

EFFECTS OF TREE SIZE AND FOREST STRUCTURE
ON FOREST DYNAMICS

By

BRADLEY NIXON

Bachelor of Science in Biology: Environmental
Conservation

Rogers State University

Claremore, Oklahoma

2020

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
December, 2022

EFFECTS OF TREE SIZE AND FOREST STRUCTURE
ON FOREST DYNAMICS

Thesis Approved:

Dr. Lu Zhai

Thesis Adviser

Dr. Rodney Will

Dr. Chris Zou

ACKNOWLEDGEMENTS

I would like to thank Dr. Zhai, Dr. Will, and Dr. Zou for guiding me through this research process. I would also like to thank them for teaching me valuable skills that can be applied to both research and to life in general. I'd also like to thank my wonderful fiancé, Lauren Mckinney, for supporting me for these past couple of years. Lastly, I'd like to thank my parents and the rest of my family for helping me out whenever I needed it.

Name: BRADLEY NIXON

Date of Degree: DECEMBER, 2022

Title of Study: EFFECTS OF TREE SIZE AND FOREST STRUCTURE ON FOREST DYNAMICS

Major Field: NATURAL RESOURCE ECOLOGY AND MANAGEMENT

Abstract: Climate change is exacerbating drought disturbances, reducing forest productivity, and causing increased forest mortality. Manipulating tree size and overall forest structure are two important components that are being considered by forest managers to help combat losses in forests. When it comes to tree size, however, there are inconsistent findings on which sizes are most vulnerable to drought; and when it comes to forest structure, there are inconsistent findings on whether stand structural diversity (SSD) is beneficial for promoting productivity. We conducted two meta-analyses to help better understand these factors, one for tree size and one for forest structure. Based on our results, we found that both tree size effects and forest structure effects are highly complex and rely on multiple biotic and abiotic factors. Notably, for tree size effects on drought induced mortality, we discovered that larger trees are initially more resistant to drought but become more vulnerable during longer droughts. They also tend to show higher mortality during drought from increasing insect disturbances. For forest structure, we found that increased SSD increases productivity in stands with larger average tree size, higher basal area, higher average temperatures, and higher levels of drought. My results indicate that forest managers will need to consider the specific factors that affect tree size and forest structure if they want to effectively manipulate forest structure and tree size to manage forests in the future.

TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION.....	1
II. A META-ANALYSIS EXAMINING THE RELATIONSHIP BETWEEN TREE SIZE AND DROUGHT INDUCED TREE MORTALITY	3
Introduction.....	3
Methods.....	6
Results.....	10
Discussion.....	12
Conclusion	16
III. A META-ANALYSIS EXAMINING THE RELATIONSHIP BETWEEN STAND STRUCTURAL DIVERSITY AND FOREST PRODUCTIVITY	18
Introduction.....	18
Methods.....	22
Results.....	25
Discussion.....	27
Conclusion	30
IV. CONCLUSION.....	31
REFERENCES	33

LIST OF FIGURES

Figure	Page
1. Tree Size Conceptual Figure	5
2. Tree Size Study Location Map	8
3. Tree Size Forest Plot and Scatter Plot	10
4. Tree Size Meta-Regression Results	12
5. SSD Conceptual Figure	21
6. SSD Study Location Map	24
7. SSD Forest Plot	26
8. SSD Meta-Regression Results	27

CHAPTER I

INTRODUCTION

Understanding forest dynamics is becoming increasingly important as climate change amplifies drought events and raises temperatures, leading to productivity losses in forests globally (Bradford *et al.*, 2020; Senf *et al.*, 2020; Hammond *et al.*, 2022). These losses could severely damage forests around the world, which would have both economic and ecological ramifications. In Oklahoma alone, forestry industries contributed \$5.6 billion to our state's economy and supports over 18,450 jobs that could be at risk (Gore *et al.* 2022). From an ecological standpoint, carbon sinks in forests provide a natural climate solution (Fargione *et al.*, 2018) and losses in forests could result in more carbon being released into the atmosphere, thus further contributing to climate change, and creating a positive feedback loop where climate change continues to damage forests which continues to escalate climate change. Additionally, forests provide habitat to wildlife and others to help sustain biodiversity necessary for maintaining healthy ecosystems (Storch *et al.*, 2018).

Understanding forest structure is important when it comes to understanding forest dynamics. For an individual tree, its size directly correlates with how much money it is worth. Larger trees can be sold as sawtimber which is worth nearly double the value per ton of pulpwood that comes from smaller trees. Additionally, the largest one percent of trees are the main predictors of carbon storage potential in a forest (Ali et al. 2019). Overall, forest structure makes up a large part of the trait variation in forests that can improve models used for predicting future vegetation and its constraints (Diaz et al. 2016) which will be essential as weather patterns and disturbance regimes continue to change.

To fully understand forest dynamics, we need to understand the effects that tree size and stand structure have on them. To accomplish this, I conducted two global-scale meta-analyses where I compiled data from all available studies on the topics and compared their results in a systematic way. My first meta-analysis is focused on the effects of tree size on drought-induced tree mortality, and it looked to answer the question of whether larger or smaller trees are more likely to die during droughts. The second analysis examined whether stand structural diversity (SSD) is beneficial to forest productivity. For both studies I examined the heterogeneity in results to investigate how biotic and abiotic factors may affect the two relationships. In doing this, we aimed to create a better understanding of how forest dynamics can be altered by tree size and forest structure. This work can be used to improve forest modeling predictions and forest management around the world.

CHAPTER II

A META-ANALYSIS EXAMINING THE RELATIONSHIP BETWEEN TREE SIZE AND DROUGHT INDUCED TREE MORTALITY

Introduction

Anthropogenic climate change -- driven by accelerated warming from human emissions -- is amplifying the frequency, intensity, and severity of droughts in many forests around the world, resulting in increased pulses of forest mortality (Brodrribb *et al.*, 2020; Senf *et al.*, 2020; Hammond *et al.* 2022). Notably, tree mortality may vary with a gradient of tree size, e.g., tree diameter or height (Grote *et al.*, 2016). Meanwhile, trees of different sizes make different ecological contributions, given the crucial roles of vegetation structure in plant dynamics (Díaz *et al.*, 2016) and ecosystem functions (Ali & Wang, 2021; Migliavacca *et al.*, 2021); including forest carbon dynamics (Slik *et al.*, 2013; Gora & Esquivel-Muelbert, 2021), tree mortality, and fecundity (Clark *et al.*, 2021), and wildlife habitat suitability (Feng *et al.*, 2020). Therefore, understanding the variation in drought-induced mortality with tree size is critical to project forest dynamics and ecosystem functions under the changing climate.

The effects of tree size on mortality arise from a range of related ecophysiological variation. Compared with small trees, large ones often have more vulnerable hydraulic structures partly owing to their more exposed canopy for transpiration, increased distance of water conductance from soil to canopy (McDowell & Allen, 2015), and wider water-transporting conduits (Olson *et al.*, 2018; Fajardo *et al.*, 2020; Guillemot *et al.* 2022). These factors hinder water movement to tree canopies and increase the risk of xylem-blocking embolisms forming, potentially leading to greater mortality of large trees rather than small ones under the same plant-level drought intensity, resulting in a positive relationship between tree size and mortality, e.g., Stovall *et al.* (2019). Therefore, increasing drought frequency and severity due to climate change may result in shorter forests in the future (Fajardo *et al.*, 2019; McDowell *et al.*, 2020). Nevertheless, this positive relationship is not consistently supported by all observations, likely due to a range of confounding factors. Although Bennett *et al.* (2015) summarized multiple studies on the tree-size effect on drought-induced mortality, the heterogeneity has not been rigorously quantified, and drivers of heterogeneity have not been thoroughly examined in previous studies. Therefore, there are important knowledge gaps in the tree-size effects on tree mortality during drought.

The relationship between tree size and mortality may be confounded by a range of abiotic and biotic factors, such as drought duration, impact of insects on the mortality process, and competition. Drought duration significantly affects forest dynamics (Gao 2019). Notably, compared with small trees, large trees tend to be less affected by short droughts because of their access to deeper soil water (Giardina *et al.*, 2018; Chitra-Tarak *et al.*, 2021; Ding *et al.*, 2021) (Fig. 1). In contrast, during a longer drought, the depletion

of deeper soil water intensifies and the water loss from deep soil may not be replenished sufficiently by small precipitation events (Fig. 1), leading to more drought stress on large trees than small ones (Chitra-Tarak *et al.*, 2018). Therefore, larger trees showed poorer recovery, particularly following extreme drought years (Bohner & Diez, 2021), and correlations between tree size and mortality are hypothesized to be more positive with longer drought duration.

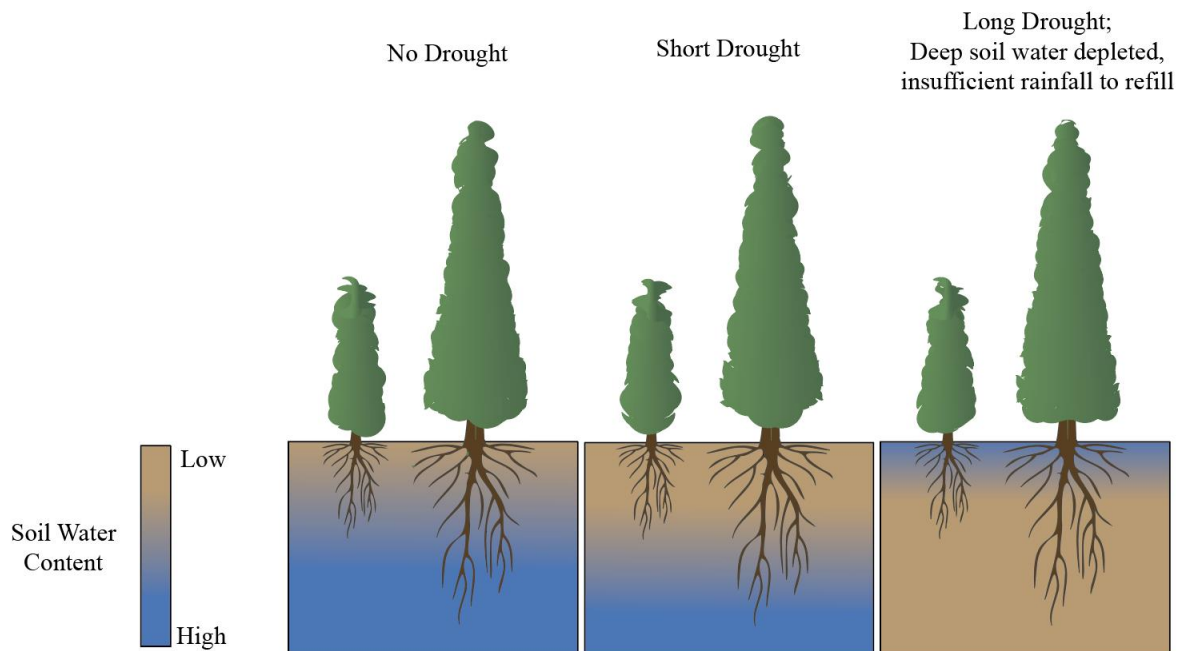


Figure 1. Conceptual figure showing a simplified comparison between small and large trees under short and long droughts. Larger trees still have access to deeper soil water during short droughts, but during prolonged droughts, the deeper soil water is depleted and the larger trees are then at a disadvantage due to their large size and limited resources to support themselves.

In addition to drought duration, we examined the interactions between tree size and drought-induced mortality with insects, basal area, and natural vs artificial droughts. Several types of insects preferentially attack larger trees (Stephenson *et al.*, 2019; Tai *et al.*, 2019; Koontz *et al.*, 2021; Trugman *et al.*, 2021). When insect-associated mortality occurs with drought, mortality among larger trees likely increases. Greater competition

for water resources occurs in stands with greater competition and stocking, i.e., higher basal area (Andrews *et al.*, 2020, Bradford 2022), potentially leading to more mortality of large trees given their more vulnerable hydraulic structure. We also examined effects of drought origin: natural vs. artificial drought. Considering that artificial drought (e.g., controlled rainfall reduction or decreased watering) may not fully simulate impacts of natural droughts, we hypothesize that the size-mortality correlation varies between natural and artificial drought.

Because the relationship between tree size and mortality is likely context-dependent identifying these factors is essential to improve the understanding and projection of forest dynamics under drought and to inform forest management from a structural perspective. To understand the complex relationship between tree size and tree mortality under drought, we reviewed 688 papers from a literature search based on multiple keyword combinations. We filtered these papers and extracted measures of tree mortality, tree diameter, sample number, site location, drought timing, whether insect presence was documented (or undocumented), and stand basal area. With the measures of tree mortality, tree diameter, and study sample size, we conducted a meta-analysis to quantify heterogeneity in the relationship between tree size and mortality. Using measures of these potentially confounding factors, we conducted a meta-regression analysis to test our hypothesis that correlations between tree size and mortality significantly vary with drought duration, insect documentation, basal area, and drought origin.

Methods

Data Collection

The data used in this meta-analysis were collected from research studies published before 2021 that reported drought-induced mortality of different sized trees. For this meta-analysis, we searched the Scopus database using keywords: (drought OR water stress) AND (forest OR tree OR rainforest OR woody OR shrub) AND (diameter OR height OR size OR DBH* OR architecture OR demography OR structure) AND (mortality OR death). This search produced 688 articles that contained the above keywords in their titles, abstracts, or listed keywords. These articles were further filtered by reading through their titles and abstracts to ensure that selected studies cover tree mortality during drought. Then, the remaining studies (205 articles) were refined further by reading their methods and results to ensure that they contained the necessary data for meta-analysis. For a study to be included in the meta-analysis, it needed to include: (a) a drought event, either natural or artificial; (b) tree mortality rates for at least three tree-size groups throughout the drought event; (c) sample sizes (or tree number) of each tree size group. Following that process, we included 19 articles, which reported 32 correlations between tree size and mortality at 24 unique locations, covering different ecoregions and forest types (Fig. 2). The data of mortality rates and sample sizes were either directly stated in the study or extracted from figures using the ImageJ program (<https://imagej.nih.gov/ij/>) to measure the lengths of bar graphs (or other graph types). Tree size group was reported as Diameter at Breast Height (DBH) classes in all studies that were used in this analysis. We used DBH as our metric for tree size because DBH is

generally related to tree height and DBH is the most widely used metric for determining tree size across the studies in our data search.

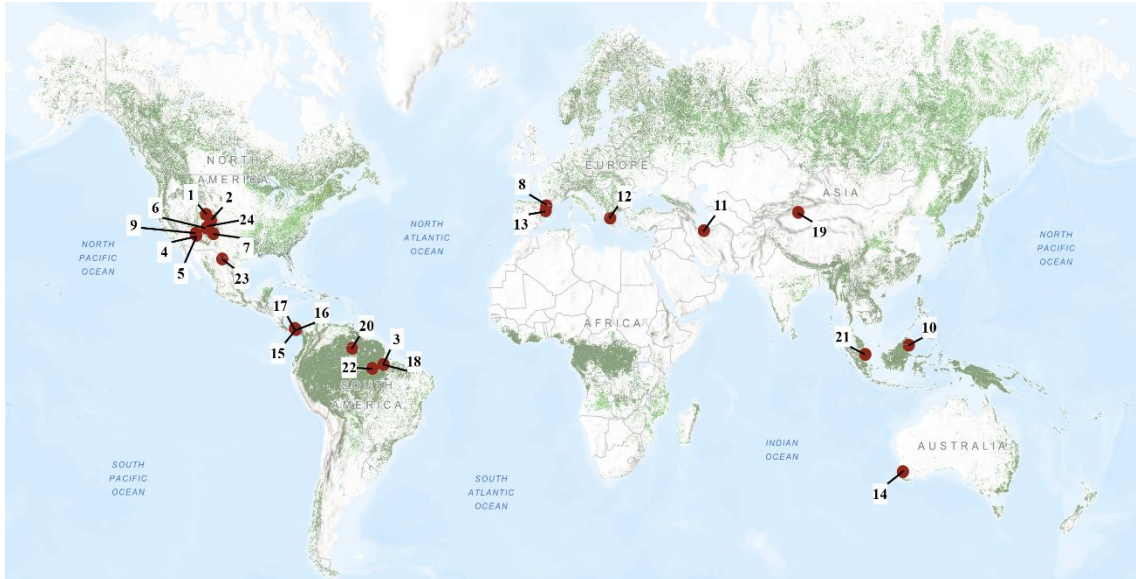


Figure 2. Locations of studies used in the meta-analysis. Each numbered point represents a drought observation. The plot numbers and their matching studies are listed in Table S1. Some studies occurred in different stands at the same location.

The drought duration was extracted directly from the text of each study and converted into months. If the drought was still ongoing at the end of the study, the duration was calculated by the last measurement of mortality that was taken. For insect information, studies were put into two groups: groups with insect presence documented and groups without. This information was directly extracted from the text of each study. Stand basal area ($\text{m}^2 \text{ha}^{-1}$) was extracted either from tables or figures included in the text. If stand density (trees ha^{-1}) was given instead of basal area, we estimated stand basal area by multiplying density by the basal area of the tree of average DBH.

Statistical Analysis

To examine the correlation between mortality rate and DBH class under drought, we quantified the effect size of the meta-analysis using the Pearson Product-Moment Correlation method (Harrer *et al.*, 2021). The correlation value of each study was calculated by a simple linear regression model. Note that some papers reported the correlations for multiple stands characterized by different stand attributes, such as species composition, stand age, etc., and these correlations were treated separately. Positive correlation values meant larger trees suffered higher mortality rates, and negative correlation values meant that smaller trees suffered more. The correlation values, along with the sample sizes, for each study were then used to run the meta-analysis to examine heterogeneity of the correlation among the studies. We used a random-effects model for our meta-analysis because a considerable amount of between-study heterogeneity was expected based on the results of previous studies (Bennett *et al.*, 2015; Giardina *et al.*, 2018). The Sidik-Jonkman (“SJ”) estimator was used to measure tau-squared (τ^2), which is the variance of the distribution of true effect sizes (Sidik & Jonkman, 2005). A Fischer’s z transformation was conducted when running the meta-analysis to ensure that the sampling distribution was approximately normal. We tested for publication bias in the meta-analysis, which results from selective publication of studies with more significant findings, using Egger’s test and checking the funnel plot. A funnel plot and Egger’s test revealed that one outlier causing publication bias. However, we ran the analysis without the outlier and it did not change the results significantly, thus this observation was kept in the analysis. As described above, we collected data of factors potentially contributing to heterogeneity of the correlation between tree size and mortality, including drought duration, insect documentation, drought origin, and basal area. The effects of these

factors were quantified by a meta-regression analysis given the heterogeneity in the effect size and random effects across the studies. One outlier was detected in the initial drought duration plot using Cook’s Distance and was removed from the final analysis for having a duration over twice as long as the average drought. The analyses were conducted using the “meta” R package (Schwarzer, 2020).

Results

Heterogeneity in the correlation between tree size and mortality

The correlations between tree size and mortality varied from negative to positive values among different studies resulting in significant heterogeneity in the correlation ($p < 0.001$). The 95% confidence interval (CI) of each correlation is also reported in Fig. 3A and shows the variation in the results. A scatter plot of the correlation from each observation shows large heterogeneity in the slopes between DBH and mortality and includes positive slopes, negative slopes, and non-significant slopes (Fig. 3B).

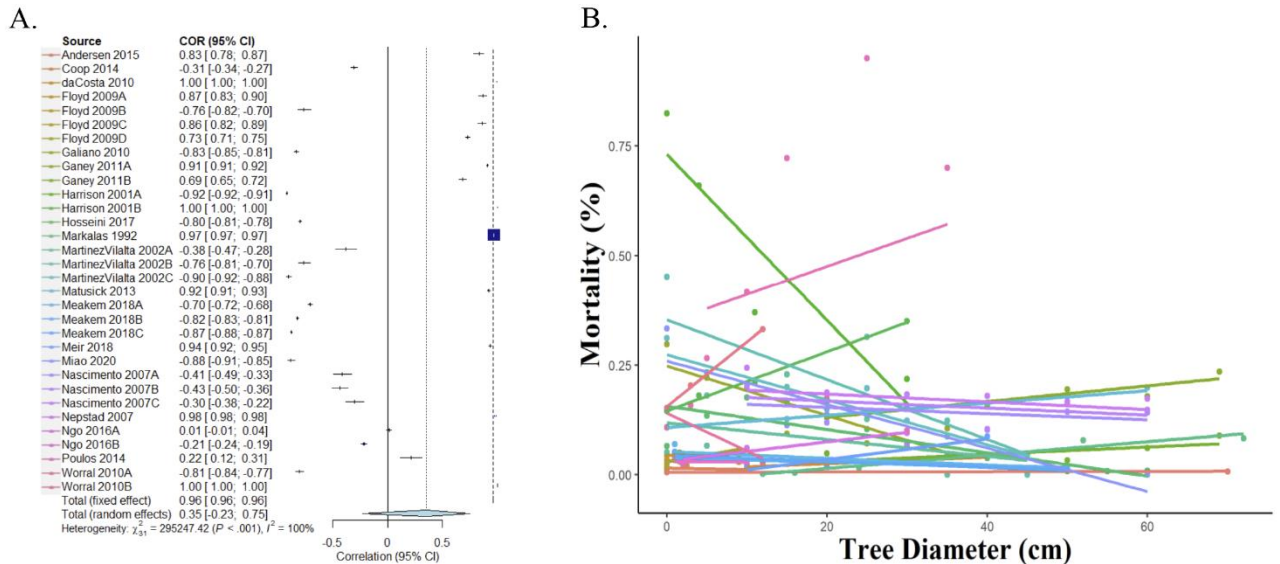


Figure 3. A) The “forest” plot showing correlation between tree size and mortality from different studies. Note that: (1) The last row shows a statistical test of the heterogeneity in

the correlation among these studies; and (2) Some studies included data from different stands which are separated using letters (i.e. Floyd 2009A, Floyd 2009B, ...). B) The scatter plot with regression lines showing correlation between tree size and mortality of the 32 observations. The legend of this figure is shown in the first column of Fig. 3A.

Effects of Drought Duration, Drought Origin, Insect Documentation, and Basal Area

The results showed that drought duration had significant effects on the correlation between tree size and mortality rate ($p = 0.006$). The correlation switched from negative to positive with longer drought duration at ~25 months (Fig. 4A). Therefore, smaller trees were more vulnerable to mortality under short droughts, but longer droughts render large trees more vulnerable. The correlation also significantly varied with drought origin ($p = 0.025$). The correlations under artificial droughts were consistently positive, but there was more heterogeneity under naturally occurring drought (Fig. 4B). In addition, studies that documented insect presence had positive correlations while those without were negative ($p = 0.016$) (Fig. 4C). Meanwhile, there was no significant effect of basal area on the correlation ($p = 0.31$, Fig. 4D).

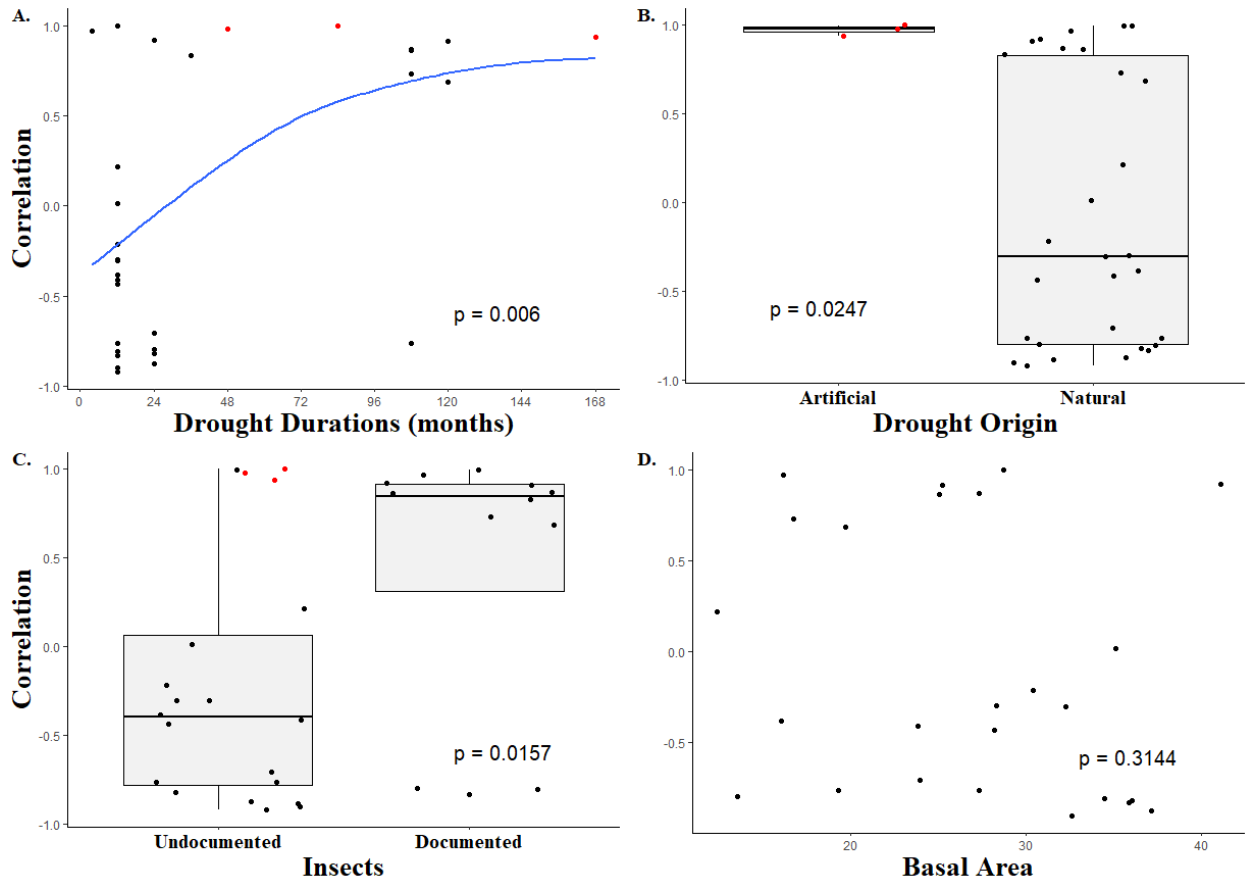


Figure 4. The heterogeneity in correlation between tree size and mortality with drought duration (A), drought origin (B), insects documented/undocumented (C), and basal area (D). Red points are artificial droughts, and black points are natural droughts on all figures.

Discussion

The significant heterogeneity in the correlation between tree size and drought-induced mortality across studies

Based on a range of studies around the world, we showed significant heterogeneity in the correlation between tree size and mortality during drought. Bennett *et al.* (2015) showed positive correlations between DBH and mortality in 65% of the droughts examined in their study, but this value dropped to 47% in our analysis that

contained more recent studies. Our analysis is based on studies from different locations that were globally distributed, but heterogeneity can even be found at regional or local scale. For example, Esquivel-Muelbert *et al.* (2020) showed a negative correlation (or decreasing mortality risk with tree size) in Western and Southern Amazon but a positive one in East-Central Amazonia. Floyd *et al.* (2009) showed a positive correlation across three piñon (*Pinus edulis*) stands, but a negative correlation in a juniper (*Juniperus monosperma*) stand in the southwestern USA. The significant heterogeneity suggests that the relationship between tree size and mortality depends on a wide range of contributing factors.

The correlation between tree size and mortality switched from negative to positive with increasing drought duration

Our analysis showed that the longer a drought persisted the more likely larger trees are to suffer higher mortality rates. With generally greater rooting depth, larger trees can more readily access deeper soil water, but deep soil water tends to become depleted during long droughts and can only be replenished by large precipitation events (Liang *et al.*, 2021). Thus, the effect of deep soil water potentially leads to the drought-duration effect, characterized by increased mortality of larger trees under longer droughts. In addition, prolonged droughts alter composition of soil microbial communities, further increasing plant drought vulnerability (Santos-Medellín, 2021). Moreover, large trees tend to store more carbon, e.g., higher total content of non-structural carbohydrates (Sala & Hoch, 2009; Niinemets, 2010). Therefore, the greater mortality of large trees during extended droughts identified in our study provides more support that drought-caused tree mortality is more likely due to hydraulic failure rather than carbon starvation (Hartman

2013, Adams et al., 2017). Overall, our study ultimately showed that larger trees are initially more resistant to droughts. However, once soil moisture becomes severely depleted, their larger size becomes a hindrance. Thus, different drought modes (e.g., short vs. long droughts) likely cause contrasting structural changes in forests. The effect of drought duration identified by our study could improve projections of drought impacts on forest dynamics (Hartmann 2022).

The correlation was positive when insects were documented under drought but reversed when they were not documented

Insects are a major causal mechanism of tree mortality during drought (Canelles et al., 2021). We found that studies documenting insect-associated tree mortality under drought showed more positive correlations between tree size and mortality. This observation aligns with other studies' findings that insects preferentially attack larger trees (Bennett et al., 2015). While the large tree preference may not be applied to all insect species (Stephenson et al., 2019), there are several possible reasons insects may prefer larger trees over smaller ones: (1) Larger trees generally have thicker bark that is better for overwintering adults (Fettig et al., 2019; Restaino et al., 2019); (2) Beetles usually prefer attacking more hydraulically stressed trees because their defense mechanisms are compromised (Netherer et al., 2015; Canelles et al., 2021, McDowell 2022), and the compromised defense mechanisms tend to occur in large trees during drought owing to their vulnerable hydraulic structure (Gaylord et al., 2013; Fettig et al., 2019). Therefore, the presence of bark beetles and other insects could affect distributions of tree size under drought. Moreover, with increasing insect-induced tree mortality under warming climate (Jaime et al., 2022; Robbins et al., 2022), considering the insect effects

could improve ecosystem models of carbon dynamics, given that large trees are crucial contributors to carbon storage (Lutz *et al.*, 2018) and efflux (Rowland *et al.*, 2018).

Artificial drought experiments had more positive correlation values than natural droughts

Our analysis found that the correlation between tree size and mortality was positive from studies based on experiments with artificial drought (e.g., throughfall exclusion), but there were only three such studies included in the analysis. A possible reason for the greater mortality rates of larger trees in the artificial drought-based studies is the longer drought duration of these studies, i.e., average 100 months in these studies compared with 36 months on average in the natural drought studies. The above results are in line with that larger trees suffer more with longer droughts. For example, one throughfall exclusion experiment lasted seven years and showed a considerably larger increase in relative tree mortality for larger trees than in smaller trees over the last four years compared to the first three (da Costa *et al.*, 2010). Therefore, future artificial drought-based studies could diversify their drought treatments to capture more impacts caused by drought. Additionally, it is challenging to simulate multivariate environmental changes associated with drought, such as vapor pressure deficit and hotter temperatures, contributing to a lack of tree mortality characterized by specific tree sizes (Meir *et al.*, 2018, Hammond *et al.* 2022). To accurately simulate drought events, many factors need to be altered and measured (heat stress, soil water deficit, solar radiation, etc.); however, these measurements could be both difficult and cost-prohibitive to manage for large-scale studies (Marchin *et al.*, 2020). Given our literature search, there have been relatively few large-scale artificial drought-based studies, particularly for ones considering tree size

effects. Meanwhile, more studies are needed to investigate comparisons between artificial versus natural droughts and to ensure that artificial droughts accurately represent natural droughts of all types.

There was no correlation between tree size and mortality with increasing basal area

Notably, our analysis found that there was no significant effect of basal area on the correlation. We hypothesized more positive correlations at higher basal areas given that greater basal area could increase competition for water resources (Olson *et al.*, 2018; Andrews *et al.*, 2020) causing more stress on large trees due to their vulnerable hydraulic structures. The non-significant effect of basal area suggests that, in addition to competition for water, other environmental conditions are modified by basal area. For example, increasing basal area could decrease light availability for small trees due to greater canopy development and that may increase their mortality (Iida *et al.*, 2014). Thus, the changes in both water competition and light availability may interact.

Conclusion

Compared with Bennett *et al.* (2015), our analysis showed less dominance of positive correlation between tree size and drought-related mortality. Moreover, we identified important factors driving correlation heterogeneity, including drought duration, drought origin, and insect documentation. With increasing data availability, future studies could explore other potential factors, such as soil conditions (depth, texture, etc.), plant functional traits, and disturbance history (Suarez *et al.*, 2004). In addition to tree-size caused changes in plant hydraulics, several functional traits (e.g., wood density, specific leaf area) could affect plant drought vulnerability (Greenwood *et al.*, 2017), and these

traits could vary with tree height via light environment and genetic factors (Reich, 2000). Another factor that needs to be assessed in the future is hotter droughts. Hotter droughts are often associated with increased tree mortality and there is evidence that droughts are getting hotter on average as time progresses (Allen *et al.*, 2010, Alizadeh *et al.*, 2020, Hammond *et al.*, 2022). This could further alter the relationship between tree size and drought-induced mortality because insect-driven mortality may be amplified by the warmer temperatures (Anderegg *et al.*, 2015) and higher temperatures can inhibit tree defenses due to the increased maintenance costs taking carbon from resin production (Allen *et al.*, 2010).

CHAPTER III

A META-ANALYSIS EXAMINING THE RELATIONSHIP BETWEEN STAND STRUCTURAL DIVERSITY AND FOREST PRODUCTIVITY

Introduction

Climate change is amplifying drought events and creating harsher temperature patterns leading to losses in forest productivity globally (Bradford *et al.*, 2020; Senf *et al.*, 2020; Hammond *et al.*, 2022). These productivity losses could be mitigated by management practices manipulating critical stand attributes, e.g., reducing stand density by thinning (Sohn *et al.*, 2016). Thinning and other management practices could also modify stand structural diversity (SSD), defined as the intra-stand variation in tree stem or canopy size (Palik *et al.*, 2021), which has been shown to be an effective predictor of forest productivity in a broad range of forest types, from tropical to boreal forests (Gough *et al.*, 2019; Larue *et al.*, 2019; Ullah *et al.*, 2021). However, the previous studies report both negative and positive relationships between SSD and forest productivity resulting in critical uncertainty in the understanding of forest dynamics from a forest structure perspective.

The relationship between SSD and forest productivity arises because SSD influences availability of critical growth resources, including light and soil resources. As SSD increases, it may have different effects on light availability and the various components of forest productivity, e.g., growth of existing trees and ingrowth of new trees. Structurally diverse forests tend to have multilayered canopies (Dănescu *et al.*, 2016; Gough *et al.*, 2019), which could increase light interception (Atkins *et al.*, 2018) and growth of individual trees. At the stand level, light penetration to the understory may increase with greater SSD due to light penetrating through gaps caused by height differences in the structurally diverse forest (Rissanen *et al.*, 2019), potentially enhancing ingrowth and growth of understories. However, homogenizing forest structure by reducing SSD is currently the most common forest management strategy used to maximize potential productivity (Puettmann *et al.*, 2015), e.g., pine plantations in the southeastern U.S.A. The availability of soil resources could increase with greater SSD because there is improved niche partitioning for belowground resources among different-sized trees due to their access to resources at different soil depths (Forrester, 2019), e.g., larger trees often have more access to deeper soil layers (Giardina *et al.*, 2018). In addition, the access to deep soil water of large trees could benefit their neighboring small trees by hydraulic redistribution (Prieto *et al.*, 2012). This enhanced niche partitioning and hydraulic redistribution with greater SSD are expected to improve forest recruitment and growth (Palik *et al.*, 2021). The above variation in the effects of structural diversity suggests there is heterogeneity in the relationship between SSD and forest productivity. However, the heterogeneity has not been rigorously quantified, and drivers of the

heterogeneity have not been thoroughly examined, leading to critical knowledge gaps in understanding forest dynamics and impacts of structural diversity.

The relationship between SSD and productivity may be confounded by a range of abiotic and biotic factors, such as basal area, mean tree size, drought, and temperature. The average tree size of stands can influence the SSD-productivity relationship, given that greater SSD in taller stands may allow the canopy to have more vertical stratification, causing greater light interception (Zeller & Pretzsch, 2019) and resulting in enhanced forest growth, particularly for dominant trees which tend to contribute more to forest productivity than the others (Ali *et al.*, 2019). Moreover, greater basal areas are expected to increase total stand light interception, given that greater basal areas may decrease the gaps caused by height differences in structurally diverse forests. As a result, greater basal areas likely to enhance forest productivity with greater SSD, i.e., more positive SSD-productivity relationship with greater basal areas. (Wang *et al.*, 2011; Ali, 2019).

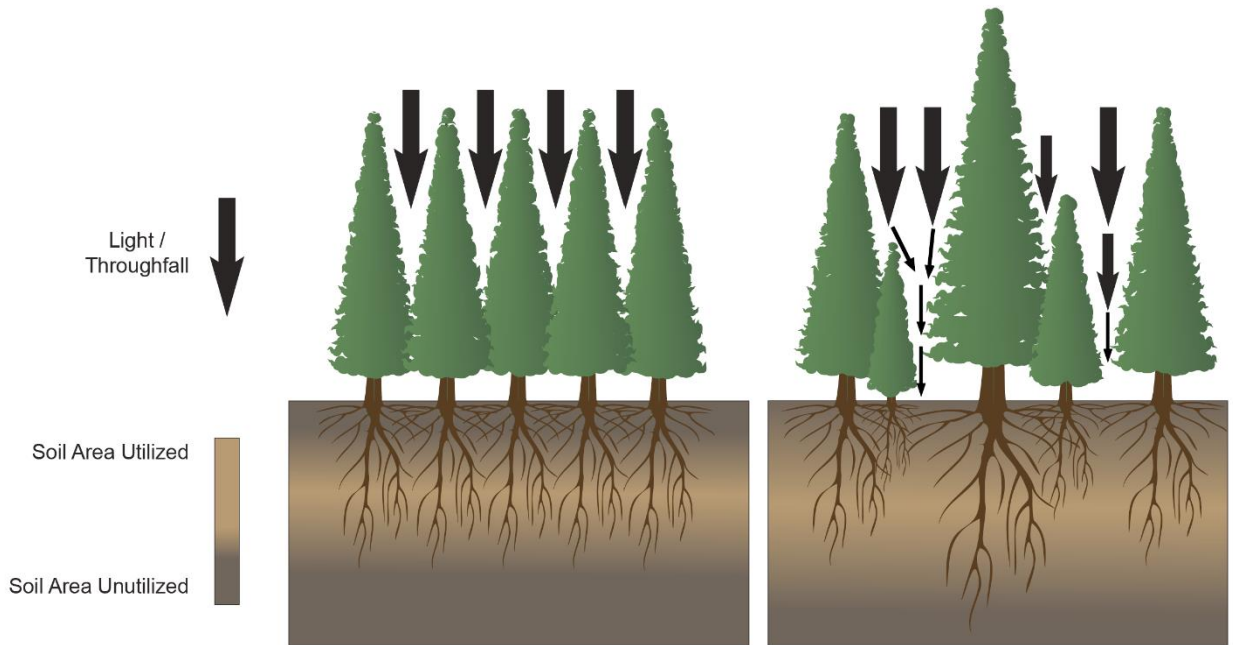


Figure 5. Conceptual figure showing a simplified comparison of a stand with low SSD (left) and one with high SSD (right). Stands with more structural diversity will have more light penetration to the understory and greater variance in rooting depths, reducing competition for vital resources. The varied rooting depths of the high SSD stand will allow for a greater use of available soil water and nutrients from all soil layers.

We also examined two abiotic factors that potentially affect the relationship between SSD and productivity: average max temperatures and drought intensity. Warmer average temperatures, usually caused by increased solar radiation, may allow for more functioning leaf area and layered canopies, contributing to greater productivity (Harms *et al.*, 2000; Park *et al.*, 2019). Thus, with warmer temperature, the SSD-productivity relationship is hypothesized to be more positive. Plant drought stress may be partially mitigated by greater SSD due to shading effects, soil water competition, and hydraulic redistribution. Understory trees in stands with higher SSD may be shaded by the trees in the dominant canopy layer that may decrease temperature within the canopy, contributing to less leaf-to-air vapor pressure deficit (VPD) and related transpiration and relieving drought stress (Grote *et al.*, 2016; Pretzsch *et al.*, 2022). Additionally, large trees may be able to lift up water from deeper soil layers to aid smaller trees whose roots are mostly

located in the shallower, drier layers (Forrester, 2019). The increased variation in rooting depths resulting from increased SSD will also reduce competition for soil water, which decreases losses in productivity during drought (Schwendenmann *et al.*, 2015; Ammer, 2019). Thus, the SSD-productivity relationship is hypothesized to be more positive with increasing drought magnitude.

The relationship between SSD and productivity is complex and could be context dependent, suggesting that there are factors altering the correlation, e.g., ones related to climate, structure, and species composition (Park *et al.*, 2019). Identifying how these factors interact is vital to improving the understanding of how SSD affects forest productivity and informing forest management from a structural perspective. To understand the complex relationship between SSD and productivity, we reviewed 850 papers from a literature search based on multiple keyword combinations. We filtered these papers and extracted measures of SSD, productivity, average tree size, basal area, average max temperatures, and climatic water deficit (CWD). We conducted a meta-analysis to quantify the significance of heterogeneity in the relationship between SSD and productivity. Using measures of these potentially confounding factors, we conducted a meta-regression analysis to test our hypothesis that correlations between SSD and productivity significantly vary with average tree size, basal area, monthly average max temperatures, and drought magnitude.

Methods

Data compilation

The data used in this meta-analysis were collected from research studies published before 2022 that reported SSD effects of forest productivity. For this meta-analysis, we searched the Scopus database using keywords: ("carbon sequestration" OR biomass OR productivity OR growth) AND (forest OR tree OR woody OR shrub) AND ("Size complexity" OR "Structur* complexity" OR "Size diversity" OR "Structur* diversity" OR "Size variation" OR "Structur* variation" OR "Size variability" OR "Structur* variability" OR "Size inequality" OR "Structur* inequality" OR "Size heterogeneity" OR "Structur* heterogeneity" OR "Size hierarchy" OR "Structur* hierarchy" OR "Size uniformity" OR "Structur* uniformity" OR "heterogeneity of stand structure"). Note that "Structur*" represents any words starting with "Structur". This search produced 850 articles that contained the above keywords in their titles, abstracts, or listed keywords. These articles were further filtered by reading through their titles and abstracts to ensure that selected studies cover the relationship between SSD and productivity. Then, the remaining studies (n = 262) were refined further by reading their methods and results to ensure that they contained the necessary data for this meta-analysis. For a study to be included in the meta-analysis, it needed to include: (a) SSD measurements; (b) productivity measurements; (c) sample sizes (or plot sizes) of each forest. Following that process, we included 11 articles which reported 22 correlations between SSD and productivity. The measurements occurred at 11 unique locations (Fig. 6), covering different ecoregions and forest types. The data of SSD and forest productivity, and sample sizes were either directly stated in the study or extracted from figures using the ImageJ program (<https://imagej.nih.gov/ij/>) to measure the lengths of bar graphs (or other graph types).

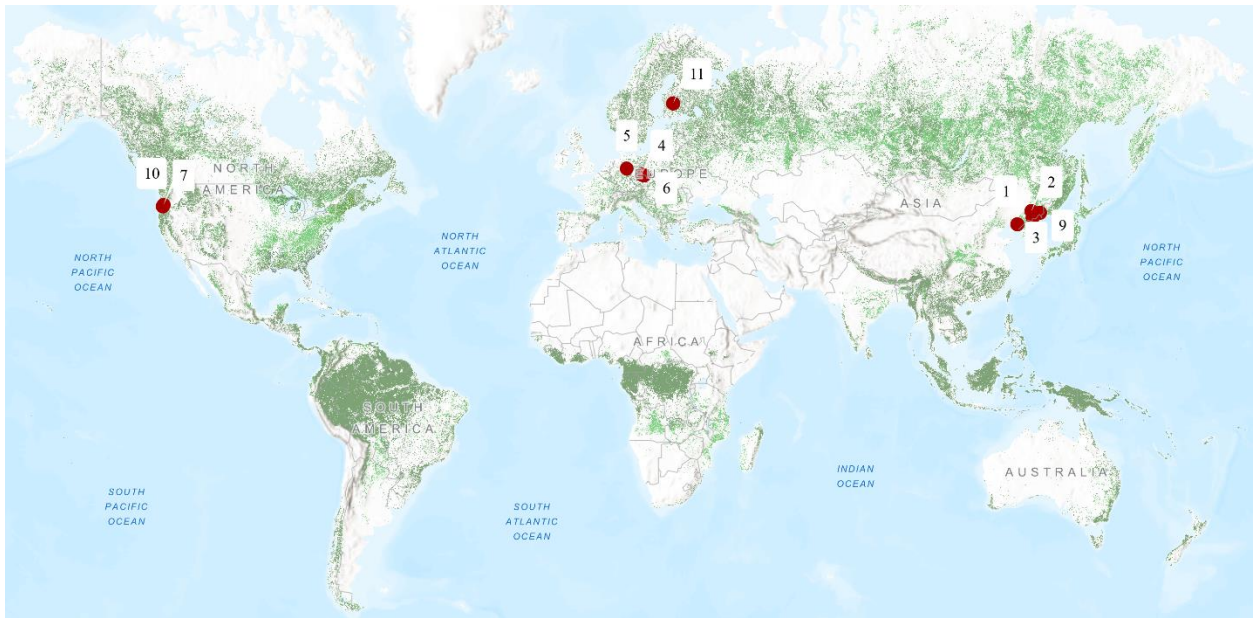


Figure 6. Locations of studies used in the meta-analysis. Each numbered point represents a drought observation. The plot numbers and their matching studies are listed in Table S1. Some studies occurred in different stands at the same location.

The basal area and tree size (i.e., mean stand diameter at breast height, DBH) data were extracted directly from either the text or tables of each study. For CWD and average max temperature, location data was taken from the study for each forest in the form of coordinates. Then the location data was used to extract the climate data for the duration of the study from the TerraClimate database (Abatzoglou *et al.*, 2018).

Statistical Analysis

To examine the correlation between SSD and forest productivity, we quantified the effect size of the meta-analysis using the Pearson Product-Moment Correlation method (Harrer *et al.*, 2021). The correlation value of each study was calculated by a linear regression model. Note that some papers reported the correlations for multiple measures of SSD, such as height variation and DBH variation, these correlations were treated separately. Positive correlation values meant that increased SSD had a positive effect on forest productivity, and negative correlations meant the opposite. The

correlation values, along with the sample sizes, for each study were then used to run the meta-analysis to examine heterogeneity of the correlation among the studies. We used a random-effects model for our meta-analysis because a considerable amount of between-study heterogeneity was expected based on the results of previous studies. The Sidik-Jonkman (“SJ”) estimator was used to measure tau-squared (τ^2), which is the variance of the distribution of true effect sizes (Sidik & Jonkman, 2005). A Fischer’s z transformation was conducted when running the meta-analysis to ensure that the sampling distribution was approximately normal. We tested for publication bias in the meta-analysis, which results from selective publication of studies with more significant findings, using Egger’s test and checking the funnel plot. As described above, we collected data of factors potentially contributing to heterogeneity of the correlation between SSD and productivity including species richness, mean tree size, basal area, CWD, monthly average max temperatures. Additionally, each stand included was classified into a forest ecozone using the FAO world ecozones map (FAO, 2010). There were three different ecozones included in this study, all were a form of temperate forest. The effects of these factors were quantified by a meta-regression analysis given the heterogeneity in the effect size and random effects across the studies. The analyses were conducted using the “meta” R package (Schwarzer, 2020).

Results

Heterogeneity in the correlation between SSD and productivity

The correlations between SSD and productivity varied from negative to positive values among different studies resulting in significant heterogeneity in the correlation ($p < 0.001$). The 95% confidence interval (CI) of each correlation is also reported in Fig. 7 and shows the variation in results.

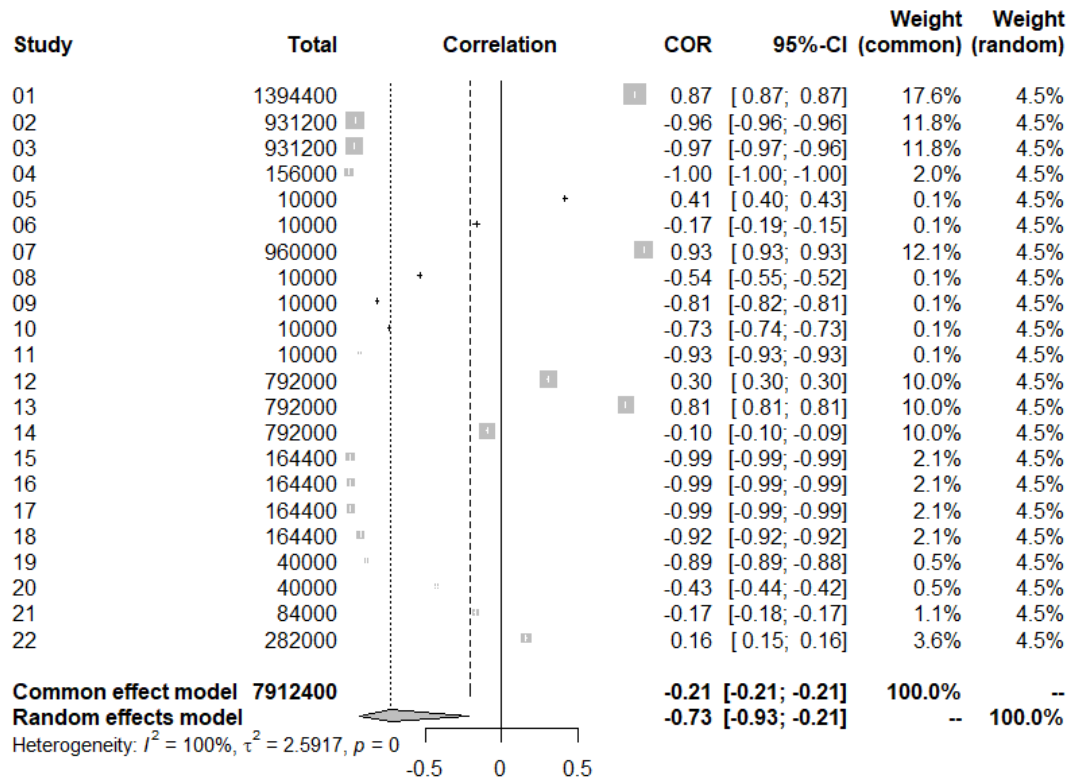


Figure 7. The “forest” plot showing correlation between SSD and productivity from different observations. Note that the last row shows a statistical test of the heterogeneity in the correlation among these studies.

Effects of basal area, mean DBH, temperature, and drought intensity

The results showed that basal area ($p = 0.027$), mean DBH ($p = 0.0017$), average max temperature ($p = 0.0086$), and CWD ($p = 0.015$) had significant effects on the correlation between SSD and productivity. With all four of these factors, the correlation changed from negative to positive with increasing values of the predictor variables (Fig. 8). Therefore, SSD had a positive effect only in stands with relatively large basal area, average tree size, average max temperatures, and drought intensity.

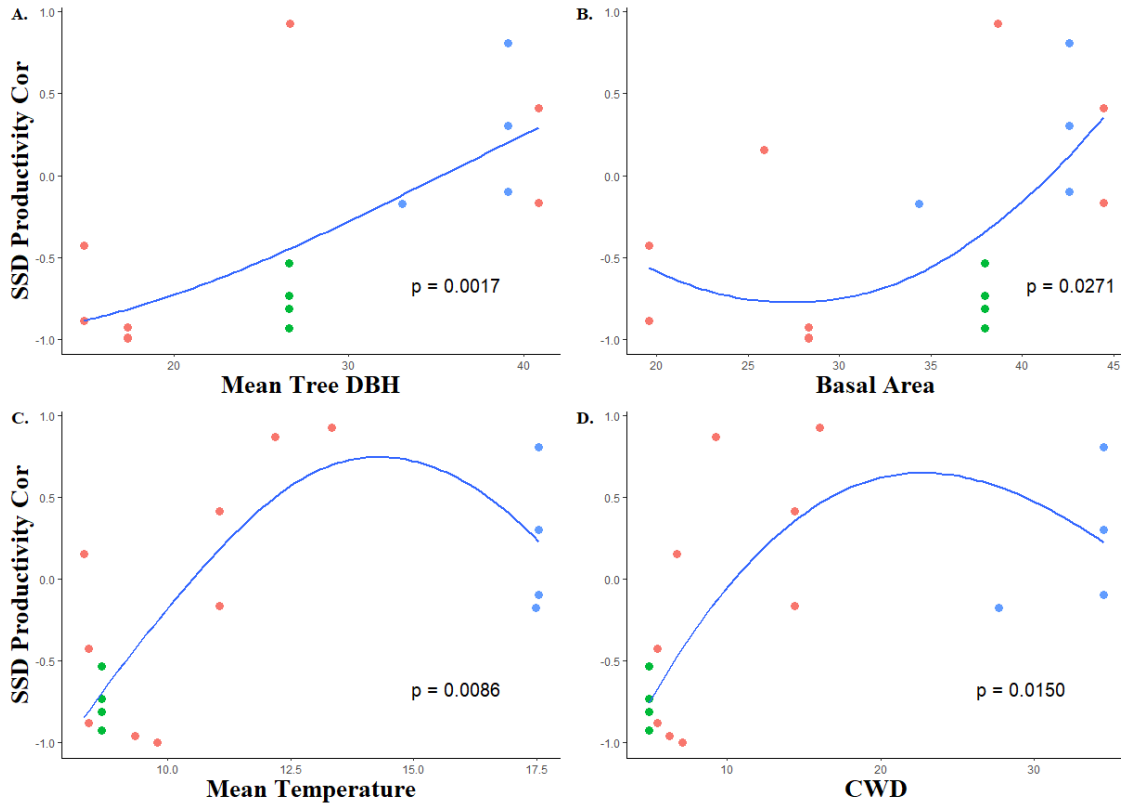


Figure 8. The heterogeneity in correlation between SSD and productivity with mean tree DBH (A), basal area (B), mean monthly max temperatures (C), and climatic water deficit (D). Point colors represent the forest ecozone where red = temperate continental forests, green = temperate mountain systems, and blue = temperate oceanic forests.

Discussion

The SSD-productivity correlation switched from negative to positive with increasing basal area

Our analysis showed that greater SSD enhanced forest productivity in stands with very high basal areas. Very high basal areas can affect productivity negatively with increasing competition and positively with increasing stand-level light interception. The positive effects may be more important than the others in forests with greater SSD because greater SSD could alleviate the competition by promoting complementary

resource utilization within a stand (Ishii *et al.*, 2004). In addition, with increased light interception, the light penetrated through canopy gaps due to size differences between neighboring trees would be better used to enhance productivity of structurally diverse forests (Ali, 2019). The effects of basal area on the SSD-productivity relationship may also stem from distribution of tree size in a stand. When comparing two stands with similarly high basal areas but different SSD, the stand with greater SSD is likely to have a few larger trees accounting for most of the basal area (Ali *et al.*, 2019). Whereas in the stand with lower SSD, the basal area tends to be made up of many similar sized trees growing more closely together. In this situation, the higher SSD stand may be more productive because the few larger trees could provide more productivity than the larger number of smaller trees (Stephenson *et al.*, 2014; Lutz *et al.*, 2018).

The correlation switched from negative to positive with increasing average tree size

Our analysis showed that with larger average tree sizes, forest productivity is more likely to benefit from increased SSD. With a taller canopy, there is greater vertical stratification that enables light to be used more efficiently (Zeller & Pretzsch, 2019). The greater vertical stratification combined with increased SSD leads to a larger overall canopy area, contributing to more light interception and greater productivity (Rissanen *et al.*, 2019). It has also been shown that the largest 1% of trees in a forest contribute to a majority of carbon storage and productivity, so the presence of extremely large trees in a structurally diverse stand would lead to increased productivity even if the remaining trees are much smaller (Stephenson *et al.*, 2014; Lutz *et al.*, 2018; Ali *et al.*, 2019).

Additionally, in younger and shorter stands, the smallest trees that are contributing to the SSD are generally expected to be more inefficient with their light and nutrient use, and

the benefits that could potentially be provided by increasing SSD would not be applicable to these stands with shorter canopy height (Zeller & Pretzsch, 2019). Thus, consistent with local studies, e.g., central Europe (Zeller & Pretzsch, 2019), our results used global-distributed data to further support that SSD is more beneficial to productivity of taller stands.

The correlation switched from negative to positive with increasing average max temperatures

Our analysis showed that the SSD-productivity relationship was more positive with increasing temperature. At a global level, higher temperatures come along with greater solar radiations which enable more complex canopy structures since more sunlight is able to penetrate to lower canopy layers (Harms *et al.*, 2000). Moreover, temperatures could become too extreme causing stress on plant growth. As discussed above, the high radiation or drought stress could be alleviated by greater SSD, due to the potentially improved shading effects and niche partitioning to increase availability and sharing efficiency of resources in structurally diverse forests (Grote *et al.*, 2016; Zellweger *et al.*, 2020; Pretzsch *et al.*, 2022).

The correlation switched from negative to positive with increasing CWD

Our analysis showed that SSD was more beneficial to productivity when stands are more stressed by drought. When water is limited, stands with higher SSD could better utilize the available water because of their varying rooting depths (Schwendenmann *et al.*, 2015; Ammer, 2019). Additionally, large trees could mitigate drought stress of their neighboring small trees by lifting water from deep soil layers to shallower drier layers

(Forrester, 2019). Layered canopies caused by increased SSD could shade understory trees to reduce radiation, leading to decreased water loss and drought stress (Grote *et al.*, 2016; Zellweger *et al.*, 2020; Pretzsch *et al.*, 2022). Therefore, forest management based on SSD could be an adaptive strategy to sustain forest productivity in response to increasing drought with climate change (Pretzsch *et al.*, 2022).

Conclusion

Our analysis showed significant heterogeneity in the SSD-productivity relationship. We also identified potential drivers of the heterogeneity given the variation in the relationship with mean tree size, basal area, temperature, and drought. Our results suggest that SSD could be another stand attribute considered in forest management to achieve resource sustainability under climate change, but the SSD effects tend to be context dependent. In addition, although the relationship between biodiversity and productivity is widely studied, structural diversity has not been well investigated as another biodiversity metric given the relatively small sample size of our meta-analysis. As more data becomes available about structural diversity effects on productivity, there are more potential factors that need to be examined, and some of them have been shown to affect the SSD-productivity relationship in local studies, e.g., functional identity (Cao *et al.*, 2022).

CHAPTER IV

CONCLUSION

Both of my analyses showed significant heterogeneity across the relationships they were investigating. For the tree size-mortality relationship the strongest drivers of heterogeneity were drought length and insect presence, where longer droughts and the presence of insects both lead to higher mortality rates in larger trees. This increased mortality of larger trees may result in shorter forests in general given longer droughts and increased insect outbreaks under climate change. In the SSD-productivity relationship mean tree size, basal area, species richness, temperature, and drought were identified as potential drivers of heterogeneity. SSD has shown that it could be a critical stand attribute to consider in forest management to achieve resource sustainability in the future. Overall, results from these two studies suggest that tree size and forest structure effects on forest dynamics are both complex and context dependent. In the end, there is no “one-size-fits-all” forest model or management strategy that can be applied to all forests. Instead, it is important to have a full understanding of how biotic and abiotic factors can alter how individual forests will react to drought, warmer temperatures, and other disturbances in

the future. Without an understanding of these interactions, it may be impossible to accurately predict how forest dynamics may shift as the climate changes.

REFERENCES

- Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. 2018. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. *Scientific Data*, 5.
- Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD, et al. 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology and Evolution* 1(9): 1285-1291.
- Ali A. 2019. Forest stand structure and functioning: Current knowledge and future challenges. *Ecological Indicators* 98: 665-677.
- Ali A, Lin SL, He JK, Kong FM, Yu JH, Jiang HS. 2019. Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests. *Global Change Biology* 25(8): 2810-2824.
- Ali A, Lohbeck M, Yan ER. 2018. Forest strata-dependent functional evenness explains whole-community aboveground biomass through opposing mechanisms. *Forest Ecology and Management* 424: 439-447.
- Ali A, Wang L-Q. 2021. Big-sized trees and forest functioning: Current knowledge and future perspectives. *Ecological Indicators* 127: 107760.
- Alizadeh MR, Adamowski J, Nikoo MR, AghaKouchak A, Dennison P, Sadegh M. 2020. A century of observations reveals increasing likelihood of continental-scale compound dry-hot extremes. *Science Advances* 6(39).
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660-684.
- Ammer C. 2019. Diversity and forest productivity in a changing climate. *New Phytologist* 221(1): 50-66.

- Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N, et al. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* 208(3): 674-683.
- Andrews CM, D'Amato AW, Fraver S, Palik B, Battaglia MA, Bradford JB. 2020. Low stand density moderates growth declines during hot droughts in semi-arid forests. *Journal of Applied Ecology* 57(6): 1089-1102.
- Atkins JW, Fahey RT, Hardiman BH, Gough CM. 2018. Forest Canopy Structural Complexity and Light Absorption Relationships at the Subcontinental Scale. *Journal of Geophysical Research: Biogeosciences* 123(4): 1387-1405.
- Bennett, A., McDowell, N., Allen, C. et al. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* 1, 15139.
- Bohner T, Diez J. 2021. Tree resistance and recovery from drought mediated by multiple abiotic and biotic processes across a large geographic gradient. *Science of the Total Environment* 789.
- Bourdier T, Cordonnier T, Kunstler G, Piedallu C, Lagarrigues G, Courbaud B. 2016. Tree size inequality reduces forest productivity: An analysis combining inventory data for ten European species and a light competition model. *PLoS ONE* 11(3).
- Bradford JB, Schlaepfer DR, Lauenroth WK, Palmquist KA. 2020. Robust ecological drought projections for drylands in the 21st century. *Global Change Biology* 26(7): 3906-3919.
- Bradford JB, Shriver RK, Robles MD, McCauley LA, Woolley TJ, Andrews CA, Crimmins M, Bell DM. 2022. Tree mortality response to drought-density interactions suggests opportunities to enhance drought resistance. *Journal of Applied Ecology* 59(2): 549-559.
- Brodribb TJ, Powers J, Cochard H, Choat B. 2020. Hanging by a thread? Forests and drought. *Science* 368(6488): 261-266.
- Canelles Q, Aquilué N, James PMA, Lawler J, Brotons L. 2021. Global review on interactions between insect pests and other forest disturbances. *Landscape Ecology* 36(4): 945-972.
- Cao J, Liu H, Zhao B, Peng R, Liang B, Anenkhonov OA, Korolyuk AY, Sandanov DV. 2022. Mixed forest suffered less drought stress than pure forest in southern Siberia. *Agricultural and Forest Meteorology* 325.

- Chitra-Tarak R, Ruiz L, Dattaraja HS, Mohan Kumar MS, Riotte J, Suresh HS, McMahon SM, Sukumar R. 2018. The roots of the drought: Hydrology and water uptake strategies mediate forest-wide demographic response to precipitation. *Journal of Ecology* 106(4): 1495-1507.
- Chitra-Tarak R, Xu C, Aguilar S, Anderson-Teixeira KJ, Chambers J, Detto M, Faybishenko B, Fisher RA, Knox RG, Koven CD, et al. 2021. Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist* 231(5): 1798-1813.
- Clark JS, Andrus R, Aubry-Kientz M, Bergeron Y, Bogdziewicz M, Bragg DC, Brockway D, Cleavitt NL, Cohen S, Courbaud B, et al. 2021. Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications* 12(1): 1242.
- da Costa ACL, Galbraith D, Almeida S, Portela BTT, da Costa M, de Athaydes Silva Junior J, Braga AP, de Gonçalves PHL, de Oliveira AA, Fisher R, et al. 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist* 187(3): 579-591.
- Dănescu A, Albrecht AT, Bauhus J. 2016. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. *Oecologia* 182(2): 319-333.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, et al. 2016. The global spectrum of plant form and function. *Nature* 529(7585): 167-171.
- Ding Y, Nie Y, Chen H, Wang K, Querejeta JI. 2021. Water uptake depth is coordinated with leaf water potential, water-use efficiency and drought vulnerability in karst vegetation. *New Phytologist* 229(3): 1339-1353.
- Drever CR, Peterson G, Messier C, Bergeron Y, Flannigan M. 2006. Can forest management based on natural disturbances maintain ecological resilience? *Canadian Journal of Forest Research* 36(9): 2285-2299.
- Esquivel-Muelbert A, Phillips OL, Brienens RJW, Fauset S, Sullivan MJP, Baker TR, Chao K-J, Feldpausch TR, Gloor E, Higuchi N, et al. 2020. Tree mode of death and mortality risk factors across Amazon forests. *Nature Communications* 11(1): 5515.
- Fajardo A, Martínez-Pérez C, Cervantes-Alcayde MA, Olson ME. 2020. Stem length, not climate, controls vessel diameter in two tree species across a sharp precipitation gradient. *New Phytologist* 225(6): 2347-2355.

- Fajardo A, McIntire EJB, Olson ME. 2019. When Short Stature Is an Asset in Trees. *Trends in Ecology and Evolution* 34(3): 193-199.
- FAO 2010. World Ecozones.
- Fargione JE, Bassett S, Boucher T, Bridgham SD, Conant RT, Cook-Patton SC, Ellis PW, Falcucci A, Fourqurean JW, Gopalakrishna T, et al. 2018. Natural climate solutions for the United States. *Science Advances* 4(11).
- Feng G, Zhang J, Girardello M, Pellissier V, Svenning J-C. 2020. Forest canopy height co-determines taxonomic and functional richness, but not functional dispersion of mammals and birds globally. *Global Ecology and Biogeography* 29(8): 1350-1359.
- Fettig CJ, Mortenson LA, Bulaon BM, Foulk PB. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *Forest Ecology and Management* 432: 164-178.
- Floyd ML, Clifford M, Cobb NS, Hanna D, Delph R, Ford P, Turner D. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon - Juniper woodlands. *Ecological Applications* 19(5): 1223-1230.
- Forrester DI. 2019. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. *Forest Ecology and Management* 447: 139-157.
- Gao J, Zhang L, Tang Z, Wu S. 2019. A synthesis of ecosystem aboveground productivity and its process variables under simulated drought stress. *Journal of Ecology* 107(6): 2519-2531.
- Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yezzer EA, Macalady AK, Pangle RE, McDowell NG. 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytologist* 198(2): 567-578.
- Giardina F, Konings AG, Kennedy D, Alemohammad SH, Oliveira RS, Uriarte M, Gentile P. 2018. Tall Amazonian forests are less sensitive to precipitation variability. *Nature Geoscience* 11(6): 405-409.
- Gora EM, Esquivel-Muelbert A. 2021. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nature Plants* 7(4): 384-391.
- Gore, Madison, Bijesh Mishra, and Omkar Joshi. 2022. Economic Contribution of Forest Sector in Oklahoma in 2020. Oklahoma Cooperative Extension Service. Print.
- Gough CM, Atkins JW, Fahey RT, Hardiman BS. 2019. High rates of primary production in structurally complex forests. *Ecology* 100(10).

- Greenwood S, Ruiz-Benito P, Martínez-Vilalta J, Lloret F, Kitzberger T, Allen CD, Fensham R, Laughlin DC, Kattge J, Bönisch G, et al. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters* 20(4): 539-553.
- Grote R, Gessler A, Hommel R, Poschenrieder W, Priesack E. 2016. Importance of tree height and social position for drought-related stress on tree growth and mortality. *Trees - Structure and Function* 30(5): 1467-1482.
- Guillemot J, Martin-StPaul NK, Bulascoschi L, Poorter L, Morin X, Pinho BX, le Maire G, R. L. Bittencourt P, Oliveira RS, Bongers F, et al. 2022. Small and slow is safe: On the drought tolerance of tropical tree species. *Global Change Biology* 28(8): 2622-2638.
- Hammond WM, Williams AP, Abatzoglou JT, Adams HD, Klein T, López R, Sáenz-Romero C, Hartmann H, Breshears DD, Allen CD. 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications* 13(1).
- Harms WR, Whitesell CD, DeBell DS. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. *Forest Ecology and Management* 126(1): 13-24.
- Harrer M, Cuijpers P, Furukawa TA, Ebert DD. 2021. *Doing Meta-Analysis With R: A Hands-On Guide*. Boca Raton, FL and London: Chapman & Hall/CRC Press.
- Hartmann H, Ziegler W, Kolle O, Trumbore S. 2013. Thirst beats hunger - declining hydration during drought prevents carbon starvation in Norway spruce saplings. *New Phytologist* 200(2): 340-349.
- Hartmann H, Bastos A, Das AJ, Esquivel-Muelbert A, Hammond WM, Martínez-Vilalta J, McDowell NG, Powers JS, Pugh TAM, Ruthrof KX, et al. 2022. Climate Change Risks to Global Forest Health: Emergence of Unexpected Events of Elevated Tree Mortality Worldwide. *Annual Review of Plant Biology* 73: 673-702.
- Iida Y, Poorter L, Sterck F, Kassim AR, Potts MD, Kubo T, Kohyama TS. 2014. Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. *Ecology* 95(2): 353-363.
- Ishii HT, Tanabe SI, Hiura T. 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science* 50(3): 342-355.
- Jaime L, Batllori E, Ferretti M, Lloret F. 2022. Climatic and stand drivers of forest resistance to recent bark beetle disturbance in European coniferous forests. *Global Change Biology* 28(8): 2830-2841.

- Koontz MJ, Latimer AM, Mortenson LA, Fettig CJ, North MP. 2021. Cross-scale interaction of host tree size and climatic water deficit governs bark beetle-induced tree mortality. *Nature Communications* 12(1): 129.
- Kovács B, Tinya F, Ódor P. 2017. Stand structural drivers of microclimate in mature temperate mixed forests. *Agricultural and Forest Meteorology* 234-235: 11-21.
- Larue EA, Hardiman BS, Elliott JM, Fei S. 2019. Structural diversity as a predictor of ecosystem function. *Environmental Research Letters* 14(11).
- Liang J, Buongiorno J, Monserud RA, Kruger EL, Zhou M. 2007. Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management* 243(1): 116-127.
- Liang M, Feng X, Gornish ES. 2021. Rainfall pulses mediate long-term plant community compositional dynamics in a semi-arid rangeland. *Journal of Applied Ecology* 58(4): 708-717.
- Lutz JA, Furniss TJ, Johnson DJ, Davies SJ, Allen D, Alonso A, Anderson-Teixeira KJ, Andrade A, Baltzer J, Becker KML, et al. 2018. Global importance of large-diameter trees. *Global Ecology and Biogeography* 27(7): 849-864.
- Marchin RM, Ossola A, Leishman MR, Ellsworth DS. 2020. A Simple Method for Simulating Drought Effects on Plants. *Frontiers in Plant Science* 10.
- Markalas S. 1992. Site and stand factors related to mortality rate in a fir forest after a combined incidence of drought and insect attack. *Forest Ecology and Management* 47(1-4): 367-374.
- McDowell NG, Allen CD. 2015. Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change* 5(7): 669-672.
- McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, Clark JS, Dietze M, Grossiord C, Hanbury-Brown A, et al. 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368(6494): eaaz9463.
- McDowell NG, Sapes G, Pivovarovoff A, Adams HD, Allen CD, Anderegg WRL, Arend M, Breshears DD, Brodribb T, Choat B, et al. 2022. Mechanisms of woody-plant mortality under rising drought, CO₂ and vapour pressure deficit. *Nature Reviews Earth and Environment* 3(5): 294-308.
- Meir P, Mencuccini M, Binks O, Da Costa AL, Ferreira L, Rowland L. 2018. Short-term effects of drought on tropical forest do not fully predict impacts of repeated or long-term drought: Gas exchange versus growth. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373(1760).

- Migliavacca M, Musavi T, Mahecha MD, Nelson JA, Knauer J, Baldocchi DD, Perez-Priego O, Christiansen R, Peters J, Anderson K, et al. 2021. The three major axes of terrestrial ecosystem function. *Nature* 598: 468-472.
- Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer J, Rosner S, Kikuta S, Schume H, et al. 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist* 205(3): 1128-1141.
- Niinemets Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* 260(10): 1623-1639.
- Olson ME, Soriano D, Rosell JA, Anfodillo T, Donoghue MJ, Edwards EJ, León-Gómez C, Dawson T, Julio Camarero Martínez J, Castorena M, et al. 2018. Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences of the United States of America* 115(29): 7551-7556.
- Palik BJ, D'Amato AW, Franklin JF, Johnson KN. 2021. *Managing for complexity, diversity, and heterogeneity in established stands Ecological silviculture: Foundations and applications*: Waveland Press.
- Park J, Kim HS, Jo HK, Jung B. 2019. The influence of tree structural and species diversity on temperate forest productivity and stability in Korea. *Forests* 10(12).
- Pretzsch H, Bravo-Oviedo A, Hilmers T, Ruiz-Peinado R, Coll L, Löf M, Ahmed S, Aldea J, Ammer C, Avdagić A, et al. 2022. With increasing site quality asymmetric competition and mortality reduces Scots pine (*Pinus sylvestris* L.) stand structuring across Europe. *Forest Ecology and Management* 520.
- Prieto I, Armas C, Pugnaire FI. 2012. Water release through plant roots: New insights into its consequences at the plant and ecosystem level. *New Phytologist* 193(4): 830-841.
- Puettmann KJ, Wilson SM, Baker SC, Donoso PJ, Drössler L, Amente G, Harvey BD, Knoke T, Lu Y, Nocentini S, et al. 2015. Silvicultural alternatives to conventional even-aged forest management - What limits global adoption? *Forest Ecosystems* 2(1).
- Reich PB. 2000. Do tall trees scale physiological heights? *Trends in Ecology and Evolution* 15(2): 41-42.
- Ren S, Yang Q, Liu H, Shen G, Zheng Z, Zhou S, Liang M, Yin H, Zhou Z, Wang X. 2021. The driving factors of subtropical mature forest productivity: Stand structure matters. *Forests* 12(8).

- Restaino C, Young DJN, Estes B, Gross S, Wuenschel A, Meyer M, Safford H. 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. *Ecological Applications* 29(4).
- Rissanen K, Martin-Guay MO, Riopel-Bouvier AS, Paquette A. 2019. Light interception in experimental forests affected by tree diversity and structural complexity of dominant canopy. *Agricultural and Forest Meteorology* 278.
- Robbins ZJ, Xu C, Aukema BH, Buotte PC, Chitra-Tarak R, Fettig CJ, Goulden ML, Goodsman DW, Hall AD, Koven CD, et al. 2022. Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California. *Global Change Biology* 28(2): 509-523.
- Rowland L, da Costa ACL, Oliveira AAR, Oliveira RS, Bittencourt PL, Costa PB, Giles AL, Sosa AI, Coughlin I, Godlee JL, et al. 2018. Drought stress and tree size determine stem CO₂ efflux in a tropical forest. *New Phytologist* 218(4): 1393-1405.
- Sala A, Hoch G. 2009. Height-related growth declines in ponderosa pine are not due to carbon limitation. *Plant, Cell and Environment* 32(1): 22-30.
- Santos-Medellín C, Liechty Z, Edwards J, Nguyen B, Huang B, Weimer BC, Sundaresan V. 2021. Prolonged drought imparts lasting compositional changes to the rice root microbiome. *Nature Plants* 7(8): 1065-1077.
- Sapijanskas J, Paquette A, Potvin C, Kunert N, Loreau M. 2014. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* 95(9): 2479-2492.
- Schwarzer G 2020. meta: General Package for Meta-Analysis, version 5.2-0. R package.
- Schwendenmann L, Pendall E, Sanchez-Bragado R, Kunert N, Hölscher D. 2015. Tree water uptake in a tropical plantation varying in tree diversity: Interspecific differences, seasonal shifts and complementarity. *Ecohydrology* 8(1): 1-12.
- Senf C, Buras A, Zang CS, Rammig A, Seidl R. 2020. Excess forest mortality is consistently linked to drought across Europe. *Nature Communications* 11(1).
- Sheil D, Burslem DF, Alder D. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83(2): 331-333.
- Sidik K, Jonkman JN. 2005. Simple heterogeneity variance estimation for meta-analysis. *Journal of the Royal Statistical Society. Series C: Applied Statistics* 54(2): 367-384.

- Slik JWF, Paoli G, McGuire K, Amaral I, Barroso J, Bastian M, Blanc L, Bongers F, Boundja P, Clark C, et al. 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography* 22(12): 1261-1271.
- Sohn JA, Saha S, Bauhus J. 2016. Potential of forest thinning to mitigate drought stress: A meta-analysis. *Forest Ecology and Management* 380: 261-273.
- Stephenson NL, Das AJ, Amperssee NJ, Bulaon BM, Yee JL. 2019. Which trees die during drought? The key role of insect host-tree selection. *Journal of Ecology* 107(5): 2383-2401.
- Stephenson NL, Das AJ, Condit R, Russo SE, Baker PJ, Beckman NG, Coomes DA, Lines ER, Morris WK, Rüger N, et al. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507(7490): 90-93.
- Stovall AEL, Shugart H, Yang X. 2019. Tree height explains mortality risk during an intense drought. *Nature Communications* 10(1): 4385.
- Suarez ML, Ghermandi L, Kitzberger T. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* - Site, climatic sensitivity and growth trends. *Journal of Ecology* 92(6): 954-966.
- Tai X, Mackay DS, Ewers BE, Parsekian AD, Beverly D, Speckman H, Brooks PD, Anderegg WRL. 2019. Plant hydraulic stress explained tree mortality and tree size explained beetle attack in a mixed conifer forest. *Journal of Geophysical Research: Biogeosciences* 124(11): 3555-3568.
- Trugman AT, Anderegg LDL, Anderegg WRL, Das AJ, Stephenson NL. 2021. Why is Tree Drought Mortality so Hard to Predict? *Trends in Ecology and Evolution*.
- Ullah F, Gilani H, Sanaei A, Hussain K, Ali A. 2021. Stand structure determines aboveground biomass across temperate forest types and species mixture along a local-scale elevational gradient. *Forest Ecology and Management* 486.
- Vacek Z, Prokúpková A, Vacek S, Bulušek D, Šimůnek V, Hájek V, Králíček I. 2021. Mixed vs. monospecific mountain forests in response to climate change: structural and growth perspectives of Norway spruce and European beech. *Forest Ecology and Management* 488.
- Wang W, Lei X, Ma Z, Kneeshaw DD, Peng C. 2011. Positive relationship between aboveground carbon stocks and structural diversity in spruce-dominated forest stands in New Brunswick, Canada. *Forest Science* 57(6): 506-515.
- Zeller L, Pretzsch H. 2019. Effect of forest structure on stand productivity in Central European forests depends on developmental stage and tree species diversity. *Forest Ecology and Management* 434: 193-204.

- Zellweger F, de Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, Baeten L, Hédli R, Berki I, Brunet J, et al. 2020. Forest microclimate dynamics drive plant responses to warming. *Science* 368(6492): 772-775.
- Zhai L, Coyle DR, Li D, Jonko A. 2022. Fire, insect and disease-caused tree mortalities increased in forests of greater structural diversity during drought. *Journal of Ecology* 110(3): 673-685.
- Zhang Y, Chen HYH. 2015. Individual size inequality links forest diversity and above-ground biomass. *Journal of Ecology* 103(5): 1245-1252.

VITA

Bradley Scott Nixon

Candidate for the Degree of

Master of Science

Thesis: EFFECTS OF TREE SIZE AND FOREST STRUCTURE ON FOREST
DYNAMICS

Major Field: Natural Resource Ecology and Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in December, 2022.

Completed the requirements for the Bachelor of Science in Biology; Environmental Conservation at Rogers State University, Claremore, Oklahoma in 2020.

Experience:

Graduate Research Assistant
Department of Natural Resource Ecology and Management, Oklahoma State University, 2020-2022

Graduate Teaching Assistant
Department of Natural Resource Ecology and Management, Oklahoma State University, 2020-2022