheightmean}$	m	vertical heterogeneity
	VCI_mean	VCI_{AVG}	-	vertical heterogeneity
2				
	VCI_mean	VCI_{AVG}	-	vertical heterogeneity
	LAI_mean	LAI_{AVG}	-	area and density
	meanZ_sd	σ_H	m	height

10				
	verticalDistMax	$\mathrm{VAI}_{\mathrm{maxheightmean}}$	m	vertical heterogeneity
	maxZ_sd	R_T	m	canopy heterogeneity
	maxZ_mean	MOCH	m	height
	VCI_mean	$\mathrm{VCI}_{\mathrm{AVG}}$	-	vertical heterogeneity
25				
	maxZ_sd	R_T	m	canopy heterogeneity
	sdZ_sd	$\mathrm{Vert}_{\mathrm{SDSD}}$	m	vertical heterogeneity
	sdZ_mean	$\mathrm{Vert}_{\mathrm{meanStd}}$	m	vertical heterogeneity
	LAI_sd	$\mathrm{LAI}_{\mathrm{SD}}$	-	area and density
50				
	maxZ_sd	R_T	m	canopy heterogeneity
	gap_fraction	Θ	ratio	cover and openness
	VCI_mean	$\mathrm{VCI}_{\mathrm{AVG}}$	-	vertical heterogeneity
	canopy_ratio_mean	$\mathrm{Canopy\ Ratio}_{\mathrm{AVG}}$	ratio	vertical heterogeneity
	LAI_sd	$\mathrm{LAI}_{\mathrm{SD}}$	-	area and density

All twelve of the site averaged CSC metrics varied depending upon the pixel size used in metric calculation. The majority of CSC metrics decreased in value as resolution became coarser, however, five of the twelve metrics (MOCH, $\mathrm{Vert}_{\mathrm{meanStd}}$, and $\mathrm{VCI}_{\mathrm{AVG},}$ Θ, and Canopy $\mathrm{Ratio}_{\mathrm{AVG}}$) displayed the opposite trend (Figure 2.5). The observed shifts in metric values with changing resolution indicated that the overall mechanistic relationships between CSC metrics and productivity could be resolution dependent. The greatest differences with shifting resolution were observed in $\mathrm{VAI}_{\mathrm{maxheightmean}}$ and $\mathrm{VCI}_{\mathrm{AVG}}$. $\mathrm{VAI}_{\mathrm{maxheightmean}}$ decreases with decreasing spatial resolution, with values being reduced to 25 – 30% of the 0.25 m resolution value by the time a 10 m resolution was reached, and all sites had the same value (5m) upon reaching the 25 m resolution. $\mathrm{VCI}_{\mathrm{AVG}}$ increased with decreasing spatial resolution, with values increasing on average by 20% with each decrease in resolution, although the difference between 10 m and 25 m was less pronounced, with an average difference of 5%, and metric values are relatively stable by 50 m resolution.

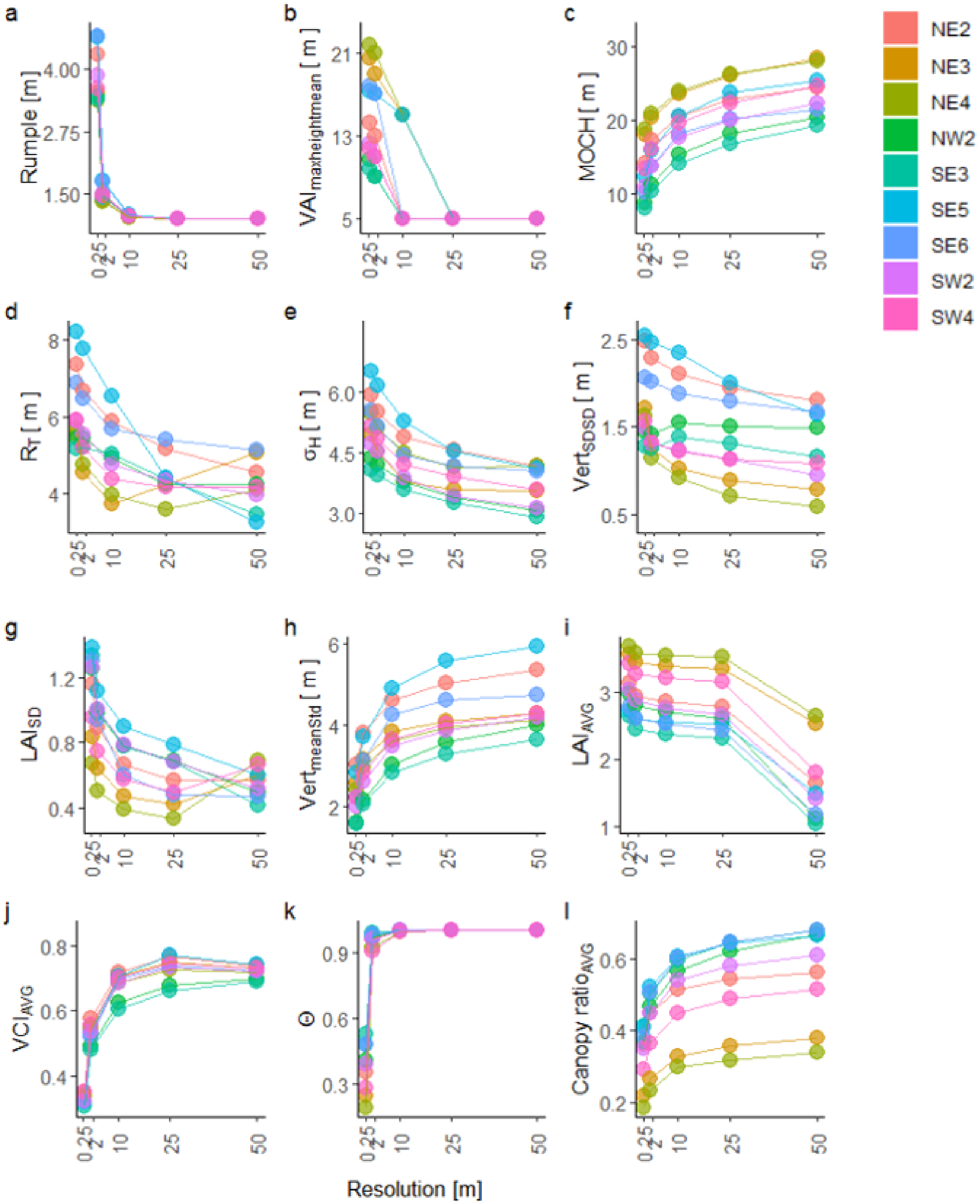


Figure 2.5: CSC metric values by site at each of the five metric calculation resolutions explored, 0.25 m, 2 m, 10 m, 25 m, and 50 m.

Vertical heterogeneity metrics describing the layering of the canopy such as σ_H, Canopy $\text{Ratio}_{\text{AVG}}$ (Schneider et al., 2017), and $\text{Vert}_{\text{meanStd}}$ generally had higher values at sites with distinct multilayered canopies such as NE2 and SE5, and lower values at sites with a more consistent single layered canopy, such as site NE4. Variability in $\text{Vert}_{\text{meanStd}}$ values generally increased with decreasing resolution, with an increase in spread between sites of 45% from 0.25 m to 50 m resolution, whereas site-to-site variability decreased by approximately 46% with decreasing resolution for σ_H.

CSC metrics VCI_{AVG} and vertical variability ($\text{Vert}_{\text{SDSD}}$) offer insight as to the degree of variability in the distribution of vegetation within each vertical column. $\text{Vert}_{\text{SDSD}}$ is similar to the metric ‘StdStd’ described in Atkins et al., 2018, but it represents the standard deviation column variability of tree height, as opposed to mean leaf height. The highest VCI_{AVG} values were observed at site NE2 (9% higher than the average of the other eight sites, at a resolution of 0.25 m), and the lowest values were typically seen at sites SE3 and NW2, depending upon spatial resolution. Variability between sites increased with decreasing resolution, largely in part to a widening spread between SE3 and NW2 and the remaining seven sites. The highest $\text{Vert}_{\text{SDSD}}$ values, indicating a less uniform vertical distribution of vegetation, were measured at sites with multilayered canopies and multiple distinct age classes present, such as SW4 and NW2, which include stands ranging in age from 7 – 110 years.

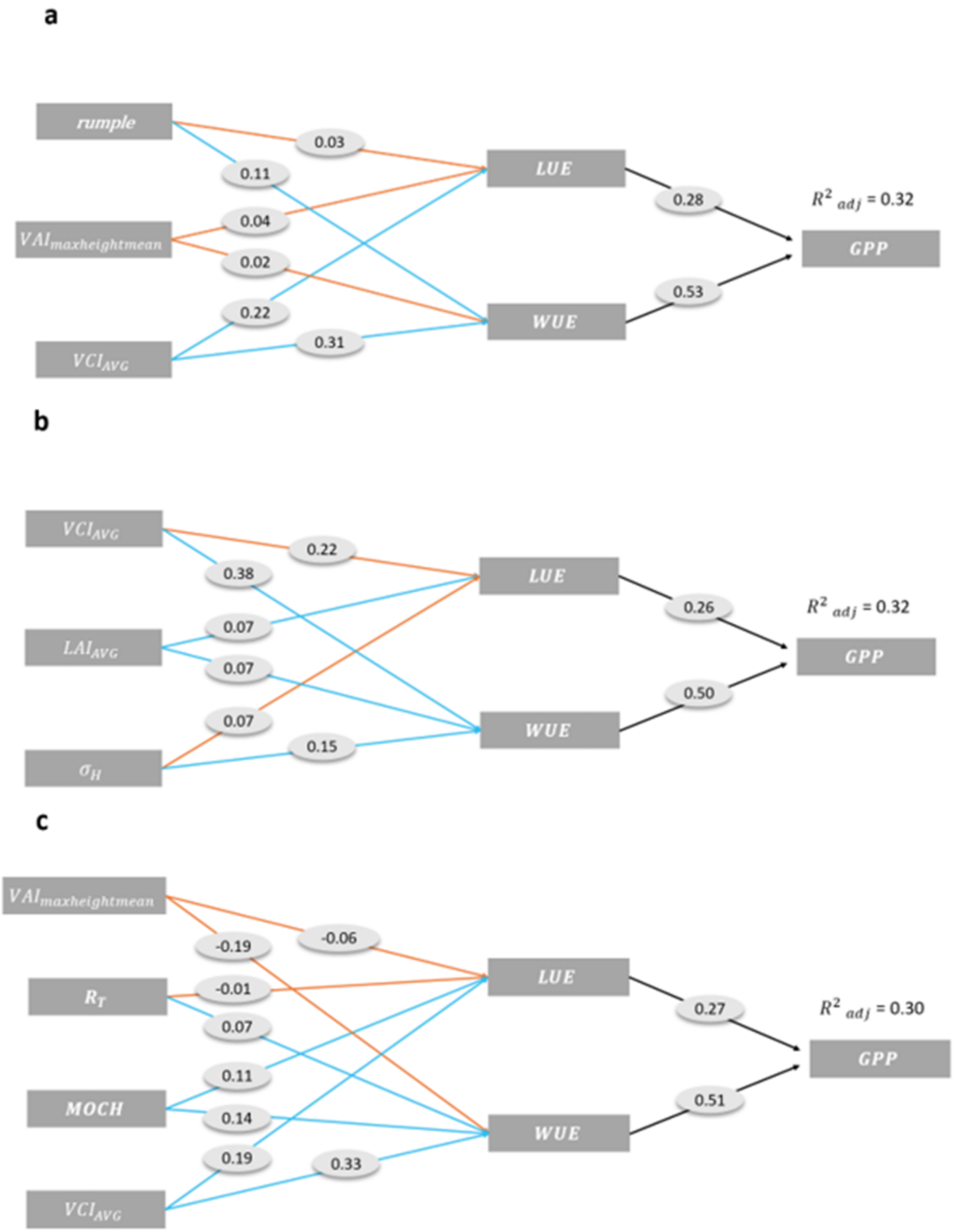
The final CSC metric addressing vertical heterogeneity is VerticalDistMax. VerticalDistMax is equivalent to the variable ‘mean height of vegetation area index maximum’ ($\text{VAI}_{\text{maxheightmean}}$) described in the *forestr* package (previously referred to as VAI_{mode} in Atkins et al., 2018). For resolutions 0.25 m and 2 m, the highest $\text{VAI}_{\text{maxheightmean}}$ values are seen at sites NE3 and NE4, and the lowest values are seen at sites NW2 and SE3. For 10 m resolution only two values of $\mathrm{VAI}_{\mathrm{maxheightmean}}$ exist, 5 m and 15 m, with three sites (NE2, NE3, and SW4) having values of 15 m and the remaining sites having values of 5 m. By 25 m model resolution all sites have the same $\mathrm{VAI}_{\mathrm{maxheightmean}}$ value of 5 m, indicating that the metric calculation resolution has a significant impact on $\mathrm{VAI}_{\mathrm{maxheightmean}}$.

Influential CSC metrics representing outer canopy complexity include rumple and top rugosity (R_T). Rumple is defined as the ratio of the outer canopy surface area to the underlying ground surface area (Parker et al., 2004), where a higher value corresponds to a more complex canopy (Kane et al., 2010). Average rumple values were significantly impacted by metric calculation resolution, and substantially decreased at resolutions coarser than 0.25 m, indicating that at coarser resolutions the outer canopy surface appears artificially smoothed. Variability between sites also decreased with decreasing resolution, and at resolutions coarser than 2 m, differences in rumple values between sites were negligible. For context, in a Douglas-fir and western hemlock dominated 500+ year old growth forest in Southern Washington (USA) with an extremely high level of outer canopy complexity, rumple values of 12 m were reported (Parker et al., 2004). R_T refers to the standard deviation of LiDAR column maximum return heights (Atkins et al., 2018a). The highest values of R_T were observed at NE3 and NE4, with an average range of 3.3 m to 8.2 m across all five resolutions.

Mean outer canopy tree height (MOCH) serves as a simple measure of vertical stand structure, by describing the maximum tree height averaged across all present species in a given stand. MOCH values increase with decreasing resolution, presumably because taller trees dominate and skew the average when a larger field of view is utilized. LAI is the ratio of the (one-sided) total leaf area per unit of ground area, and describes the amount of leaf tissue exposed to ambient light in the forest canopy. The highest values of $\mathrm{LAI}_{\mathrm{AVG}}$ were observed at sites NE3 and NE4, both among the oldest sites, and the lowest values were seen at sites SE3 and SE5, both fairly young aspen sites, with an overall range of 1.0 m to 3.7 m across all five resolutions. LAI_{SD} describes the standard deviation, or the variability in LAI, and offers insight into how photosynthetic tissues are distributed in the forest canopy. The highest values were observed at site SW4, and the lowest values were seen at sites NE2 and NE3, with a total range of 0.34 to 1.4. LAI_{SD} values generally decrease with decreasing resolution, with a reduction in variability between sites (decrease in variability of 36% from 0.25 m to 25 m resolution). Θ showed the greatest variability between sites at a resolution of 0.25 m, and at resolutions of 10 m and greater differences between sites became indistinguishable.

2.3.3 Structural equation modeling

Comparison of SEM models showed that the reduced model, where CSC metrics were restricted to influencing GPP through RUE as opposed to exerting direct influence over GPP, had a better overall fit than the fully saturated model. In other words, LUE and WUE actively mediate the mechanistic relationship between CSC variables and GPP, and changes in CSC result in changes in RUE and ultimately in GPP.


a
rumple
$VAI_{maxheightmean}$
VCI_{AVG}
0.03
0.11
0.04
0.02
0.22
0.31
LUE
WUE
0.28
0.53
R^2_{adj} = 0.32
GPP
b
VCI_{AVG}
LAI_{AVG}
σ_H
0.22
0.38
0.07
0.07
0.07
0.15
LUE
WUE
0.26
0.50
R^2_{adj} = 0.32
GPP
c
$VAI_{maxheightmean}$
R_T
MOCH
VCI_{AVG}
-0.06
-0.19
-0.01
0.07
0.11
0.14
0.19
0.33
LUE
WUE
0.27
0.51
R^2_{adj} = 0.30
GPP

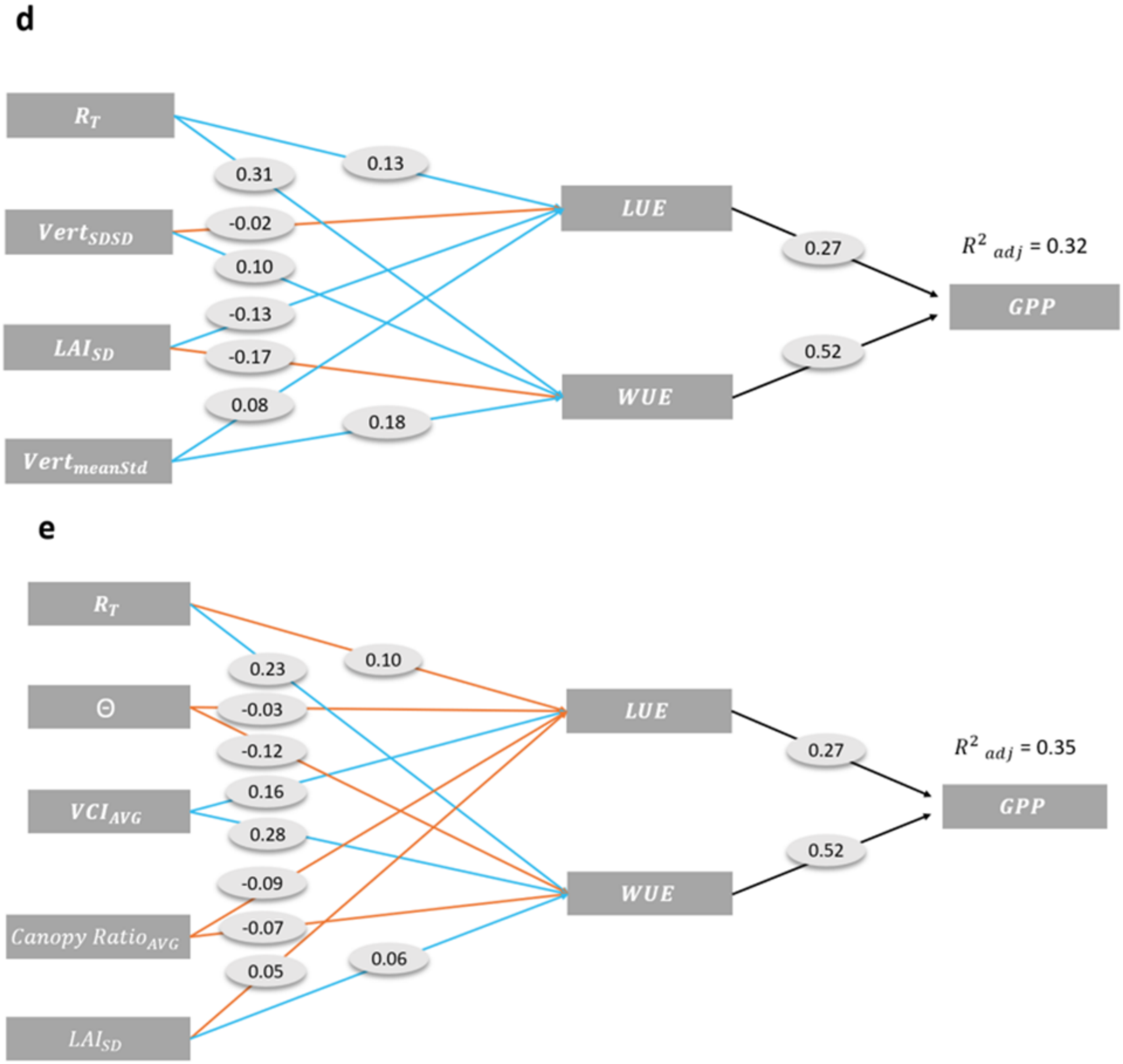


Figure 2.6: Reduced SEM diagrams at CSC metric calculation resolutions of 0.25 m **(a)**, 2 m **(b)**, 10 m **(c)**, 25 m **(d)**, and 50 m **(e)**. CSC predictor variables are on the far left, mediating variables (LUE and WUE) are in the center, and the response variable, GPP, is on the far right. Standardized regression coefficients are shown in gray circles. Blue lines indicate a statistically significant ($P < 0.01$) mediation effect between mediating and predictive variables, while orange lines indicate that mediation either does not exist or is not statistically significant.

Across all five models, 38 mediation relationships were tested in total; 19 WUE mediated relationships and 19 LUE mediated relationships. The strength of mediation is determined by the magnitude of the indirect effect, where the indirect effect is calculated as the product of standardized beta coefficients representing the path between the predictor and mediation variables and the path between mediation variables and the response variable. 14 of the 19 WUE mediated relationships were significant (Figure 2.6), with all cases being partial mediation, complete mediation was not observed for either WUE or LUE. WUE as a mediator between GPP and the metrics $VAI_{maxheightmean}$ (present in 0.25 m and 10 m resolution models), LAI_{SD} (present in the 25 m resolution model), Θ and Canopy $Ratio_{AVG}$ (both only present in the 50 m resolution model) were never shown to be significant. Mediation strength, characterized by the magnitude of the indirect effect of a given CSC metric on GPP through WUE as a mediator was 0.10 on average, with a range of 0.14.

Eight of the 19 LUE mediated relationships were significant (Figure 2.6), and metrics directly tied to light interception such as those related to LAI (LAI_{AVG} and LAI_{SD}) were always significantly mediated by LUE. LUE significantly mediated relationships between GPP and VCI_{AVG}, MOCH, R_T, and $Vert_{meanStd}$ as well, but the significance of mediation was not always consistent when a given CSC metric was present in different resolution models. LUE never significantly mediated relationships between GPP and $VAI_{maxheightmean}$, rumple, σ_H, $Vert_{SDSD}$, Θ, or Canopy $Ratio_{AVG}$, regardless of spatial resolution. Mediation strength of LUE on the relationship between a given CSC metric and GPP was 0.03 on average, with a range of 0.08. WUE was shown to be a substantially stronger mediator between CSC and GPP than LUE, with a standardized mediation strength 290% larger than that of LUE when averaged across all nine plots. Averaged across all sites, the correlation between daily WUE and daily LUE was 0.40.

Mediation analysis by resolution showed differing trends between WUE and LUE as mediators. The significance of WUE as a mediator did not appear to be resolution dependent, whereas the significance of LUE as a mediator did appear to be dependent upon the spatial resolution of the model in question. For example, LUE was a significant mediator of R_T in the 25 m resolution model, but not in the 10 m resolution model. The presence of LUE as a significant mediator was more prevalent at coarser spatial resolutions (10 m and 25 m) than at finer resolutions (0.25 m and 2 m), but LUE only significantly mediated one of the five predictive variables included in the 50 m resolution best fit model (VCI_{AVG}). Cases where the structure-function relationship was mediated by both WUE and LUE were observed more frequently at coarser resolutions than at finer resolutions, with the exception of the 50 m resolution model.

In summary, for CSC metrics that experienced mediation (all but $VAI_{maxheightmean}$) the presence of a mediating factor in the overarching relationship between forest structure and function was consistent regardless of CSC metric calculation resolution, but which individual relationships were significantly mediated changed with resolution shifts when LUE was the mediating variable in question. Mediation effects were the least pronounced at a metric calculation resolution of 50 m, but this is potentially influenced by the higher prevalence of edge effects at such a coarse resolution, and the associated influence on metric uncertainty. Due to the variety of measurement units involved, beta coefficients were standardized to facilitate comparison and outliers were removed. Standardized beta coefficients show that at a resolution of 0.25 m, VCI_{AVG} and rumple were the strongest drivers of GPP ($\beta = 0.33$, $\beta = 0.11$), at 2 m VCI_{AVG} was the strongest driver of GPP ($\beta = 0.35$) followed by σ_H ($\beta = 0.16$), at 10 m^2 VCI_{AVG} and H_{AVG} were the strongest drivers of GPP ($\beta = 0.33$, $\beta = 0.16$), at 25 m spatial resolution R_T

and $\text{Vert}_{\text{meanStd}}$ were the strongest drivers ($\beta = 0.22$, $\beta = 0.18$), and at 50 m VCI_{AVG} and Θ were the strongest drivers ($\beta = 0.30$, $\beta = -0.11$). Additionally, all CSC metrics were stronger drivers of WUE than of LUE.

2.4 Discussion

Our findings support the emerging consensus that a positive mechanistic relationship exists between CSC and productivity in mixed temperate forests (Gough et al., 2019, Gough et al., 2016), but suggest that this is a multifaceted relationship impacted by additional factors such as species diversity and management history. As well, we found that this relationship is not direct but rather is mediated by the effective acquisition and assimilation of both light and water resources, and that RUE generally is enhanced by increasing CSC. Furthermore, we show that in a heterogenous mixed temperate forest subject to disturbance, metrics describing the vertical profile of heterogeneity are the strongest drivers of productivity, as opposed to CSC metrics that are constrained to the outer canopy.

Through analysis of the structure-function relationship at five structural metric calculation resolutions ranging from 0.25 m to 50 m, we demonstrate that the scale of metric calculation has a significant impact on the metric values themselves, and thus on which CSC metrics are ultimately included in predictive models of productivity. We showed that shifting the spatial resolution also changes the dynamics of the relationship between RUE and CSC. Lastly, it was established that even in a study domain where sites have shared climatic and environmental conditions, differences in management and disturbance history as well as species diversity result in substantial variability in land-atmosphere exchanges of CO_2. This is likely due to changes in forest composition and trait diversity in response to disturbance.

2.4.1 Structural complexity

VCI_{AVG} was the most frequently observed CSC metric in the models, and consistently proved to be the most robust driver of both RUE and GPP in models where it was present, irrespective of spatial resolution. However, CSC metrics related to outer canopy heterogeneity such as and rumple were also imperative. Four out of the five best fit models included CSC metrics related to both vertical and outer canopy heterogeneity, although vertical metrics were more prevalent in all cases. VCI_{AVG} describes how the vertical distributions of LiDAR returns differ from a uniform distribution, which is representative of the overall evenness of the vertical distribution of vegetation (van Ewijk et al., 2011, Kane et al., 2010a, Kane et al., 2010b). In an example presented by van Ewijk et al. (2011), a low VCI_{AVG} could correspond to the stand initiation stage, where the majority of point returns are congregated in the lowest vertical bins, whereas a mid to high VCI_{AVG} could correspond to a stand in the midst of understory re-initiation or even a transition into old growth, where vegetation is distributed between multiple height bins. The VCI_{AVG} values observed within the study domain are consistent with the relative dominance of stands in the young to middle age classes.

The CSC metric $VAI_{maxheightmean}$ conveys important information about biomass allocation patterns. Models that did not contain $VAI_{maxheightmean}$ did contain CSC metrics related to LAI, suggesting that incorporating a variable that accounts for the complexity in arrangement of vegetative tissues is essential when describing a stand's ability to absorb incoming light. VAI is similar to the more commonly used LAI, but vegetative tissues include branches and stems in addition to photosynthesizing leaves (Scheuermann et al., 2018). However, it's worth noting that several studies have shown that the influence of LAI on production saturates in importance over time, but the same trend has not been observed in VAI (Hardiman et al., 2011), potentially making it a more reliable metric overall when describing the area-related distribution of vegetative tissues. σ_H is the standard deviation of the mean height of lidar returns for raster pixels, and builds on the canopy layering information provided by $VAI_{maxheightmean}$ by representing the variability associated with the height of greatest leaf density. High values (corresponding to a multilayered canopy) were observed at sites with a variety of age classes present, where harvest practices have resulted in patches with unique canopy features, such as site NE2 (Figure 2.3).

$Vert_{meanStd}$ is a reliable indicator of the spread between distinct canopy layers, high values were observed at sites such as NE2, which includes a dense canopy between 5 m – 10 m tall with an additional canopy around 25 m tall, and a fairly sparse degree of vegetation between the two canopies (Figure 3). Pairing this metric with $Vert_{SDSD}$ illustrates the variability in vertical forest profiles, and offers insight into the arrangement of the understory. For example, high values of $Vert_{SDSD}$ were observed at sites with dense non-uniform understories, such as site SW4. In addition to conveying information about forest successional stage when combined with species information, MOCH is important to consider when interpreting the significance of observed rumple values (Kane et al., 2010b), as rumple generally increases with increasing tree height. At first glance sites NE4 and NW2 could be classified as having similar levels of complexity, with rumple values of 3.4 m and 3.5 m respectively at 0.25 m resolution. However, the large differences in MOCH between the sites (19 m versus 8.8 m) draws attention to the fact that the variance in complexity between the two sites is more pronounced, as a similar rumple value for a stand with less than half the MOCH of NE4 indicates that NW2 has a higher degree of CSC than is present at NE4.

The prevalence of vertical heterogeneity metrics focused on canopy layering and vegetation distribution in the models explored here further supports recent findings indicating that vertical complexity is a strong driver of productivity in mixed temperate systems (Fahey et al., 2019), that it plays an important role in determining seasonal dynamics in forest productivity (Smith et al., 2019, Tang and Dubayah, 2017) and emphasizes the role of vertical variation in driving biomass growth (Stark et al., 2012). All twelve influential CSC metrics explored here were sensitive to changes in metric calculation resolution, highlighting the need for consistency in the spatial resolution at which CSC metrics are calculated, and for the disclosure of metric calculation resolutions when reporting CSC metric values and interpreting the significance of findings.

For most CSC metrics, values decreased as resolution became coarser (with MOCH, $\text{Vert}_{\text{meanStd}}$, and VCI_{AVG} as exceptions), as did variability between sites. Moreover, differences between sites became indistinguishable for rumple, $\text{VAI}_{\text{maxheightmean}}$, and Θ at resolutions coarser than 10m. This suggests that for research questions centered around discerning differences in CSC between sites and the potential impacts of those differences on ecosystem function, a finer resolution should be used for CSC metric calculation. However, which sites are classified as most or least structurally complex overall is relatively consistent regardless of metric calculation resolution. Sites SE5 and NE2 consistently rank as the sites with the highest complexity, and sites SE3 and NW2 dependably rank as the sites with the lowest complexity. For some sites, such as NE3 and NE4, the comparative complexity ranking differs depending on which metric is being examined, for example both sites have very high complexity rankings in metrics LAI_{AVG}, $\text{VAI}_{\text{maxheightmean}}$, and MOCH regardless of resolution, but consistently rank low in metrics R_T, LAI_{SD}, rumple, and $\text{Vert}_{\text{SDSD}}$.

Ultimately CSC can’t be encapsulated by a single metric, and a select set of metrics will provide a more comprehensive representation. For instance, pairing a variable like that offers insight as to whether a canopy is single or multi-layered with a variable like $\mathrm{LAI}_{\mathrm{AVG}}$ that describes the density and arrangement of photosynthetic tissues will reveal more about a stand’s potential productivity than either variable in isolation could. However, which metrics should be included in predictive models of productivity isn’t a one size fits all situation, as shown here it is contingent upon spatial resolution.

2.4.2 The structure function relationship

Here we showed that a positive mechanistic relationship exists between CSC and forest productivity in mixed temperate forests, and that CSC metrics which describe the vertical profile of heterogeneity are better predictors of GPP than metrics that are limited to the outer canopy alone. This is potentially due to vertical complexity metrics providing greater information content in terms of describing a forest’s successional stage and ability to capture light as it moves beyond the outer surface of the canopy and penetrates into the forest below (Zimble et al., 2003). As early successional species overtake forest gaps created by disturbance to establish multi-canopied stands, the more biodiverse forest with greater structural complexity and range of shade tolerances will make the forest more resource efficient under variable light conditions, increasing net carbon uptake (Hardiman et al., 2011, Hardiman et al., 2013b, Hooper et al., 2005). For example, NE2, which has the highest GPP, WUE, and LUE, also exhibits high levels of CSC across the majority of the metrics evaluated. NE2 is predominantly pine, with aspen and paper birch intermixed (Figure 2.2). Due to a history of timber harvest and replanting (Table 2.2) there is a significant secondary pine canopy (Figure 2.3) with an average age of 22 years. This multi-layered canopy is captured in the second highest values of VCI_{AVG} observed across all nine sites (at a spatial resolution of 0.25 m $VCI_{AVG} = 0.35$, 10% higher than the following seven sites), while MOCH and rumple were also comparatively high, at 10% higher than average and 4.4% higher than average respectively.

Mediation of the structure-function relationship by RUE existed at all five CSC metric calculation resolutions, but was the least pronounced at a resolution of 50 m, where mediation was present in fewer than half of the mediation pathways that were tested (Figure 2.6). At a resolution of 50 m, CSC metrics are calculated within a 2,500 m^2 pixel. With such a large pixel size, edge effects are more pronounced, and can affect metric values, which can ultimately impact the mechanistic relationships that are derived using those values. Pixels located at the edge of a site contain a portion of the available LiDAR data, but a portion of the total pixel area lies outside of the available LiDAR data range, meaning that data collected in these edge pixels is essentially weighted higher than data collected across the rest of the site, because the pixels contain less LiDAR data but still cover the same total area. These edge effects manifest as uncertainty in CSC metric values. While negligible at fine resolutions such as 2 m or 10 m, at larger scales the added uncertainty is amplified.

SEM highlighted WUE as a considerably stronger driver of GPP than LUE, but it's important to pause here and consider that the temperate mixed forests of Northern Wisconsin are not water limited ecosystems, and previous studies have shown that stand-scale productivity is predominantly a function of the capacity to harvest light and fix carbon (Reich et al., 2012), so why does WUE show up as highly influential when predicting GPP? The answer lies primarily in the relationship between WUE and LUE. The tiny stomata covering the leaf surface exist in a constant tradeoff between opening and sacrificing water for the chance to take up CO_2, both of which are necessary ingredients for photosynthesis (Monteith 1965). Regardless of available light, when plants are water stressed, stomata close in an attempt to conserve existing resources, at the cost of reducing CO_2 uptake and thus photosynthetic capacity (Hatfield and Dold, 2019, Kukal and Irmak, 2020). However, when a plant has a steady supply of water, stomata will more readily open and a greater amount of atmospheric CO_2 can be fixed per unit of incident light (Binkley et al., 2004). A recent study by Ehbrecht et al. (2021) examining climatic controls on CSC at the global scale found that CSC was strongly correlated with water availability across all biomes examined, and that the relationship between water availability and use and CSC can be tied to mechanisms determining tree size. This is because water availability effectively controls functional diversity and shade tolerance as well as tree size following the hydrological limitation hypothesis (Ehbrecht et al., 2021). Shade tolerant trees are found in greater abundance in systems where growth is not limited by factors other than light, such as the non-water limited systems present in Northern Wisconsin. All three of these factors (functional diversity, shade tolerance, tree size) contribute to CSC (Thom et al., 2021). In addition, a recent study by Smith et al. (2019) showed that vertical heterogeneity in particular plays an important role in modulating seasonal responses to water availability. Although the Smith et al. (2019) study took place in a tropical forest, comparable relationships may also exist in temperate forests such as our site, which experiences a warm, humid growing season and is not typically water limited.

However, the importance of the relationship between CSC and LUE cannot be understated, as it shows that the functional diversity driven by complexity is able to better capitalize on available resources (Williams et al., 2016, Penone et al., 2019). As well, although this study was limited in duration, other studies such as the Zhang et al. (2012) global meta-analysis of diversity productivity relationships showed that almost 30% of the variation in productivity between monocultures and polycultures was explained by heterogeneity of shade tolerance, and that high shade tolerance variation within a community is likely one of the most important life-history traits, leading to more efficient resource use when scaled to the ecosystem level (Stark et al., 2012).

For most CSC metrics examined here, increasing CSC is associated with increasing RUE, although the magnitude of the trend is dependent upon resolution. The exception is LAI_{SD}, which has a negative relationship with both WUE and LUE at all resolutions. The strongest positive relationship exists between VCI_{AVG} and WUE, and the weakest relationship exists between R_T and LUE. Mediation analysis showed that neither WUE or LUE significantly mediated the relationship between $VAI_{maxheightmean}$ and GPP (Figure 6), suggesting that either the relationship is direct, or additional unaccounted for factors play the role of mediator. The most complex sites (SE5 and NE2) have differing relationships to productivity. Site NE2 has the highest GPP of all nine sites, but also has the highest Reco, resulting in its classification as a small net source of CO_2 to the atmosphere. Site SE5 has the second lowest seasonal GPP as well as the second lowest Reco. The two least complex sites, SE3 and NW2, have among the lowest total seasonal GPP and Reco. SW2 and SW4 have the second and third highest seasonal GPP, yet consistently display only moderately levels of CSC at all five spatial resolutions. However, both of these sites contain stands in a wide range of age classes (Table 2.2), indicating heterogeneity in successional stages, and both sites are noted as containing very wet areas, with older (>100 years) mixed conifer swamp stands.

2.4.3 Disturbance impacts

With the exception of NE2, sites with a record of greater disturbance severity and intensity, presented as clearcutting or shelterwood harvest, exhibit lower levels of complexity across the majority of CSC metrics, and across all metrics addressing vertical complexity. One reason for this could be that the harvests at NE2 were all selective harvests, and resulted in distinct structurally heterogeneous ‘patches’ within the site at different successional stages and with a high degree of canopy cover. In contrast to the primarily broadleaf understory present at multiple other sites, several patches within NE2 feature a prominent conifer understory. As mixed conifers tend to show higher levels of vertical complexity than many purely broadleaf stands do (Ehbrecht et al., 2017, Pommerening and Murphy, 2004, Zenner 2016), the presence of a developing conifer understory could be contributing to a higher overall VCI_{AVG}. This is supported by the presence of a substantial conifer understory at one other site, SW4, which exhibits the highest degree of VCI_{AVG} amongst the nine sites (0.35). Again, with the exception of NE2, sites with a record of more substantial disturbance had lower levels of productivity, and lower levels of RUE. For example, site NW2, which had the highest frequency of both clear cuts and harvest events, had the lowest GPP of all nine sites and also had the lowest average daily LUE (0.33 g C MJ^{-1}) and WUE (2.9 g C kg H_2O^{-1}) values.

More moderate disturbances such as thinning and selective harvest could be contributing to increased CSC within the study area, through assisting in the transition to uneven aged stands (Gough et al., 2021). This is observed at site SE6, which consists of a 19-year-old mixed aspen, white spruce, and balsam fir stand, a 22-year-old jack pine stand, a 75-year-old aspen stand, and a 92-year-old mixed upland hardwood stand (Figure 2.2). SE6 underwent species-specific commercial thinning to reduce stand density, which has been shown to impact stand growth and structure (Wisconsin Department of Natural Resources, 2020). SE6 also experienced salvage cutting to remove dead or damaged trees following a severe hail storm in 2000. Sites SE5 and NE2 consistently ranked as the most complex sites regardless of spatial resolution, and both sites have experienced moderate management disturbances such as thinning as well as manual planting.

2.5 Conclusions

Quantifying mechanistic relationships between forest CSC and productivity is essential to advancing our ability to scale measurements from the leaf to stand to landscape level. This will greatly enhance our capacity to directly assess landscape-level ecosystem functions and implications for natural climate solutions. We approached this challenge using a combination of UAS LiDAR-derived CSC metrics from nine forested sites within a 10 × 10 km study domain, land-atmosphere exchange data from nine EC towers located within those forested sites, and SEM. Through employing a high density of EC towers across a relatively small spatial domain, we were able to separate variability in climate, soil fertility, and forest functional types from structural controls on productivity, allowing for a more representative physiological understanding than has been previously demonstrated.

We conclude that **(a)** structural metrics describing the vertical complexity of a forest (specifically $\mathrm{VCI}_{\mathrm{Avg}}$) are the strongest drivers when predicting productivity in temperate mixed forests with a significant degree of heterogeneity and a long history of management; **(b)** variability in the type and intensity of management and disturbance legacies contribute to substantial differences in CSC metric values as well as productivity; **(c)** the relationship between forest structure and function is not direct, but is actively mediated by light and water RUE, with WUE being a stronger driver of GPP; and **(d)** CSC metric values change with shifts in the resolution of metric calculation, resulting in changes to the mechanistic relationship between forest structure and function. This emphasizes the need for consistency in the spatial resolution at which CSC metrics are calculated, and for the disclosure of resolutions of metric calculation when reporting CSC metric values and interpreting the significance of findings. These findings will allow us to improve mechanistic representation in ecosystem models of how CSC impacts light and water-sensitive processes, and ultimately GPP. This will strengthen the ability of models to mimic true ecosystem responses to management and disturbance, allowing for a more accurate assessment of the response of forests to various management regimes and representative concentration pathways, enhancing our ability to assess climate mitigation and adaptation strategies.

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Supplemental figures

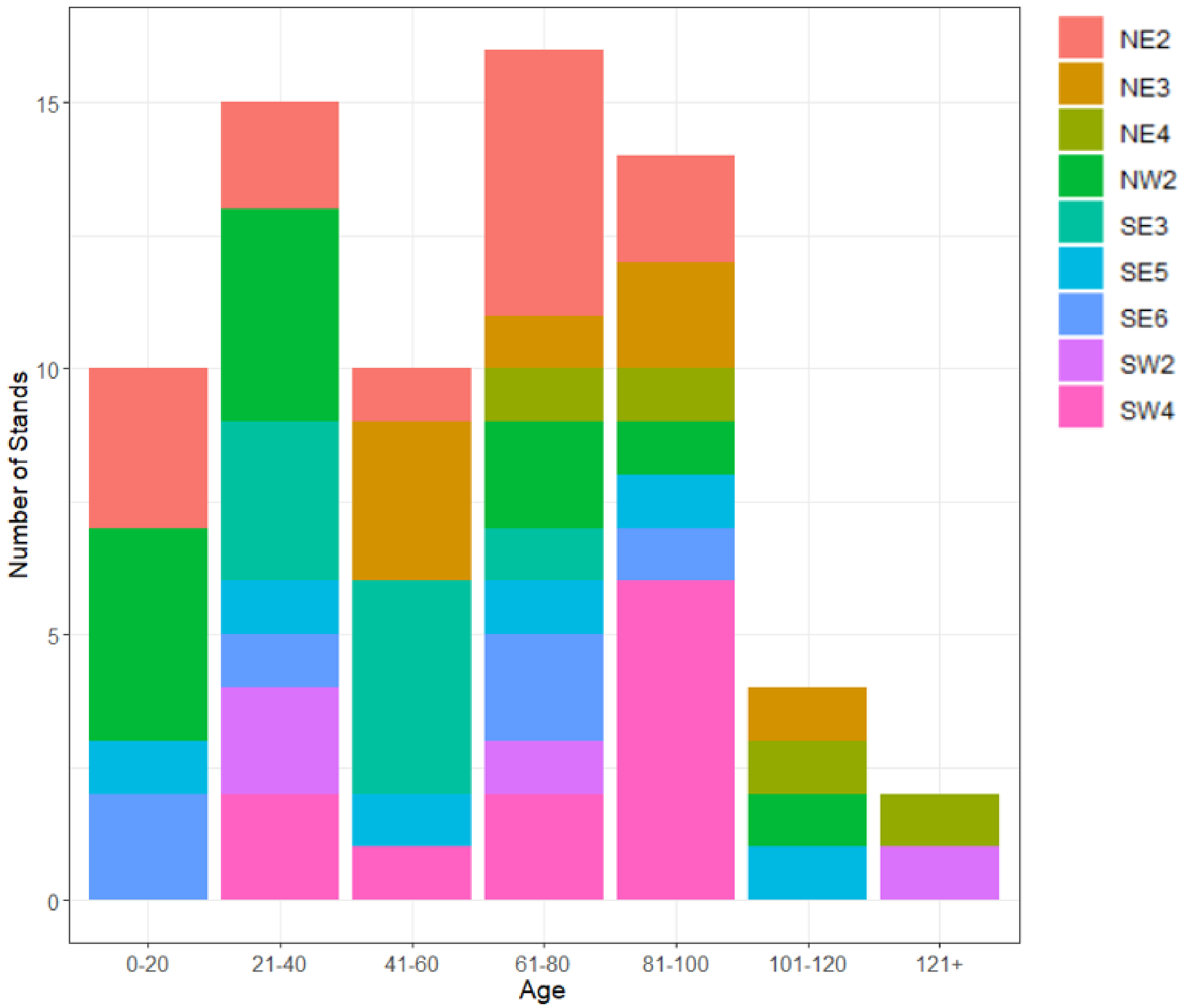
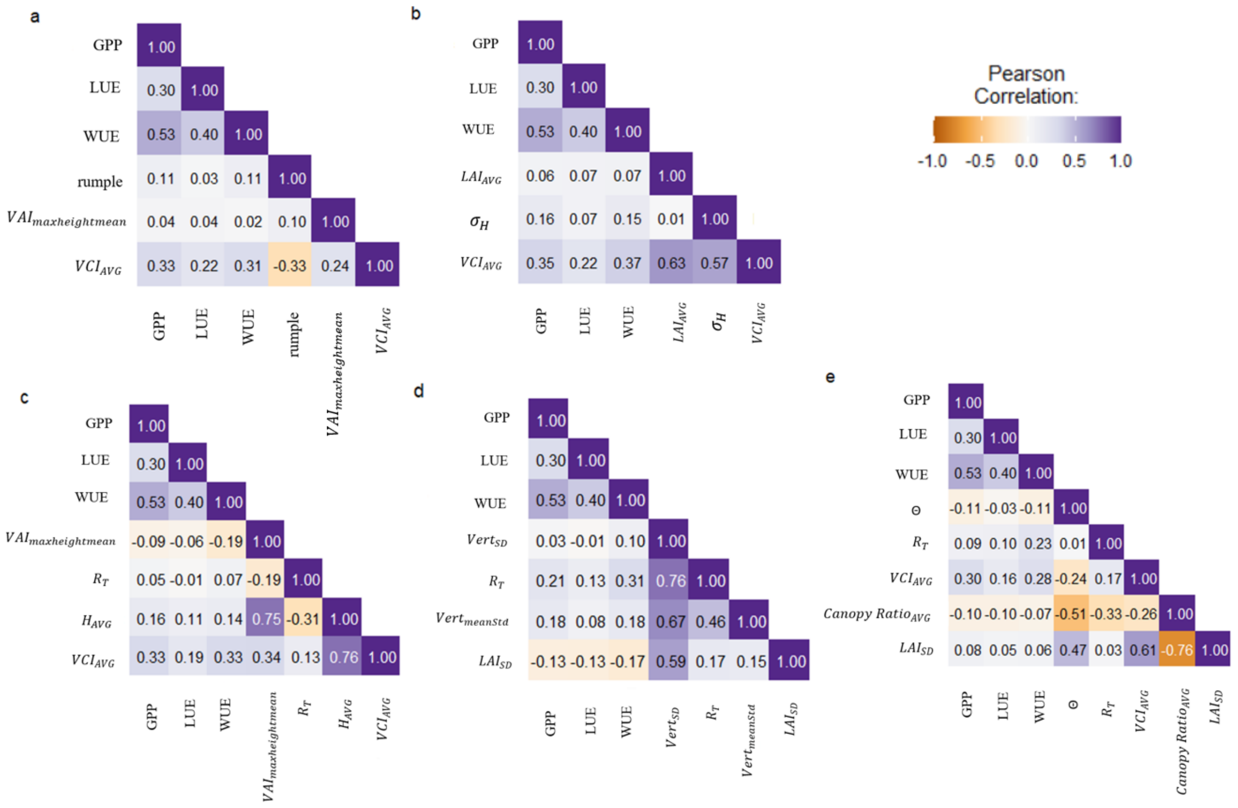


Figure S2.1: Age distribution at the nine selected forest sites, where colors represent different sites to highlight the presence of multiple forest age classes within a single site.



a

	GPP	LUE	WUE	rumple	$VAI_{maxheightmean}$	VCI_{AVG}
GPP	1.00					
LUE	0.30	1.00				
WUE	0.53	0.40	1.00			
rumple	0.11	0.03	0.11	1.00		
$VAI_{maxheightmean}$	0.04	0.04	0.02	0.10	1.00	
VCI_{AVG}	0.33	0.22	0.31	-0.33	0.24	1.00

b

	GPP	LUE	WUE	LAI_{AVG}	σ_H	VCI_{AVG}
GPP	1.00					
LUE	0.30	1.00				
WUE	0.53	0.40	1.00			
LAI_{AVG}	0.06	0.07	0.07	1.00		
σ_H	0.16	0.07	0.15	0.01	1.00	
VCI_{AVG}	0.35	0.22	0.37	0.63	0.57	1.00

c

	GPP	LUE	WUE	$VAI_{maxheightmean}$	R_T	H_{AVG}	VCI_{AVG}
GPP	1.00						
LUE	0.30	1.00					
WUE	0.53	0.40	1.00				
$VAI_{maxheightmean}$	-0.09	-0.06	-0.19	1.00			
R_T	0.05	-0.01	0.07	-0.19	1.00		
H_{AVG}	0.16	0.11	0.14	0.75	-0.31	1.00	
VCI_{AVG}	0.33	0.19	0.33	0.34	0.13	0.76	1.00

d

	GPP	LUE	WUE	$Vert_{SD}$	R_T	$Vert_{meanStd}$	LAI_{SD}
GPP	1.00						
LUE	0.30	1.00					
WUE	0.53	0.40	1.00				
$Vert_{SD}$	0.03	-0.01	0.10	1.00			
R_T	0.21	0.13	0.31	0.76	1.00		
$Vert_{meanStd}$	0.18	0.08	0.18	0.67	0.46	1.00	
LAI_{SD}	-0.13	-0.13	-0.17	0.59	0.17	0.15	1.00

e

	GPP	LUE	WUE	Θ	R_T	VCI_{AVG}	$Canopy\ Ratio_{AVG}$	LAI_{SD}
GPP	1.00							
LUE	0.30	1.00						
WUE	0.53	0.40	1.00					
Θ	-0.11	-0.03	-0.11	1.00				
R_T	0.09	0.10	0.23	0.01	1.00			
VCI_{AVG}	0.30	0.16	0.28	-0.24	0.17	1.00		
$Canopy\ Ratio_{AVG}$	-0.10	-0.10	-0.07	-0.51	-0.33	-0.26	1.00	
LAI_{SD}	0.08	0.05	0.06	0.47	0.03	0.61	-0.76	1.00

Figure S2.2: Pearson correlation matrices for predictive models corresponding to CSC metric calculation resolutions of 0.25 m **(a)**, 2 m **(b)**, 10 m **(c)**, 25 m **(d)**, and 50 m **(e)**. Purple shades indicate positive correlations between variables, while orange shades indicate negative correlations, with the exact correlation strength displayed within each box.

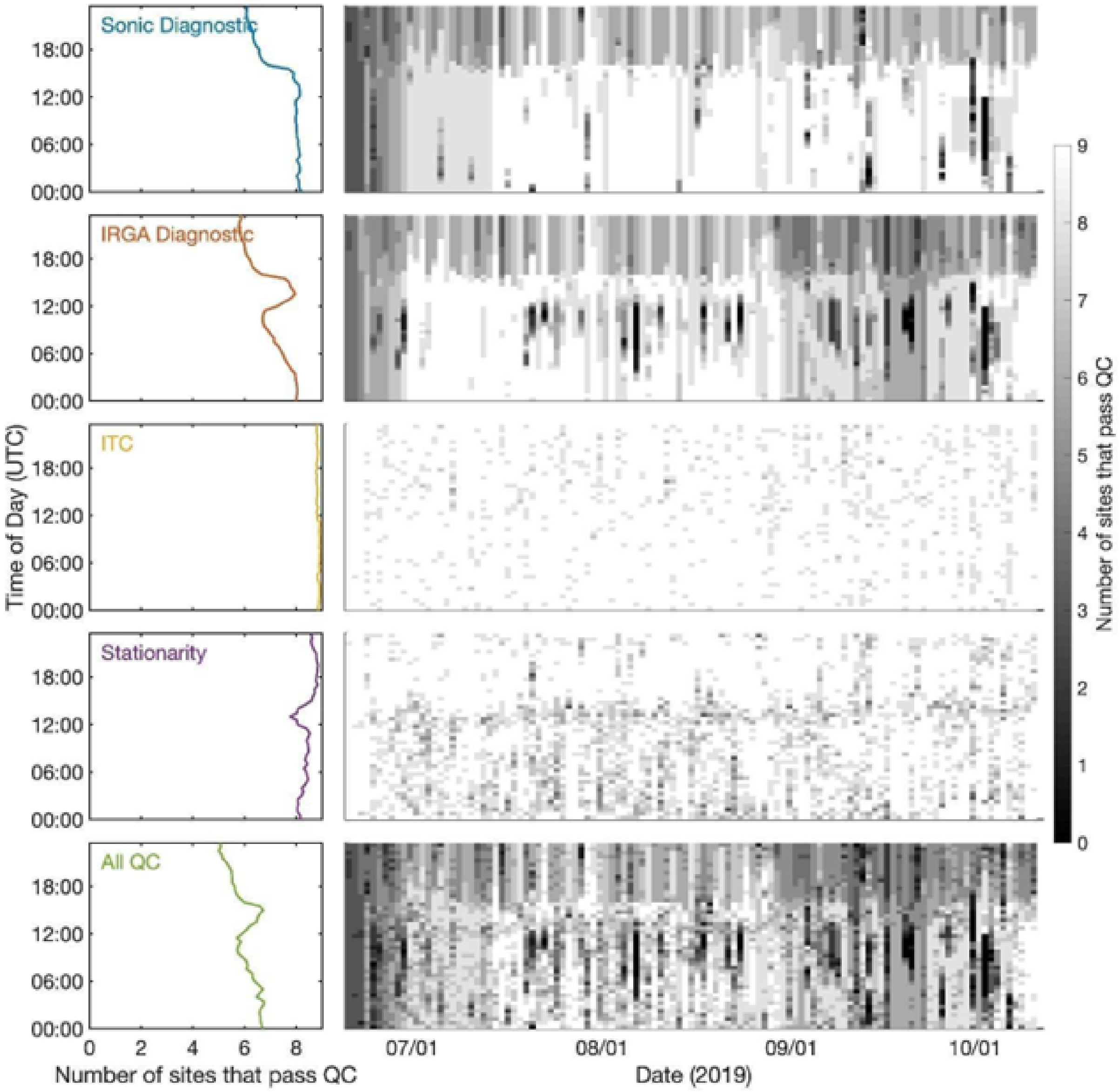


Figure S2.3: Results of the four quality control (QC) checks that were assessed for EC data, as well as the combined QC assessment for each site. The gray scale represents the number of sites that passed or failed the QC assessment for each date and time during the measurement period.

Supplemental tables

Table S2.1: Description of LiDAR-derived forest complexity metric

Metric	Description	Source
Rumple	Ratio of the top surface area of the canopy to the projected ground area	*Kane et al., 2010*
VerticalDistMax	Height with the most points, using 0.5m bins above a cutoff height of 5m	*Atkins et al., 2018*
maxZ_mean	Mean of max height of points in each pixel	*Parker et al., 2004*
maxZ_sd	Standard deviation of max height of points in each pixel	*Atkins et al., 2018*
sdZ_mean	Mean of standard deviation of height of points in each pixel	*Atkins et al., 2018*
sdZ_sd	Standard deviation of standard deviation of height of points in each pixel	*Atkins et al., 2018*
meanZ_mean	Mean of mean of height of points in each pixel	*Atkins et al., 2018*
meanZ_sd	Standard deviation of mean of height of points in each pixel	*Atkins et al., 2018*
density_mean	Mean of density of points in each pixel	*Roussel et al., 2020*
density_sd	Standard deviation of density of points in each pixel	*Roussel et al., 2020*
gap_fraction	Fraction of pixels with returns below a cutoff height	*Atkins et al., 2018*

VCI_mean	Mean of vertical complexity index	*van Ewijk et al., 2011*
VCI_sd	Standard deviation of vertical complexity index	*van Ewijk et al., 2011*
LAI_mean	Mean of leaf area index	*Atkins et al., 2018*
LAI_sd	Standard deviation of leaf area index	*Atkins et al., 2018*
RH25	Mean of 25th quantile of point heights	*Schneider et al., 2017*
RH50	Mean of 50th quantile of point heights	*Schneider et al., 2017*
RH75	Mean of 75th quantile of point heights	*Schneider et al., 2017*
RH95	Mean of 95th quantile of point heights	*Schneider et al., 2017*
canopy_ratio_mean	Mean of 95th quantile of heights minus the 25th quantile of heights divided by the 95th quantile of heights	*Schneider et al., 2017*

Chapter 3

Ecosystem demography model overview, experimental design, and site description

Abstract

The purpose of this chapter is to provide an overview of the modeling approach used to generate the data evaluated in chapters four and five. Chapters four and five utilize output from the same set of simulations conducted with the Ecosystem Demography model (ED2) version 2.1 (Moorcroft et al., 2001, Hurtt et al., 2002, Albani et al., 2006, Medvigy et al., 2009, Longo et al., 2019), a process-based model capable of simulating dynamic responses of vegetation to disturbance events and resource competition. This chapter provides a brief overview of the ED2 model, the modeling experimental design implemented in this study, and site descriptions.

3.1 Introduction

Model simulations were initialized using National Ecological Observatory Network (NEON) data from core forested terrestrial sites across two U.S. regions, the Southeastern and Great Lakes regions, to capture a range of ecoclimate zones and representative forestry practices. Simulations were used to compare management and climate change impacts on forest function across ecological and climate gradients. To conduct simulations from 2006 - 2100 under multiple radiative forcing scenarios, downscaled output from a subset of 10 Coupled Model

Intercomparison Project Phase 5 (CMIP5) (Taylor et al., 2012) general circulation models (GCMs) were used for meteorological forcing in model simulations. In the CMIP5 protocol, simulations were conducted under four future greenhouse gas concentration trajectories, referred to as representative concentration pathways (RCPs). Outputs from two of these concentration trajectories, RCP4.5 and RCP8.5 (where numbers correspond to the approximate radiative forcing in W m^{-2} reached by the year 2100), were used to explore interactions between climate change and management. RCP4.5 corresponds to a medium stabilization scenario where some climate mitigation policies are implemented, while RCP8.5 corresponds to a high baseline emissions scenario, resulting in high concentrations of greenhouse gasses in the atmosphere (van Vuuren et al., 2011).

Four management types were defined to represent a spectrum of existing management practices: production, ecological, preservation, and passive forestry, with distinct harvest parameters corresponding to each management type within each region. The four management types defined here reflect varying balances between ecosystem goods and services, such as demand for wood products, recreation, habitat and biodiversity support, or hydrologic regulation (Becknell et al., 2015). Data from interviews with forestry experts (VonHedemann and Schultz, 2021) were distilled to develop regionally specific ED2 model parameters corresponding to each management scenario.

3.2 Site description

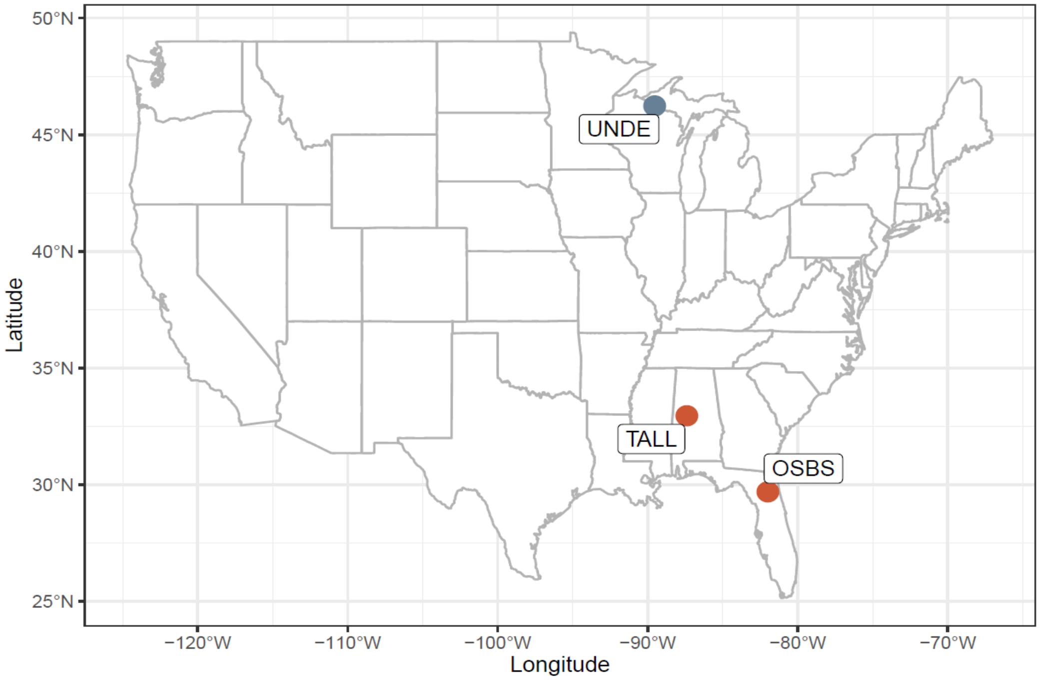


Figure 3.1: Locations of forested NEON sites used in this analysis. Sites are colored by region; blue corresponds to the Great Lakes region and red corresponds to the Southeast.

Our goal was to simulate the interaction of management and climate change at representative locations with sufficient observations for model initialization and parameterization. NEON core terrestrial sites provide this (Figure 3.1), as core site locations were designed to capture key aspects of the U.S. ecological landscape along multiple axes of climate, edaphic, topographic, vegetation, wildlife, and management practices (Schimel et al., 2007), and collect a wealth of observational data related to biogeochemical processes, land-atmosphere interactions, habitat structure, climate, and more.

The Great Lakes (GL) region is represented by the University of Notre Dame Environmental Research Center (UNDE, 46.23˚N, 89.54˚W) site, a Northern Mesic Forest site located in Michigan's Upper Peninsula near the Wisconsin border. UNDE is primarily second-growth forest, regrown following a period of intensive clear-cutting at the beginning of the 20th century experienced across most of the Great Lakes region (Mahon 2003), although current management is minimal. UNDE experiences an average annual temperature of 40˚F, an average precipitation rate of 31.6 inches per year, and significant snowfall in the winter. Soils are predominantly Spodosols (lesser proportions of Histosols and Inceptisols exist as well) with sandy textures, and formed in glaciofluvial deposits (Parsley 2016). The area is characterized primarily as forested, but also includes an abundance of lakes, ponds, and bogs. Dominant tree species include red and sugar maple (*Acer rubrum* and *A. saccharum*), aspen (*Populus tremuloides* and *P. grandidentata*), and paper birch (*Betula papyrifera*). The evergreen forests are typically balsam fir (*Abies balsamea*), with cedar (*Thuja accidentalis*) and black spruce (*Picea mariana*) in wetter areas (Krauss 2018).

The Southeastern (SE) U.S. is represented by the Ordway-Swisher Biological Station (OSBS, 29.69 ˚N, 81.99 ˚W) and Talladega National Forest (TALL, 32.95 ˚N, 87.39 ˚W) sites. OSBS is a longleaf pine site located in North-central Florida that experiences a humid subtropical climate, characterized by hot summers and mild winters (average annual temperature is 70˚F), an average precipitation rate of 51 inches per year, and intense summer storms. Soils are a mix of sandy soil types with either very thin organic horizons, or completely eroded organic horizons due to silviculture (Prink and Figueroa, 2019). Longleaf pine (*Pinus palustris Mill.*) and turkey oak (*Quercus laevis*) are the dominant tree species (Krauss 2018). OSBS has historically been managed for recreation, habitat, and biodiversity (Livingston 2014), and is currently closed to the public. TALL is a predominantly longleaf and loblolly pine site located in West-central Alabama, with an understory of mixed oak and other hardwoods including sweetgum (*Liquidambar*) (Hatcher 2017). TALL is a humid subtropical site, with hot summers, mild winters (average annual temperature is 63˚F), an average precipitation rate of 54.3 inches per year, and frequent storms and flooding. Soils developed from marine sediments and are a mix of sandy, loamy, and clayey, with Maubila, Boykin, Wadley, and Smithdale as the major soil series (Hatcher 2017). TALL has a long history of intensive harvest, the area is currently managed for multiple purposes including recreation, active logging, some preservation, and cockaded woodpecker habitat, which involves midstory harvest and regular prescribed fire (Pasquill 2006).

3.3 Model overview and experimental design

To test the impact of human management on forest function and elucidate potential interactions with climate change across multi-decadal timescales, we ran a series of dynamic vegetation model simulations using the ED2 model at sites in two U.S. regions under four representative management scenarios and two future radiative forcing climate change scenarios (Figure 3.2).

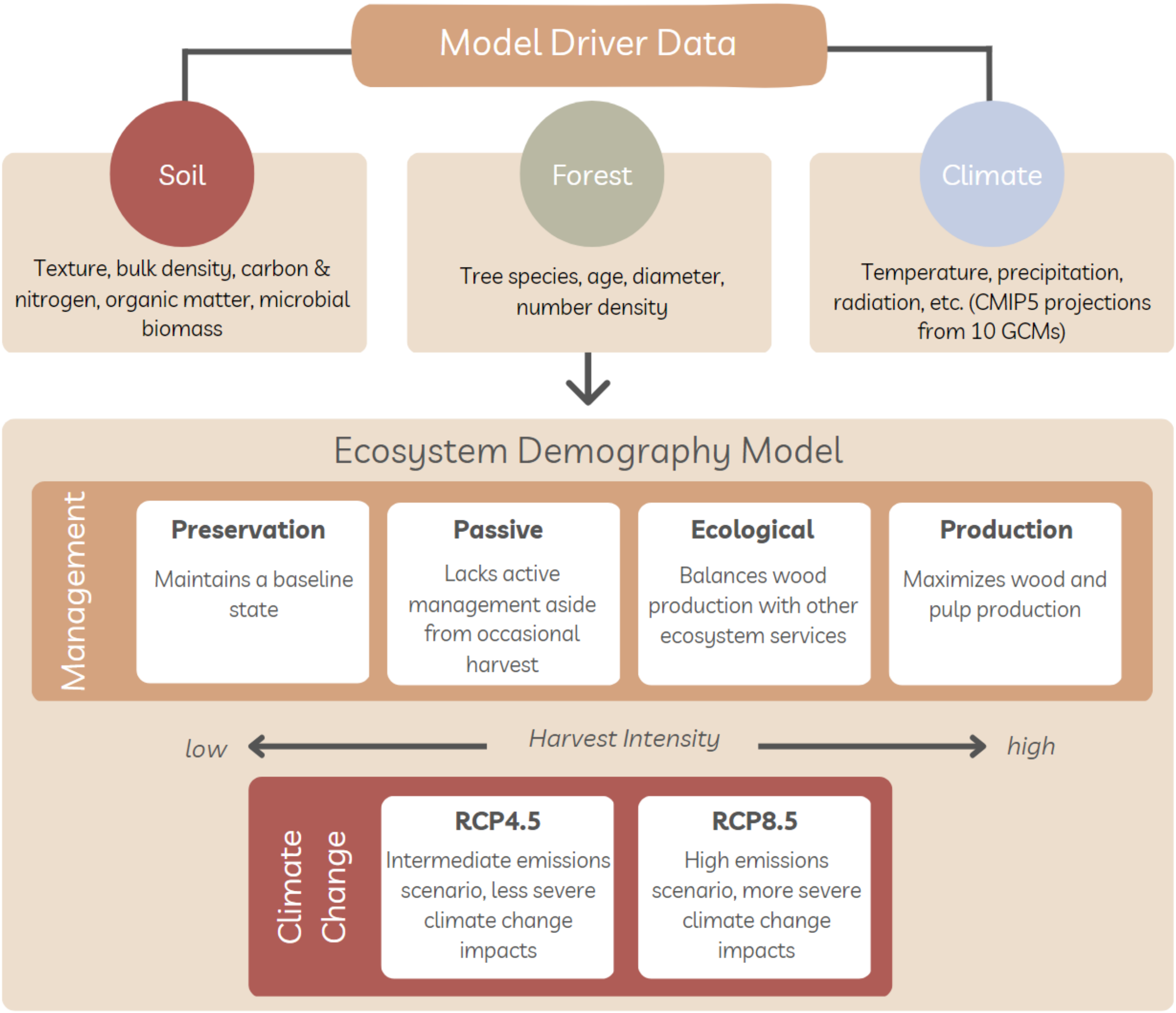


Figure 3.2: Infographic depicting the data types and modeling design implemented in this study.

ED2 was selected for this study due to its realistic representation of ecosystem processes, ability to capture non-linear impacts of fine-scale heterogeneity in ecosystem structure on land-atmosphere exchanges of carbon, water, and energy over time, ease of spatial scaling, and model outputs that aligned with the primary variables of scientific interest. ED2 is a size and age structured approximation of an individual-based vegetation model (often referred to as forest gap models), meaning that biophysical and physiological processes are resolved across cohorts instead of at the scale of individual trees (Longo et al., 2019, Fisher et al., 2017). Cohorts are defined as groups of trees within the same plant functional type (PFT), where a PFT is a group of species with similar physical, phylogenetic and phenological characteristics (Wullschleger et al., 2014), and of similar sizes.

Ecosystem descriptors such as carbon pool magnitudes and net ecosystem productivity are emergent properties that result from simulated competition for resources between plant types with differing abilities to survive (Longo et al., 2019). Within a site, disturbance related heterogeneity is represented by a series of patches, which are defined by type of disturbance that occurred and the time since the last disturbance (Moorcroft et al. 2001), and consist of multiple cohorts. Examples of disturbance types in ED2 that generate new patches include harvest, treefall, fire, land abandonment, and cropland or pasture land conversion (Longo et al., 2019). To account for fine-scale variability within the landscape, a series of differential equations representing the energy, water, and carbon cycles are resolved separately for each patch, and flux and storage terms are resolved for each cohort within a given patch. Detailed information on the spatial hierarchy and representation of thermodynamic properties and ecosystem fluxes within ED2 can be found in Moorcroft et al. (2001), Medvigy et al. (2009) and Longo et al. (2019).

Default plant trait parameters associated with PFTs were used to compare model outputs from simulations conducted in different regions of the US; site-specific optimization of ED2 parameters was not performed as it was unclear if these would scale to larger regions. Model simulations spanned from 2006 to 2100, with outputs saved at monthly timesteps. To allow time for climate drivers and land surface properties to stabilize in relation to each other, simulation of management did not begin until the year 2020, following a short spin-up period commonly applied to ED2 in these types of experiments. Because simulations started from existing forest conditions as opposed to bare ground, and there was no significant land use change, a prolonged spin-up period was not necessary to build up carbon pools. Further, extended spin-up was not required to resolve erroneous interactions with atmospheric components, since meteorological drivers were in steady state for the time period utilized, and static CO_2 conditions circumvented potential complications due to unstable radiative forcing responses to increasing atmospheric CO_2 concentrations.

ED2 is sensitive to increases in CO_2 concentration, which can result in unrealistic plant productivity responses (i.e., strong CO_2 fertilization effects) and dominate uncertainty in predictions of productivity over long timescales (Rollinson et al., 2017, De Kauwe et al., 2013, Walker et al., 2020, Zaehle et al., 2014, De Kauwe et al., 2014). To isolate the climate and management factors driving variability in forest function that might be obscured by productivity responses to elevated CO_2 concentrations, model runs were conducted with a static leaf-level CO_2 concentration of 380 ppm. Soil and vegetation data used to initialize ED2 were derived from plot and site-level observational data provided by NEON (Table 3.1). Soil physical and chemical data came from a single ‘megapit’, or large temporary soil pit dug at each site, whose sampling location is representative of the distributed sensor-equipped soil plots that exist at each site. Soil variables include the number of soil layers, soil texture, carbon and nitrogen content, bulk density, and microbial biomass. ED2 organizes soil carbon into three distinct reservoirs based on decay rate: fast, intermediate (also referred to as structural), and slow soil carbon pools. The fast soil carbon pool is composed of metabolic litter (both non-lignified leaf and fine-root litter) that decomposes quickly, the intermediate soil pool is composed of decaying structural tissues and lignified materials, and the slow soil carbon pool consists of dissolved soil organic matter (SOM; Moorcroft et al., 2001).

To determine the size of the fast soil carbon pool for model initialization, NEON microbial biomass data was averaged to find the microbial biomass per kg of soil for each site. Total average microbial biomass was then segregated into microbial biomass of carbon and microbial biomass of nitrogen using ecosystem–specific average microbial carbon:nitrogen:phosphorus ratios from a global synthesis by Wang et al. (2021). The microbial biomass of carbon at each site was then multiplied by soil bulk density at each site. The fast soil carbon pool was initialized based solely on the microbial biomass of carbon at each site.

The size of the slow soil carbon pool was determined using the total soil carbon per horizon reported by NEON, doing a weighted average based on soil layer thickness across all soil horizons to arrive at a single value for each site, and multiplying by soil bulk density to align with ED2 units. The microbial biomass of carbon was then subtracted from the total soil carbon to arrive at a final estimate for the size of the slow soil carbon pool at each site. To determine the size of the intermediate soil carbon pool, soil organic matter was estimated from total organic soil carbon data, and multiplied by ten for a rough estimate of structural and lignified soil carbon content. Additional details on how soil carbon dynamics are represented in ED2 can be found in the supplement at the end of this chapter.

Vegetation data came from in-situ measurements, tree structure and mapping data are reported per individual per plot. Vegetation data include tree species and density, diameter at breast height, and tree height. Detailed information on sampling protocols can be found through the DOI's provided in Table 3.1.

Table 3.1: NEON soil and vegetation data product information

Data Product ID	Data Product Name	DOI	Site ID
DP1.00096.001	Soil physical and chemical properties (megapit)	https://doi.org/10.48443/t70z-np08	UNDE, OSBS, TALL
DP1.10104.001	Soil microbial biomass	https://doi.org/10.48443/rwbj-ry66	UNDE, OSBS, TALL
DP1.10098.001	Vegetation structure	https://doi.org/10.48443/73zn-k414	UNDE, OSBS, TALL

To conduct simulations out to the year 2100 under multiple future radiative forcing scenarios, downscaled output from a subset of 10 CMIP5 GCMs (Table 3.2) was used for meteorological forcing in ED2. Utilizing output from an ensemble of GCMs allows for a more representative understanding of interactions between management and climate change by reducing bias in results introduced by model sensitivities and structural differences that might otherwise dominate if using a time series from model simulations forced by a single GCM. Additionally, using dynamic meteorological forcing spanning 80 years as opposed to cycled single-year meteorology as other studies have done (Dorheim et al., 2021) captures the impacts of interannual variability of weather on carbon dynamics, which have been shown to significantly affect fluxes (Desai et al., 2010, Desai et al., 2022, Shiga et al., 2018).

Meteorological variables required at a sub-daily resolution by ED2 include air temperature, precipitation rate, incoming shortwave and longwave radiation, specific humidity, air pressure, and zonal and meridional wind speed. Meteorology data was temporally downscaled to three-hourly averages (aside from GFDL-CM3 all GCMs had a daily native temporal resolution) using a multivariate regression based approach (Simkins 2017).

Table 3.2: General circulation models used in this study. All 10 GCMs are from the CMIP5 collection of simulations. Models were selected based on availability of the necessary parameters to initialize ED2 and inclusion of projections under both RCP4.5 and RCP8.5.

General Circulation Model	Developer
ACCESS1-0	Commonwealth Scientific and Industrial Research Organisation and Bureau of Meteorology (Australia)
Bcc-csm1-1	Beijing Climate Center and China Meteorological Administration (China)
BNU-ESM	Beijing Normal University (China)
CNRM-CM5	National Center for Meteorological Research (France) and European Center for Research and Advanced Training in Scientific Computing
CSIRO-Mk3-6-0	Commonwealth Scientific and Industrial Research Organisation and the Queensland Climate Change Centre of Excellence (Australia)
GFDL-CM3	National Oceanic and Atmospheric Administration Geophysical Fluid Dynamics Laboratory (USA)
Inmcm4	Institute of Numerical Mathematics of the Russian Academy of Sciences and the Main Geophysical Observatory (Russia)
IPSL-CM5B-LR	Institut Pierre Simon Laplace Climate Modelling Center (France)
MIROC5	Center for Climate System Research, University of Tokyo, National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology (Japan)
MRI-CGCM3	Meteorological Research Institute (China)

The four forest management types defined in this study, production, ecological, preservation, and passive forestry, reflect varying balances between ecosystem structure and function, and the ecosystem goods and services that result. Production forestry is focused on maximizing the production of timber and wood products to provide raw materials for consumer goods. Ecological forestry also involves timber harvest, but harvest practices are less invasive and attempt to simulate structure and function within the natural range of variability (Franklin et al., 2002). Ecological forestry typically results in higher levels of structural complexity and species diversity (Franklin et al., 2007) than production forestry. Preservation management involves no active harvest and seeks to maintain plant and animal biodiversity and other ecosystem services (recreation access and quality, aesthetic and cultural value, etc.) at a baseline state determined by historical conditions. In the context of this study, preservation management is akin to a 'no management' control scenario, as it involves no active harvest in either geographic region evaluated here. Lastly, passive management involves periodic full or selective timber harvest, with minimal-to-no management between harvests (Carey 2006). While actual on-the-ground management has numerous nuances that vary by prescriptions and site conditions, the goal here is to provide a consistent set of management types that encompass a reasonable range of potential harvest and management regimes for a wide variety of forests.

Management in the version of ED2 used here is primarily defined by the presence or absence of harvest, and the specifications of how harvest impacts stand structure if it does take place. Management is prescribed by altering harvest parameters such as the timing, frequency, and spatial extent of harvest, as well as the PFT, age, and size groups targeted for harvest. Management parameters are established at the start of model simulations, and do not evolve over time.

Regionally specific management parameters (Table 3.3) were derived from remote interviews (6 – 20 per region depending on region size) with forestry experts across the U.S. – including forest extension specialists, researchers, silviculturists, federal, state, and tribal forest managers, forestry consultants, and industry experts – to evaluate local and regional forest management practices (vonHedemann and Schultz, 2021). Interviews were conducted by Dr. Nicolena von Hedemann from the Department of Forest and Rangeland Stewardship at Colorado State University. Interviewees were asked questions regarding standard silvicultural approaches in their region, the impact of economic markets and infrastructure on forest management, climate change impacts and forestry adaptation practices, and more. Information regarding regional silvicultural practices was then distilled into numerical parameters that could be implemented in ED2 (Table 3.3) to simulate harvest by Paul Duffy of Neptune and Company, Incorporated. For example, from these discussions, production forestry in the Great Lakes region is characterized in ED2 by a rotation length of 57 years and a fractional harvest area of 1.8% per year, where trees with a DBH above 26.67 cm have an 80% probability of harvest, trees with a DBH below 26.67 cm have a 20% probability of harvest.

Table 3.3: Regionally specific harvest parameters for the management types implemented in this study. Trees were targeted for harvest based on size and plant functional type (PFT), and harvest prescriptions were applied annually from 2020 through 2100.

Management	Region	ED2 PFTs Harvested	Fractional Area Harvested	Rotation	Min. DBH for Harvest	Harvest Probability Above Min.DBH	Harvest Probability Below Min.DBH
			per year	*years*	*cm*	*fraction*	*fraction*
Passive	SE	7-9-10-11	0.014	72.5	15	1	1
Ecological	SE	7-9-10-11	0.1	10	15.24	0.7	0.7
Production	SE	7-9-10-11	0.014	70.75	15.88	0.875	0
Preservation	SE	7-9-10-11	0	NA	200	0	0
Passive	GL	6-7-9-10-11	0.015	66	15	1	1
Ecological	GL	6-7-9-10-11	0.016	64.2	31.5	0.72	0.12
Production	GL	6-7-9-10-11	0.018	57	26.67	0.8	0.2
Preservation	GL	6-7-9-10-11	0	NA	200	0	0

PFT 6 = Northern pine, PFT 7 = Southern pine, PFT 9 = Early successional hardwood, PFT 10 = Mid successional hardwood, PFT 11 = Late successional hardwood

Unlike in the Great Lakes region, production forestry in the Southeastern U.S. is predominantly intensively managed pine plantations (Wear and Greis, 2002). To represent this in ED2, adjustments were made to ‘seed rain’ and ‘seedling mortality’, two reproduction parameters in the ED2 settings file. Seed rain is the density of seedlings added each year, and was set to zero for non-pine PFTs and 0.2 kg C m^{-2} $year^{-1}$ for pine PFTs. Seedling mortality odds were set to 99% for non-pine PFTs and 50% for pine PFTs, to encourage survival of pine seedlings. This facilitated the rapid dominance of pines in comparison to other tree species, to simulate a pine plantation. Wildfire as a disturbance type was not included in the simulations performed in this study, due to wildfire not being a primary disturbance regime in either region (Frelich 1995).

With four different management scenarios (production, ecological, preservation, and passive forestry), two future climate scenarios (RCP4.5 and RCP8.5), and 10 GCMs, 80 model simulations were conducted at each study site, spanning from 2006 to 2100, for a total of 240 model simulations overall. Model output from sites within the same region were averaged to obtain regional-scale representations.

3.4 Model-data comparison

To assess whether ED2 predictions of regional net carbon and water exchanges were within the range of observed values, simulations under preservation management (akin to a 'no management' scenario here) for both RCP scenarios were compared to NEON observational data from each region. Carbon exchanges were represented by the variable net ecosystem exchange (NEE) and water exchanges were represented by evapotranspiration (ET). Observational land-atmosphere exchange data was obtained from NEON's bundled eddy covariance product (data product ID DP4.00200.001) for UNDE, TALL, and OSBS. Level four data from the eddy covariance bundle was used to obtain fluxes; this level includes the turbulent and storage flux components as well as the net surface-atmosphere exchange of carbon and water. Level one air temperature data was also used to calculate evapotranspiration from measurements of latent heat flux. Observational flux data was grouped by region and averaged to a monthly time step to align with the temporal resolution of ED2 outputs, but observational data were not gap filled. To ensure a full five years of observational data for comparison against simulations, data were subset to the years 2018-2022 (approximately 5.5 years of processed NEON observational data are currently available for each of the three sites).

Model predictions were within a similar range of observations in both regions for ET and NEE (Figure 3.3). Averaged across the five year evaluation period, ED2 overestimated ET in the GL region, and underestimated ET in the SE region. ED2 predictions of monthly ET were approximately twice as large as observed ET in the GL region, while observed ET was approximately 1.8 times larger than modeled ET in the SE. Averaged across the five year period, both observations and model predictions showed the GL region was a slight net carbon sink. However, model simulations predicted the GL region to be 3.4 – 3.6 times less of a net carbon sink than was indicated by observations. Average observed NEE in the GL was -0.019 ± 0.05 kg C m^{-2} $month^{-1}$, while model predicted values were -0.005 ± 0.08 kg C m^{-2} $month^{-1}$ on average, where a more negative value indicates a greater net transfer of carbon from the atmosphere to the land surface. Both observations and model predictions showed that the SE region was also a net carbon sink. Differences between model predictions and observations were less pronounced in the SE, model simulations predicted the SE to be a 15.9% greater net carbon sink than was observed.

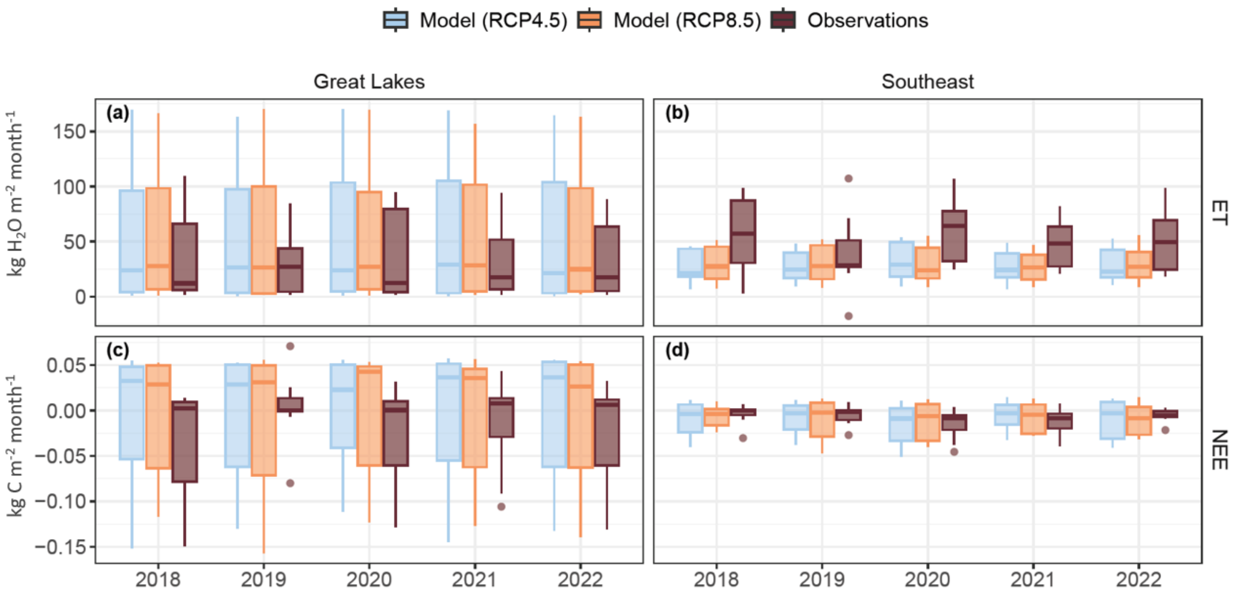


Figure 3.3: Comparison of observed and modeled monthly evapotranspiration (ET) and net ecosystem exchange (NEE) grouped by year. Columns are organized by geographic region, and color corresponds to data source.

Figure 3.4 shows that the difference between modeled and observed ET in the GL region is primarily due to an overestimation of ET by ED2 in the summer months (June, July, August). ET is consistently underestimated compared to observations in the SE, but the largest discrepancies also occur during the growing season. Averaged across the five year observational period, ED2 successfully captures seasonal carbon dynamics in both regions.

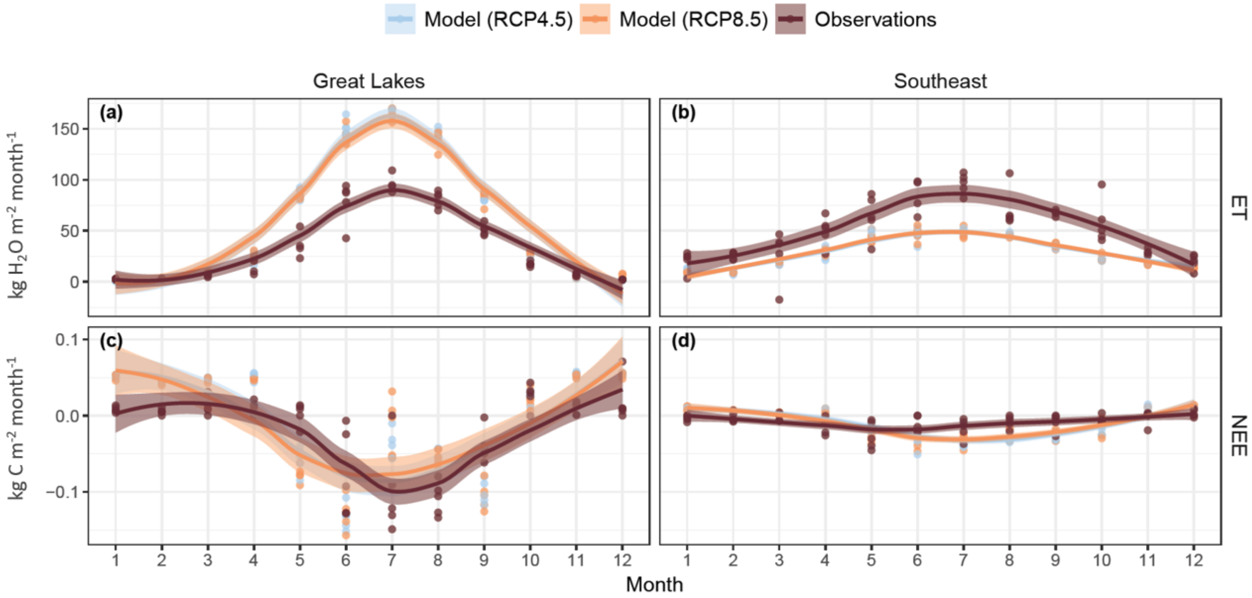


Figure 3.4: Comparison of seasonal observed and modeled monthly evapotranspiration (ET) and net ecosystem exchange (NEE) grouped by month. Columns are organized by geographic region, and color corresponds to data source. Points represent monthly values for each of the five years analyzed, and lines represent monthly values averaged over the entire time period.

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Supplemental information

Soil carbon in ED2

ED2 organizes soil carbon into three distinct reservoirs based on decay rate: fast, intermediate (also referred to as structural), and slow soil carbon pools. The fast soil carbon pool is composed of metabolic litter (both non-lignified leaf and fine-root litter) that decomposes quickly, the intermediate soil pool is composed of decaying structural tissues and lignified materials, and the slow soil carbon pool consists of dissolved soil organic matter (SOM; Moorcroft et al., 2001). Vegetation mortality, shedding of living tissues (such as leaf fall due to drought or phenology), and vegetation maintenance at the cohort level all contribute carbon to the fast and intermediate soil carbon pools, while the slow soil carbon pool grows by input of decayed material from the fast and intermediate soil carbon pools. Each soil carbon pool directly contributes to ED2's CO_2 cycle (a subset of the full carbon cycle) through heterotrophic respiration (Longo et al., 2019).

Heterotrophic respiration is represented by a simplified implementation of the CENTURY model (Bolker et al., 1998), and is the result of decomposition of carbon in the three soil carbon pools. Carbon loss from each pool is determined by a characteristic decay rate, which corresponds to the typical half-life for metabolic litter, structural litter, and dissolved SOM. Decay rates are impacted by the average temperature and relative soil moisture of the top 0.2 m of soil, meaning decay rates can be reduced under extreme soil moisture or temperature conditions, for example warm, moist soil conditions accelerate decomposition. Although CENTURY accounts for the influence of temperature and soil moisture on decomposition rates, the effects of microbial activity on decomposition are not explicitly represented.

Incoming plant material is divided into intermediate and fast pools based on the carbon to nitrogen ratio (a function of available nutrients) and lignin content (a function of soil moisture). Flows of carbon between soil carbon pools are represented as linear transfers, and rates of transfer are modified by soil texture. Soil carbon pools are resolved at the patch level, so they are able to respond to management-driven shifts in vegetation dynamics. An evaluation of five soil carbon models including DAYCENT (the daily version of CENTURY; Parton et al., 1998) against observations by Sulman et al. (2018), where observational data was the result of experimental manipulations of temperature and litter inputs, showed that the variability in soil carbon responses to warming and litter addition were similar in magnitude between models and observations. The modeled response to increased litter inputs were similar to the experimental results, but respiration rates increased more rapidly in the model simulations. Additionally, observational data showed an increase in SOM in response to warming, while models predicted a decrease; this discrepancy could potentially be due to the elevated heterotrophic respiration in the model simulations compared to observations.

Chapter 4

Is it us or is it us? Management versus climate change as drivers of multi-decadal variability in forest function

Abstract

Forests blanket approximately 30% of the land surface, interact with the atmosphere to provide multiple climate feedbacks, and serve as a significant global carbon sink. Management alters land-atmosphere exchanges of carbon, water, and energy, as well as the resultant interactions with climate. However, gaps remain in our understanding of the long-term effects of management on forest function, how management interacts with climate change, and the spatial scales that define relationships.

Here, we assessed the response of forest function, defined as carbon and water cycling, to four management regimes and two climate change scenarios across two U.S. regions: the Southeast and Great Lakes. Regionally specific management parameters were derived from interviews with more than 100 forest management experts. We used the Ecosystem Demography model to simulate forest dynamics from 2006 – 2100, and defined the dominant axes of future variability in function over time. Random forests were used to determine the relative importance of climate and management as drivers of functional variability.

Our results show that the majority of the future variability in ecosystem functions is captured by two axes. The first axis primarily represents water exchange and respiration, and the second axis reflects the net carbon balance, light and carbon use efficiency. We found that management and climate impacts were regionally dependent, and whether climate or management was a stronger driver of ecosystem function depended on spatial scale as well as the functional axis. The effect of management on function was 1.2 – 16.3 times greater than the effect of climate at the regional scale; however, at broader spatial scales, the gradients in future climate conditions became critical. This work advances the understanding of how forest function will respond to management and climate change across scales, a key component of improving representation of the impact of management on land-atmosphere interactions in Earth system models.

4.1 Introduction

The comparatively large size of the global forest carbon sink in combination with the complementary climate feedbacks forests provide gives improved forest management significant potential as a Nature-based Climate Solution (NbCS) to enhance the magnitude of the terrestrial carbon sink (Fargione et al., 2018; Novick et al., 2022) and help mitigate the effects of climate change (although it's essential that any NbCS strategies are implemented in conjunction with emissions reductions). However, substantial uncertainty persists surrounding future variability of the terrestrial carbon sink and other ecosystem services, vulnerabilities in the face of climate change, how management will interact with climate change across long timescales, and how specific management strategies will impact forest structure and function across broad spatial scales. The successful implementation of improved forest management as an NbCS hinges on addressing these uncertainties (Giebink et al., 2022).

Within the contiguous U.S. most forests are considered managed (Becknell et al., 2015, FAO 2020), where management is mainly for wood products, water resources, fire hazard reduction, and recreation services, with carbon uptake as a secondary outcome (FAO 2020, Ryan et al., 2010). However, management of terrestrial ecosystems fundamentally alters ecosystem structure (Ehbrecht et al., 2017, Fahey et al., 2018), which changes the dynamics of key ecosystem functions such as carbon and water cycling (Forrester et al., 2013, Ford and Keeton, 2017) while also impacting ecosystem services including biodiversity and water regulation (Mori et al., 2016). For example, Murphy et al. (2022) showed that differences in forest structure between co–located sites with a shared climate altered light and water resource use efficiency, resulting in substantial differences in seasonal net carbon uptake. Echbrecht et al. (2017) showed that management–induced changes in forest structure also altered microclimate at the stand scale; stands with higher structural complexity had lower mean daily temperature and vapor pressure deficit amplitudes compared to stands of lower structural complexity. In the case of temperature, 39% of the variation in mean daily amplitude was explained by the degree of stand structural complexity.

The impacts of a specific forest management approach can be highly spatially variable depending on local climate, the existing forest state, species composition, and disturbance regimes. For example, Gutsch et al. (2018) showed that the impacts of two management strategies (one promoting biomass production and the other prioritizing habitat diversity) on forest function (carbon uptake, timber production, water regulation, and habitat) across 85 forested regions in Germany varied substantially by region, as did trade–offs and co-benefits between management types. The authors showed that the same management strategy often promoted net carbon uptake in one region, while failing to enhance or even reducing carbon uptake in a neighboring region. Much of what we know about the relationship between management and function comes from studies limited in time or space, so given the inherent non-stationarity of carbon dynamics, gaps remain in our understanding of how specific management strategies will impact forest function beyond the stand scale, or across timescales relevant for climate change. It is also unclear if management strategies that are effective at the plot scale can be "scaled up" to larger scales in space that are necessary for mitigating regional and global-scale impacts.

Characterizing the long-term interactions between management, function, and climate is essential to reduce the predictive uncertainty surrounding the future realities of climate change, and facilitate the development of robust and scalable climate mitigation strategies (Novick et al., 2022, Wu et al., 2023, Anderegg et al., 2020). Additionally, we need an improved understanding of the relative importance of forest management versus climate change as drivers of future variability in ecosystem function, and whether this relative importance persists across spatial scales.

To test the impact of human management on forest function and elucidate potential interactions with climate change across multi-decadal timescales, we ran a series of dynamic vegetation model simulations using the Ecosystem Demography model version 2.1 (ED2) (Moorcroft et al., 2001, Hurtt et al., 2002, Albani et al., 2006, Medvigy et al., 2009, Longo et al., 2019) at sites in two U.S. regions (Great Lakes and Southeast), representing a gradient in forest type, edaphic factors, and climate. Simulations were conducted under four representative management scenarios spanning a range of management intensities, and using meteorological drivers under two future radiative forcing scenarios, RCP4.5 and RCP8.5. This approach allowed us to characterize the impacts of both management and climate change on forest function across large spatial and temporal scales, in a way that has not been previously demonstrated.

Specifically, we address the following questions: 1) How do variations in climate and management intensity and severity impact forest function (defined as carbon and water cycling), and are relationships regionally dependent? 2) What are the dominant axes of future variability in ecosystem function in managed forests?, and 3) What is the relative importance of management versus climate change as drivers of variability in forest function over multi-decadal timescales, and is driver importance scale dependent?

Given that the response of forest function to management varies by management intensity and severity, we hypothesize that active management strategies that promote uneven-aged stands and a multi-layered structure through periodic harvest of individual large trees (such as ecological forestry) will have higher resource use efficiency and be less susceptible to reductions in ecosystem function in response to climate variability, whereas more passive management strategies (such as passive and preservation forestry) will have greater sensitivity to climate change and lower levels of resource use efficiency. We also expect that both the impact of management on forest function and interactions between climate and management will vary in relative strength by geographic region, due to the pace and pattern of climate change by region and differences in treatments (harvest rates, rotation, targeted species, etc.) applied to managed forests. We hypothesize that forest productivity and resource use efficiency will be key axes of future functional variability in managed forests, as these encapsulate the mechanistic basis of how management and climate change influence forest carbon exchanges. Finally, we hypothesize that management will be a stronger overall driver of changes in forest function than climate change, as forest structure is largely determined by management, and forest structure and composition are important factors that shape forest function (Felipe-Lucia et al., 2018). However, we expect driver importance to vary spatially, with climate change importance being more pronounced at higher latitudes.

4.2 Methods

4.2.1 Experimental design

ED2 model simulations were initialized using National Ecological Observatory Network (NEON) data from core forested terrestrial sites across two U.S. regions, the Southeastern and Great Lakes regions, to capture a range of ecoclimate zones and representative forestry practices. Simulations were used to compare management and climate change impacts on forest function across ecological and climate gradients. Simulations spanned from 2006 – 2100 and were conducted under two alternate radiative forcing scenarios (RCP4.5 and RCP8.5), using four representative management types (preservation, passive, ecological, and production forestry). A detailed description of the model driver data and experimental design is provided in chapter three, along with site descriptions.

Principal component analysis (PCA) was used for multivariate analysis of ecosystem function variables to reduce data dimensionality and determine the dominant axes of variability in ecosystem function. Random forests (RF) were used to identify and rank the importance of dominant climate and structural drivers of variability in ecosystem function, where axes of variability in ecosystem function were represented by individual principal components, and comparison across regionally grouped data isolated spatial trends. RF is a supervised machine learning (ML) algorithm that utilizes an ensemble of decision trees to make predictions, and has proven adept at dealing with potential nonlinearities among variables (Breiman, 2001).

4.2.2 Impact of management and climate change on forest function

In addition to being common outputs across ecosystem and land surface models, several of the variables selected to represent ecosystem function (Table 4.1) are frequently included in observational measurements, creating opportunities for benchmarking. Many of these variables are direct outputs of ED2, but ecosystem respiration (Reco), carbon use efficiency (CUE), inherent water use efficiency (IWUE), ecosystem-scale stomatal slope (G1), and light use efficiency (LUE) were calculated from existing ED2 outputs; more information can be found in Table 4.1. Soil carbon is segregated into three reservoirs in ED2 based on characteristic decay rates. Fast soil carbon, intermediate (also referred to as structural), and slow soil carbon pools. The fast soil carbon pool is composed of metabolic litter (both non-lignified leaf and fine-root litter) that decomposes quickly, the intermediate soil pool is composed of decaying structural tissues and lignified materials, and the slow soil carbon pool consists of dissolved soil organic matter (SOM; Moorcroft et al., 2001). More information on the representation of soil carbon in ED2 can be found in the supplement to chapter three.

Variables that inform function were subset to the active growing season and averaged for each year spanning from 2020 – 2100. The growing season was broadly defined as periods where air temperature was above 5˚C and GPP was greater than 0.031 kg C m^{-2} $month^{-1}$ (Nelson et al., 2018). This definition of growing season was used to accommodate regional differences in growing season length or timing, and potential seasonal shifts over time in response to climate change.

Table 4.1: Ecosystem function variables used in analysis

Variable	Symbol	Description	Units	Calculation	Source
Ecosystem respiration	Reco	Sum of respiration by living organisms, includes both heterotrophic (Rh) and autotrophic respiration (Ra)	$kg\ C\ m^{-2}\ month^{-1}$	Ra + Rh	
Carbon use efficiency	CUE	Ratio between net primary production (NPP) and GPP, indicates how efficiently atmospheric C is converted into plant biomass	$kg\ C\ m^{-2}\ month^{-1}$	$\frac{NPP}{GPP}$	*DeLucia et al., 2007*
Evapotranspiration	ET	Total movement of water from the land surface to the atmosphere through evaporation (E) and transpiration (T)	$kg\ H_2O\ m^{-2}\ month^{-1}$	E + T	
Inherent water use efficiency	IWUE	Ecosystem level proxy of intrinsic WUE, represents the ratio of C assimilation rate to stomatal conductance at the leaf level	$kg\ C\ Pa\ kg\ H_2O^{-1}\ month^{-1}$	$\frac{(GPP*VPD)}{ET}$	*Beer et al., 2009*
Stomatal slope (ecosystem scale)	G1	Slope of the relationship between stomatal conductance and photosynthetic rate, interpreted as the marginal carbon cost of water to plant C uptake	–	$\frac{ca*\sqrt{VPD}}{1.6*GPP} * (Gs - g0) -1$	*Medlyn et al. 2011*
Light use efficiency	LUE	Ratio of NPP to photosynthetically active radiation (PAR)	$kg\ C\ MJ^{-1}$	$\frac{NPP}{PAR}$	*Medlyn, 1998*
Net canopy conductance	Gc	Stomatal conductance to water vapor and CO_2 scaled to the ecosystem level	$W\ m^{-2}$	Direct ED2 output	
Gross primary production	GPP	Total amount of C fixed via photosynthesis	$kg\ C\ m^{-2}\ month^{-1}$	Direct ED2 output	
Net ecosystem exchange	NEE	NPP minus C losses through Rh	$kg\ C\ m^{-2}\ month^{-1}$	Direct ED2 output	
Fast soil carbon	FSC	Total amount of C in the soil C pool with the fastest decay rate, comprised of metabolic litter	$kg\ C\ m^{-2}$	Direct ED2 output	
Structural soil carbon	STSC	Total amount of C in the soil C pool with an intermediate decay rate, comprised of decaying structural tissues and lignified materials	$kg\ C\ m^{-2}$	Direct ED2 output	
Slow soil carbon	SSC	Total amount of C in the soil C pool with the slowest decay rate, comprised of dissolved soil organic matter	$kg\ C\ m^{-2}$	Direct ED2 output	

Comparison of model predictions across management scenarios highlighted differences in function that emerged as a result of management, and comparison across radiative forcing scenarios highlighted the impact of climate change on the relationship between management and forest function. The response of forest function to management and climate change was evaluated through regionally-grouped simulations. A five-year moving average was calculated to isolate trends in variable response from start to end of the century, and bootstrapping provided confidence intervals for summary statistics. Annual growing season averages for function variables calculated at each site were grouped by geographic region, RCP scenario, and management type for principal component analysis (PCA), with region, RCP scenario, and management type retained as supplementary categorical variables. The R package *FactoMineR51* (Lê et al., 2008) was used for conducting and visualizing PCA. Function variables were scaled to unit variance.

Significance testing was performed to determine the ideal number of components that should be retained to minimize redundancy but avoid information loss. The component significance testing method used here was developed by Dray (2008) and implemented in the R package *ade4*. The Dray (2008) method is based on the computation of RV coefficients (multivariate generalizations to the R^2) as similarity measures, and the suggested number of axes to keep is estimated using a sequential Bonferroni procedure. The significance of PCA loadings was evaluated using a simple fixed threshold approach and a (more rigorous) bootstrapped eigenvector method. The significance threshold is determined by the dimensions of the dataset, and loadings are deemed significant when their absolute value and contribution are larger than the set threshold value (Migliavacca et al., 2021). The bootstrapped eigenvector method (Peres-Neto et al., 2003) performs 1,000 permutations on the extracted loadings from PCA, and p-values are estimated as the number of bootstrapped loadings less than or equal to zero for loadings that were positive in the original matrix, or the number of loadings greater than or equal to zero for loadings that originally were negative, divided by the total number of bootstrap samples.

ANOVA was conducted on a generalized additive model (GAM) implemented using the R package *mgcv()* (Wood 2011) and fit for each region using the restricted maximum likelihood method to determine the degree of variance in PC values that could be attributed to management type, climate change scenario, and interactive effects between the two. Year was included as a smoothed predictor to account for the effects of temporal autocorrelation. The statistical significance of differences in average PCs across management types, geographic regions, and RCP scenarios was determined using a Tukey's HSD test with an alpha value of 0.05.

4.2.3 Relative strength of management and climate change as drivers of forest function

Random forests (RF) were used to identify and rank the importance of dominant climate and structural drivers of variability in ecosystem function. RF was conducted with individual principal components (PC) as dependent variables, and annually averaged forest structural and climate metrics from model simulations as independent variables, using the R package *randomForest* (Breiman 2001). Climate variables include photosynthetically active radiation (PAR, W m^{-2}), air temperature (T_A , ℃) vapor pressure deficit (VPD, Pa), precipitation (P, mm $month^{-1}$), and surface soil matric potential (SMP, MPa). Forest structural variables include tree age (Age_{Tree}, years), leaf area index (LAI), tree height (H_{Tree}, m), coarse woody debris (CWD, kg C m^{-2}), the total number of unique cohorts ($Cohort_{total}$), and above ground biomass (AGB, kg C m^{-2}). Driver variables were grouped by region, RCP scenario, and management type for annual averaging. All possible model formulations were tested using 1,000 decision trees, and in-sample and out-of-sample R^2 values were calculated on both out-of-sample and full model predictions to assess the performance of each potential model formulation. Data was divided for training and testing using interleaved K-fold cross-validation (CV), a resampling method that splits data into K groups to train and test each model on multiple iterations (Hastie et al., 2009). The value of K is determined by the size of the dataset, with the goal of having groups of approximately equal size. K was set equal to 10 for model formulation testing.

For a predictive model to be considered causal, it must be invariant across different data environments (Peters et al., 2016). Two distinct data environments, or subsets of the full dataset, were defined for testing invariance of all RF model formulations, where an invariant model is one that is stable in its formulation regardless of differences in data heterogeneity (Migliavacca et al., 2021). Geographic regions (Great Lakes and Southeast) were used to define data environments, as each datapoint could be assigned to only one environment, and latitudinal differences in climate and forest type as well as differences in management practices and histories introduced heterogeneity in the predictor variables. The R package *CondIndTests* (Heinze-Deml et al., 2017) was used to test for conditional independence among random predictor variables, and a p-value for invariance was computed for each combination of response variable and predictors. Out-of-sample R^2 was calculated based on 10-fold CV.

After determining the best-fit RF model, driver variable importance was assessed. Variable importance was assessed for both individual predictive variables and for groups of variables. Group organization was based on whether variables represent climate or structural factors, with structural variables serving as a proxy for management, as management directly alters forest structure. The *importance()* function in the *randomForest* R package was used to compute a permutation-based variable importance measure, which is done by calculating the change in model predictive mean square error (MSE) before and after randomly permuting the value of each predictor variable, averaging across all decision trees, and normalizing by the standard deviation of the differences (Breiman 2001). This metric is essentially a model sensitivity measure, as it conveys how sensitive model accuracy is (in terms of changes in MSE) to small changes in individual predictor variable values. The permutation-based approach is less biased than using variable selection frequency or changes in node impurities that result from splitting decision trees on a given variable to quantify variable importance (Strobl et al., 2007), but if predictor variables exist across a range of measurement scales or categorical groups, then the reliability of this permutation-based variable importance measure decreases. To account for this, driver variables were scaled to unit variance. The predictive performance of grouped driver variables was estimated for each PC using 1,000 decision trees and 5-fold CV to calculate model R^2 for each group and PC combination.

4.3 Results

4.3.1 Net changes in climate and productivity by region

By the end of the century, growing season median monthly precipitation was 8.2 to 8.7 times higher on average in the SE than in the GL region (Table 4.2), and regional differences were typically larger under the more severe climate change scenario (RCP8.5). Precipitation increased from the start to the end of the century in both regions, under RCP4.5 precipitation increased by 2.0% from the start to the end of the century in the GL region, compared to a 1.0% increase under RCP8.5, while the SE saw a 20.5% increase in monthly growing season precipitation from start to end of century for RCP4.5 and a 16.1% increase under RCP8.5.

Monthly average growing season temperatures were 15.5 to 19.8% higher in the GL than the SE. In both regions, air temperature increased more under the more severe climate change scenario (RCP8.5), and differences between RCP scenarios become more pronounced over time in the GL. In the GL region, growing season air temperature increased by 5.2% for RCP4.5 and 10.5% for RCP8.5 from start to end of the century, while in the SE, air temperature increased by 2.6% for RCP4.5 and 4.1% for RCP8.5.

Table 4.2: Regional growing season average monthly air temperature and median monthly precipitation values (± 1 standard deviation) for start and end of century

Region	Climate change scenario	Period	Temperature (˚C)	Precipitation (mm)
SE	RCP4.5	start of century	14.3 ± 0.3	803.2 ± 109.1
SE	RCP4.5	end of century	14.6 ± 0.1	1010.4 ± 85.2
SE	RCP8.5	start of century	14.4 ± 0.3	918.9 ± 127.6
SE	RCP8.5	end of century	15.1 ± 0.2	1095.5 ± 50.8
GL	RCP4.5	start of century	16.2 ± 0.5	120.2 ± 6.6
GL	RCP4.5	end of century	17.1 ± 0.1	122.6 ± 7.0
GL	RCP8.5	start of century	16.4 ± 0.6	125.2 ± 8.1
GL	RCP8.5	end of century	18.4 ± 0.4	126.5 ± 5.6

Average productivity values (GPP) were typically 14.69 – 22.56% higher in the GL than the SE, with the difference becoming less pronounced over time, although trends varied by RCP and management scenario (Figure 4.1). In the GL, productivity experienced a minor increase of 1.23% from the start to the end of the century, whereas in the SE productivity values increased by 9.60%. Average productivity differences between RCP scenarios were minimal by the second half of the century in the GL (<1%), while in the SE, end-of-century productivity was 5.14% higher under the RCP8.5 climate change scenario (0.31 ± 0.01 kg C m^{-2} $month^{-1}$) compared to the RCP4.5 scenario (0.30 ± 0.01 kg C m^{-2} $month^{-1}$). AGB is 31.18 – 79.96% higher in the GL than the SE, but regional differences decreased over time as AGB steadily increased in the SE. Differences across management types and climate scenarios is broader in the GL compared to the SE, with differences in AGB primarily organized by management type. AGB decreased from start to end of century in the GL, with greater net decreases seen for RCP8.5 than RCP4.5 (17.39% and 13.27%, respectively). However, AGB increased from the start to the end of the century in the SE, with an average net increase of 47.36% for RCP4.5 and 40.74% for RCP8.5.

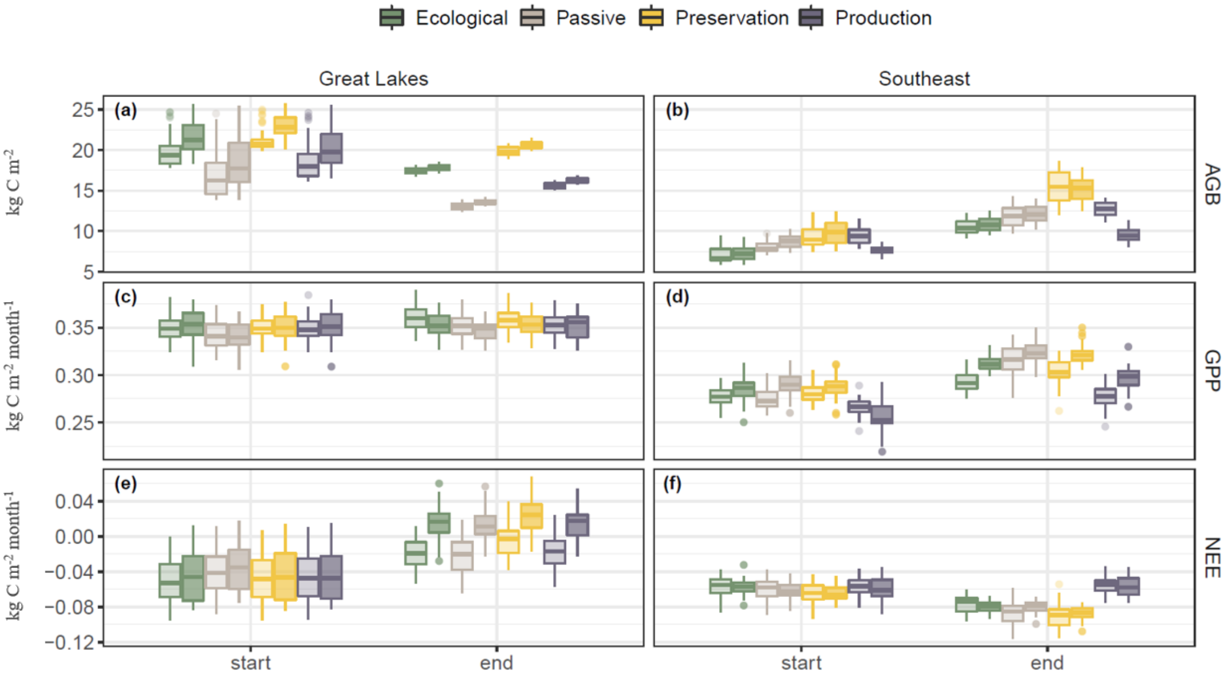

Figure 4.1: Aboveground biomass (AGB), gross primary productivity (GPP), and net ecosystem exchange (NEE) for the start and end of the century. Columns are organized by geographic region, color hue corresponds to management type, and color tone corresponds to climate change scenario, where lighter tones represent RCP4.5 and darker tones represent RCP8.5

The GL region was initially a slight carbon sink under both climate change scenarios (average NEE = –0.04 ± 0.02 kg C m^{-2} $month^{-1}$), but due to Reco increases outpacing productivity, the region became on average a slight net carbon source by the second half of the century under the RCP8.5 climate change scenario (0.02 ± 0.01 kg C m^{-2} $month^{-1}$), yet remained a net sink of carbon under the RCP4.5 scenario (–0.02 ± 0.01 kg C m^{-2} $month^{-1}$). The SE was a consistent carbon sink that increased in size over time, with NEE values ranging between –0.06 to –0.08 kg C m^{-2} $month^{-1}$ on average. End of century differences in SE NEE were less pronounced between the two climate change scenarios than what was observed in the GL, the SE was a 2.67% larger net sink of carbon under RCP4.5 compared to RCP8.5.

4.3.2 Dominant axes of ecosystem functional variability

The key axes of forest ecosystem function were identified through PCA. The first two principal components (PCs) were statistically significant and captured 83.80% of the total variance in ecosystem function across all region, climate, and management scenarios. The first axis of ecosystem function, PC1, represents the majority of the observed variability (71.3%) and is primarily defined by variables related to water exchange (IWUE and ET) and respiration (Reco), as well as productivity (GPP and G1) and slow (SSC) and fast (FSC) decaying soil carbon, as indicated by Figure 4.2. The second axis of ecosystem function, PC2, captures 12.5% of the observed variability in ecosystem function and is dominated by NEE, a variable describing the balance of carbon exchange between the land surface and the atmosphere, the net conductance to water vapor and CO_2 (Gc), and light (LUE) and carbon (CUE) use efficiency. Stomatal slope (G1), a variable representing tradeoffs between carbon gain and water loss, structural soil carbon (STSC), and GPP also contribute significantly to the variability captured by PC2.

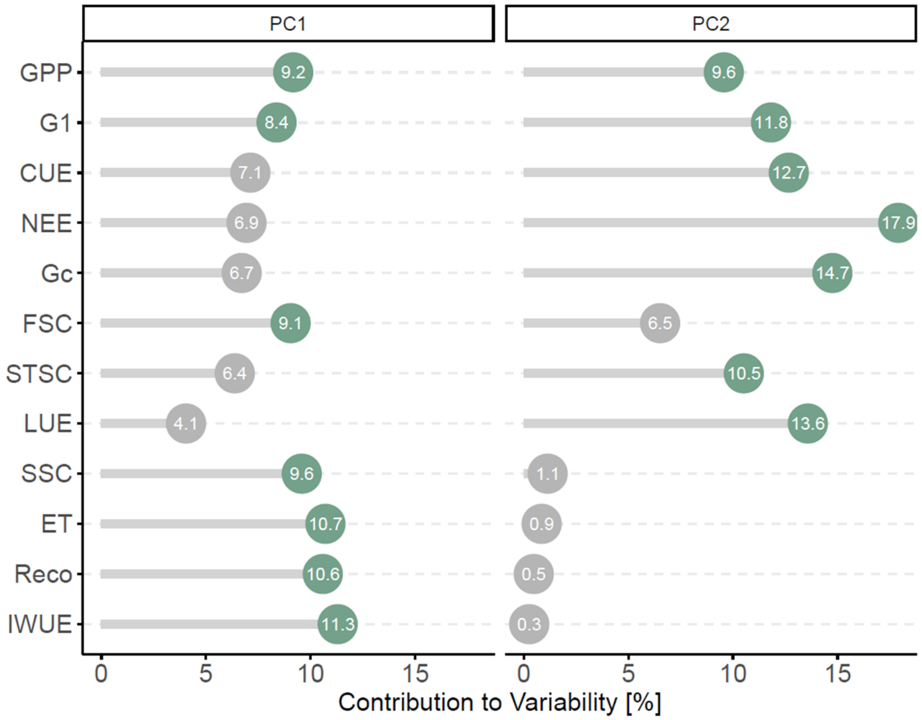

Figure 4.2: Contribution of individual ecosystem function variables to each principal component. Significant function variable loadings are colored green

4.3.3 Differences in functional variability by region, climate change scenario, and management

Whether variance in ecosystem function over time differs significantly by climate change scenario or management type depends on region as well as the functional axis in question, as does the portion of the total variance that can be attributed to each categorical factor. For example, PC1 values differed significantly among management types in both regions, but differences among RCP scenarios for PC1 were only significant in the SE (Table 4.3). Management explained a greater portion of the total variability compared to RCP scenario for both functional axes in both regions, however, the effect of management was more pronounced in the SE. Management explained 9.5 times more PC1 variability than RCP scenario in the SE, and 5.6 times more variability than RCP scenario in the GL. For PC2, the functional axis defined by the net exchange of carbon and resource use efficiency, management explained 16.3 times more variability than RCP scenario in the SE, and 1.26 times more variability than RCP scenario in the GL. Production forestry tended to differ the most from the other three management types, and was often characterized by lower average PC2 values in the SE and higher average PC2 values in the GL.

Table 4.3: Management type, climate change scenario (RCP), and interactive effects on the two axes of ecosystem functional variability. '*' symbols next to F-values denote statistical significance at an alpha value of 0.05, and ':' symbols between predictors indicate interaction effects between categorical factors. Df = degrees of freedom and SS = sum of squares

			PC1			PC2		
Predictor	Region	Df	SS	F-value	η2	SS	F-value	η2
RCP	GL	1	1.9	3.39	0.003	52.3	149.364*	0.054
Management	GL	3	10.6	6.186*	0.017	65.7	62.558*	0.068
Management:RCP	GL	3	1.4	0.817	0.002	2.3	2.219	0.002
RCP	SE	1	3.04	32.69*	0.030	15.6	46.01*	0.017
Management	SE	3	28.92	103.6*	0.281	254	250.19*	0.273
Management:RCP	SE	3	6.8	24.37*	0.066	3	2.92*	0.003

$*p < 0.05$

Differences among RCP scenarios in the GL were only statistically significant for PC2. Interaction effects between management and climate change scenarios were only significant in the SE. The relative differences in PC1 values among management types change with RCP scenario in the SE, PC1 values become more similar between ecological and preservation management under RCP8.5, and passive, preservation, and ecological management all experience an increase in PC1 values under RCP8.5, whereas PC1 values decrease under production management. The more severe climate change scenario increases PC2 values across all management types. The influence of the climate change scenario alone was more distinct for PC1 than PC2 in the SE, but the reverse was true in the GL (Table 4.3). Variability in PC2 was greater under RCP8.5 in the GL region, possibly driven by the comparatively high (more positive) NEE and Reco values observed under RCP8.5.

Regional differences in average PC values are the most distinct for the first axis of ecosystem functional variability (PC1; Figure 4.3), where group mean values are always statistically different between the two regions regardless of RCP scenario or management type (Figure S4.3). Greater variability in PC1 values is associated with the GL than the SE region. The GL region tends to have higher STSC, CUE, GPP, G1, ET, IWUE, Reco and SSC and lower FSC, LUE, and Gc, and is less of a net carbon sink, while the SE displays the opposite trend, with high values for FSC, LUE, and Gc, is a greater net carbon sink, with comparatively lower values for the remaining variables (Figure S4.2). The significance of mean pairwise differences between all combinations of region, RCP scenario, and management type groups determined using a Tukey's HSD test is shown in Figure S4.3.

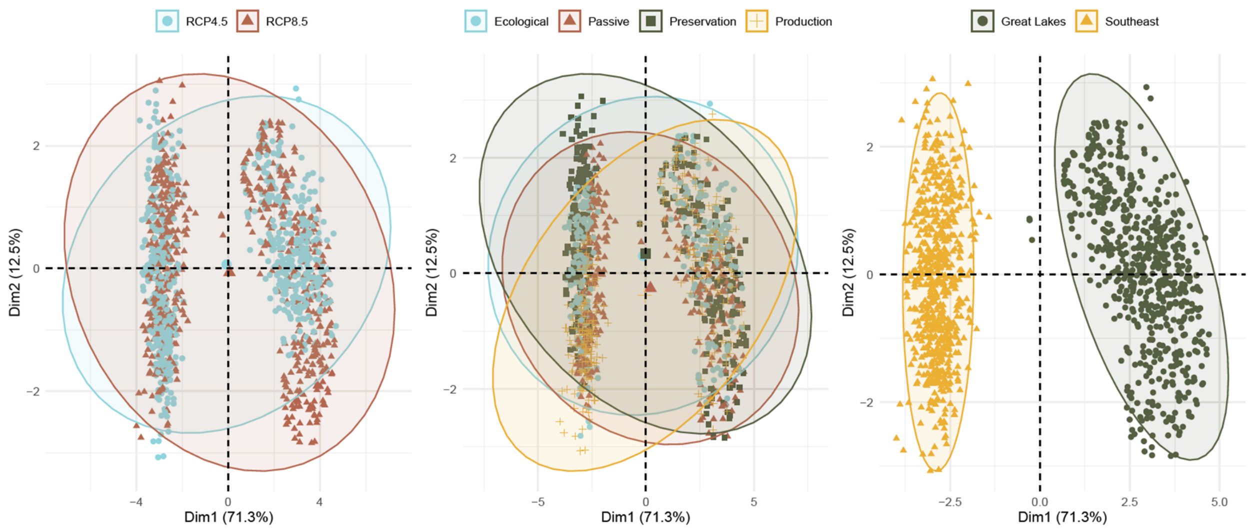

Figure 4.3: Biplots showing the organization of data points along the first two principal components. Points are colored by the RCP scenario **(a)**, management type **(b)**, or by geographic region **c)**. Ellipsoids are defined by a 95% confidence interval

4.3.3.1 Land-atmosphere exchange and resource use efficiency

Productivity varied more over time in the SE than in the GL (Figure S4.1), and differences between management types were more pronounced, average productivity (GPP) differences across management types and RCP scenarios were minimal (± 0.01 kg C m^{-2} $month^{-1}$) in the GL. Net carbon source and sink magnitudes also differed minimally between management types in the GL, but differences were more pronounced between RCP scenarios. Under RCP4.5, management types in the GL were on average net carbon sinks of –0.02 ± 0.01 kg C m^{-2} $month^{-1}$ while under RCP8.5 management types were on average net carbon sources of 0.02 ± 0.01 kg C m^{-2} $month^{-1}$. This can be attributed to differences in ecosystem respiration rates between the two RCP scenarios, Reco was 8.07% higher on average under RCP8.5 than RCP4.5 in the GL. In the SE, productivity was highest for passive forestry (0.31 – 0.32 kg C m^{-2} $month^{-1}$)

and lowest for production forestry (0.28 – 0.30 kg C m^{-2} $month^{-1}$) under both RCP scenarios (Figure 4.1). Production forestry was also the smallest net sink of carbon (–0.06 ± 0.01 kg C m^{-2} $month^{-1}$), likely due to its comparatively high levels of Reco (0.22 – 0.24 kg C m^{-2} $month^{-1}$), while preservation forestry was the largest net carbon sink (–0.09 ± 0.01 kg C m^{-2} $month^{-1}$).

ET was 70.69% higher in the GL compared to the SE, values did not change significantly over time in either region. Differences in ET across management types were minimal in both regions, but ET was 7.44% higher under RCP8.5 compared to RCP4.5 in the SE. Canopy conductance (Gc) decreased by 4.89 – 11.05% from the first to the second half of the century in the GL (the decrease was more pronounced under RCP8.5), but increased slightly across all management types and RCP scenarios in the SE, with an average increase of 8.12%.

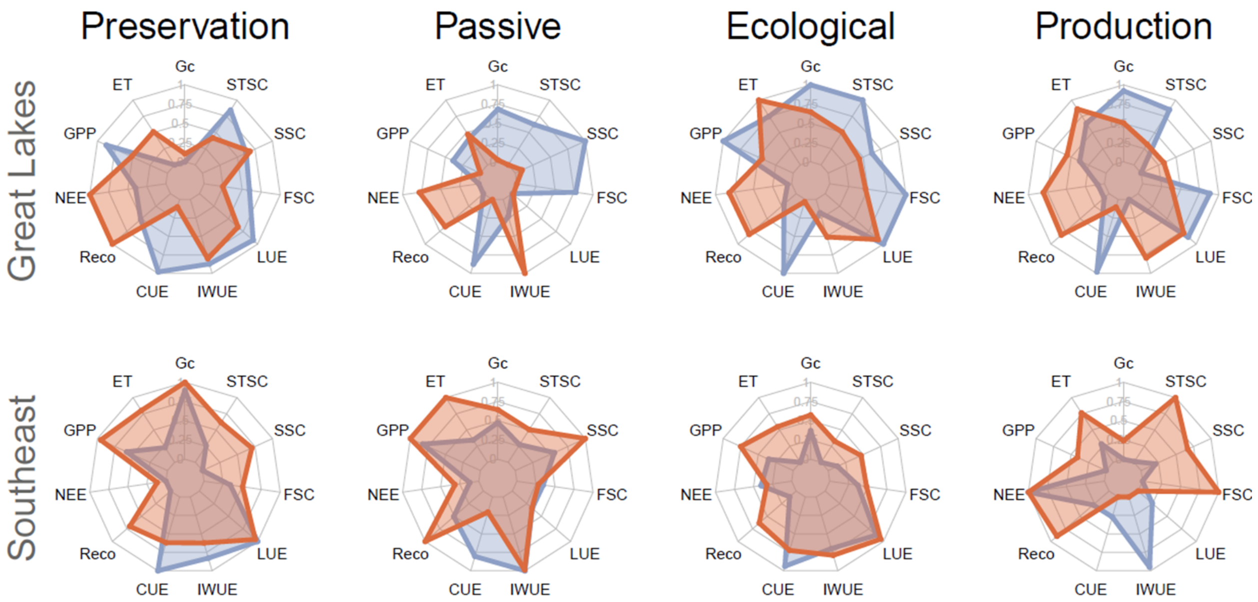

Figure 4.4: Comparison of relative ecosystem functional variables between management types. Figure rows correspond to geographic region and figure columns correspond to management type. Blue polygons represent relative variable values under RCP4.5 and red polygons represent relative variable values under RCP8.5. Each ecosystem functional variable is grouped by region and scaled from 0 – 1 (grid lines on the plots are in increments of 0.25)

Water use efficiency was 52.88% higher on average in the GL than in the SE, and IWUE increased by 5.29% on average from the start to the end of the century in the GL region. Higher average IWUE tended to be associated with the more severe climate change scenario (RCP8.5), but differences were minimal across management types in both regions. CUE differed primarily by RCP scenario in the GL region (CUE was 3.46% higher under RCP4.5) with minimal differences between management types, and values decreased by 0.96% to 3.48% from the start to the end of the century for RCP4.5 and RCP8.5, respectively. CUE differences by RCP scenario were less pronounced in the SE, but the largest differences were seen for passive and preservation management. CUE was lowest under production forestry (0.70 ± 0.01 kg C m^{-2}

month^{-1}), and highest for preservation and ecological forestry (both 0.71 ± 0.01 kg C m^{-2} month^{-1}) in the SE. Of the three RUE variables, LUE differed most substantially across the four management types, with greater differences between management types observed in the SE. LUE was lowest under passive management in the GL region regardless of RCP scenario (0.02 kg C MJ^{-1}), and highest for ecological management. LUE was 42.64% higher on average in the SE, and was lowest for production management (0.02 kg C MJ^{-1}), and highest under preservation and ecological forestry (0.04 kg C MJ^{-1}). Overall, production forestry had the lowest RUE levels in the SE.

4.3.3.2 Soil carbon

Both axes of ecosystem functional variability include at least one significant variable describing carbon stored in soil. Changes in stored soil carbon from the start to the end of the century were more dramatic in the GL region than in the SE, particularly for SSC and STSC. In the GL region, FSC and STSC decreased by 21.90 – 32.65% on average across all management types and RCP scenarios from the start to the end of the century, while SSC increased by 53.54%. Both FSC and STSC were 7.06 – 15.20% lower on average in the GL under RCP8.5 than under RCP4.5, and differences were more pronounced between RCP scenarios than between management types, but ecological forestry had the highest average values of FSC and STSC (0.62 ± 0.06 kg C m^{-2} and 39.06 ± 5.02 kg C m^{-2}), passive forestry had the smallest STSC stores (36.77 ± 5.11 kg C m^{-2}), and preservation had the lowest FSC (0.57 ± 0.04 kg C m^{-2}). Differences between management types were negligible for SSC in both regions under both RCP scenarios.

In the SE, FSC differed the most across management types and climate change scenarios. Under RCP4.5 FSC stores in the SE were lowest for production forestry (0.91 ± 0.08 kg C m^{-2}) and highest for ecological management (1.02 ± 0.03 kg C m^{-2}), but under RCP8.5, FSC was highest for production forestry (1.12 ± 0.07 kg C m^{-2}) and lowest for passive forestry (0.98 ± 0.07 kg C m^{-2}). Differences between management and RCP scenarios were minimal for STSC in the SE, but STSC was slightly higher for production forestry.

4.3.4 Relative strength of management and climate as drivers of variability in forest function

The best fit RF model across both PCs (average out-of-sample $R^2 = 0.95$) includes the structural variables tree age (Age_{Tree}), leaf area index (LAI), mean tree height (H_{Tree}), coarse woody debris (CWD), above ground biomass (AGB), and the total number of unique cohorts ($Cohort_{total}$), and the climate variables photosynthetically active radiation (PAR), air temperature (T_A), vapor pressure deficit (VPD), precipitation (P), and surface soil matric potential (SMP). The predictive model was invariant across the two data environments (defined as SE and GL geographic regions), meaning the best-fit model formulation was not regionally dependent. However, most of the possible model formulations tested were statistically invariant ($p < 0.01$) across the two data environments, which means that we cannot deduce with certainty that the full model formulation is in fact causal, and instead can only say that it is a plausible causal model.

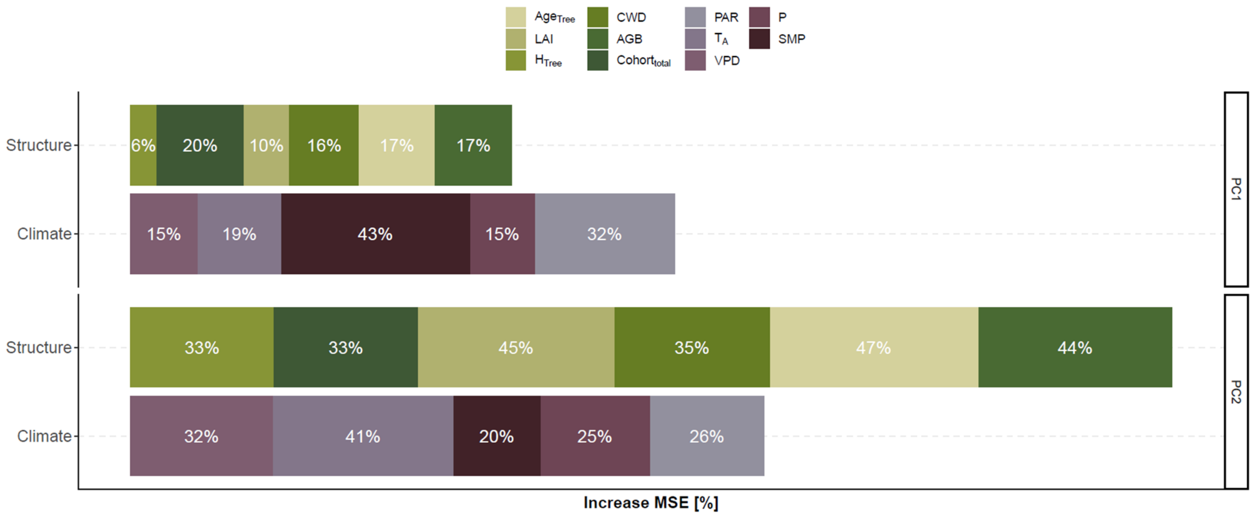

Figure 4.5: Random forest variable importance (evaluated as the percent increase in MSE associated with small permutations to individual variable values) to predict the two primary axes of ecosystem functional variability defined through PCA. Variables representing forest structure are shades of green and variables representing climate are shades of purple. The white numbers indicate the relative importance of individual variables.

Grouped climate variables were stronger drivers of the variability in ecosystem function captured by PC1 (Figure 4.5), the axis primarily defined by variables related to water exchange, respiration, and productivity, while grouped structural variables were stronger drivers for PC2, the functional axis dominated by NEE as well as light and carbon use efficiency. However, the importance of climate variables over structural variables for PC1 was narrow, grouped climate variables alone explained 98.94% of the total variance in PC1 while grouped structural variables explained 97.83% of the total variance, as determined using 1,000 decision trees and 5-fold CV to calculate model R^2 for each group and PC combination. The difference in the explanatory power of grouped predictor variables was broader for PC2; structural variables predicted PC2 values with an average R^2 of 0.889 while climate variables predicted PC2 values with an average R^2 of 0.736.

The importance of individual drivers was assessed as the change in model accuracy (% MSE) after variable permutation. For PC1, SMP and PAR were the most important individual drivers (42.74% and 31.87% increase in MSE respectively), but $\text{Cohort}_{\text{total}}$ and T_A were also important drivers. LAI and H_{Tree} were the least important drivers of function variability for PC1. H_{Tree} and LAI were the strongest drivers of PC2 (47.44% and 44.64% increase in MSE respectively), followed by AGB (43.95% increase in MSE) and T_A (41.07% increase in MSE). P and SMP were the least important drivers of the function variability represented by PC2.

4.4 Discussion

Comparison of model predictions across management scenarios highlighted differences in function that emerged as a result of management, where forest function is evaluated here primarily through the lens of carbon and water cycling, as these processes are central to land-atmosphere interactions (Reichstein et al., 2014). Comparison across radiative forcing scenarios highlighted the impact of climate change on the relationship between management and forest function, and assessment of regionally grouped simulations illuminated regional dependencies associated with the relationship among management, function, and climate change.

4.4.1 Impacts of management and climate change on forest function

Our first research objective was to determine how variations in climate and management intensity and severity impact forest function, and if relationships are regionally dependent. As hypothesized, the response of forest function to management and climate change varied regionally. Regional differences were the most pronounced for functional variables that aligned with PC1, such as evapotranspiration, respiration, and water use efficiency, all of which had strong responses to changing climatic conditions. There was also greater variability in PC1 values in the GL compared to the SE region. The GL region tends to have larger structural (intermediate decay rate) and slow soil carbon stores (STSC and SSC), higher productivity (GPP), stomatal slope (G1), evapotranspiration (ET), carbon and inherent water use efficiency (CUE and IWUE), and respiration (Reco), and smaller fast soil carbon (FSC) stores, light use efficiency (LUE), and stomatal conductance (Gc), and is less of a net carbon sink. The SE displays the opposite trend, with high values for FSC, LUE, and Gc, a greater net carbon sink, and comparatively lower values for the remaining variables.

We hypothesized that the response of ecosystem function to climate change severity would vary by functional category, but that generally speaking we'd observe a decrease in carbon storage and an increase in resource use efficiency in response to more severe climate change conditions. We found that total carbon storage did decrease in the GL region in response to the more severe climate change scenario, but that while IWUE was higher on average under RCP8.5, CUE was lower across all management types, and LUE was slightly lower, but varied more by management type. In the SE, productivity increased under RCP8.5 as did stored soil carbon, but whether carbon sink magnitudes increased or decreased under RCP8.5 relative to RCP4.5 depended on management type. CUE in the SE was again lower under the more severe climate change scenario, but changes in IWUE and LUE depended on management type.

Lastly, we hypothesized that active management strategies that promote uneven-aged stands and a multi-layered structure through periodic harvest of individual large trees (such as ecological forestry) would have higher resource use efficiency and be less susceptible to reductions in ecosystem function in response to climate variability, whereas more passive management strategies (such as passive and preservation forestry) would have greater sensitivity to climate change and lower levels of resource use efficiency.

Consistent with our hypothesis, ecosystem function was the most sensitive to climate change under passive forestry in the GL, meaning passive forestry simulations differed the most substantially between RCP scenarios. Under the more severe climate change scenario in the GL, passive forestry resulted in decreased overall carbon storage; soil carbon and productivity both decreased, while respiration increased. In contrast, ecological forestry was the least sensitive to changes in climate, and maintained comparatively high levels of ecosystem function. However, resource use efficiency trends under ecological forestry were not significantly different from production or preservation management. The high sensitivity of passive forestry to changes in climate is concerning because a large percentage of forested lands in the GL region are managed by private owners (Hoover and Riddle, 2021) who typically rely on passive management strategies (vonHedemann and Schultz, 2021), while our analysis suggests that more active management approaches that such as ecological forestry, should be considered in the GL region to sustain ecosystem function in the face of climate change. Resource use efficiency was the most sensitive to climate change under production forestry in the SE, with significant declines in IWUE, CUE, and LUE observed under RCP8.5, while ecological forestry maintained high levels of resource use efficiency. Trends in other ecosystem functions were more variable between management types, and depended on the specific ecosystem function.

Productivity was higher in the GL, and the region was initially a slight carbon sink under both climate change scenarios, but due to Reco increases outpacing productivity (GPP), the GL became on average a slight net carbon source by the second half of the century under the more severe climate change scenario (RCP8.5) (where Reco was 8% higher than under RCP4.5), suggesting higher climate-driven carbon losses. Projections of future carbon uptake in the GL region through other methods, such as Earth System Models, predict substantial increases in regional productivity (Wu et al., 2022), however, this is likely due to CO_2 fertilization effects, which were not represented here. In contrast, the SE was a consistent carbon sink that increased in size over time, a trend that has been reported in other studies (Wu et al., 2022). The expanding size of the SE carbon sink is likely attributed to enhanced precipitation (Bond-Lamberty et al., 2014, Wu et al., 2022) and increased canopy conductance, whereas productivity in the GL was likely curtailed by high growing season temperatures. The high evaporative demand coupled with increasing aridity from temperature increases outpacing precipitation increases likely became a limiting factor for productivity in the GL (Rollinson et al., 2016). This is evidenced by the decrease in Gc and increase in IWUE observed in the GL, which suggests that forests became water stressed, and sacrificed carbon gain to conserve water resources.

Reco was more responsive to changes in climate than to changes in management in both regions, with greater loss of carbon to the atmosphere under the more severe climate change scenario. This is consistent with global analyses of soil carbon flux (the second largest terrestrial carbon flux and one component of Reco), which show an amplification of soil respiration in response to rising air temperatures (Bond-Lamberty and Thomson, 2010). This suggests that enhancing net carbon uptake by managing for increased productivity is likely more achievable than managing to reduce respiration. Productivity differences between management types were minimal in the GL, but in the SE the less intensive management practices (passive and preservation forestry) had higher average GPP by the end of the century, while the more intensive management practices that prioritized wood products (production and ecological forestry) resulted in lower average GPP, with the lowest productivity observed for production forestry.

Changes in stored soil carbon from the start to the end of the century were more dramatic in the GL region than in the SE; fast and structural soil carbon decreased over time, while slow soil carbon increased. This indicates that the observed increases in respiration in the GL were driven by accelerated decomposition of more readily available metabolic litter and structural tissues, rather than mobilization of older stored carbon. Fast and structural soil carbon were also 7 – 15% lower under the more extreme climate change scenario in the GL, but soil carbon stores were larger on average under RCP8.5 in the SE. Fast soil carbon stores had the broadest range across management and RCP scenarios in both regions, likely due the role of management in controlling rates of above ground biomass production and thus litter input, and RCP scenario controlling litter mass loss by influencing decomposition rates (Lu et al., 2013). In the SE, fast and slow soil carbon stores increased slightly from the start to the end of the century, but changes in structural soil carbon were minimal. Variations in management intensity had less of an impact on soil carbon than variations in climate in both regions.

Resource use efficiency was represented as light, water, and carbon use efficiency. LUE differed primarily by management type in both regions, whereas trends in IWUE and CUE were less consistent. Ecological and preservation forestry often promoted higher LUE, while passive forestry had lower LUE. LUE was higher on average in the SE. IWUE tended to increase under the more severe climate change scenario in both regions, with the exception of production forestry in the SE. In the GL, production and passive forestry had similar IWUE, while ecological forestry often had the lowest values. In the SE, IWUE was higher under passive forestry and lower under production forestry. IWUE was 53% higher on average in the GL than in the SE, which is not surprising considering the higher evaporative demand in the GL. High IWUE in the GL likely buffered the impact of increasing Reco on NEE to a certain extent by sustaining productivity. CUE differed primarily by RCP scenario in the GL, whereas differences were more pronounced between management types in the SE, which suggests that management could be used to increase CUE in the SE, and further enhance the net carbon uptake. CUE decreased under RCP8.5 relative to RCP4.5 in both regions, with the lowest values under passive forestry in the GL and production forestry in the SE. In the SE, CUE was highest under ecological and preservation forestry. CUE was higher on average in the GL.

With regards to opportunities for using management to enhance resource use efficiency, LUE is most responsive to management in both regions. Passive forestry actually decreased LUE relative to the control (preservation management) in both regions, whereas ecological management enhanced LUE. This is likely due to the multi-canopy structure encouraged by ecological management, which could foster a more diverse mix of shade tolerant trees that are able to capitalize on understory light more efficiently. Passive forestry had the strongest positive impacts on IWUE in the SE regardless of RCP scenario, whereas passive forestry enhanced IWUE in the GL only under RCP8.5. Generally speaking, ecological forestry had the best outcomes for RUE relative to preservation forestry in the SE, while production forestry had the worst (except for IWUE under RCP4.5, which it did enhance). Trends were weaker in the GL, preservation forestry generally had higher RUE than the active management types, and outcomes were much more dependent on RCP scenarios. Ecological and production forestry had high LUE, and high CUE under RCP4.5, while passive forestry had high IWUE under RCP8.5.

4.4.2 Dominant axes of ecosystem functional variability in managed forests

The dominant axes of variability in forest function over time at the regional scale were 1) tradeoffs between carbon accumulation (in both biomass and soils) and water loss, and the flux of carbon from the land surface back to the atmosphere through respiration, and 2) the net carbon balance of ecosystems, as well as light and carbon use efficiency. As hypothesized, both forest productivity and resource use efficiency were key components of ecosystem functional variability in managed forests, but resource use efficiency, and in particular water use efficiency, was ultimately representative of a larger proportion of the observed variability.

Regional differences in forest function were the most pronounced for functional axes representing tradeoffs between carbon gain and water loss. As variability in this functional axis was driven more by climate related variables than by management, this likely reflects the regional differences in how the pace and pattern of climate change will be expressed. Regional differences were much less distinct for functional axes related to light and carbon use efficiency, which differed more by management type. This suggests that while climate change is an important driver of variability in ecosystem function, the degree of impact it has on ecosystem function is tempered by how it interacts with management.

4.4.3 Relative strength of management and climate as drivers of variability in forest function

Our final research objective was to characterize the relative importance of management versus climate change as drivers of variability in forest function over multi-decadal timescales, and determine if driver importance was scale dependent. ANOVA of two GAMs fit with regional data showed that management explained 1.2 – 16.3 times more variability than RCP scenario for both axes of future variability in ecosystem function. However, the effect of management was more pronounced in the SE, and interaction effects between management and climate change scenarios were only significant in the SE. This supports our hypothesis that management is a stronger overall driver of changes in forest function than climate change, and is consistent with recent work in boreal forests by Triviño et al. (2023) and temperate forests by Gutsch et al. (2018). Triviño et al. (2023) showed that the future of ecosystem services in boreal forests was primarily driven by management, with management effects that were 11 times stronger on average than climate change effects. A similar study in Germany evaluating tradeoffs between ecosystem services (Gutsch et al., 2018) also concluded that management had a comparatively larger influence on ecosystem services than climate change scenarios. Both authors deduced that the relative importance of drivers varied between biogeographical zones. Contrary to our hypothesis that the importance of climate change would increase with latitude, RCP scenario alone was more important in the SE than in the GL for the dominant axis of future functional variability (PC1), although the RCP scenario was more important in the GL for PC2.

Our application of a random forest (RF) model to predict future variability in ecosystem function told a slightly different story regarding the importance of management versus climate change for the first axis of functional variability (PC1). The predictive model was built using climate and structural data from both geographical regions combined, and was invariant across the two data environments ($p < 0.001$), meaning that the best-fit model formulation was not regionally dependent. Analysis showed that grouped climate variables were stronger drivers of the variability in ecosystem function captured by PC1, the axis primarily defined by variables related to water exchange, respiration, and productivity, while grouped structural variables were stronger drivers for PC2 ($R^2 = 0.889$ for structural variables compared to $R^2 = 0.736$ for grouped climate variables), the functional axis dominated by NEE as well as light and carbon use efficiency. However, the importance of climate variables over structural variables for PC1 was narrow ($R^2 = 0.989$ versus $R^2 = 0.978$), suggesting that both management and climate play an important role in driving PC1.

The difference in conclusions between the two methods could be partially attributed to differences in spatial extent of the data used in analysis. The conclusion that management is a more important driver of function than climate at the regional scale is supported by similar studies (Triviño et al., 2023, Gutsch et al., 2018), but when expanding to the sub-continental scale to incorporate data from multiple regions, the broad gradients in future climate conditions become more critical. The narrow difference in driver strength of climate versus management suggests that the effects are likely not independent of one another. This is supported by other studies showing that interactions between climate and forest structure and demography explain forest functional responses better than each factor individually (Rollinson et al., 2016, Clark et al., 2013, Bond-Lamberty et al., 2014), and that functional responses to climate (especially precipitation changes) are mediated by competition and structural factors such as tree size (Mérian and Lebourgeois, 2011), elements that are directly impacted by management. It's worth noting that the two drivers likely have different timescales of importance and interaction, although this was not explicitly explored here. Management effects on forest function are often more immediate than climate change effects, but management-induced changes in carbon cycle dynamics can alter the functional response to climate across longer timescales (Seidl et al., 2017, Desai et al., 2022).

At the level of individual variable importance, soil matric potential (SMP) and photosynthetically active radiation (PAR) were the most important individual drivers for predicting ecosystem functions related to water exchange, respiration, and productivity (PC1). SMP represents how readily available water is for plants to utilize in photosynthesis, meaning it links productivity responses to climatic conditions such as increasing aridity or drought. Its importance over a more general variable like precipitation, which has been shown by others such as Wu et al. (2022) to be a strong driver of productivity, likely comes from the more direct relationship to productivity and water exchange. Additionally, SMP influences the decomposition of soil organic matter, which has implications for Reco and soil carbon storage. Considering PAR is the primary energy source for photosynthesis, its importance as a driver of PC1 isn't surprising. PAR varies due to seasonal changes in vegetation phenology and solar radiation, but PAR availability also varies substantially depending on canopy architecture. Structural variables such as tree height, density, leaf orientation, LAI, and abundance of gaps all determine the interception and distribution of PAR within the forest.

Average tree height (H_{Tree}) and leaf area index (LAI) were the strongest drivers of functional variability related to net carbon exchange and resource use efficiency (PC2). H_{Tree} influences a broad range of factors contributing to net carbon exchange and resource use efficiency, including leaf area, shading, competitive advantage, and demand for available resources, all of which shape carbon uptake and storage capacity. LAI correlates with the ability of trees to intercept incoming light, as well as the degree of light limitation due to shading, both of which shape LUE, a significant contributor to PC2.

4.5 Conclusions

In summary, the research findings presented here indicate that the response of forest function to management and climate change is highly dependent on biogeographic region. The Great Lakes (GL) region tends to have larger carbon stores, higher productivity, and greater water use efficiency, but it is less of a net carbon sink by the end of the century compared to the Southeast (SE) region. Respiration increases outpaced productivity gains in the GL region, leading to a transition from a carbon sink to a slight net carbon source under the more severe climate change scenario. On the other hand, the SE region remained a consistent carbon sink that increased in magnitude over time. These regional differences can be attributed to factors such as higher evaporative demand and temperature-induced water stress in the GL region.

We also highlight the relative importance of management and climate change as drivers of forest function across multi-decadal timescales. Management was found to explain more variability in forest function than climate change at the regional scale, with management effects being more pronounced in the SE region. However, when combining data from multiple regions, the broad gradients in future climate conditions became more critical. The narrow precedence of climate over management as a driver of forest function at the sub–continental scale suggests that their effects are likely not independent of one another. Our analysis also showed that climate variables had a stronger influence on the variability related to water use efficiency, respiration, and evapotranspiration, while structural variables were more important for the variability related to net carbon exchange, trade offs between carbon gain and water loss, and light and carbon resource use efficiency.

Overall, this chapter supports the consensus that considering both management and climate change impacts at the regional scale is important for understanding and predicting variability in forest function. Management practices can significantly influence forest productivity and resource use efficiency, while climate change impacts vary by region and interact with management practices to alter outcomes. These findings emphasize the need to incorporate both factors when assessing the viability of forest management strategies to sustain ecosystem function in the face of changing climatic conditions.

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Supplemental figures

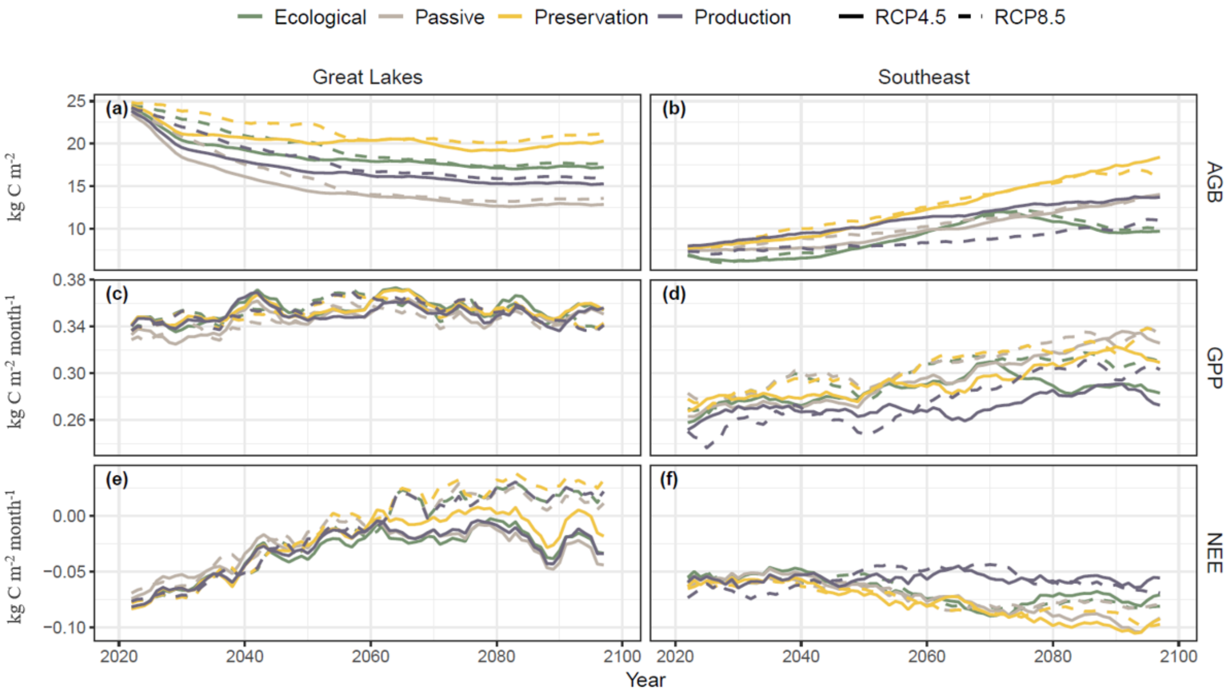

Figure S4.1: Above ground biomass (AGB), gross primary productivity (GPP), and net ecosystem exchange (NEE) across both regions from the implementation of active forest management in 2020 through the duration of the modeling temporal extent. Lines indicate 5-year moving averages. Color corresponds to management type and line style represents climate change scenarios

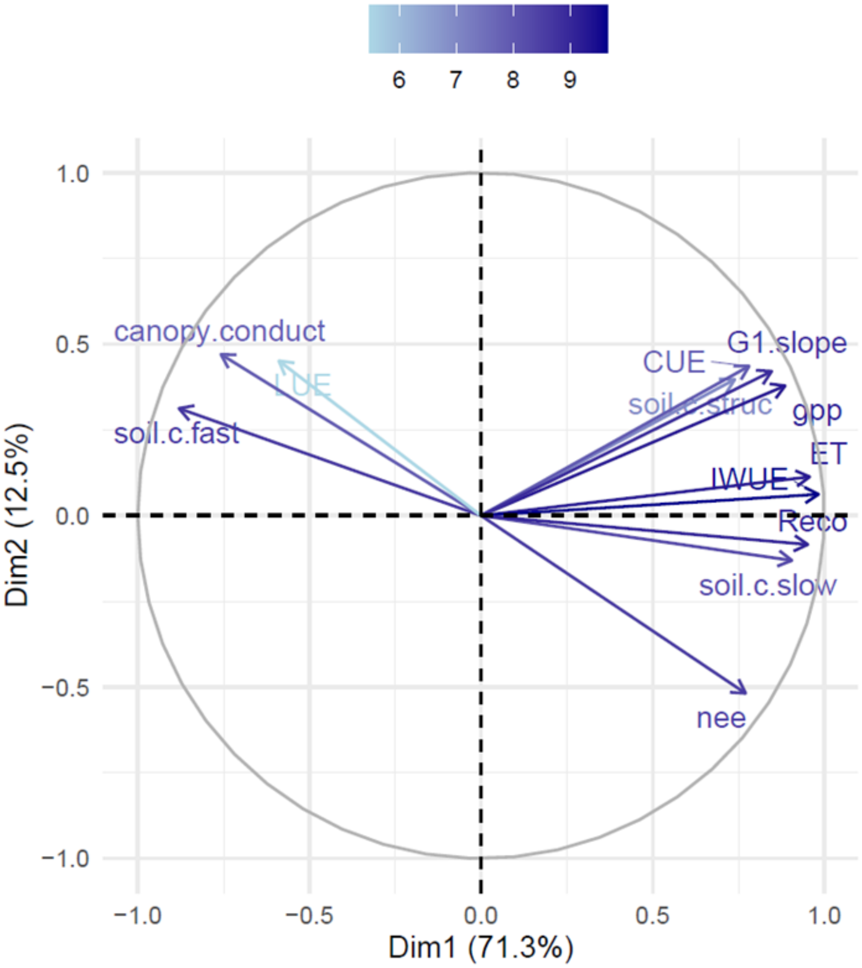

Figure S4.2: Variable factor map for PC1 (Dim1) and PC2 (Dim2). The labeled variables are those that best represent the plane, and variable color corresponds to the strength of their contribution to the principal components shown.

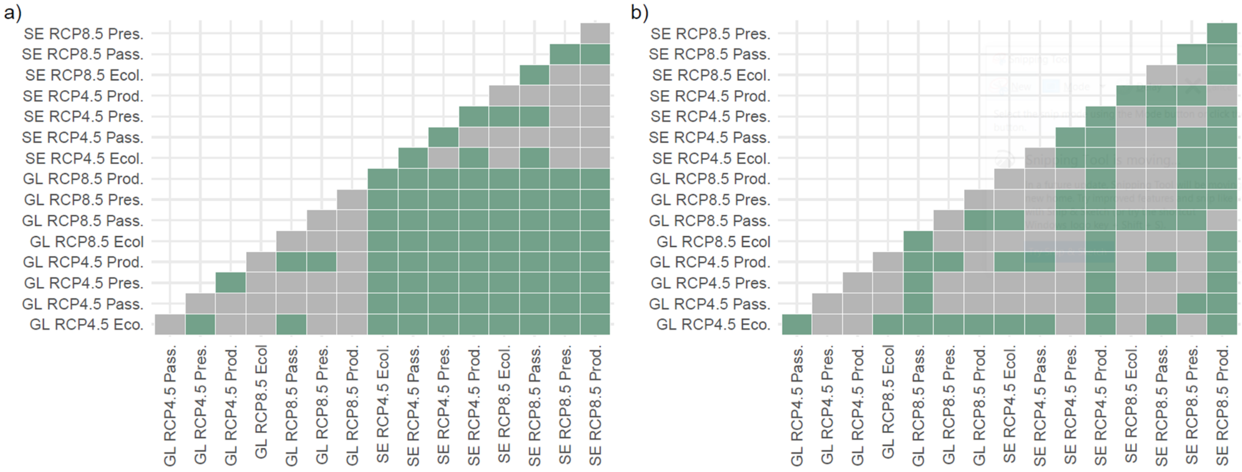

Figure S4.3: Tukey's HSD comparison of region, RCP scenario, and management type group means for **a)** PC1 and **b)** PC2. Green boxes indicate statistically significant differences in average PC values between groups ($p < 0.05$)

Chapter 5

Forest management as a Nature – based Climate Solution: Impacts on forest structure, functional stability, and regional interactions with climate change

Abstract

Nature-based Climate Solutions (NbCS), which increase carbon sequestration in natural systems through activities such as improved forest management, have been garnering increasing attention for their climate mitigation potential. Additionally, NbCS could be designed to increase resilience to future climate change impacts, which have been shown to negatively impact some ecosystem functions. However, large-scale implementation of forest management as a NbCS is dependent on the durability of management induced changes in forest carbon and water cycling, and much remains unknown about how forest function will respond to management, or how that response will evolve across long timescales through interactions with climate change. To adequately address potential durability concerns related to forest management as an NbCS, we need to identify emergent relationships between functional stability and forest structure and improve understanding of how the strength of relationships varies under alternate management configurations, as well as across spatiotemporal scales.

Here, we used a process-based model to simulate multi-decadal projections of forest dynamics in response to management. Simulations were conducted across gradients in forest

type, edaphic factors, and climate under two alternate radiative forcing scenarios (RCP4.5 and RCP8.5). This allowed us to quantify shifts in ecosystem stability in response to climate change and compare regional differences in how specific management strategies modulated that response, where ecosystem stability is characterized using a multidimensional framework. Our results show that management can be used to increase functional resilience and minimize the release of stored carbon by reducing mortality, but also highlight the regional dependency of management-induced changes in forest structure and ultimately resilience.

5.1 Introduction

Emissions reductions alone are insufficient to avoid the most catastrophic effects of climate change (National Academies of Sciences 2018, Rockström et al., 2021, Canadell and Schulze, 2014). Therefore, active removal of atmospheric CO_2 must also be a core component of any feasible climate mitigation strategy (IPCC 2022, Smith et al., 2016). Many proposed approaches to this challenge require significant technological advances, or are still largely experimental (Fuss et al., 2014). Although some of these ideas are exciting and potentially viable solutions, several hinge on technological innovations that aren't currently capable of operating at the scale required for a measurable impact (ex: direct carbon capture), have a substantial degree of associated uncertainty regarding interactions with the rest of the Earth system (ex: stratospheric aerosol injection), or are limited in their application potential due to exorbitant expense.

Nature-based climate solutions (NbCS), which manipulate natural systems through management and design to increase carbon sequestration and decrease greenhouse gas emissions (Novick et al., 2022), do not suffer these same limitations. NbCS have the potential to sequester up to 1.2 Pg CO_2 e year-1 in the United States, which is approximately 21% of net annual emissions (Fargione et al., 2018), while also supporting a range of environmental and social co-benefits, such as cleaner air and water, enhanced biodiversity, and improved ecosystem quality for recreational and cultural purposes (Becknell et al., 2015, Novick et al., 2022). Furthermore, NbCS such as forest management could potentially be designed to increase resilience to future climate change impacts, whether that be rising temperatures, increased storm severity, or enhanced vulnerability to pest and pathogen infestation.

However, there is no silver bullet in life or in science, and large-scale implementation of forest management as a NbCS is dependent on the durability of management induced changes in forest carbon and water cycling (Canadell and Raupach, 2008, Novick et al., 2022, Anderegg et al., 2023). Forest area is increasing globally, expanding the potential magnitude of the terrestrial carbon sink (Keenan and Williams, 2018, Friedlingstein et al., 2022, Fernandez-Martinez et al., 2019), but is that forest sink also becoming more vulnerable? Climatic conditions affect how forests respond to disturbance (Seidl et al., 2017, Anderson-Teixeira et al., 2013, Dorheim et al., 2022), and rapidly changing environmental conditions could potentially decrease ecological stability (Bauman et al., 2022, Reich et al., 2022), hindering an ecosystem's ability to recover from disturbance events (Seidl et al., 2017). Feedbacks between decreased ecosystem stability and climate change have also been demonstrated, increases in forest mortality across the globe have been linked to climate-induced acceleration of environmental change (Liu et al., 2019, Anderegg et al., 2023).

Much remains unknown about how forest resilience to perturbations (both natural and anthropogenic) will shift in response to climate change (Dorheim et al., 2022, Thom and Seidl, 2016, Reyer et al., 2015, Forzieri et al., 2022), but recent evidence indicates that for many forest types (temperate, tropical, and arid) resilience is declining, potentially in response to increased variability and magnitude of extremes in large scale climate drivers (Forzieri et al., 2022, McDowell et al., 2020). As forests become less resilient, the likelihood of large-scale mortality in response to climate-change driven disturbance increases (Reich et al., 2022, Bauman et al, 2022, Forzieri et al., 2022), meaning a significant portion of stored carbon could be released, potentially nullifying mitigation efforts (Anderegg et al., 2023, Reichstein et al., 2013). For example, the death of an estimated 320 million trees due to Hurricane Katrina resulted in the Southeastern United States becoming a large enough net source of carbon that it negated the entire annual terrestrial carbon sink of the United States in 2005 (Running 2008).

The response of forests to disturbance is a prolific area of research, and one that has intensified in recent years (Seidl et al., 2017). Work has been conducted across short to intermediate timescales empirically (Gough et al., 2013, Gough et al., 2007, Matheny et al., 2014), using chronosequences (Amiro et al, 2010) and models (Dietze and Matthes, 2014, Dorheim et al., 2022), and on links between disturbance and climate (Brice et al., 2020, Anderson-Teixeira et al., 2013, Andrews et al., 2018, Temperli et al., 2015, Turner 2010). However, relatively few studies have examined human management as a disturbance regime across multi-decadal timescales (Gough et al., 2021, Naudts et al., 2016) while accounting for subsequent interactions with climate, which given the inherent non-stationarity of both carbon cycling in response to disturbance (Gough et al., 2021) and climate change, is important for understanding the durability of forestry related NbCS (Hicke et al., 2012). Additionally, climate change impacts are highly spatially variable, and differ across gradients in topography, latitude, etc., meaning that forest management strategies designed to mitigate climate change likely have relatively greater potential in some regions compared to others. To adequately address potential durability concerns related to forest management as an NbCS, we need to identify emergent relationships between functional stability and forest structure, and improve understanding of how the strength of relationships varies under alternate management configurations, as well as across spatial and temporal scales.

Here, we used a process-based vegetation demography model to simulate multi-decadal projections of forest dynamics in response to management. Simulations spanned from 2006 – 2100 and were conducted across gradients in forest type, edaphic factors, and climate under two alternate radiative forcing scenarios (RCP4.5 and RCP8.5). This allowed us to quantify shifts in ecosystem stability in response to climate change, and compare regional differences in forest response across a spectrum of management intensities.

This study focuses on functional stability rather than compositional stability, as shifts in composition are inevitable as ecosystems adjust to pervasive changes in climate and environmental conditions in the coming decades (Falk et al., 2022). Considering this, traditional approaches to ecosystem management that seek to maintain or restore systems to a historical compositional baseline state are no longer appropriate (Williams et al., 2020). Instead, we seek to understand how key ecosystem functions such as carbon and water cycling will respond to pressure from ongoing climate change (referred to herein as 'climate forcing'), and how management might buffer that response.

Ecosystem stability is characterized here as both resilience (S_R, speed of functional recovery following perturbation) and temporal stability (S_T, persistence over time of ecosystem function). Several recent studies have adopted a multi-dimensional framework (Hillebrand et al., 2018) to evaluate ecosystem functional stability in response to discrete disturbance events, such as stem girdling through the Forest Accelerated Succession Experiment (FASET; Gough et al.,

2013) (Mathes et al., 2021), or simulated mortality events across a range of severities (Dorheim et al., 2021). However, this study is among the first to evaluate the multidimensional stability response of forest carbon cycling to sustained management over multi-decadal timescales in the context of alternate climate change scenarios at the regional scale. Therefore, this work provides novel insights into not only how active management impacts the structure and functional stability of forests across long timescales but also how future climate change might affect stability trajectories. Additional information on the implemented modeling design, model overview, and site descriptions are provided in Chapter 3.

Specifically, we address the following questions: 1) How does forest management across a range of intensities impact forest structure on multi-decadal timescales, and do impacts vary regionally or by climate change scenario?, and **2)** how do the ensuing structural changes alter ecosystem functional resilience and temporal stability in the face of a changing climate, and are impacts regionally dependent?

We hypothesize that management intensity and severity is a stronger driver of shifts in forest structure than climate change, but that structural responses to management will diverge regionally over time due to differences in regional climate change impacts. We also expect that management is the most important factor shaping functional resilience (S_R), but that regional interactions between management and climate change will alter stability outcomes over time (S_T), and that more intensive management practices (e.g. production forestry) will decrease functional stability. Finally, we expect to see a positive correlation between functional stability and structural complexity and diversity.

5.3 Methods

5.3.1 Experimental design

To assess the impact of management on forest structure across long time scales, forest structural variables output by ED2 were scaled from the cohort to the site level using area weighted averaging and evaluated under each of the four management types at both the start and the end of the century. To determine whether ecosystem functional stability in the face of shifting climate regimes is dependent on management, we examine resilience and temporal stability of three key ecosystem functional variables; evapotranspiration (ET), gross primary productivity (GPP), and ecosystem respiration (Reco). Collectively, these variables represent salient pathways that define land-atmosphere exchange: the uptake of atmospheric carbon by the land surface through photosynthesis, release of terrestrial carbon to the atmosphere through respiration, and the movement of water between the land surface and the atmosphere. Ecosystem stability metrics are calculated using 80 years of modeled data from simulations conducted in two regions, the Great Lakes and Southeastern United States, to evaluate regional differences in the relationship between management, climate change, and ecosystem stability, as management-induced changes in ecosystem function have been shown to be regionally dependent (Chapter 4). A detailed description of the model driver data and experimental design is provided in Chapter 3, along with site descriptions.

5.3.2 Representation of forest structure and function

Forest structure is characterized by a set of 12 variables output by ED2: tree age (Age_{Tree}), above ground biomass (AGB), leaf area index (LAI), mortality rate ($Mort_R$), tree density

(DENS), coarse woody debris (CWD) and both the mean and standard deviation of tree diameter at breast height (DBH_{Avg} and DBH_{SD}), crown area (CA_{Avg} and CA_{SD}), and tree height (H_{Avg} and H_{SD}) (Table 5.1). Inclusion of DBH_{SD}, CA_{SD} and H_{SD} represents diversity in tree PFT and size variability, which are indicators of canopy complexity that are directly impacted by management and have demonstrated links to forest productivity (Murphy et al., 2022, Hardiman et al., 2013, Atkins et al., 2018, 2020, Gough et al., 2019). All structural metrics natively exist at the cohort or patch scale in ED2, and were scaled to the site level using area weighted averaging. Seedlings and saplings smaller than 12.7 cm DBH and 1.37 m height (values based on Forest Inventory and Analysis thresholds) were excluded to remove bias from overrepresented seedlings.

Table 5.1: Ecosystem structure and function variables used in analysis.

Variable	Symbol	Units	Group
tree age	$\mathrm{Age}_{\mathrm{Tree}}$	*years*	structure
above ground biomass	AGB	$kg\ C\ m^{-2}$	structure
leaf area index	LAI	--	structure
mortality rate	$\mathrm{Mort}_{\mathrm{R}}$	*n trees dead since previous month*	structure
tree density	DENS	$trees\ m^{-2}$	structure
coarse woody debris	CWD	$kg\ C\ m^{-2}$	structure
average diameter at breast height	$\mathrm{DBH}_{\mathrm{Avg}}$	*cm*	structure
standard deviation diameter at breast height	$\mathrm{DBH}_{\mathrm{SD}}$	*cm*	structure
average crown area	$\mathrm{CA}_{\mathrm{Avg}}$	*m*	structure
standard deviation crown area	$\mathrm{CA}_{\mathrm{SD}}$	*m*	structure
average tree height	$\mathrm{H}_{\mathrm{Avg}}$	*m*	structure
standard deviation tree height	H_{SD}	*m*	structure
ecosystem respiration	Reco	$kg\ C\ m^{-2}\ month^{-1}$	function
evapotranspiration	ET	$kg\ H_2O\ m^{-2}\ month^{-1}$	function
gross primary production	GPP	$kg\ C\ m^{-2}\ month^{-1}$	function

Ecosystem function is defined by three variables characterizing the land-atmosphere exchange of carbon and water. Functional variables include evapotranspiration (ET), gross primary productivity (GPP), and ecosystem respiration (Reco) (Table 5.1). ET represents the total movement of water from the land surface to the atmosphere through evaporation and transpiration. GPP is the total amount of atmospheric carbon fixed by photosynthesis, and Reco is the sum of autotrophic and heterotrophic respiration, and represents the total respiration by living organisms in an ecosystem.

Monthly model output was subset to the active growing season for each region based on minimum temperature and productivity thresholds, where the growing season was defined as periods where air temperature was above 5˚C and GPP was greater than 0.031 kg C m^{-2} $month^{-1}$ (Nelson et al., 2018). This broad definition of growing season was employed to accommodate regional differences in growing season length, and potential shifts in phenological timing that might occur due to climate change. Monthly growing season ecosystem structure data was grouped by geographic region, RCP scenario, and management type, and annual averages for each structural variable of interest were obtained using a 5-year moving average. 1-way t-tests were applied to determine if forest structure differed significantly between management types within each region.

5.3.3 Ecosystem functional stability

Resilience in forest function (S_R) is calculated as the regression slope of relative function over time, following Hillebrand et al. (2018), as shown by Equation 5.1.

Equation 5.1: Mathematical representation of ecosystem functional resilience. $F_{\text{Perturbed}}$ is the perturbed function value, F_{Control} is the control function value, *i* is the intercept of the resilience regression line, *t* is time, and S_R is functional resilience.

$$ln(\frac{F_{Perturbed}}{F_{Control}}) = i + S_R * t$$

F_{Control} is represented by regional output from model simulations conducted using preservation forestry settings under RCP4.5, as preservation forestry is akin to a 'no management' scenario in this study, and using RCP4.5 disentangles the effects of amplified climate change associated with RCP8.5 simulations. $F_{\text{Perturbed}}$ corresponds to regional output from model simulations conducted under alternate management and climate forcing treatments, where each treatment denotes a combination of management type (passive, ecological, or production forestry) and emissions scenario (RCP4.5 or RCP8.5), for a total of six treatments applied in each geographic region, with 10 replicates each, where model output from individual GCMs represent treatment replicates.

S_R is a dimensionless quantity and can be positive, negative, or 0. A zero value indicates no recovery of pre-disturbance function following perturbation, a positive value indicates a more rapid recovery than the control scenario, and a negative value indicates lower resilience than the control scenario in response to forcing or perturbation (Hillebrand et al., 2018). Calculating S_R from the log ratio of disturbance to control fluxes allows for responses to be standardized for comparison across variables with different units and flux magnitudes. Functional stability over time (S_T) is calculated as the inverse of the coefficient of variation of the functional value over a set timestep, as shown by Equation 2 (Tilman et al., 2006, Lehman and Tilman, 2000, Tilman 1999).

Equation 5.2: Mathematical representation of temporal stability. S_T is temporal stability, μ is the mean functional value over a set time period, and σ is the standard deviation of the functional value over the same time period

$$S_T = \frac{\mu}{\sigma}$$

This measure of S_T is used rather than representing S_T as the inverse of the standard deviation of resilience residuals (Hillebrand et al., 2018, Mathes et al., 2021), as it is more applicable when measuring stability over long time periods in the face of multiple fluctuating disturbances (Tilman et al., 2006), as opposed to capturing stability responses to single pulse disturbance events (Hillebrand et al., 2018). S_T is a dimensionless quantity that's inherently positive, larger values correspond to lower fluctuations around the mean trend in ecosystem function over time.

Monthly growing season ecosystem function data was grouped by geographic region, RCP scenario, management type, and GCM to calculate log ratios between treatment and control function values, then annually averaged across GCMs to obtain annual ecosystem function resilience values corresponding to each combination of geographic region, RCP scenario, and management type. To calculate temporal stability, monthly growing season data was grouped by geographic region, RCP scenario, management type, and GCM and divided into non-overlapping five year intervals (across which temporal trends were small to non-existent) spanning from the start of active management in 2020 to the year 2100, and S_T was calculated for each interval. Data was organized into start (2020 – 2059) and end of century (2060 – 2100) bins and averaged to calculate net changes in ecosystem structure, S_T , and S_R associated with each region, RCP scenario, and management type.

To determine whether dimensions of ecosystem functional stability (S_R and S_T) were better predicted by management type or climate change scenario, ANOVA was conducted on a generalized additive model (GAM) implemented using the R package *mgcv()* (Wood, 2011) and fit using the restricted maximum likelihood method. Interactive effects between management type, region, and RCP scenario were also included as predictors, and year was included as a smoothed predictor to account for temporal autocorrelation. Pearson correlation was used to determine the directionality and strength of relationships between functional resilience metrics and ecosystem structure variables. The statistical significance of differences in average S_R and S_T across management types, geographic regions, and RCP scenarios was determined using a Tukey's HSD test with an alpha value of 0.05. All analyses were performed in R (R Core Team, 2021).

5.4 Results

5.4.1 Climate trends

Average monthly growing season precipitation increased from the start to the end of the century in both regions, with greater increases observed in the SE (16 – 20%) than in the GL region (1 – 2%) (Figure 5.1). This represents a marked intensification of growing season precipitation in the SE. Precipitation increases were more pronounced under RCP4.5 than RCP8.5 in both regions, and regional differences in average monthly precipitation were larger under the more severe climate change scenario. Average monthly growing season temperatures also increased from the start to the end of the century in both regions. Temperatures increased more under the more severe climate change scenario (2.6 – 5.2% increase under RCP4.5 compared to 4.1 – 10.5% increase under RCP8.5), and temperature differences between regions became more pronounced over time. By the end of the century average growing season air temperatures were 17.1 ± 0.1˚C (RCP4.5) to 18.4 ± 0.4˚C (RCP8.5) in the GL and 14.6 ± 0.1 ˚C (RCP4.5) to 15.1 ± 0.2˚C (RCP8.5) in the SE. These changes are consistent with regional trends reported in the Fourth National Climate Assessment released by the U.S. Global Change Research Program (2018).

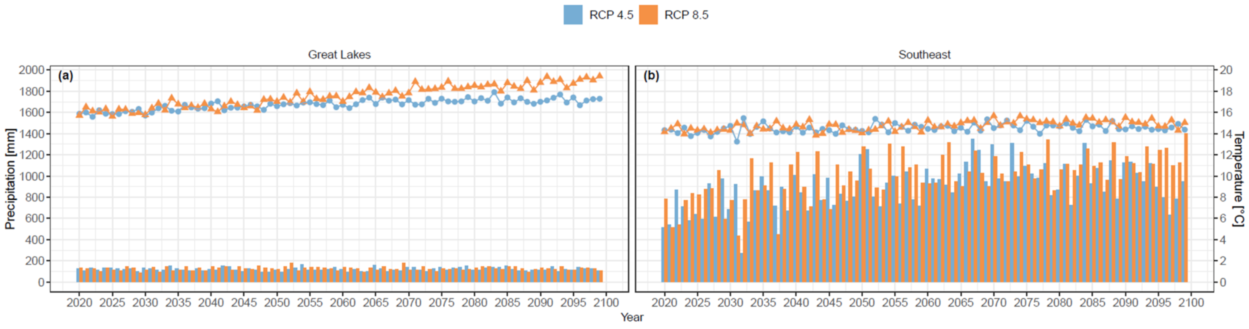

Figure 5.1: Trends in regional average monthly growing season temperature and median monthly precipitation under RCP4.5 (blue) and RCP8.5 (orange).

5.4.2 Management impacts on forest structure

A one-way Kruskal-Wallace t-test showed that forest structure differed significantly between management types in both regions ($p < 0.05$). Forest structural metrics describing the physical arrangement of vegetation in the forest include AGB, DENS, and LAI. AGB differed primarily by management type in both regions, and differences between management types were more pronounced in the GL (Figure S5.1). AGB was highest under preservation forestry (15.115 – 20.550 kg C m^{-2} $month^{-1}$), akin to the 'no management' control scenario, in both regions. AGB was lowest under passive management (13.324 ± 0.328 kg C m^{-2} $month^{-1}$) in the GL, and lowest for ecological management (10.583 ± 0.840 kg C m^{-2} $month^{-1}$) under RCP4.5 and production management (9.481 ± 0.811 kg C m^{-2} $month^{-1}$) under RCP8.5 in the SE. DENS decreased by 41.686% from the start to the end of the century in the GL region, but increased by 23.064% on average in the SE. DENS was lowest for ecological and production management (0.032 – 0.091 trees m^{-2}) and highest for passive and preservation management (0.056 – 0.100 trees m^{-2}) in both regions. Changes in LAI from the start to the end of the century were minimal in the GL as were differences between management and RCP scenarios. LAI increased by 9.431% over time averaged across all management types in the SE, ecological forestry promoted the highest average LAI (4.968 ± 0.100) and production forestry had the lowest average values (4.513 ± 0.152).

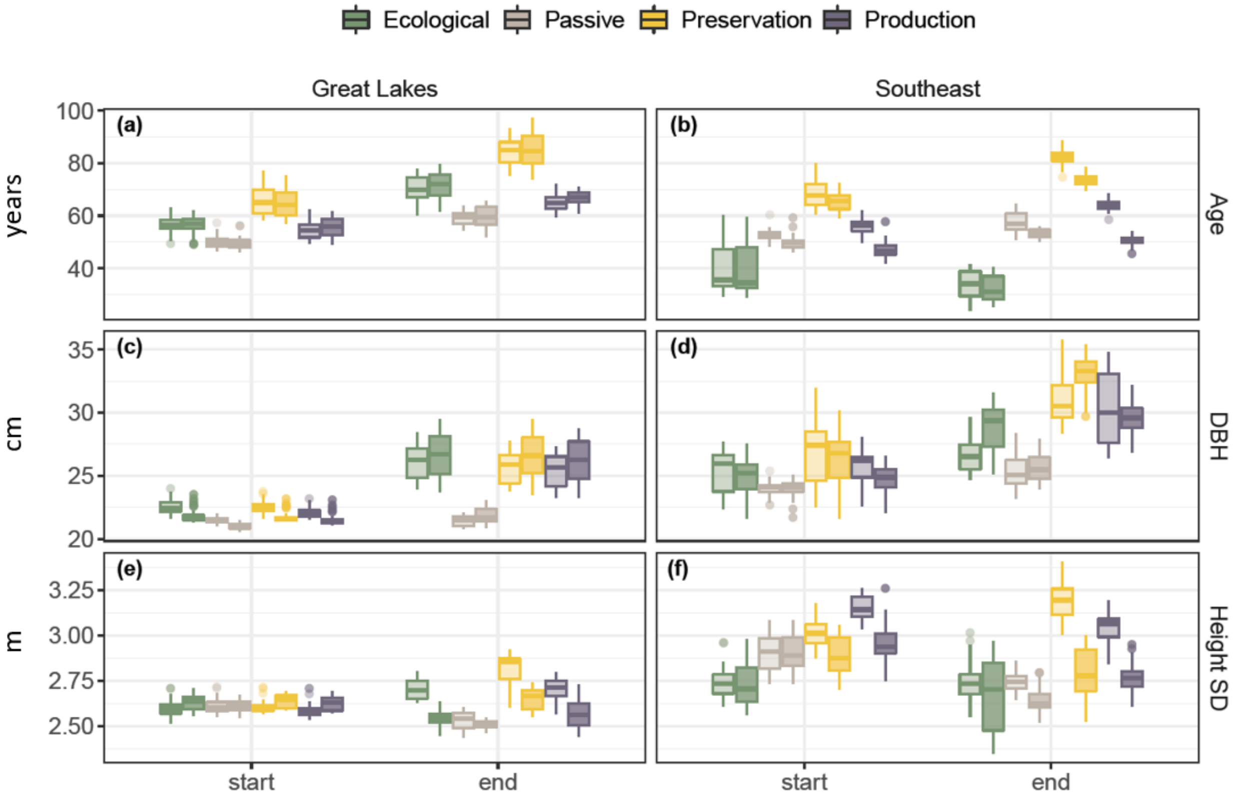

Figure 5.2: Average age, diameter at breast height (DBH), and standard deviation of height for the start and end of the century. Columns are organized by geographic region, color hue corresponds to management type, and color tone corresponds to climate change scenario, where lighter tones represent RCP4.5 and darker tones represent RCP8.5

Forest structural metrics describing the age and size distributions of trees include Age_{Tree}, CA_{Avg}, H_{Avg}, and DBH_{Avg} (Figure S5.4). Age_{Tree} differed primarily by management type in both regions (Figure 5.2), with preservation forestry supporting the oldest stands (73.592 – 84.405

years). Passive forestry resulted in the youngest average stands in the GL (59.221 ± 3.076 years), while ecological forestry resulted in the youngest stands in the SE (33.406 ± 4.732 years). CA_{Avg} decreased by 24.626% from the start to the end of the century in the GL region across all management types, but changes in CA_{Avg} over time were minimal in the SE. Passive forestry supported larger CA_{Avg} in both regions, while ecological and production forestry resulted in smaller CA_{Avg}. DBH_{Avg} and H_{Avg} increased by 3.413 – 13.671% from the start to the end of the century in both regions. In the GL, ecological forestry resulted in taller trees with DBH_{Avg} comparable to preservation forestry (26.199 cm), while in the SE, DBH_{Avg} was highest under preservation and production forestry (29.858 – 31.868 cm). Passive forestry resulted in smaller, shorter trees in both regions (21.391 – 25.595 cm).

Forest structural metrics describing mortality include $Mort_R$ and CWD (Figure S5.2). CWD decreased by 13.360% from the start to the end of the century in the GL, with differences primarily between RCP scenarios. Changes in CWD in the SE were minimal from start to the end of the century, and the highest values were observed for production forestry. $Mort_R$ increased by 70.253% from the start to the end of the century in the GL, and by 98.210% in the SE. In the GL, $Mort_R$ was 5.600% higher under RCP8.5, but in the SE $Mort_R$ was 15.183% higher on average under RCP4.5. Preservation management had the highest $Mort_R$ in the GL region (0.097 ± 0.013 trees m^{-2} $month^{-1}$) and passive management had the lowest (0.055 ± 0.004 trees m^{-2} $month^{-1}$), ecological and production management had comparable $Mort_R$. In the SE, $Mort_R$ was highest for preservation (0.043 ± 0.011 trees m^{-2} $month^{-1}$) and passive (0.039 ± 0.010 trees m^{-2} $month^{-1}$) forestry and lowest for ecological forestry (0.023 ± 0.004 trees m^{-2} $month^{-1}$).

Structural metrics describing the diversity and complexity of forests include CA_{SD}, H_{SD}, and DBH_{SD} (Figure S5.3). CA_{SD} was 29.401% higher on average in the GL than in the SE, but DBH_{SD} and H_{SD} were 7.33. – 37.644% higher in the SE. CA_{SD} decreased by 5.756% from the start to the end of the century in the GL. Variability in crown size was 3.452 – 6.673% greater on average under RCP4.5 than RCP8.5, with the lowest values seen under passive and production management in the GL and under ecological management in the SE. Passive management promoted high CA_{SD} in the SE, while preservation management had the highest CA_{SD} in the GL. DBH_{SD} increased by 17.884 – 20.231% over time on average, and values were typically higher under RCP4.5. Preservation management had the highest DBH_{SD} (10.822 ± 0.945 cm) and H_{SD} (2.729 ± 0.072 m) in the GL (Figure S5.3), ecological and production forestry resulted in similar levels of DBH_{SD} and H_{SD}, while passive management had the lowest average values (8.589 ± 0.190 cm and 2.520 ± 0.033 m). DBH_{SD} and H_{SD} were highest under preservation and production forestry (15.164 – 17.366 cm and 3.043 – 3.197 m) for RCP4.5 in the SE and lowest under passive and production forestry for RCP8.5 (12.040 – 12.676 cm and 2.642 – 2.769 m).

5.4.3 Ecosystem functional stability

By the second-half of the century the ensemble mean fluxes for GPP, Reco, and ET in the GL region were 0.347 – 0.359 kg C m^{-2} $month^{-1}$, 0.331 – 0.377 kg C m^{-2} $month^{-1}$, and 123.237 – 132.677 kg H_2O m^{-2} $month^{-1}$ (respectively). The ensemble mean fluxes for GPP, Reco, and ET in the SE region were 0.276 – 0.323 kg C m^{-2} $month^{-1}$, 0.213 – 0.243 kg C m^{-2} $month^{-1}$, and 57.479 – 65.594 kg H_2O m^{-2} $month^{-1}$.

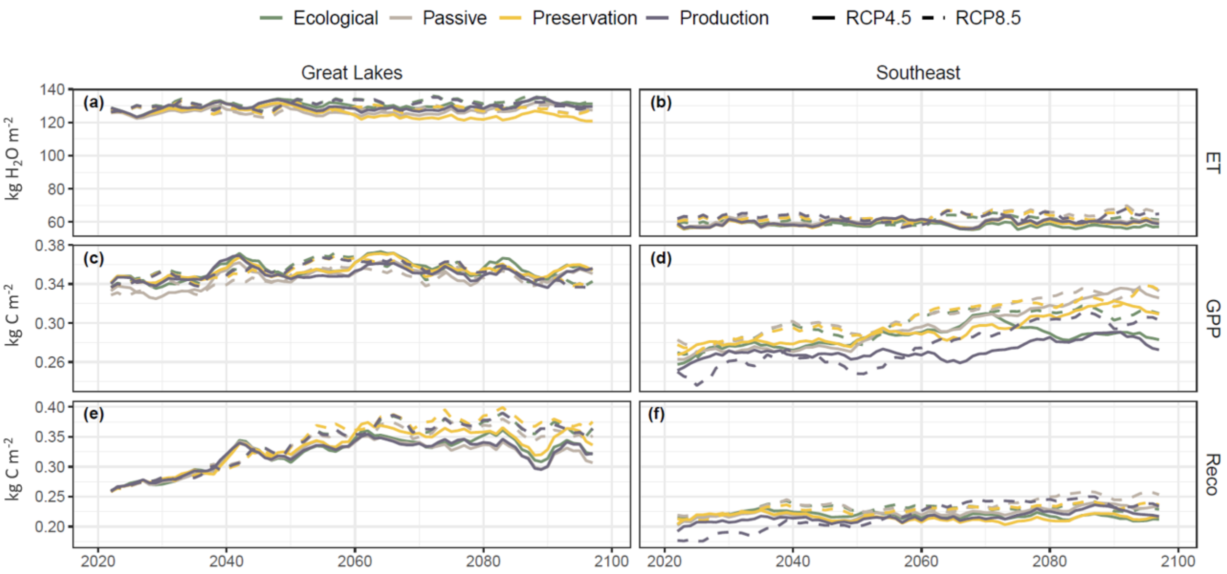

Figure 5.3: Average monthly growing season fluxes of evapotranspiration (ET) (**a – b**), gross primary productivity (GPP) (**c – d**), and ecosystem respiration (Reco) (**e – f**) ED2 simulations from the start of active management in 2020 through 2100. Color corresponds to management type, solid lines are regional ensemble mean fluxes (5-year moving average) under RCP4.5, and dotted lines represent regional ensemble mean fluxes under RCP8.5.

Although both transpiration and evaporation were consistently higher in the GL region than in the SE, the comparatively high ET in the GL region is likely due to substantially higher rates of transpiration. The hot, dry, and windy conditions in the GL resulted in higher average transpiration and thus ET than in the SE, where conditions were more humid and temperature increases were not as pronounced.

5.4.3.1 Functional resilience

Average functional resilience (S_R) differed significantly between geographic regions based on a one-way Kruskal-Wallace t-test ($p < 0.05$). By the second half of the century, average

S_R was higher in the SE region than in the GL region for all three ecosystem function variables that were evaluated (GPP, Reco, and ET), and regionally averaged S_R values were positive in the SE and negative in the GL. GPP S_R averaged 0.004 ± 0.008 in the SE compared to –0.007 ± 0.009 in the GL, Reco S_R averaged 0.005 ± 0.007 in the SE and –0.005 ± 0.008 in the GL, and ET S_R averaged 0.001 ± 0.010 in the SE and –0.002 ± 0.008 in the GL.

S_R decreased from the start to the end of the century on average for all three dimensions of ecosystem function in the GL, but temporal trends in resilience varied by management type in the SE (Figure 5.4). All resilience metrics were positively correlated with one another in the GL region regardless of management type or RCP scenario, meaning increasing one dimension of S_R increased other dimensions of S_R in return. In the SE, resilience metrics were positively correlated with one another under RCP4.5, but under the more severe climate change scenario (RCP8.5) higher ET S_R came at the cost of lower Reco S_R . GPP and ET S_R were lower on average under RCP8.5 than RCP4.5 in both the SE and GL regions, but Reco S_R was 37.92 – 67.10% higher under the more severe climate change scenario.

S_R differed significantly between all management types in the SE based on a one-way t-test ($p < 0.05$), but in the GL region differences in average S_R were significant between passive and ecological forestry as well as between passive and production forestry, but production and ecological forestry were not significantly different.

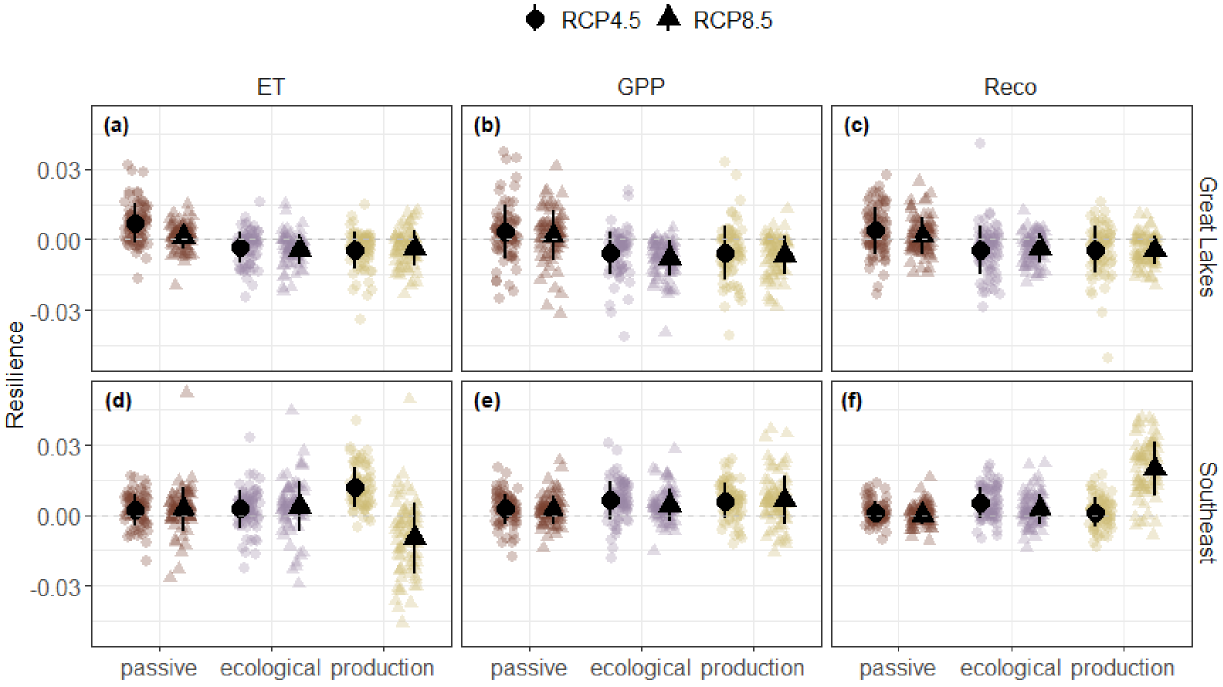

Figure 5.4: Mean annual ET, GPP, and Reco functional resilience (S_R) by management type and RCP scenario. Individual points correspond to annual averages, where circles represent RCP4.5 and triangles represent RCP8.5. Black points represent overall group means from 2020 – 2100 (error bars denote ± 1 σ).

Passive forestry in the GL had higher S_R than both production and ecological forestry across all three functional dimensions (Table 5.2), while ecological and production forestry often had similar S_R values. Differences in S_R by RCP scenario for a given management type were minimal in the GL. ET and GPP S_R were lowest under production management in the GL, and Reco S_R was equally low under ecological and production management.

Table 5.2: Mean end of century annual resilience (unitless) ± 1 standard deviation for gross primary productivity (GPP), evapotranspiration (ET) and ecosystem respiration (Reco) by management type, RCP scenario, and region.

		RCP4.5		RCP8.5	
Variable	Management	GL	SE	GL	SE
ET	ecological	-0.005 ± 0.009	0.001 ± 0.010	-0.005 ± 0.008	0.001 ± 0.010
ET	passive	0.006 ± 0.008	0.001 ± 0.007	0.001 ± 0.006	0.000 ± 0.007
ET	production	-0.006 ± 0.010	0.012 ± 0.009	-0.005 ± 0.010	-0.008 ± 0.015
GPP	ecological	-0.008 ± 0.011	0.007 ± 0.010	-0.011 ± 0.008	0.004 ± 0.005
GPP	passive	-0.001 ± 0.009	0.002 ± 0.008	-0.002 ± 0.010	0.000 ± 0.006
GPP	production	-0.010 ± 0.010	0.005 ± 0.008	-0.010 ± 0.009	0.008 ± 0.010
Reco	ecological	-0.009 ± 0.009	0.007 ± 0.007	-0.005 ± 0.006	0.002 ± 0.006
Reco	passive	0.001 ± 0.010	0.002 ± 0.005	0.001 ± 0.008	-0.001 ± 0.004
Reco	production	-0.009 ± 0.011	0.002 ± 0.006	-0.007 ± 0.005	0.020 ± 0.011

In contrast to what was observed in the GL, passive forestry in the SE often had lower average S_R compared to the other management types (Figure 5.4). ET S_R was highest under production management and lowest for passive management, but under the more severe climate change scenario ET S_R was lowest under production management and highest under ecological management. Both GPP resilience and Reco resilience were highest under ecological management and lowest under passive management for RCP4.5, but under RCP8.5 resilience for GPP and Reco was higher under production management.

5.4.3.2 Temporal stability

Average temporal stability (S_T) differed significantly between geographic regions based on a one-way Kruskal-Wallace t-test ($p < 0.05$). Regional differences in S_T were the most pronounced for Reco and the least pronounced for ET, which differed more by RCP scenario. Reco stability was 56.25% lower in the GL than in the SE. GPP S_T was 17.25% higher on average in the SE than in the GL, and GPP S_T differed the most by management type, although primarily in the SE. GPP had the highest average S_T values overall (Table 5.3).

Table 5.3: Mean end of century annual temporal stability (unitless) ± 1 standard deviation for gross primary productivity (GPP), evapotranspiration (ET) and ecosystem respiration (Reco) by management type, RCP scenario, and region.

		RCP4.5		RCP8.5	
Variable	Management	GL	SE	GL	SE
ET	ecological	2.960 ± 0.708	2.540 ± 1.212	2.713 ± 0.533	2.686 ± 1.871
ET	passive	2.945 ± 0.698	2.552 ± 1.168	2.716 ± 0.526	2.549 ± 0.916
ET	production	2.949 ± 0.673	2.644 ± 1.345	2.728 ± 0.531	2.590 ± 1.380
GPP	ecological	3.351 ± 0.847	3.725 ± 0.798	3.192 ± 0.916	3.960 ± 1.593
GPP	passive	3.320 ± 0.859	3.617 ± 0.718	3.197 ± 0.871	3.973 ± 0.817
GPP	production	3.346 ± 0.825	3.641 ± 0.810	3.239 ± 0.890	4.437 ± 1.300
Reco	ecological	1.859 ± 0.268	3.359 ± 0.865	1.803 ± 0.249	3.198 ± 0.905
Reco	passive	1.893 ± 0.263	3.382 ± 0.872	1.836 ± 0.240	3.187 ± 0.870
Reco	production	1.866 ± 0.266	3.345 ± 0.898	1.814 ± 0.244	3.265 ± 0.929

S_T differed significantly between RCP scenarios in both regions based on a one-way t-test ($p < 0.05$), but differences by management type were only significant between production and passive management in the SE, S_T did not differ significantly by management at all in the GL region. ET S_T changes from the start to the end of the century were minimal under RCP4.5, but S_T decreased by 10.75% on average from the start to the end of the century under RCP8.5 (Figure 5.5). GPP S_T increased by 2.56 – 5.10% on average from the start to the end of the century in the SE, and decreased by 3.95 – 6.31% in the GL region. S_T changes were minimal for Reco in the GL. In the SE, Reco S_T increased from the start to the end of the century under RCP4.5 and decreased under RCP8.5. S_T was lower on average under RCP8.5 than RCP4.5 across all three functional variables in the GL region, but in the SE S_T was higher under RCP8.5 for ET and GPP.

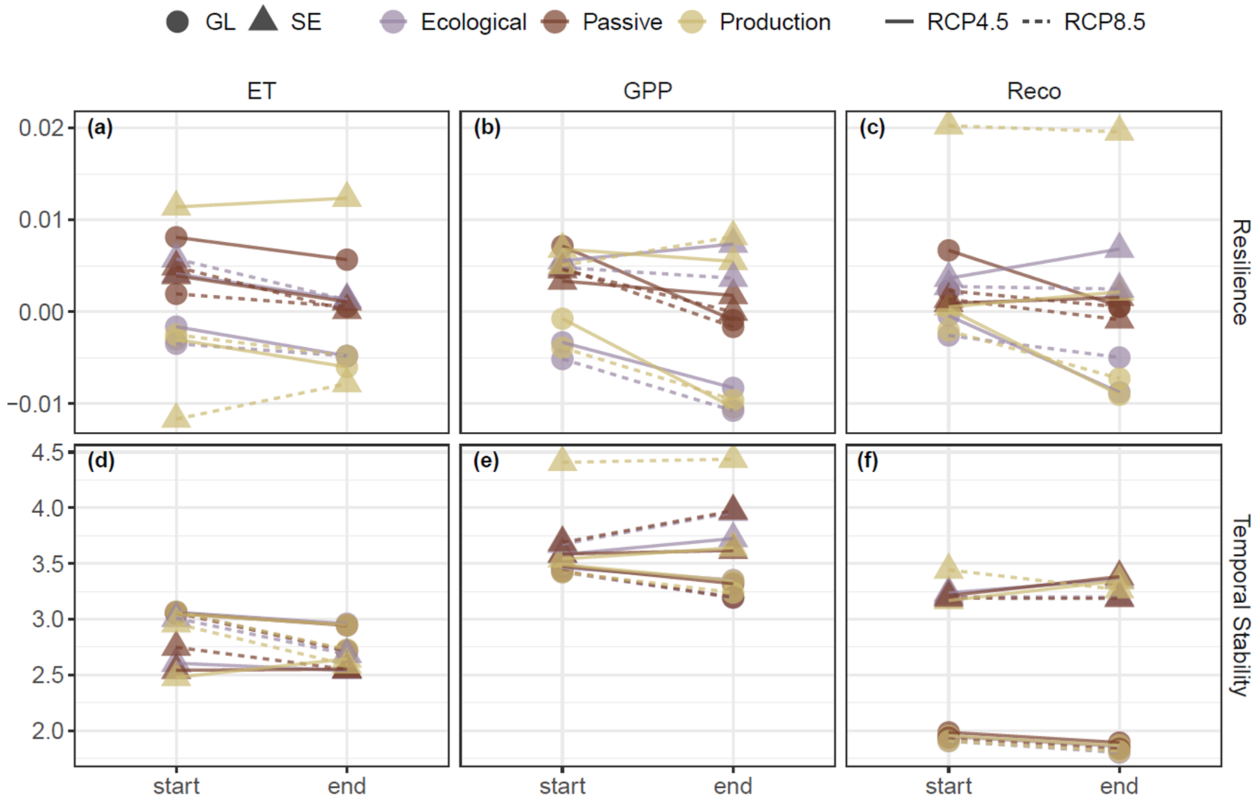

Figure 5.5: Average start versus end of the century resilience **(a – c)** and temporal stability **(d – f)** values by region (point shape), management type (color) and RCP scenario (line type) for ET **(a, d)**, GPP **(b, e)**, and Reco **(c, f)**. Positive resilience values indicate greater functional resilience for a given treatment compared to the control.

In the SE, management related trends in S_T varied by ecosystem function, ET S_T was highest under production management, GPP S_T was highest under ecological management, and Reco S_T was highest under passive management (Table 5.3). However, under the more severe climate change scenario ET S_T was highest under ecological management, while GPP and Reco S_T were highest under production management. ET S_T was lowest under ecological management, GPP S_T was lowest under passive management, and Reco S_T was lowest under production management. Under RCP8.5, ET and Reco S_T were lowest under passive management, and GPP S_T was lowest under ecological management. Differences in S_T by management type in the GL were not significant.

5.4.3.3 Predictors of ecosystem stability

A generalized additive model (GAM) was used to predict functional resilience with management type, RCP scenario, and region as independent factors (including interactive effects) as well as a smoothed year variable. ANOVA showed that while RCP scenario was a significant predictor ($p = 0.001$), functional resilience overall was shaped more by management than by RCP scenario (Table 5.4). However, regional differences dominated, meaning the strength of management as a predictor of resilience was regionally dependent.

Table 5.4: Strength of management type, climate change scenario (RCP), and region group membership as predictors of ecosystem functional stability. '*' symbols next to F-values denote statistical significance at an alpha value of 0.05, and ':' symbols between predictors indicate interaction effects between categorical factors. Df = degrees of freedom and SS = sum of squares.

		S_R			S_T		
Predictor	Df	SS	F-value	Partial η2	SS	F-value	Partial η2
Region	1	0.028	334.546*	0.209	152.3	232.993*	0.163
RCP	1	0.001	10.472*	0.008	0.7	1.05	0.001
Management	2	0.004	23.33*	0.035	3.9	2.979	0.005
Region:RCP	1	0.000	0.453	0.000	9.5	14.573*	0.012
Region:Management	2	0.020	118.502*	0.158	4.8	3.637*	0.006
RCP:Management	2	0.000	1.056	0.002	5.2	3.974*	0.007
Region:RCP:Management	2	0.000	2.554	0.004	5	3.801*	0.006

*$p < 0.05$

ANOVA of a similar GAM predicting temporal stability showed that S_T was best predicted by regional climate change impacts (Table 5.4). Interactions between RCP scenario and management type (p = 0.019), as well as the regionally dependent interaction between RCP scenario and management type (p = 0.022), were also significant predictors of temporal stability.

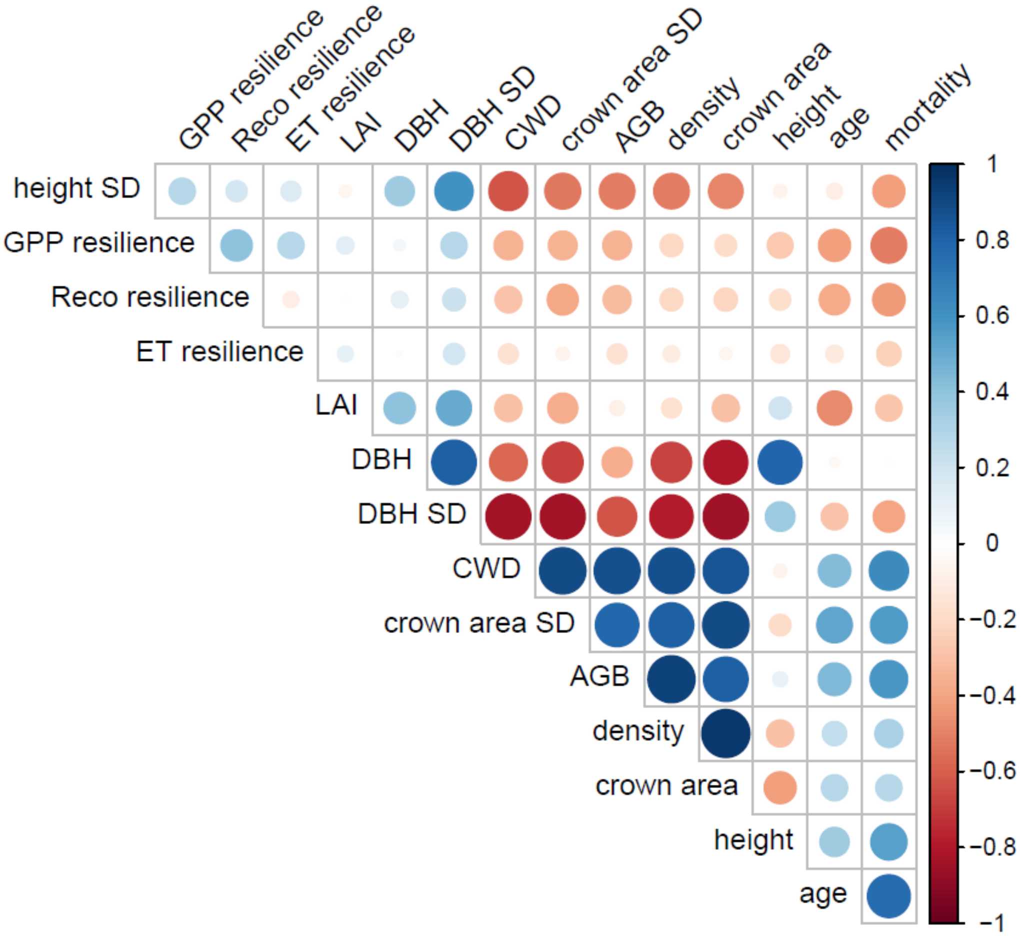

Figure 5.6: Correlation plot of relationships between ecosystem structural variables and GPP, Reco, and ET S_R. Circle size and color shade correspond to Pearson correlation strength, color hue depicts whether a relationship is positive (blue) or negative (red).

Across all three metrics of functional resilience, lower resilience resulted in higher mortality and higher CWD (Figure 5.6). Regardless of climate change scenario, resilience was promoted by higher variability in tree height and DBH (Table S5.1). Higher LAI also was correlated with higher Reco resilience under RCP4.5 and higher ET resilience under RCP8.5 (Figure S5.5). Lower ET resilience was associated with higher average tree height and higher AGB. Lower GPP and Reco resilience was correlated with higher average age as well as higher AGB, and larger variability in tree crown size. Correlations between forest structure and ET resilience were weaker under the more severe climate change scenario.

5.5 Discussion

Using a process based model to simulate the dynamic response of forest structure and function to ongoing management across multi-decadal timescales, we showed that changes in both forest structure and functional stability were regionally dependent, varied over time and by management intensity, and interacted with climate change to produce alternate outcomes.

5.5.1 Management and forest structure

Our first research objective was to address how management of varying levels of intensity impacts forest structure across multi-decadal time scales, and determine whether impacts were regionally dependent or varied by climate change scenario. Comparison of 12 variables representing the physical arrangement of vegetation (AGB, LAI, DENS), age and size distributions of trees (Age_{Tree} , DBH_{Avg}, CA_{Avg}, and H_{Avg}), mortality (CWD and $Mort_R$), and the diversity and complexity of forests (DBH_{SD}, CA_{SD}, and H_{SD}) under preservation, passive, ecological, and production management showed that forest structure differed significantly between management types in both regions ($p < 0.05$).

Most structural variables differed more between management types than between climate scenarios, consistent with Danneyrolles et al. (2019) which showed anthropogenic disturbance was a stronger driver of compositional changes than climate at the century scale. However, $\mathrm{Mort_R}$ and DENS differed primarily between RCP scenarios (and regions). This is indicative of a greater climate sensitivity for these two components of forest structure, and a particularly strong climate driven mortality signal in the GL, which saw amplified $\mathrm{Mort_R}$ for most management types under RCP8.5. Temperature increases outpacing precipitation in the GL is likely a factor in the reduction of DENS over time. Drier areas tend to have less densely populated understoreys (Malhi et al., 2002) in response to changes in competition for available resources and differential survival of species (McDowell et al., 2008), which could lead to shifts in water use efficiency over time (Seidl, 2017). Additionally, rising temperatures prompt stomatal closure (McDowell et al., 2020), which reduces growth and increases mortality through carbon starvation.

Furthermore, the same management strategy often produced divergent structural outcomes over time when applied in different regions, likely due to interactions with regional climate change impacts. These findings support our hypothesis that the response of forest structure to management depends on management intensity and severity, and that structural responses to management will diverge regionally over time due to differences in regional climate change impacts.

Preservation management, akin to a “no management” control, was characterized in both regions by forests with large, tall, older trees and high AGB. $\mathrm{DBH_{SD}}$ and $\mathrm{CA_{SD}}$ were also high under preservation management in both regions, and $\mathrm{H_{SD}}$ was high in the GL and in the SE under RCP4.5. The highest mortality values were observed under preservation management in both regions, and $\mathrm{Mort_R}$ increased substantially from the start to the end of the century. The higher mortality rates in the control compared to simulations with ongoing active management suggests that management could be buffering the acceleration of climate-driven mortality, although the extent to which this is observed depends on management type and region. The combination of high biomass and large trees alongside steadily increasing mortality could also suggest that the enhanced growth in response to warmer temperatures and greater precipitation becomes unsustainable over time as competition for available resources increases, and the ecosystem begins to self-thin in response.

Passive management, which involves occasional harvest with little to no management in the interim, is characterized in both regions by dense stands of comparatively shorter and smaller trees with large crowns, and low DBH_{SD}. The trend towards young shorter-statured stands is consistent with recent studies evaluating global forest demographic responses to increased climate variability (McDowell et al., 2020). This compositional shift is likely more prominent under passive management compared to preservation forestry because larger more desirable trees are periodically removed for harvest, accelerating community transition. In the GL, passive management resulted in stands of young trees with low average AGB, low DBH_{SD}, CA_{SD}, and H_{SD}, and low $Mort_R$. This suggests successful recruitment as well as a simplification of canopy structure in response to intermittent management, where the degree of canopy structural complexity is represented by DBH_{SD}, CA_{SD}, and H_{SD}, which were 6.024 – 20.634% lower under passive management compared to the control. This contrasts with the idea that small scale intermittent disturbance often results in increased canopy complexity (Hardiman et al., 2013, Ehbrecht et al., 2017), but is likely to be a consequence of disturbance being of the same intensity, severity, and targeting the same PFTs and size classes for removal with each recurrence.

Passive management in the GL resulted in larger CA_{Avg} compared to the control regardless of RCP scenario. Passive management also resulted in low DBH_{SD} and H_{SD} in the SE, but the same reduction in CA_{SD} compared to the control was not observed, rather both CA_{Avg} and CA_{SD} were greater than the control. This could be because warming was not as pronounced in the SE, nor was the region water stressed, both consistent warming and drought have been shown to result in crown dieback (Matusick et al., 2018). In the SE, DENS and CWD were also higher under passive management compared to the control, although CWD was only higher under RCP4.5.

Ecological management is characterized by tall to moderately tall trees with smaller crowns in both regions. In the GL, AGB is high under ecological management, trees are older on average than under passive or production management, and DBH_{SD} is similar between ecological and production management. LAI and CWD are both higher under ecological management compared to the control in the GL, as are tree DBH_{Avg} and H_{Avg}. Higher average LAI has been linked to increased productivity (Gough et al., 2021), as evidenced by comparatively high AGB under ecological management. This could be explained by an increase in carbon use efficiency resulting from successional transition, which is supported by the abundance of tall, large, older trees. In the SE, ecological management resulted in young stands with high LAI, high DBH_{SD} but low CA_{SD}, and low $Mort_R$. Similar to the GL, ecological management in the SE resulted in increased LAI compared to the control. The combination of high LAI, high DBH_{SD}, and comparatively younger average Age_{Tree} suggest successful recruitment and survivorship under ecological management in the SE.

Production management, the management type representing the most intensive harvest, is characterized by low density stands with smaller average crowns in both regions. Similar to ecological management, production management in the GL also resulted in higher LAI and taller average trees compared to the control. In the SE, LAI was lowest under production management and CWD was highest, surpassing average control values. The combination of shallow soils, increased soil moisture due to enhanced precipitation, low stand density, and abundance of tall trees could result in increased wind damage risks (Panferov et al., 2009, Seidl et al., 2017) under production management in the SE, where summer storms are characterized by high winds that are projected to intensify with climate change (USGCRP, 2018). $\mathrm{DBH}_{\mathrm{SD}}$ was similar between production and ecological management in both regions.

Each management strategy produced different canopy complexity and productivity outcomes. While preservation management had the highest overall canopy complexity and productivity (represented by AGB) in both regions, the highest structural complexity amongst the active management strategies was either ecological or production forestry (depending on structural variable), and passive management frequently had the lowest complexity and lowest productivity in both regions. Temporal changes were the most pronounced for $\mathrm{Mort}_{\mathrm{R}}$, DENS, and AGB. $\mathrm{Mort}_{\mathrm{R}}$ experienced dramatic increases in both regions from the start to the end of the century, DENS exhibited a large decrease over time in the GL, and AGB increased substantially in the SE.

5.5.2 Ecosystem functional stability

Our second research objective was to determine how forest management alters ecosystem functional stability in the face of a changing climate, and if relationships are regionally dependent. We quantified the response of forest functional stability to management and climate change using both resilience (S_R) and temporal stability (S_T) metrics, which allowed for standardization of functional responses across different treatment combinations.

We hypothesized that management is the most important factor shaping functional stability, but found that while management is the most important driver of S_R, S_T is more closely linked to climatic factors. We also expected that regional interactions between management and climate change would alter stability outcomes over time, and that more intensive management practices (e.g. production forestry) would decrease functional stability. We found that regional differences were important for both measures of functional stability. The strength of management as a predictor of S_R was regionally dependent, and regional climate change impacts as well as regional interactions between management and climate change scenarios were more important predictors of S_T than climate change scenario alone. This means that the relationship between management and functional stability needs to be evaluated on a regional basis, and that managing to increase S_R is not one-size-fits-all.

We showed that interactions between management and climate change alter stability outcomes over time, but found that decreases in functional stability over time in response to management weren't limited to the more intensive management practices (e.g. production forestry), but instead depended on the region a given management practice was implemented under, as well as how management interacted with regional climate change impacts. Finally, a positive relationship between functional stability and structural complexity and diversity was observed, but only for S_R.

Regional comparison showed that functional stability and its relationship to management was regionally dependent. Average S_R was higher in the SE than in the GL for all three ecosystem function variables, and regionally averaged S_R values were positive in the SE and negative in the GL. This means that management amplified S_R compared to a no management scenario in the SE, but that the management types evaluated here actually decreased S_R in the

GL. This suggests that additional management strategies need to be evaluated for increasing S_R in the GL region, and in areas with similar climatic and forest conditions. The comparatively higher S_R in the SE could be related to the observed increase in water availability, which has been shown to accelerate recovery rates following disturbance (Anderson-Teixeira et al. 2013). S_R values were within the range of similar studies evaluating the response of S_R to disturbance (Dorheim et al., 2021, Mathes et al., 2022). The second dimension of functional stability, S_T, was also higher in the SE for two out of the three functional variables (GPP and Reco). Both stability metrics decreased from the start to the end of the century on average in the GL region, but temporal trends were less uniform in the SE and tended to vary by management type and functional variable, this is likely due to functional responses to management having a broader range in the SE than in the GL overall (Chapter 4).

The impact of management on ecosystem functional stability depended on the intensity and severity of management as well as how management interacted with regional climate change impacts. Management had a greater impact on S_R in the SE than in the GL, where only passive management produced significantly different S_R outcomes. Passive forestry in the SE often had lower average S_R than the other management types, but whether S_R was comparatively higher or lower under production versus ecological management depended on RCP scenario and the ecosystem function variable in question. Passive forestry in the GL had higher S_R than both production and ecological forestry across all three functional dimensions. Ecological and production forestry often had similar effects on S_R, but ET and GPP S_R were slightly lower under production management in the GL. Only passive forestry increased S_R compared to a no management scenario on average in the GL, ecological and production forestry decreased average S_R across all functional variables for both RCPs.

Differences in S_T by management type were only significant between production and passive management in the SE, S_T did not differ significantly by management at all in the GL region. S_T differed significantly between RCP scenarios in both regions and was lower on average under RCP8.5 than RCP4.5 across all three functional variables in the GL region, but in the SE S_T was higher under RCP8.5 for ET and GPP. GPP S_T differed the most by management type (although only significantly in the SE), and was the most temporally stable functional metric. This suggests that the S_T of carbon sink magnitudes will likely depend more on climate-induced changes in respiration than on productivity, as Reco was less temporally stable and differed more regionally. In the SE, GPP S_T was highest under ecological management for RCP4.5 and under production management for RCP8.5.

Although management was a stronger predictor of S_R, regional interactions between management and climate change scenarios had important implications for S_R. S_R was positive for all ecosystem function variables under RCP4.5, but under RCP8.5, ecological management continued to increase overall S_R compared to a no management scenario, while passive management had a near neutral effect for ET and GPP S_R, and had a negative effect for Reco S_R, meaning passive management was decreasing Reco S_R compared to a no management scenario, and production management decreased S_R for ET. This suggests that active management is needed to bolster ecosystem S_R in the face of climate change in the SE, but that managing for increased S_R likely involves tradeoffs in wood products production. Under RCP4.5, ecological forestry promoted higher GPP and Reco S_R in the SE while production forestry promoted higher ET S_R. However, this trend was reversed under the more severe climate change scenario, under RCP8.5 ecological forestry promoted higher ET S_R, while production forestry promoted higher GPP and Reco S_R. This could be due to changes in forest structure under production management (typically lower density stands with tall trees) altering tree susceptibility to water deficit issues (Seidl et al., 2017), which became more salient under RCP8.5, particularly in the GL. Production forestry in the SE frequently had the largest difference in S_R between RCP scenarios, suggesting the functional resilience of forests under production management is more sensitive to changes in climate.

Structural complexity had meaningful consequences for functional resilience. Overall, S_R was promoted by higher variability in tree height and DBH. This suggests that managing to increase structural complexity could increase S_R in the face of climate change. Considering the positive effects of structural complexity on resource use efficiency and productivity (Murphy et al., 2022), these findings are promising for the potential of forest management as a NbCS.

5.6 Conclusions

Paleoecological records show that ecosystems can gradually reorganize in response to shifts in mean conditions due to climate change (Iglesias and Whitlock, 2020), a process that will likely accelerate under future climate stress (Nolan et al., 2018). However, environmental conditions are changing too rapidly for successful reorganization to occur autonomously, resulting in widespread mortality (McDowell et al., 2020, Forzieri et al., 2022) as many forests approach ecological tipping points (Reyer et al., 2015). Management can be used to promote or alter these trajectories and rates of organization, increasing functional resilience and minimizing the release of stored carbon by reducing mortality. However, temporal stability is driven more by climate than by management, meaning management strategies must evolve over time as environmental conditions shift in response to climate change.

Furthermore, our findings highlight the regional dependency of management-induced changes in forest structure and ultimately functional resilience, as well as the dependence of temporal stability on regional climate change impacts. We showed that some management types lead to reductions in resilience, cautioning that the same management approach is not necessarily viable everywhere, and that the durability of management related NbCS has to be assessed at the regional scale. This information can help forest managers evaluate trade offs between ecosystem goods and services, assess climate risks of applying management practices in different regions, and potentially identify specific components of ecosystem function to bolster through targeted management practices.

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Supplemental figures

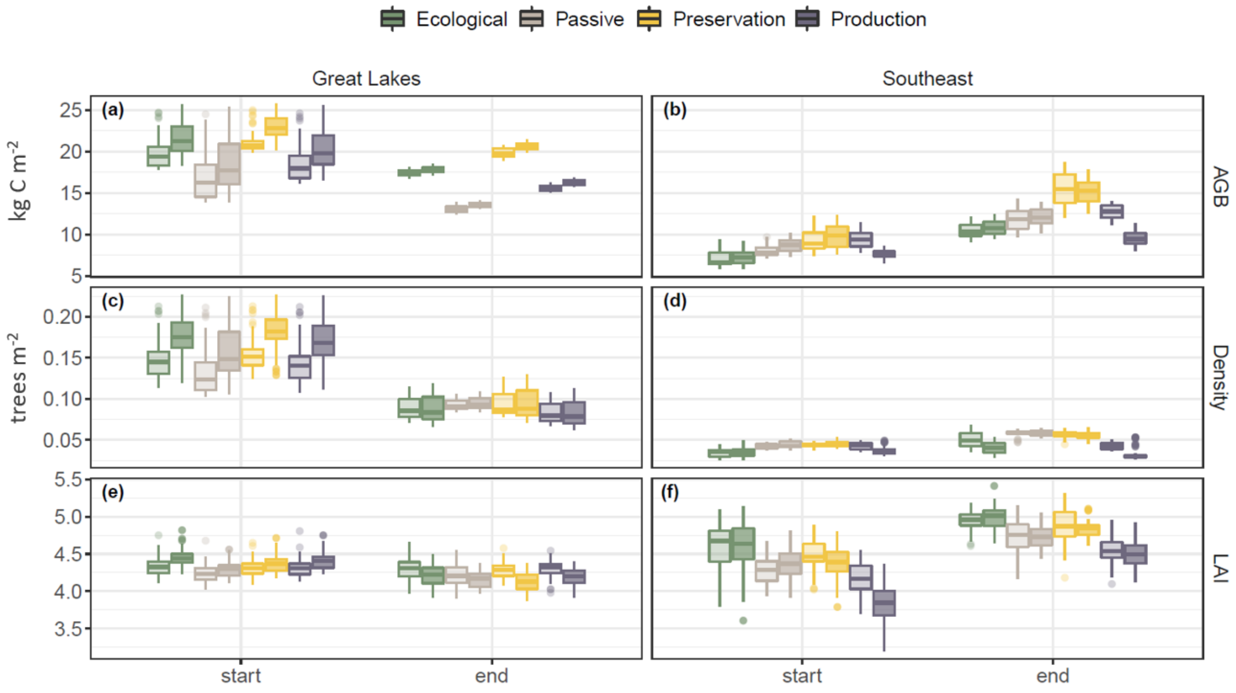

Figure S5.1: Above ground biomass (AGB), tree density, and leaf area index (LAI) for the start and end of the century. Columns are organized by geographic region, color hue corresponds to management type, and color tone corresponds to climate change scenario, where lighter tones represent RCP4.5 and darker tones represent RCP8.5.

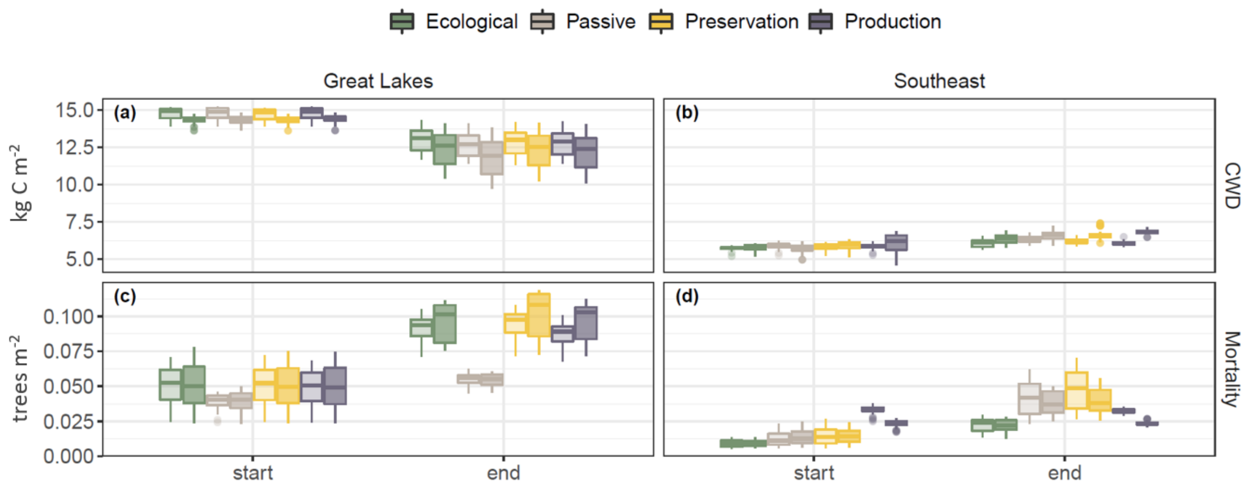

Figure S5.2: Coarse woody debris (CWD) and mortality rate for the start and end of the century. Columns are organized by geographic region, color hue corresponds to management type, and color tone corresponds to climate change scenario, where lighter tones represent RCP4.5 and darker tones represent RCP8.5.

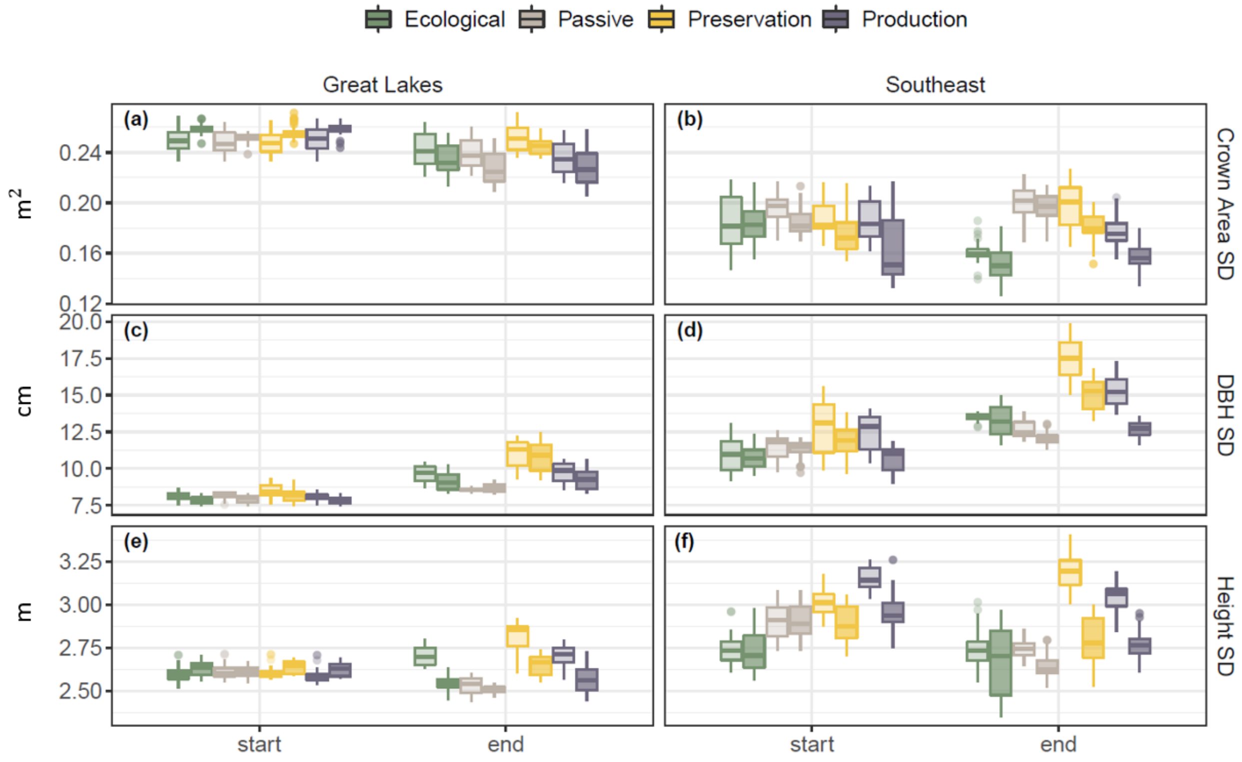

Figure S5.3: Standard deviation of crown area,diameter at breast height (DBH), and tree height for the start and end of the century. Columns are organized by geographic region, color hue corresponds to management type, and color tone corresponds to climate change scenario, where lighter tones represent RCP4.5 and darker tones represent RCP8.5.

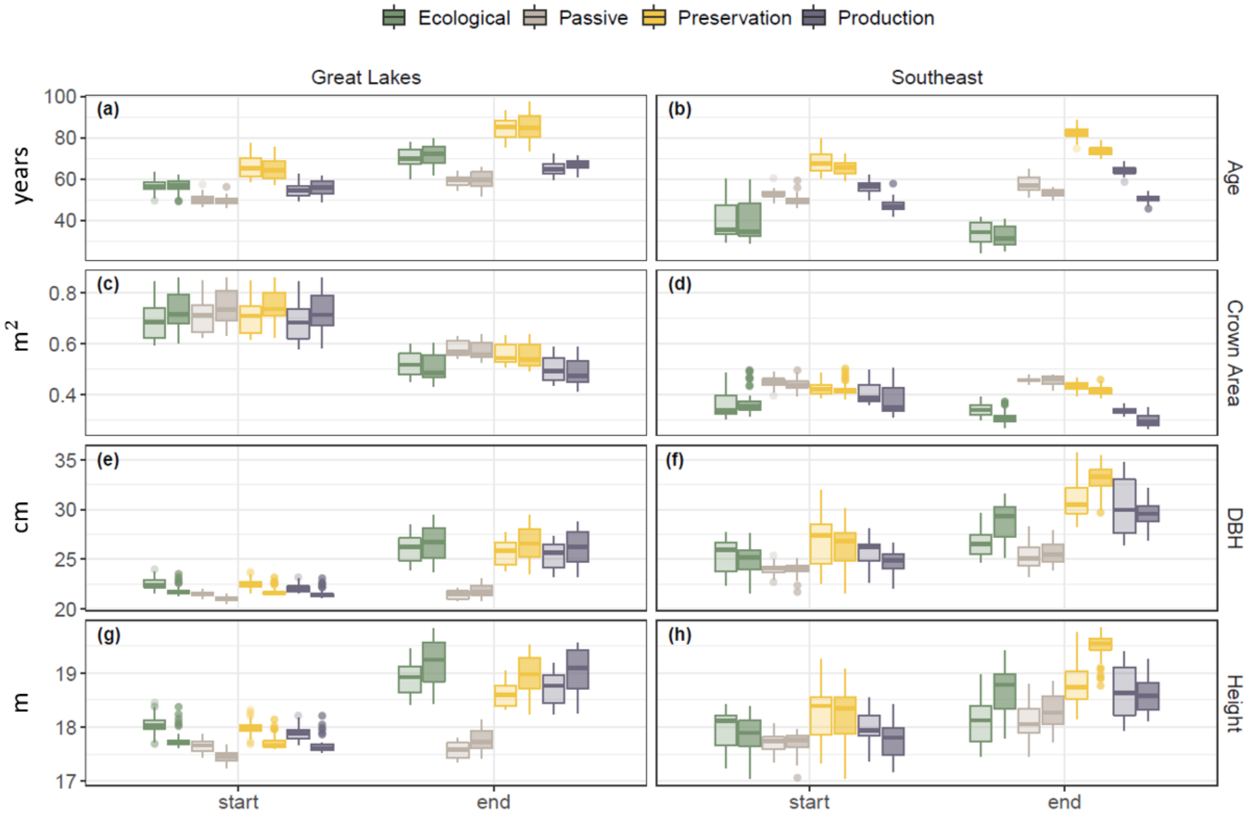

Figure S5.4: Average tree age, crown area, diameter at breast height (DBH), and tree height for the start and end of the century. Columns are organized by geographic region, color hue corresponds to management type, and color tone corresponds to climate change scenario, where lighter tones represent RCP4.5 and darker tones represent RCP8.5.

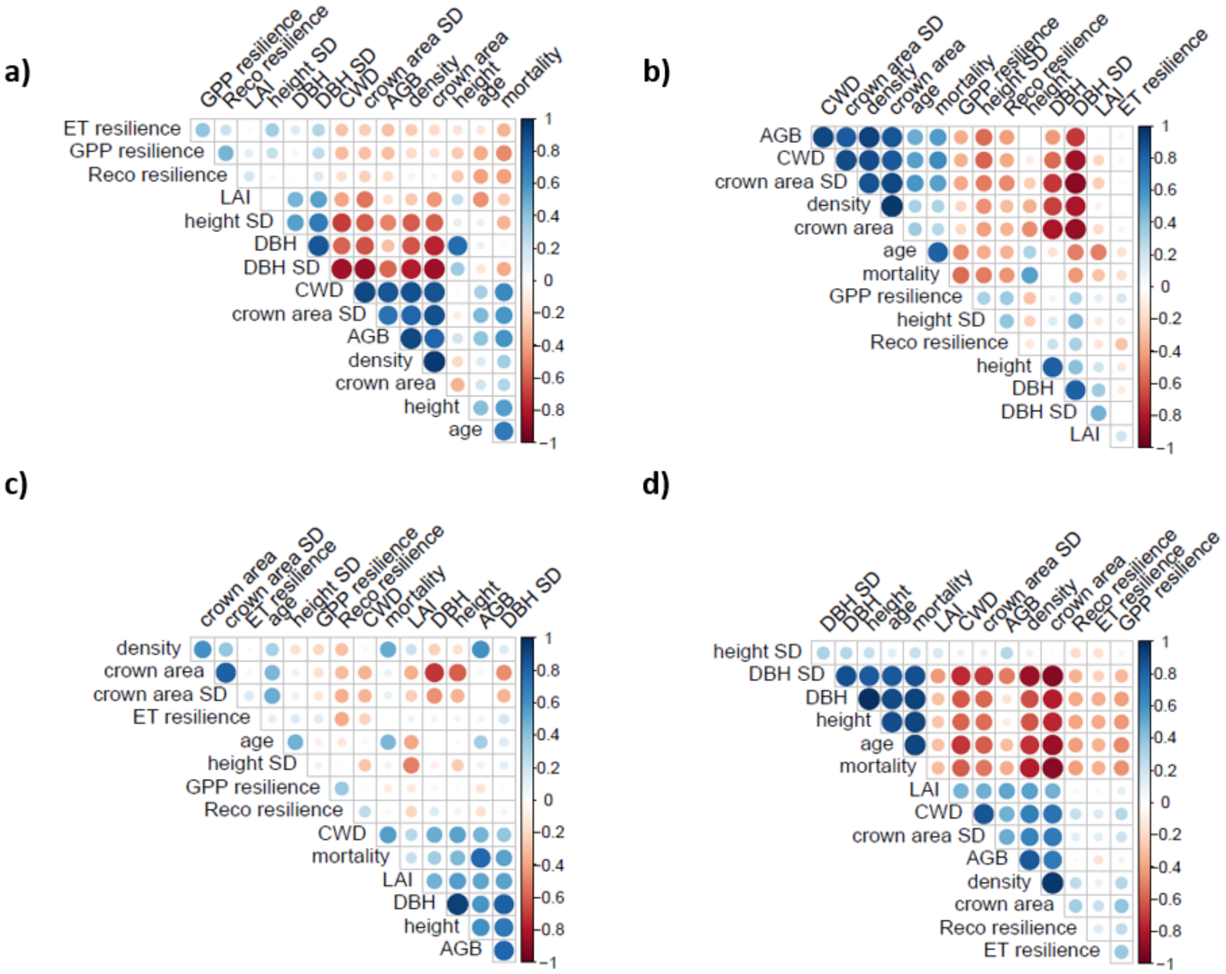

Figure S5.5: Correlation plot of relationships between ecosystem structural variables and GPP, Reco, and ET S_R subset to only **a)** RCP4.5, **b)** RCP8.5, **c)** the Southeast, and **d)** the Great Lakes. Circle size and color shade correspond to Pearson correlation strength, color hue depicts whether a relationship is positive (blue) or negative (red).

Supplemental tables

Table S5.1: Pearson correlation matrix of relationships between ecosystem structural variables and GPP, Reco, and ET S_R.

AGB	age	CWD	DENS	LAI	$Mort_R$	CA_{Avg}	CA_{SD}	DBH_{Avg}	DBH_{SD}	H_{Avg}	H_{SD}	ET S_R	GPP S_R	Reco S_R
1	0.44	0.87	0.92	-0.09	0.58	0.82	0.78	-0.37	-0.63	0.09	-0.52	-0.16	-0.34	-0.32
0.44	1	0.43	0.24	-0.48	0.76	0.28	0.52	-0.04	-0.29	0.35	-0.1	-0.12	-0.42	-0.38
0.87	0.43	1	0.87	-0.3	0.63	0.85	0.89	-0.58	-0.84	-0.07	-0.63	-0.16	-0.34	-0.29
0.92	0.24	0.87	1	-0.16	0.32	0.96	0.82	-0.67	-0.78	-0.3	-0.52	-0.11	-0.21	-0.21
-0.09	-0.48	-0.3	-0.16	1	-0.28	-0.3	-0.37	0.4	0.5	0.2	-0.06	0.1	0.12	-0.01
0.58	0.76	0.63	0.32	-0.28	1	0.28	0.56	-0.01	-0.4	0.54	-0.42	-0.24	-0.52	-0.43
0.82	0.28	0.85	0.96	-0.3	0.28	1	0.89	-0.8	-0.85	-0.42	-0.49	-0.06	-0.19	-0.22
0.78	0.52	0.89	0.82	-0.37	0.56	0.89	1	-0.68	-0.84	-0.19	-0.53	-0.07	-0.34	-0.39
-0.37	-0.04	-0.58	-0.67	0.4	-0.01	-0.8	-0.68	1	0.82	0.79	0.35	0.01	0.05	0.11
-0.63	-0.29	-0.84	-0.78	0.5	-0.4	-0.85	-0.84	0.82	1	0.36	0.6	0.18	0.28	0.21
0.09	0.35	-0.07	-0.3	0.2	0.54	-0.42	-0.19	0.79	0.36	1	-0.07	-0.14	-0.27	-0.18
-0.52	-0.1	-0.63	-0.52	-0.06	-0.42	-0.49	-0.53	0.35	0.6	-0.07	1	0.16	0.28	0.18
-0.16	-0.12	-0.16	-0.11	0.1	-0.24	-0.06	-0.07	0.01	0.18	-0.14	0.16	1	0.28	-0.1
-0.34	-0.42	-0.34	-0.21	0.12	-0.52	-0.19	-0.34	0.05	0.28	-0.27	0.28	0.28	1	0.4
-0.32	-0.38	-0.29	-0.21	-0.01	-0.43	-0.22	-0.39	0.11	0.21	-0.18	0.18	-0.1	0.4	1

Chapter 6

Conclusions

In this dissertation I have incorporated both observational and model-derived data to explore the dynamic relationships between forest management, structure, function, and climate change across spatiotemporal scales. I have utilized a variety of statistical and methodological approaches to pursue three overarching questions:

1. What is the mechanistic relationship between forest structure and function?

2. What is the primary driver of future variability in forest function?

3. How does management impact the stability of forest function in the face of climate change?

This final chapter summarizes the key findings of the work presented in this dissertation, contextualizes these key findings within the broader field, and discusses implications, limitations, and directions for future research.

6.1 Research synopsis

The objective of chapter two was to identify mechanistic relationships between forest structure and function, explore potential controls or mediating factors on that relationship, and determine whether the observed relationships were scale dependent. The study design of the

2019 Chequamegon Heterogenous Ecosystem Energy-balance Study Enabled by a High-density Extensive Array of Detectors (CHEESEHEAD19) field experiment provided a unique opportunity to partially control for the influence of variability in climate, edaphic factors, and forest functional types on productivity, allowing for a more representative physiological understanding of the structure- function relationship than has been previously demonstrated.

Studies have shown that integrating information obtained from canopy structural complexity (CSC) metrics can serve as a powerful indicator of ecosystem-scale functions such as gross primary productivity (GPP), augmenting other commonly measured characteristics including species composition and diversity (Atkins et al., 2018a, Atkins et al., 2018b, Eitel et al., 2016, Fahey et al., 2019, Gough et al., 2019, Hardiman et al., 2011, Silva Pedro et al., 2017). Identifying not only which CSC variables have the greatest potential to predict GPP, but what potential controls or influential factors of the structure-function relationship might exist is a vital aspect of this effort. Previous work has addressed pertinent issues related to classification and standardization of CSC metrics (Atkins et al., 2018a, Atkins et al., 2018b, Hardiman et al., 2013a, Hardiman et al., 2013b, Parker et al., 2004, van Ewijk et al., 2011), but few studies have explored the issue of spatial scale in calculating and representing CSC metrics, especially when using aerial-based LiDAR systems.

By pairing high-frequency flux tower measurements of land-atmosphere exchange with high resolution LiDAR measurements of CSC taken within the same spatial domain, we were able to isolate mechanistic connections between forest structure and function. Mechanistic relationships were explored using structural equation modeling (SEM), and the viability of resource use efficiency (RUE) as a mediator of the structure-function relationship was evaluated, as previous studies have demonstrated it to be a strong predictor of forest productivity (Atkins et al., 2018a, Atkins et al., 2018b, Gough et al., 2019). Both water use efficiency (WUE) and light use efficiency (LUE) were used to represent overall stand RUE, and relationships were tested at five different spatial resolutions.

Chapters four and five expand in scale through comparison of multi-decadal vegetation demography model simulations of forest dynamics in response to management in two regions, the Great Lakes and Southeastern U.S. Simulations were conducted across gradients in forest type, edaphic factors, and climate under two alternate radiative forcing scenarios (RCP4.5 and RCP8.5). Management was represented by four distinct scenarios constituting a range of intensities: preservation, passive, ecological, and production forestry. This approach allowed us to characterize the impacts of both management and climate change on forest structure and function in two substantially different geographic regions, representing a novel contribution, as recent studies that have explored similar questions have been conducted using sites within a region of similar climate and environmental conditions (Triviño et al., 2023, Gutsch et al., 2018, Morán-Ordóñez et al., 2020).

The use of dynamic meteorological forcing spanning 80 years as opposed to cycled single-year meteorology as other studies have done (Dorheim et al., 2021) captures the impacts of interannual variability of weather on carbon dynamics, which have been shown to significantly affect fluxes (Desai et al., 2010, Desai et al., 2022, Shiga et al., 2018). Finally, the incorporation of meteorological forcing data under alternate radiative forcing scenarios from a collection of 10 GCMs allows for a more representative understanding of interactions between management and climate change by reducing bias in results introduced by model sensitivities that might otherwise dominate if using a time series from model simulations forced by a single GCM, as previous studies have done (Triviño et al., 2023, Morán-Ordóñez et al., 2020).

Chapter four focused on understanding future variability in forest function in response to human management and shifting climatic conditions. This chapter outlined the dominant axes of future functional variability using principal component analysis, then applied a combination of generalized additive modeling and random forests to determine whether management or climate change is the dominant driver of the observed functional variability, and whether conclusions were spatially dependent. This chapter addressed critical knowledge gaps related to how specific management strategies will impact forest function beyond the stand scale, across timescales relevant for climate change, and the relative strength of management and climate change as drivers of future ecosystem function, all of which are essential for facilitating the development of robust and scalable climate mitigation strategies (Novick et al., 2022, Wu et al., 2023, Anderegg et al., 2020, Giebink et al., 2022).

Finally, chapter five outlined the response of forest structure to variations in management and climate intensity, and related structural changes to shifts in ecosystem functional stability over time. This chapter utilized a multidimensional framework that included both resilience and temporal stability to characterize functional stability, and compared regional differences in forest response across a spectrum of management intensities. Several recent studies have adopted a multi-dimensional framework (Hillebrand et al., 2018) to evaluate ecosystem functional stability in response to discrete disturbance events, such as stem girdling through the Forest Accelerated Succession Experiment (FASET; Gough et al., 2013, Mathes et al., 2021), or simulated mortality events across a range of severities (Dorheim et al., 2021). However, this work is among the first to evaluate the multidimensional stability response of forest carbon cycling to sustained management over multi-decadal timescales in the context of alternate climate change scenarios at the regional scale. Therefore, this chapter provides novel insights into not only how active management impacts the structure and functional stability of forests across long timescales but also how future climate change might affect stability trajectories.

6.2 Summary of key findings and implications

1. **The mechanistic relationship between forest structure and function is mediated by resource use efficiency, is dependent upon the spatial resolution used to calculate structural metrics, and structural metrics representing the degree of vertical heterogeneity are the most influential productivity drivers for heterogeneous temperate forests.**

Through pairing LiDAR-derived CSC metrics from nine forested sites within the 10 × 10 km CHEESEHEAD19 study domain with high frequency land-atmosphere exchange data from nine EC towers located within those forested sites, we were able to separate variability in climate, soil fertility, and forest functional types from structural controls on productivity, allowing for a more representative physiological understanding of the relationship between forest structure and function than has been previously demonstrated. Our findings support the emerging consensus that a positive mechanistic relationship exists between CSC and productivity in mixed temperate forests (Gough et al., 2019, Gough et al., 2016, Ehbrecht et al., 2021), but suggest that this is a multifaceted relationship impacted by additional factors such as species diversity and management history. As well, we found that this relationship is not direct but rather is mediated by the effective acquisition and assimilation of both light and water resources, and that RUE generally is enhanced by increasing CSC.

Furthermore, we show that in a heterogenous mixed temperate forest subject to disturbance, metrics describing the vertical profile of heterogeneity (specifically the vertical complexity index, VCI_{Avg}) are the strongest drivers of productivity, as opposed to CSC metrics that are constrained to the outer canopy, supporting recent results from other studies regarding the importance of vertical heterogeneity (Fahey et al., 2019, Smith et al., 2019, Tang and Dubayah 2017). This is potentially due to vertical complexity metrics providing greater information content in terms of describing a forest's successional stage and ability to capture light as it moves beyond the outer surface of the canopy and penetrates into the forest below (Zimble et al., 2003, van Ewijk et al., 2011). Previous studies have focused on the utility of single outer canopy structural metrics such as rugosity (Atkins et al., 2020, Hardiman et al., 2013, Hardiman et al., 2011) to relate forest structure and function and facilitate scaling of ecosystem functions, while indices such as VCI_{Avg} are less explored (van Ewijk et al., 2011). However, outer canopy metrics such as rumple and rugosity fail to suitably characterize the variation within multi-layered complex stands such as the stands evaluated in this study. The superior performance of VCI_{Avg}, which captures variability in tree height and the evenness of biomass distribution, shows promise for scaling the structure-function relationship in complex forests subject to shifting disturbance regimes.

Finally, through analysis of the structure-function relationship at five structural metric calculation resolutions ranging from 0.25 m to 50 m, we demonstrated that the scale of metric calculation has a significant impact on the metric values themselves, and thus on which CSC metrics are ultimately included in predictive models of productivity. We showed that shifting the spatial resolution also changes the dynamics of the relationship between RUE and CSC. This finding emphasizes the need for consistency in the spatial resolution at which CSC metrics are calculated, and for the disclosure of resolutions of metric calculation when reporting CSC metric values and interpreting the significance of findings.

Through the exploration of mechanistic relationships between forest CSC and function, this chapter highlighted which complexity metrics provide important information about RUE and productivity. The persistent superior performance of the reduced SEM, where the relationship between CSC and GPP is moderated by RUE, suggests that although specific CSC metric values change slightly with metric calculation resolution shifts, the existence of a mediation effect itself is not scale dependent. This indicates that the mechanistic relationships outlined here can be scaled from the stand to the ecosystem level to provide novel insights into forest function and carbon storage potential. These metrics can then be integrated as flexible structural parameters in mechanistic ecosystem models that simulate light and water-sensitive processes, improving the ability of models to mimic true ecosystem responses to management and disturbance. This improved representation will allow us to explore the future response of forests to a variety of management regimes and representative concentration pathways, enhancing our ability to assess mitigation and adaptation strategies beyond direct observational studies, which often take many years to produce outcomes. Additionally, these findings provide new opportunities to validate and apply information obtained from satellites, such as the GEDI high resolution ecosystem LiDAR, which is capable of measuring global forest canopy height and vertical structure (Dubayah et al., 2020).

2. Management is the strongest driver of future variability in forest function at the regional scale, but at broader spatial scales gradients in future climate become critical.

To evaluate the strength of management and climate change as drivers of future variability in forest function, we first had to isolate the dominant axes of variability in future ecosystem function. Using principal component analysis, we showed that the dominant axes of variability in forest function over time at the regional scale were 1) tradeoffs between carbon accumulation (in both biomass and soils) and water loss, and the flux of carbon from the land surface back to the atmosphere through respiration, and 2) the net carbon balance of ecosystems, as well as light and carbon use efficiency. Both forest productivity and resource use efficiency were key components of ecosystem functional variability in managed forests, but resource use efficiency, and in particular water use efficiency, was ultimately representative of a larger proportion of the observed variability. Regional differences in forest function were the most pronounced for functional axes representing tradeoffs between carbon gain and water loss. As variability in this functional axis was driven more by climate related variables than by management, this likely reflects the regional differences in how the pace and pattern of climate change will be expressed.

ANOVA of two generalized additive models fit with regional data showed that management type explained 1.2 – 16.3 times more variability than RCP scenario for both axes of future variability in ecosystem function, and that the effect of management was more pronounced in the Southeast. This supported our hypothesis that management is a stronger overall driver of changes in forest function than climate change, and is consistent with recent work in boreal forests by Triviño et al. (2023) and temperate forests by Gutsch et al. (2018). However, our application of a random forest model to predict future variability in ecosystem function told a slightly different story regarding the importance of management versus climate change for the first axis of functional variability (PC1). The predictive model was built using climate and structural data from both geographical regions combined, and analysis showed that grouped climate variables were stronger drivers of the variability in ecosystem function captured by PC1, the axis primarily defined by variables related to water exchange, respiration, and productivity, while grouped structural variables were stronger drivers for PC2 , the functional axis dominated by NEE as well as light and carbon use efficiency. However, the importance of climate variables over structural variables for PC1 was narrow, suggesting that both management and climate play an important role in driving PC1.

The difference in conclusions between the two methods could be partially attributed to differences in spatial extent of the data used in analysis. The conclusion that management is a more important driver of function than climate at the regional scale is supported by similar studies (Triviño et al., 2023, Gutsch et al., 2018), but when expanding to the sub-continental scale to incorporate data from multiple regions, the broad gradients in future climate conditions become more critical. The narrow difference in driver strength of climate versus management suggests that the effects are likely not independent of one another. This is supported by other studies showing that interactions between climate and forest structure and demography explain forest functional responses better than each factor individually (Rollinson et al., 2016, Clark et al., 2013, Bond-Lamberty et al., 2014), and that functional responses to climate (especially precipitation changes) are mediated by competition and structural factors such as tree size (Mérian and Lebourgeois, 2011), elements that are directly impacted by management.

Overall, findings from chapter four support the consensus that considering both management and climate change impacts at the regional scale is important for understanding and predicting variability in forest function. Management practices can significantly influence forest productivity and resource use efficiency, while climate change impacts vary by region and interact with management practices to alter outcomes. These findings emphasize the need to incorporate both factors when assessing the viability of forest management strategies to sustain ecosystem function in the face of changing climatic conditions.

3. **The impact of management on forest functional stability is regionally dependent and varies by management intensity and severity. Temporal stability is driven more by climate than by management, while resilience is shaped primarily by management.**

We quantified the response of forest functional stability to management and climate change using both resilience (S_R) and temporal stability (S_T) metrics, which allowed for standardization of functional responses across different treatment combinations. We found that regional differences were important for both measures of functional stability. The strength of management as a predictor of S_R was regionally dependent, and regional climate change impacts as well as regional interactions between management and climate change scenarios were more important predictors of S_T than climate change scenario alone. We showed that the same management type could lead to reductions in S_R in one region while bolstering S_R in another region, cautioning that managing to increase S_R is not one-size-fits-all, and that the durability of improved forest management as a Nature-based Climate Solution (NbCS) has to be assessed at the regional scale.

We showed that interactions between management and climate change alter stability outcomes over time, but found that decreases in functional stability over time in response to management weren't limited to the more intensive management practices (e.g. production forestry), but instead depended on the region a given management practice was implemented under, as well as how management interacted with regional climate change impacts. Finally, a positive relationship between functional stability and structural complexity and diversity was observed, but only for S_R, where higher S_R was promoted by greater variability in tree height and diameter. This suggests that managing to increase structural complexity could increase S_R in the face of climate change. Considering the positive effects of structural complexity on resource use efficiency and productivity (Murphy et al., 2022), these findings are promising for the potential of forest management as a NbCS. Ultimately, this information can help forest managers evaluate trade offs between ecosystem goods and services, assess climate risks of applying management practices in different regions, and potentially identify specific components of ecosystem function to bolster through targeted management practices.

6.3 Limitations and future work

6.3.1 The eddy covariance method

Chapter two used observational land-atmosphere gas exchange data collected by flux towers to characterize ecosystem function when evaluating mechanistic relationships between forest structure and function. Flux towers collect this data using the eddy covariance (EC) method, which is the most well-established method for taking continuous measurements of energy and trace gas exchange (Desai et al., 2008), but it is not without drawbacks. All measurements have associated uncertainty, and in the context of EC measurements these uncertainties can be segregated into several categories, including uncertainty due to instrument or calibration error, technological limitations of the instruments themselves, inadequate sample size, and environmental conditions that violate the assumptions at the core of EC theory (Richardson et al., 2012). Some of these errors are stochastic and appear as random noise in the data, while other errors are systematic and result in a bias that is relatively constant over time. Numerous studies have explored these uncertainties at length (Hollinger and Richardson, 2005, Loescher et al., 2006, Massman & Lee, 2002, Richardson et al., 2006), but it is worth noting general trends in overall EC uncertainty here.

Random error in 30-min fluxes ranges from 10% to 20% (Loescher et al., 2006), with annual estimates around 10% (Richardson et al., 2006), as error generally decreases with longer time series and averaging (Loescher et al., 2006). Flux uncertainty follows a strong seasonal pattern (uncertainty is generally higher during the growing season), and is sensitive to land cover type and wind speed (Hollinger and Richardson, 2005, Richardson et al., 2006). Error is also associated with the partitioning of NEE into GPP and Reco and varies by partitioning method, but a survey of 23 methods conducted by Desai et al. (2008) showed that on average the difference in GPP was <10%, with additional uncertainty depending on the abundance of gaps in the data. In this study, there was an average of 37% gaps in measured NEE values across the nine sites.

6.3.2 Evaluation of the structure–function relationship

Chapter two primarily examined the influence of biotic forest factors to define the relationship between forest structure and function, but the inclusion of prominent abiotic factors such as nutrient regimes could further enhance understanding. Combining chemical analysis of leaves with the remote sensing of CSC and EC measurements of land-atmosphere carbon exchange would account for the influence of factors such as nitrogen availability in determining controls on RUE and productivity (Reich 2012). Another key limitation of chapter two is the relatively short window in which data were collected. Although this observational window supported the primary goals of CHEESEHEAD19 related to addressing issues of energy balance closure, from a carbon cycle perspective it failed to capture winter effects on net carbon budgets. Incorporating multi year data sets would address this problem as well as allow for a more thorough examination of the influence of stand age on RUE and productivity, whereas here the analysis was inconclusive.

Moreover, as neither disturbance and management or stand age were expressly controlled for, the impacts of management and disturbance on the structure-function relationship explored in chapter two are largely qualitative. Although the high density of EC towers in a small study domain controlled for several factors such as differences in soil type, forest type, and mesoclimate, differences in microclimate still existed between sites. This is presented as variability in temperature, latent and sensible heat flux, and wind properties including turbulence. Although heterogeneity in land cover existed, there was very little difference in topography to drive variability in air circulation or relative humidity, so the observed differences in microclimate were likely due to diversity in vegetation type and density, as well as proximity to and abundance of water. Lastly, the somewhat small site sample size involved in chapter two suggests caution should be exercised when evaluating SEM fit statistics.

6.3.3 Modeling limitations

The potential effects of increasing atmospheric CO_2 on ecosystem function are not accounted for in the modeling design utilized in chapters four and five. Inclusion of dynamic atmospheric CO_2 would likely result in amplified productivity and altered carbon dynamics. This is a plausible explanation for why our conclusions regarding the future magnitude of the regional carbon sink in the Great Lakes region don't align with average Earth system model predictions, which anticipate the region becoming a larger net carbon sink by the end of the century (Wu et al., 2023). However, due to the sensitivity of ED2 to increases in CO_2 concentration (Rollinson et al., 2017), inclusion of dynamic atmospheric CO_2 would likely dominate uncertainty in predictions of productivity over long timescales (Rollinson et al., 2017, De Kauwe et al., 2013, Walker et al., 2020, Zaehle et al., 2014, De Kauwe et al., 2014). Furthermore, several studies have shown that long term productivity increases under elevated CO_2 concentrations may ultimately be offset by increased competition for resources and mortality in response to climate change (van der Sleen et al., 2014, Fernández-de-Uña et al., 2016, Terrer et al., 2019, Ainsworth and Long 2005, Peñuelas et al., 2017, Walker et al., 2020).

Models are a key tool to reveal patterns in demographic responses to disturbance and interactions with climate change across long timescales, but it is important to note that even the best models have limitations in simulating the complex interactions between ecosystem functions. For example, considerable challenges persist in the representation of environmental responses to disturbance, including management (Fisher et al., 2017). These limitations arise from the structural representation of processes within the model and an insufficient representation of the true variability in vegetation traits. This can also be attributed to the general parameterization of PFTs and an inability to capture the full range of vegetation characteristics.

ED2 is also not capable of simulating factors such as species migration, which occurs as species natural ranges shift in response to changing local climate conditions. Finally, the modeling design employed in chapters four and five examines the direct land-atmosphere exchange of carbon but does not consider the rate of carbon export through harvest. This omission may result in an incomplete assessment of the overall carbon source-sink dynamics of the ecosystem.

6.3.4 Exclusion of natural disturbance

The modeling design utilized here does not consider the compounding effects of natural disturbances such as fire or insect or pathogen outbreaks. This means that the indirect effects of natural disturbances on structure and stability through interactions between climate intensification and management such as increases in vulnerability to insects or pathogens are not accounted for, although they can substantially alter forest dynamics (Hicke et al., 2012, Pugh et al., 2019). For example, pine trees in the western United States that are already suffering the effects of drought are made even more vulnerable to mortality from mountain pine beetle infestation, as water stressed trees have lower resistance to beetle infestation (Powell and Logan 2005). Interaction effects with natural disturbances could potentially amplify climate sensitivity (Seidl et al., 2017), which is particularly concerning in the GL region, as climate related disturbance effects have been shown to increase with latitude, and we showed here that the GL is already displaying low functional resilience. With climate change increasing the frequency and intensity of natural disturbance events (Seidl et al., 2017), their exclusion here may limit understanding of the potential effects of enhanced climate stress on carbon and water dynamics. However, this dissertation focuses on human management as disturbance, and incorporation of natural disturbance regimes that are shifting in response to climate change would require significant assumptions, contributing additional uncertainty.

6.3.5 Directions for future work

Overall, this work describes general patterns in the response of forest structure and function to management and climate change. Future work could focus on expanding the modeling scope to include sites in additional regions, representation of forms of natural disturbance such as wildfire, isolation of functional resilience risk factors or thresholds, and evaluation of timescales of importance including any lag dependencies or associated non-linearities that characterize the regional relationships between forest structure and function. This would allow for a more robust evaluation of how relationships between forest structure and function could be scaled, and illuminate weaknesses in existing ecological theory. This information could then be used to develop and test a theoretical framework for representation of forest structure and function relationships in Earth system models (ESMs), to serve as a constraint on forest functional shifts in response to human management and improve the reliability of model predictions regarding the future of the terrestrial carbon sink.

6.3.5.1 Incorporation of additional sites

Model simulations were restricted to two U.S. regions; the Great Lakes and Southeastern U.S. While these regions differ substantially in climatic and edaphic conditions, forest types, and disturbance histories, analysis of forest structure and function responses to management and climate in two regions is not sufficient to address scaling stand-level ecological hypotheses to the continental scale. In order to accomplish this, additional simulations in other U.S. regions are required, as are spatially explicit representations of management types and distributions in each region. This is an area of continuing work, vegetation structure and climate data required to drive model simulations has already been compiled in the Pacific Northwest (PNW), Northeast, and Rocky Mountains regions, and management prescriptions for ED2 are nearing completion for the

PNW. Additionally, forest functional data from model output will be combined with high resolution (250 m) regional management maps derived from Moderate Resolution Imaging Spectroradiometer (MODIS; Knight et al., 2006) and LANDSAT satellite imagery (Marsik et al., 2018) to obtain continental-scale estimates of forest function (GPP, NPP, ET, etc.) based on management type.

6.3.5.2 Representation of structure-function relationships in Earth system models

One strategy for improving management and disturbance impacts in ESMs and reducing predictive uncertainty could be through representing the connection between forest management and function with the use of structural complexity metrics, which are directly altered by management and have been shown to exert strong controls over forest resource use efficiency and productivity. Many elements of forest structure are already incorporated in land surface models, either explicitly or through plant functional traits that are directly related to structure. I hope to explore a framework for how mechanistic relationships between forest structure and function could be integrated as a constraint in ESMs to modulate how management and functional responses interact, and how interactions change under different climate futures, with the goal of keeping predictions grounded in reality and reducing predictive uncertainty.

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