Forest composition and diversity buffer microclimates and enhance productivity

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Conflict of Interest

The authors declare no conflict of interest.

ABSTRACT

Trees can buffer forest ecosystems against climate extremes, creating microenvironments that support diverse plant communities. We asked how diverse tree communities could influence the above- and below-ground moisture environment, thereby linking tree diversity and ecosystem function. To address this question, we integrated remotely sensed forest structure, growth inventories, microclimate measurements, and leaf-level physiology in a forest biodiversity experiment. We found that fast-growing, early successional tree species buffered daily amplitudes of vapor pressure deficits (VPD) within forest plots, increasing the annual wood production of slow-growing, shade tolerant tree species. In assemblages with more stable microclimates, several tree species showed increased leaf water content and reduced physiological stress. Plots with reduced amplitude in VPD had greater complementarity and overyielding relative to those with higher variability. A mechanistic understanding of how tree diversity and community composition contribute to VPD amplitude and overyielding can inform conservation and restoration efforts in a rapidly changing world.

1 | INTRODUCTION

Biodiversity supports the cycling of energy, nutrients, and water through ecosystems (Schuldt et al. 2018; Tilman et al. 2014). Climate change, habitat loss, and a suite of compounding factors are causing rapid declines in biodiversity (Bellard et al. 2012; Isbell et al. 2023; Segan et al. 2016). Informed stewardship of landscapes can sustain ecosystems under increasingly extreme environments (Hong et al. 2022; Wright et al. 2017).

Relationships between biodiversity and ecosystem function are well established in both experimental and observational systems (Liu et al. 2018; Mori et al. 2018; Schnabel et al. 2021; Tilman et al. 1996), yet the mechanisms by which forest ecosystems become productive beyond the sum of their parts remain poorly understood (Williams et al. 2017). We have only begun to discern how biodiversity changes local environments and contributes to ecosystem functioning (Guzmán et al. 2025; Isbell et al. 2015; Urgoiti et al. 2022; Zheng et al. 2024**.** Improving our understanding of the mechanisms by which biodiversity results in overyielding will fill critical gaps in ecological theory and enhance urgently needed sustainable forestry, conservation, and restoration efforts.

Coexistence theory explains how diverse species can survive together in an environment with shared resources (Chesson 2000; HilleRisLambers et al. 2012; Levine et al. 2017; Mayfield and Levine 2010; Tilman 1980). Studies have described how organisms engage in direct competition or respond to their abiotic environment, often without simultaneously testing how organisms shape their local environment and thereby influence neighbors and drive ecosystem functions.

We designed the present study to examine how organisms alter their local microclimate, which in turn impacts the functioning of organisms. This mechanistic approach to studying coexistence and biodiversity-ecosystem function examines the feedback loops between abiotic and biotic factors in an ecosystem (Goldberg 2012). Interactions between species and the local environment can influence individual growth and scale up to the ecosystem level (Goldberg 2012; Hacker and Gaines 1997). Complementary among tree crowns of different species has been shown to result in overyielding, a critical net biodiversity effect based on productivity (Loreau and Hector 2001; Williams et al. 2017). In addition, complementarity in resource usage and facilitation between species can enhance the survival and growth of trees, particularly under drought conditions (Blondeel et al. 2024; Kothari et al. 2021).

Warmer and drier conditions are increasing in many parts of the world, increasing vapor pressure deficits (VPD) and negatively impacting the growth and reproduction of numerous plant species (López et al. 2021). The ability of plants to reduce fluctuations in VPD may be critical to the survival of species that are adapted to live in cool and wet environments, and those at the rear-edges of their growing zones (Maclean et al. 2015; Sánchez-Salguero et al. 2017). Plants can act as ecosystem engineers in their local environments through shading and restricting air movement, reducing variation in VPD and decreasing solar irradiation available to neighbor plants (Connell 1983; Gilad et al. 2004; Holmgren et al. 1997; Wright et al. 2014; Zhang et al. 2024). Recent research shows how tree composition, diversity, and structure can buffer microclimates (Schnabel et al. 2025, Wang et al. 2025). What is not yet clear is how tree diversity and composition influence microclimate variation, and how this variation influences productivity in forest communities (De Frenne et al. 2021; Losapio et al. 2021).

Long term, large-scale biodiversity experiments provide opportunities for testing the mechanisms linking biodiversity and ecosystem function. In this study, we utilized the ecosystem-scale Forest and Biodiversity Experiment 2 (FAB2) (Cavender-Bares et al. 2024) after 8 years of growth as a platform to examine potential drivers of overyielding in forest ecosystems (Fig. 1). We asked how tree diversity and community composition may influence above-ground water availability (VPD), which in turn may influence tree physiology and overyielding. First, we hypothesized that tree diversity and **fa**st-growing early **s**uccessional **t**ree (FAST) species – acting as ecosystem engineers – increase forest cover due to their resource-acquisitive strategies (Zheng et al. 2024). Second, we hypothesized that more forest cover decreases local light availability and reduces microclimate variability. Third, we hypothesized that buffered microclimates – which we define as dampened daily amplitude in VPD – arising from greater forest cover reduce leaf-level stress, increase productivity, and contribute to complementarity.

2 | METHODS

2.1 | Site Description and Study Species

We conducted research in the Forest and Biodiversity experiment (FAB2) at Cedar Creek Ecosystem Science Reserve, located in Anoka County, Minnesota (45.406299, -93.191309). The soil is characterized as sandy with limited nutrient availability and is classified as a mixed frigid Lamellic Udipsamment on the Zimmerman series (SoilWeb: An Online Soil Survey 2025). Established in 2016, the long-term experiment includes 12 tree species native to Minnesota and was designed to tease apart the influences of species richness, functional diversity, functional variability, phylogenetic diversity, and phylogenetic variability on forest ecosystem processes (Cavender-Bares et al. 2024). Phylogenetic species variability differs from phylogenetic diversity by capturing evolutionary differences independently of species richness. The represented angiosperm species included *Tilia americana, Acer rubrum, Acer negundo, Quercus rubra, Q. ellipsoidalis, Q. alba, Q. macrocarpa,* and *Betula papyrifera*. The gymnosperm species included *Juniperus virginiana, Pinus banksiana, P. resinosa,* and *P. strobus*. More details on how dimensions of tree diversity were calculated and the experimental design of FAB2 can be found in Cavender-Bares et al. 2024. For this study, we studied 148 100 m^2 (10 m × 10 m) plots that were originally planted with 100 trees each, including 36 monocultures, 46 bi-cultures, 46 6-species polycultures, 10 6-species polycultures, and 10 12-species polycultures. We chose a subset of those plots spanning the range of multiple dimensions of tree diversity to install sensors and conduct physiology measurements (Supplementary Table 1).

The proportion of fast-growing early successional tree (FAST) species was selected as a measure of community composition to understand the potential role of FAST species as ecosystem engineers that could shape local environmental conditions, thereby influencing the growth and physiology of slower growing tree species (Kothari et al. 2021). FAST proportion was calculated as the fraction of wood volume in a plot composed of pines (*Pinus*) and birches (*Betula*), as these species were able to grow swiftly despite the nutrient-poor, sandy soil of the experimental site (Fig. 1, Goldberg 1982). To understand the role of gymnosperms in determining ecosystem function, the proportion of gymnosperms was calculated as the fraction of wood volume in a plot composed of gymnosperm species.

2.2 | Forest Structure and Environment

To determine how tree diversity and composition affected forest structure**,** we performed an Uncrewed Aerial Vehicle LiDAR survey (UAV-LiDAR) over FAB2 on July 9, 2024 to derive tridimensional point clouds of LiDAR returns. Following the methods of Guzmán et al. 2025, plant fractional cover (FC) was computed for each plot as a ratio of LiDAR returns from vegetative structure to LiDAR returns from the ground. FC is a descriptor of light attenuation and vegetation density, where values close to 1 represent plots with higher vegetation density or lower light availability at the forest floor than values close to 0 (Boucher et al. 2023; Guzmán Q. et al. 2025; Venier et al. 2019).

To study associations of forest composition, diversity and FC with microclimate, we deployed microclimate sensors to monitor air and soil conditions within experimental plots. Between April and May 2024, we installed SensorPush HT.w microclimate sensors (SensorPush, NY, USA) in the centers of 75 selected plots (Supplementary Table 1). The sensors measured air temperature, relative humidity, and vapor pressure deficit (VPD) at 1-minute intervals and were housed within AcuRite solar radiation shields (AcuRite, WI, USA) attached to shepherd hooks (Fig. 1). The sensors were suspended at an average height of 84.2 cm, aligning with the average heights of slower growing tree species in monocultures. The minimum, mean, median, 95th percentile, range, and amplitude for each microclimate metric were calculated across the field sampling days (July 16 - July 19, 2024). Sampling days were chosen to represent the peak growing season. The 95th percentile was used to approximate the maximum because logged maximum microclimate values may have been influenced by excess solar irradiation and ground re-radiation. The amplitudes of temperature, relative humidity, and VPD (VPD_{amp}) were calculated by fitting a sine curve to the daily fluctuations of each microclimate metric and extracting the amplitude coefficients. VPD_{amp} and range of VPD were highly correlated ($R^2 = 0.99$, $p < 0.001$), but VPD_{amp} was selected as a representative measure of microclimate due to its strong correlations with FC.

On April 12, 2024, we installed 24 GS 1 and TEROS 10 soil moisture sensors at the centers of experimental plots to pair with aboveground microclimate measurements (Supplementary Table 1) (METER, WA, USA). Soil moisture calibration curves were created for both sensor types by correlating sensor voltage readings to known volumetric water contents (VWC) (Supplementary Table 2). Data loggers attached to the sensors recorded VWC on 30-minute intervals from April 12 to September 3, 2024 (Chen et al. 2025). Statistics of minimum, mean, median, maximum, and range (VWC_{range}) were calculated for VWC in each plot, corresponding to the month of July 2024. VWC statistics were averaged over the month due to staggered data logger malfunctions.

To determine how FC was associated with light availability in the plots, we used an AccuPAR LP-80 photometer (METER, WA, USA) to measure photosynthetically active radiation (PAR). PAR measurements were taken between 10:00 and 15:00 h on cloudless days from July 11 – 22, 2024 within experimental plots in which soil moisture was monitored. PAR was measured at the height of microclimate sensors (~84.2 cm) in the northeast and southwest quadrants of each plot. The within-plot PAR measurements were divided by PAR measurements of open sky conditions outside of the plot, resulting in ratios characterizing PAR transmission through the forest canopy.

2.3 | Plant Physiological Measurements

We studied four slow-growing deciduous tree species (*Tilia americana, Acer rubrum, Quercus alba, Quercus rubra*) to understand how changes in microenvironmental conditions could influence tree physiology. During the peak of the 2024 growing season, we measured sun-exposed leaves in the upper canopies of three trees of each focal species per plot, unless fewer than three individuals were alive in the selected plot. Measurements were averaged to generate an average metric for each species per plot.

Gas exchange measurements (photosynthesis, stomatal conductance) were taken on July 17 and July 19, 2024 between 9:00 and 13:00 h using a LI-COR 6800 (LI-COR, NE, USA). The LI-COR 6800 was set with light levels at 1200 μmol m^{-2} s^{-1}, flow rate at 500 m s^{-1}, fan speed at 10000 rpm, relative humidity at 60%, temperature at 20 °C, and reference CO_2 at 400 μmol mol^{-1}. One leaf from each of the three trees was collected before sunrise, scanned, dried, and weighed to calculate leaf mass per area (LMA). Leaf area was determined using ImageJ software and the magick and LeafArea packages in R (Katabuchi 2015; Ooms 2016; R Core Team 2023; Schneider et al. 2012).

Reflectance spectra measurements on leaves (400-2500 nm) were taken in the field using a PSR+ Spectroradiometer on July 16, 2024 (Spectral Evolution, MA, USA). The Carter Miller Stress Index (CMSI), which gives information on water stress and the decline of photosynthetic activity, was calculated using spectral reflectance values (R694 / R760; Carter and Miller 1994).

Based on methods in the literature, partial least squares regression models were developed from leaf reflectance spectra of woody species across central Minnesota using the pls package (Appendix S1; Kothari et al. 2023; Mevik and Wehrens 2007; Serbin et al. 2014). The coefficients from the partial least squares regression models were used to derive leaf-level traits of lignin and water content for selected trees.

2.4 | Growth and Net Biodiversity Effects

We used growth inventories of FAB2 to understand the productivity of tree species in plots with differences in diversity, composition, and microclimate. For this study, we analyzed trees measured at the ends of the 2023 and 2024 growing seasons. Growth metrics included height, diameter at root collar, and diameter at breast height. Because diameter at breast height was not measured in 2024 due to funding limitations, we developed species-specific regression models to predict $\log_{10}$(diameter at breast height) using $\log_{10}$(diameter at root collar) and $\log_{10}$(height). The wood volume of each tree was estimated using geometric equations for conoid and conoidoid volumes as described in Cavender-Bares 2025 and Guzmán et al. 2025. Tree inventory data were quality controlled by reviewing trees identified as having outlier volume and annual wood productivity estimates.

Net biodiversity effects of forest plots were calculated for the 2024 growing season based on equations from Loreau and Hector 2001 that partition biodiversity effects into complementarity and selection. Following the methods of Guzmán et al. 2025, we used calculated tree volumes to estimate annual wood productivity (AWP, m^3 y^{-1}) and net biodiversity effects of productivity, hereafter called overyielding (m^3 y^{-1} ha^{-1}). The average AWP of monoculture plots was considered the "expected" AWP for each species. The difference between observed and expected AWP (AWP_{O-E}) was calculated for polycultures of each tree species.

2.5 | Statistical Analysis

To test our hypotheses, we ran multiple linear regressions in R between metrics of diversity, community composition, forest structure, microenvironment, physiology, and overyielding (R Core Team 2023). Quantile regressions were performed to model the relationships between plot diversity metrics and FC using the quantreg package in R (Koenker 2025). Twenty-fifth quantile regressions allowed us to examine how diversity related to FC while accounting for zero-inflated diversity data (Fig. 2). Generalized additive models were used to observe changes in variance of FC residuals as they related to diversity and were fit using the mgcv package (Wood 2011).

We regressed FC with VPD_{amp} to understand how forest structure influenced microclimate variation. FC was transformed to reduce skew and linearize the relationship between FC and VPD_{amp}. Transformed fractional cover (TFC) was calculated using the equation:

$$\text{Transformed Fractional Cover} = -\text{sqrt}(1 - \text{FC}) \qquad (1)$$

We examined how microclimate influenced the productivity of different tree species. Due to limited replication of microclimate sensors in polycultures, we used FAST proportion, TFC, and

VPD_{amp} to create a multiple linear regression that predicted VPD_{amp} for all 148 100 m^2 plots in the experiment. The R^2 for this regression was 0.8446, with $p < 0.001$.

$$VPD_{amp} = 0.79986 - (0.43435 * TFC) - (0.26989 * FAST\ Proportion) \qquad (2)$$

This model was used to infill VPD_{amp} values in plots without microclimate sensors. Infilled VPD_{amp} values were used to examine relationships between VPD_{amp} and $AWP_{O\text{-}E}$ of tree species (Supplementary Fig. 2).

To understand the relationships between tree diversity, community composition, forest structure, microclimate, and net biodiversity effects, we built a structural equation model using the lavaan package in R (Rosseel 2012). Phylogenetic species variability describes evolutionary dissimilarity and was previously shown to explain variation in FC (Guzmán et al. 2025) and was therefore selected as a representative metric of diversity. FAST proportion was chosen as a measure of community composition, TFC was included as a descriptor of forest structure, VPD_{amp} was incorporated as a metric of microclimate, and overyielding was included as a measure of net biodiversity effects.

3 | RESULTS

3.1 | Tree diversity and community composition influence forest structure, reducing variability in microclimates

Greater tree diversity resulted in more canopy cover (i.e., fractional cover; FC) (Fig. 2). Quantile regression analysis at the 25th percentile showed that tree communities with higher species richness, functional diversity, phylogenetic diversity, and phylogenetic variability were associated with increased FC ($p < 0.001$). Greater tree diversity also reduced variation in FC ($p < 0.001$). Plots with higher proportions of fast-growing early successional (FAST) species also maintained higher FC (Supplementary Fig. 1, $p < 0.001$). In addition to increasing FC, FAST proportion contributed to the reduction of microclimate variation (VPD_{amp}). FAST species had significantly lower VPD_{amp} in monocultures compared to non-FAST species ($p < 0.001$), and greater FAST proportion in plots significantly reduced VPD_{amp} ($R^2 = 0.76$, $p < 0.001$)

FC buffered the microclimate against large fluctuations in VPD_{amp} and decreased local light availability. Increases in FC decreased the 95th percentile and mean VPD in plots ($p < 0.001$). The daily amplitudes of temperature and relative humidity—drivers of VPD_{amp}—were both strongly influenced by transformed fractional cover (TFC) ($p < 0.001$). However, a multiple linear regression revealed that trends in VPD_{amp} were primarily driven by the amplitude of relative humidity ($R^2 = 0.98$, $p < 0.001$) compared to temperature ($p > 0.05$). TFC was strongly negatively correlated with VPD_{amp} (Fig. 3, $R^2 = 0.75$, $p < 0.001$). Included together in a multiple linear regression, TFC and FAST proportion robustly predicted VPD_{amp} ($R^2 = 0.84$, $p < 0.001$). Increases in FC decreased understory light availability ($R^2 = 0.70$, $p < 0.001$). A multiple linear regression including VPD_{amp} and FC predicted PAR transmission well ($R^2 = 0.81$, $p < 0.001$). There was a strong positive correlation between VPD_{amp} and PAR transmission within the canopy, highlighting a potential tradeoff between microclimate buffering and light availability (Fig. 3, $R^2 = 0.77$, $p < 0.001$).

3.2 | Buffered microclimates and tree diversity are associated with more annual wood production of some species

VPD_{amp} showed a strong negative relationship with overyielding ($R^2 = 0.69$, $p < 0.001$), indicating that lower values of VPD_{amp} were associated with more overyielding in forest plots (Fig. 3). *T. americana, A. negundo,* and *P. banksiana* showed significant declines in annual wood production ($AWP_{O\text{-}E}$) with increasing VPD_{amp} ($p < 0.05$). The $AWP_{O\text{-}E}$ of the remaining species was not strongly influenced by VPD_{amp} (Supplementary Fig. 2, $p > 0.05$).

Tree diversity also influenced the annual wood production of some species. Increases in phylogenetic species variability resulted in $AWP_{O\text{-}E}$ gains for *P. strobus* ($p < 0.05$), and *T. americana* ($p = 0.051$). Increased phylogenetic diversity resulted in significantly decreased $AWP_{O\text{-}E}$ of *Q. ellipsoidalis* and *Q. macrocarpa* ($p < 0.05$). The $AWP_{O\text{-}E}$ of *A. rubrum* increased with higher phylogenetic diversity ($p < 0.05$), although a monoculture plot with exceptionally high AWP caused $AWP_{O\text{-}E}$ to be negative.

3.3 | Deciphering mechanisms underlying Biodiversity-Ecosystem Function

Overyielding resulted from the interactions between local biotic and abiotic factors in the forest diversity experiment. Structural equation modeling showed that the proportion of FAST species – rather than phylogenetic species diversity – was responsible for increased canopy cover (Fig. 4, $p < 0.001$). Increases in FAST proportion and canopy cover reduced microclimate variation

($\mathrm{VPD}_{\mathrm{amp}}$) within the forest plots during the peak growing season ($p < 0.001$). Buffered microclimates influenced the annual wood production of tree species, as described above. Overall, higher variation in microclimate negatively influenced overyielding ($p < 0.05$), indicating a net positive relationship between buffered microclimates and overyielding (Fig. 4). A linear regression between $\mathrm{VPD}_{\mathrm{amp}}$ and overyielding corroborated the relationship (Fig. 3, $R^2 = 0.69$, $p < 0.001$). Canopy cover and FAST proportion had non-significant correlations with overyielding ($p > 0.05$).

Although both complementarity and selection effects were present in the plots, trends in overyielding were driven by complementarity effects (Supplementary Fig. 3). Compared to plots with less than 50% FAST proportion, plots in which FAST species composed 50% or more of the wood volume displayed higher complementarity effects ($p < 0.01$), more negative selection effects ($p < 0.05$), and greater net biodiversity effects ($p < 0.001$).

3.4 | Species exhibit physiological responses to variation in local environments modified by tree diversity and composition

Differences in plot-level environmental conditions caused responses in the physiology of four focal tree species: *A. rubrum, Q. alba, Q. rubra,* and *T. americana*. Physiological responses to variations in the local environment were largely species-specific, but some general trends were also observed. Greater $\mathrm{VPD}_{\mathrm{amp}}$ significantly decreased leaf water content in most focal species (Fig. 5, $p < 0.01$ for *A. rubrum*, *Q. alba*, *Q. rubra*, $p < 0.1$ in *A. rubrum*), and greater leaf water content was significantly correlated with a lower Carter Miller Stress Index (CMSI) in most focal species ($p < 0.05$ for *A. rubrum*, *Q. alba*, *Q. rubra*, $p = 0.06$ in *T. americana*). Greater VPD_{amp} was associated with higher LMA in *A. rubrum*, *Q. rubra* ($p < 0.05$), and *T. americana* ($p = 0.05$). Increases in LMA were tightly linked to photosynthesis in *T. americana* ($p = 0.01$) and *Q. rubra* ($p < 0.1$). Increased LMA of species was also highly correlated with greater leaf lignin content in *Q. alba* ($p < 0.01$) and *T. americana* ($p < 0.1$). Leaf lignin content was negatively correlated with CMSI in *A. rubrum* ($p < 0.01$) and *T. americana* ($p < 0.05$).

Higher proportions of gymnosperm species in the plot lowered mean and minimum VWC values ($R^2 = 0.51$, $p < 0.001$; $R^2 = 0.52$, $p < 0.001$) and increased the range of VWC (VWC_{range}) (Supplementary Fig. 4, $R^2 = 0.20$, $p < 0.05$). Maximum VWC was not significantly influenced by higher proportions of gymnosperm species ($p > 0.05$). VWC_{range} decreased moderately with more PAR transmission in the plot ($R^2 = 0.15$, $p < 0.1$), but was not correlated with tree diversity metrics or VPD_{amp} ($p > 0.05$). No strong correlations were observed between VWC_{range} and leaf water content or LMA. However, increases in VWC_{range} significantly increased the average stomatal conductance of *A. rubrum* (Fig. 5, $p < 0.05$). Increases in stomatal conductance contributed to greater photosynthesis in only *T. americana* ($p < 0.01$).

4 | DISCUSSION

We found that tree species composition increased fractional cover more than diversity, fractional cover decreased microclimate variation within the forest canopy, and more stable microclimates contributed to increased forest productivity. The results from this study supported our three hypotheses. Fast-growing early successional tree (FAST) species served as ecosystem engineers to increase forest cover. Greater forest cover decreased light availability and reduced microclimate variability, buffering against extreme microclimates, which in turn reduced physiological stress in some species and increased overyielding. These findings highlight the importance of forest composition and structure in shaping microclimates and demonstrate the roles of facilitation and biotic-abiotic interactions in diverse ecosystems (Basnet et al. 2025; Goldberg 2012; Wright et al. 2017). Increased complementarity and productivity in more diverse plots with high proportions of FAST species contributed to higher overyielding.

4.1 | Consequences of tree diversity and community composition

We showed how tree diversity and especially community composition influenced forest fractional cover (FC), supporting previous findings (Guzmán et al. 2025). The proportion of FAST species had a stronger effect on FC than multiple dimensions of tree diversity, highlighting the importance of community composition on forest structure. However, phylogenetic species variability was significantly associated with overyielding, indicating that diversity can influence ecosystem functions beyond microclimate buffering.

Considering the influence of tree diversity on the difference between observed and expected annual wood production (AWP_{O-E}) for individual species can provide insight into potential BEF mechanisms. The significant positive associations between AWP_{O-E} and phylogenetic species variability suggest that the productivity of some species, such as *P. strobus* and *T. americana*, was positively influenced by large evolutionary differences between these trees and their neighbors. Phylogenetic diversity – but not phylogenetic variability – includes species richness as a factor. Consequently, the significant relationships between $AWP_{O\text{-}E}$ and phylogenetic diversity show that a greater number of species in a community increased the productivity of *A. rubrum*, but decreased the productivity of *Q. ellipsoidalis, Q. macrocarpa*. These findings highlight the importance of understanding multiple aspects of diversity, such as species variability and richness, which can have distinct consequences for different species.

Not all species increased $AWP_{O\text{-}E}$ in response to greater tree diversity. Heightened interspecies competition for resources could explain decreases in $AWP_{O\text{-}E}$ of *Q. ellipsoidalis* and *Q. macrocarpa.* These drought-tolerant *Quercus* species grew less in plots with more species, indicating a preference for open canopies, consistent with their shade intolerance (Kothari et al. 2021) and frequent establishment in savanna ecosystems (Peterson and Reich 2001).

4.2 | Buffered microclimates promote the growth of shade-tolerant and water-limited tree species, contributing to overyielding

Complementarity increased in plots with higher FAST proportion, which contributed to higher fractional cover, and consequently decreased local light availability and reduced microclimate variability. The reduced microclimate variation contributed to overyielding in forest plots. This finding supports prior studies of gap-filling and crown complementarity between different tree species (Williams et al. 2017) and highlights the facilitative effect of FAST species on other tree species through microclimate buffering.

The negative relationship between microclimate variability (VPD_{amp}) and overyielding indicates that reduced VPD_{amp} is associated with increased productivity of trees. With ongoing climate change, microclimate buffering will become more important as species are pushed to the edges of their climate envelopes (Koo et al. 2017). Previous research has highlighted the importance of topography for climate refugia (Ackerly et al. 2020; Suggitt et al. 2018) and microclimate buffering by plant cover (Bernath-Plaisted et al. 2023; De Frenne et al. 2021; De Lombaerde et al. 2022).

In line with successional theory, FAST species may alter their local climate and environment in ways that promote their own survival, including buffering of microclimate (Connell and Slatyer 1977). A FAST species, *P. banksiana*, showed significant declines in AWP_{O-E} associated with increases in VPD_{amp}, indicating vulnerability of the species to drought (McCollum and Ibáñez 2020). Similar to the results from the higher density FAB1 experiment (Kothari et al. 2021), shade tolerant tree species in FAB2 grew more under the canopy cover of their taller counterparts. FAST proportion influenced the local microclimate by creating canopy cover that provided shade and reduced evaporative demand (Lin 2010). Reduced VPD_{amp} was associated with increased AWP_{O-E} of *T. americana* and *A. negundo*, which are shade tolerant angiosperms found in moist sites and riparian ecosystems (Crow 1990; Niinemets and Valladares 2006; Ward et al. 2002). Sitewide soil water limitation, vulnerability to drought, and shade tolerance characteristics could explain how these tree species benefited from buffered microclimates that alleviated atmospheric drought stress.

4.3 | Buffered microclimates reduce leaf-level stress of focal species

Reduced microclimate variation was associated with changes in leaf-level physiology indicating lower levels of water and light stress. Variability in leaf form and function can be important contributors to growth and overyielding (Chitwood and Sinha 2016; Rozendaal et al. 2006; Williams et al. 2021). Although we did not observe strong correlations between the leaf traits and growth in this study, possibly due to low sample size, the decreased leaf-level stress resulting from reduced VPD_{amp} may have indirectly contributed to the growth of the focal trees. Buffered microclimates resulted in higher leaf water content and reduced drought-related photosynthetic stress for all focal species, as indicated by the CMSI (Carter and Miller 1994). Trees living in microclimates buffered by FAST species had more water in their leaves and were less stressed than their counterparts in more open environments.

Dampened VPD_{amp} significantly decreased LMA in multiple species (Fig. 5). Reduced VPD_{amp} was strongly correlated with lower PAR transmission through the forest canopy, thus decreases in LMA may have been responses to coupled declines in drought and light stress. Leaves with higher LMA invest more in structural support mechanisms such as lignin and are better able to withstand drought and other physical stressors (Wright et al. 2004). *Q. alba* and *T. americana* increased leaf lignin content in leaves with higher LMA. Despite *Q. rubra* and *A. rubrum* not displaying within-species relationships between LMA and leaf lignin, the overall positive relationship between LMA and leaf lignin held true (Fig. 5). This result simultaneously emphasizes species-specific differences in leaf traits and the ability of some species to shift their resource allocation strategies in response to changes in their environment.

In this system, soil moisture variation (VWC_{range}) did not influence leaf-level physiology as much as microclimate variation. Given that the proportion of gymnosperms did not significantly influence the maximum VWC but significantly lowered the mean and minimum VWC in plots, the relationship between gymnosperms and VWC_{range} may have been driven by increased water uptake by well-established gymnosperm roots (Bond 1989). Redistribution of soil water by gymnosperm roots may have alleviated drought stress in *A. rubrum*, increasing the species' stomatal conductance (Caldwell et al. 1998). For *A. rubrum*, increases in stomatal conductance in gymnosperm-dominated plots did not translate to increased photosynthesis, perhaps due to light limitation. Despite the lack of intraspecific relationships between stomatal conductance and photosynthesis in *Q. rubra, Q. alba,* and *A. rubrum*, the positive correlation across species between these variables remained strong. These results highlight the differences between species in physiological responses to environmental stress as well as consistent mechanisms governing plant function that persist across diversity treatments and environmental conditions.

4.4 | Conclusions

Plant traits, evolutionary histories, and coexistence theory all inform understanding of species interactions and growth dynamics. We show that plants exhibit complementarity in how they influence and respond to the microenvironmental conditions they collectively shape. In this study, we hypothesized and found strong connections between diversity, community composition, forest cover, and microclimate variability (VPD_{amp}), with influences on plant growth and overyielding. We thus demonstrated a clear mechanistic relationship between decreased VPD_{amp} and overyielding, caused by tree diversity and composition. Our findings, combined with previous work explaining how reduction in light stress increases productivity of shade tolerant tree species (Kothari et al. 2021), indicate that tree diversity and composition drive overyielding through amelioration of both atmospheric drought and light stress. Specifically, we show that in young experimental forests, fast-growing early successional tree (FAST) species shape the microenvironment of their neighbors, influencing species growth rates, increasing complementarity, and contributing to overyielding. These relationships could shift over time, with slower-growing later successional species dominating and influencing both microclimate and productivity in the future (Zheng et al. 2024).

In the face of a changing climate, FAST species may play an important role in buffering microclimates in young forests, benefiting the FAST species themselves and facilitating the growth of species that are less tolerant of drought or light stress. While FAST species may differ between sites, they play an important role in early successional forests as ecosystem engineers, influencing local microenvironments and ecosystem function (Gilad et al. 2004; Losapio et al. 2021). This study creates a window into the complex relationships between overyielding, microclimate, forest structure, community composition, and tree species diversity: a critical step in understanding and protecting our biodiverse ecosystems.

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FIGURES

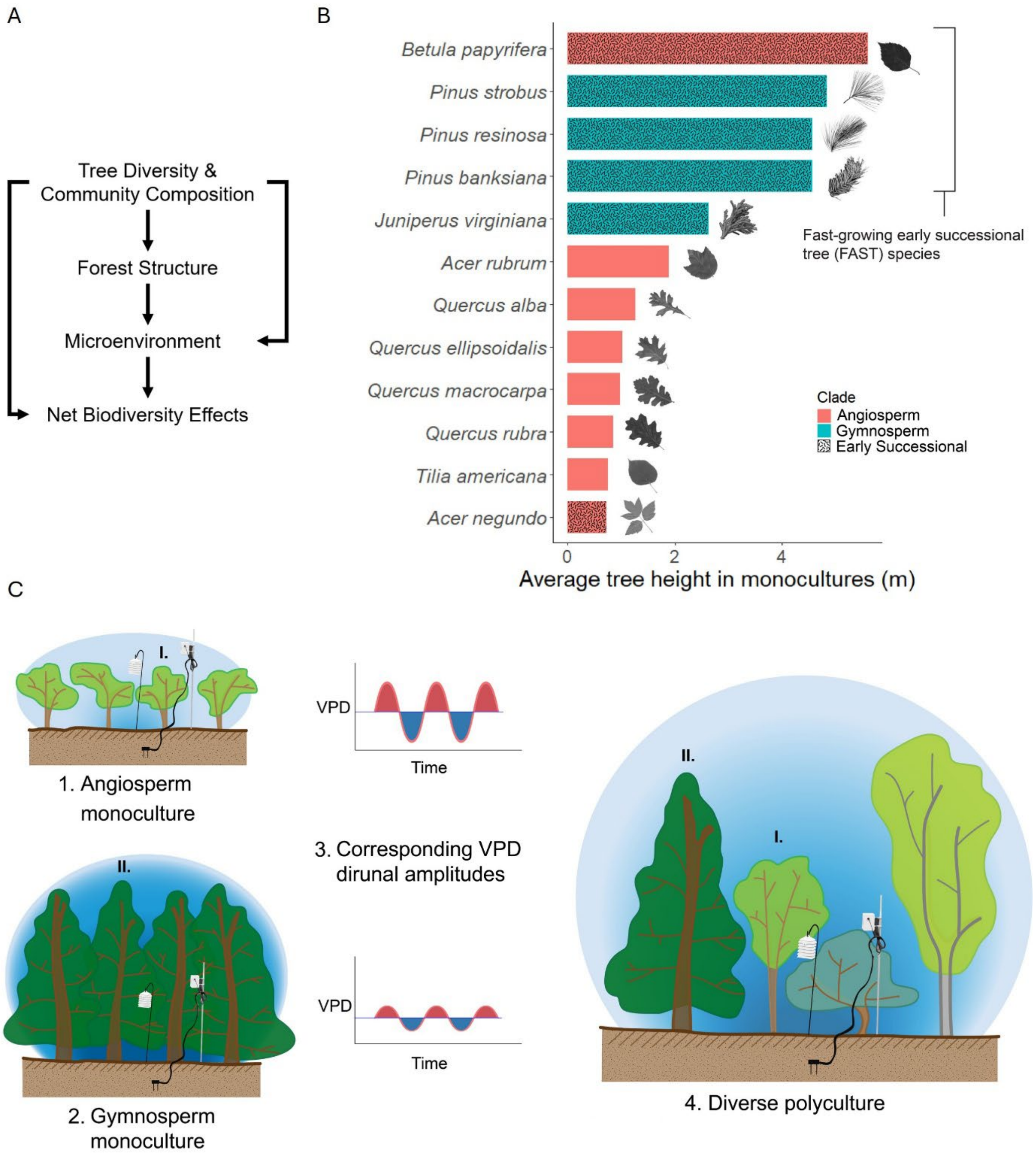


Figure 1. This study used a forest biodiversity experiment to examine the mechanisms linking biodiversity and ecosystem functioning. (A) We hypothesized that forest structure and its effects

on microenvironment served as links between tree diversity, community composition, and net biodiversity effects. (B) We predicted that the fast growing early successional (FAST) species would act as ecosystem engineers, decreasing local light availability and buffering against extremes in microclimate. (C) Sensors were installed in forest plots to measure microclimate and soil moisture. We predicted that (1) plots with shorter angiosperm trees would experience more (3) extreme daily fluctuations in vapor pressure deficit (VPD) than (2) taller gymnosperm monocultures with more canopy cover to buffer local VPD. (4) Diverse polycultures would bring together tree species that would create variation in local environments that could influence the physiology of individual trees (I, II) and contribute to net biodiversity effects through increases in complementarity. Leaf scans courtesy of Jake Grossman.

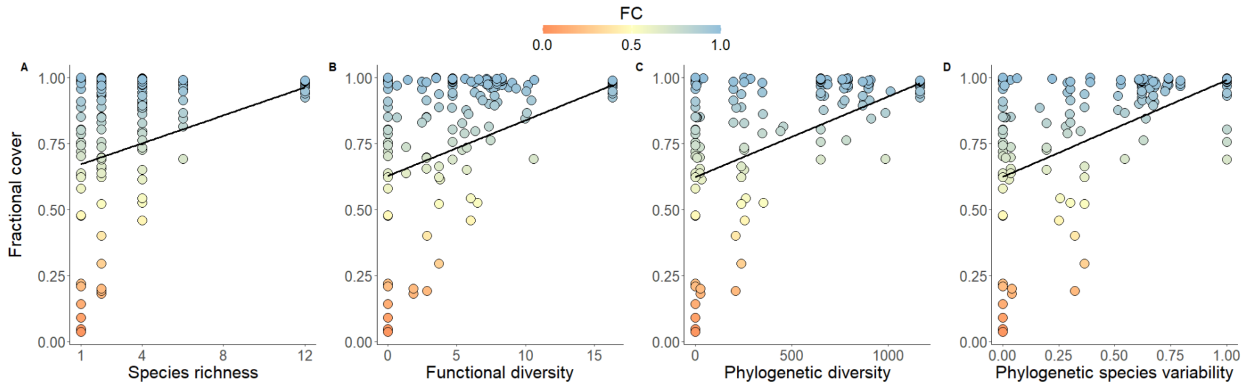


Figure 2. Quantile regressions at the 25th percentile show that different metrics of tree diversity are significantly correlated with increases in fractional cover (FC) ($p < 0.001$). In addition, variation in fractional cover decreases with increasing tree diversity ($P < 0.001$).

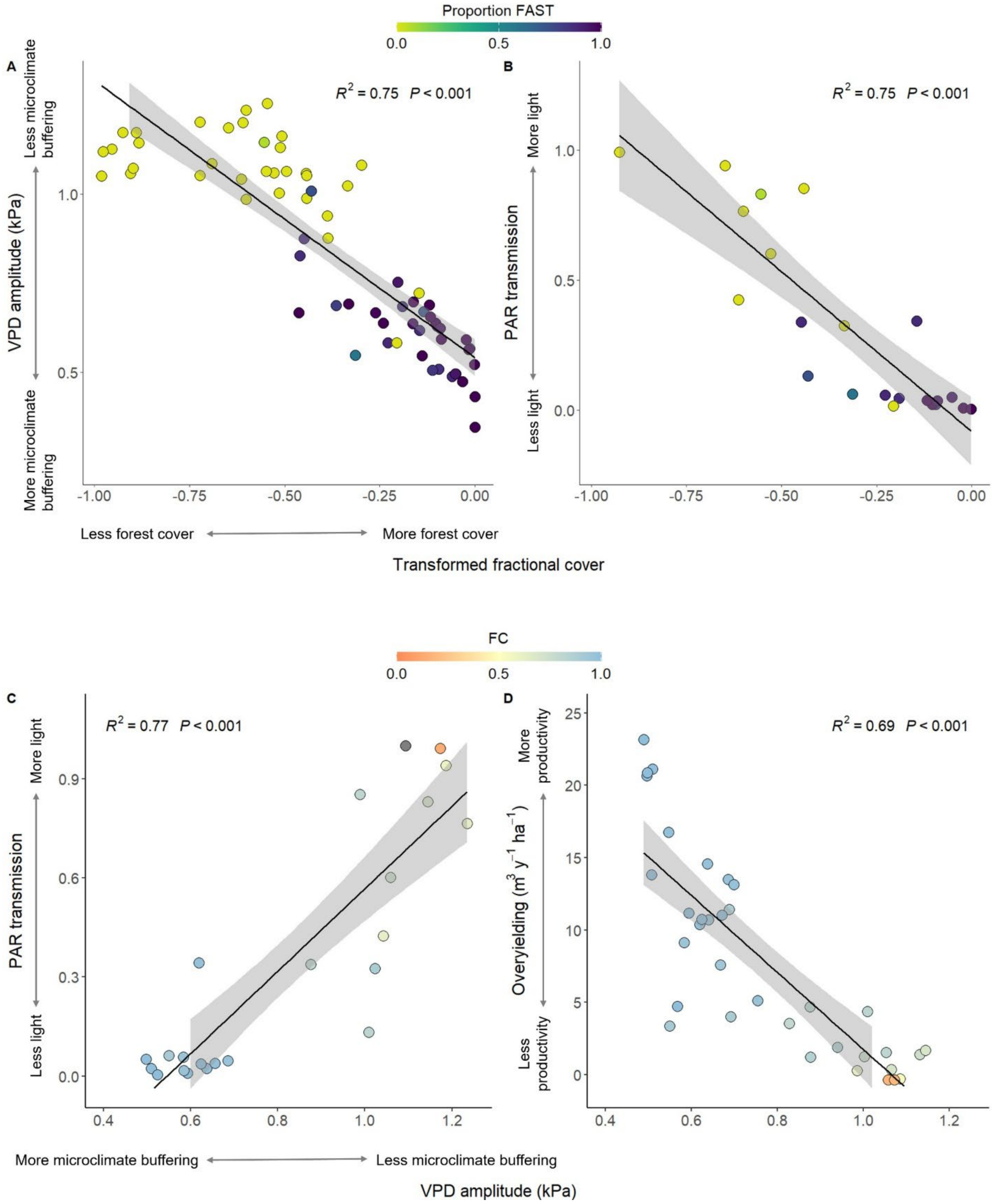


Figure 3. Linear regressions show the strong relationships between transformed fractional cover (TFC), VPD amplitude (VPD_{amp}), PAR transmission, and overyielding. A higher FAST

proportion in a forest plot contributes to increased TFC. Increased TFC is linked with declines in (A) VPD_{amp} and (B) PAR transmission through the forest canopy. Higher VPD_{amp} is associated with (C) more PAR transmission and (D) decreased overyielding. Connecting these panels, we reason that FAST species contribute to buffered microclimates that are associated with increased wood productivity. FAST species also lower PAR transmission through the canopy, lowering light related stressors, but also potentially posing a challenge of light limitation for some tree species.

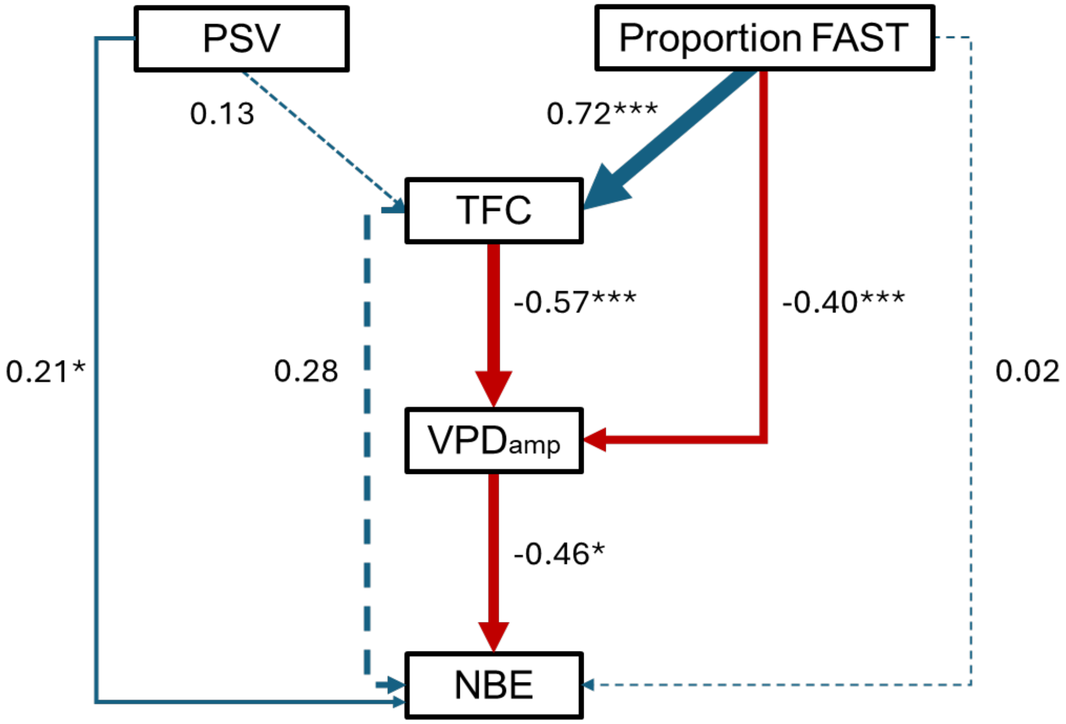


Figure 4. A structural equation model was built to understand the mechanisms linking biodiversity and ecosystem function. Blue lines indicate positive relationships, and red lines indicate negative relationships between variables. Solid lines and asterisks indicate significant correlations between variables. Line thickness denotes the size of standardized estimates of paths between variables. Phylogenetic species variability (PSV) was chosen as a diversity metric, and FAST proportion was selected as a metric of community composition. Transformed fractional cover (TFC) is a metric of forest structure, and VPD amplitude (VPD_{amp}) is a measure of microclimate. Overyielding is the net biodiversity effect (NBE) in this model. Greater FAST proportion significantly increased TFC and decreased VPD_{amp} ($p < 0.001$). TFC also greatly reduced VPD_{amp} ($p < 0.001$). Higher VPD_{amp} was associated with lower NBE ($p < 0.05$), and greater PSV positively influenced NBE ($p < 0.05$). This model shows that tree diversity, community composition, and the interactions between trees and their local environment can influence tree growth and overyielding.

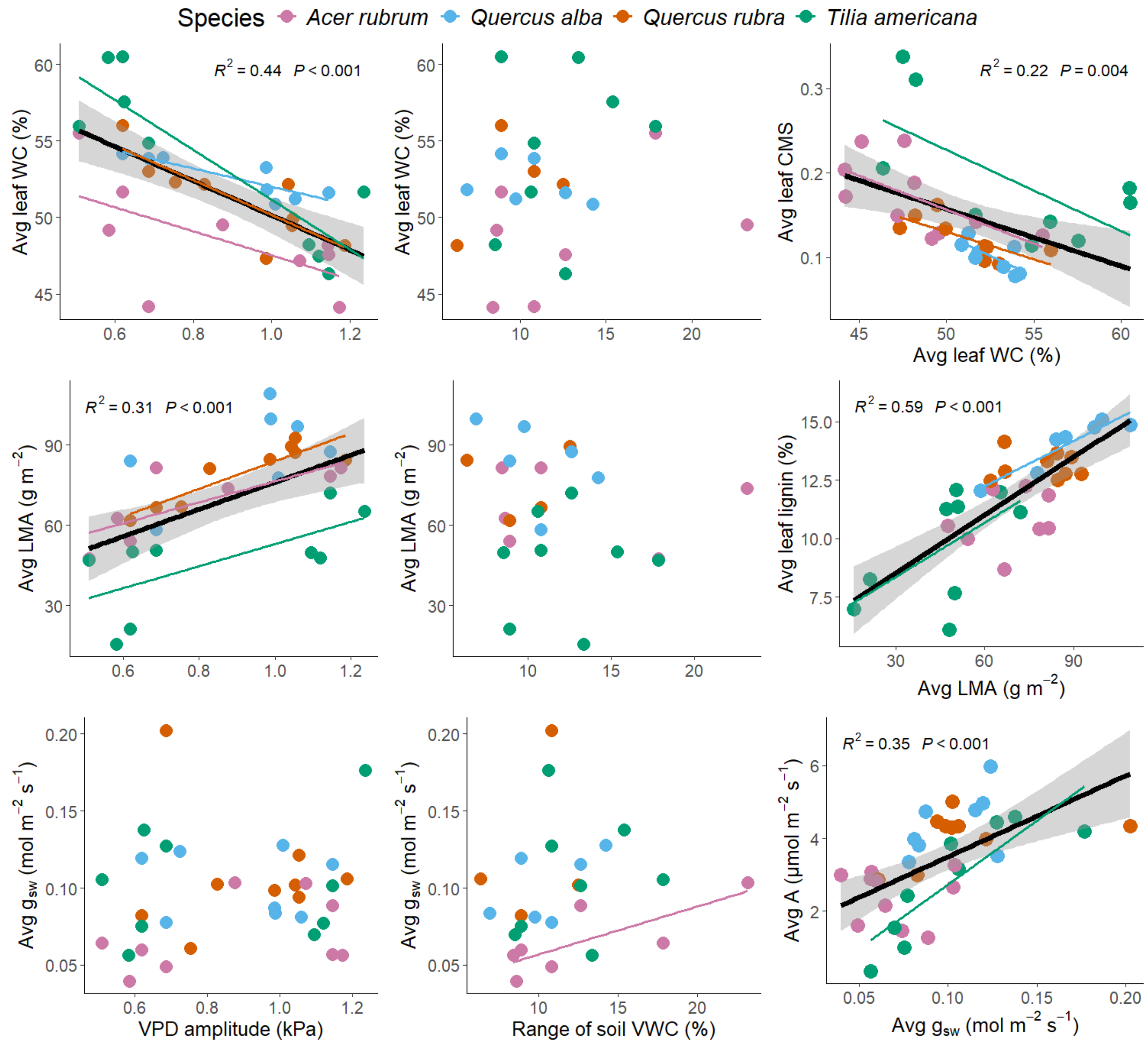
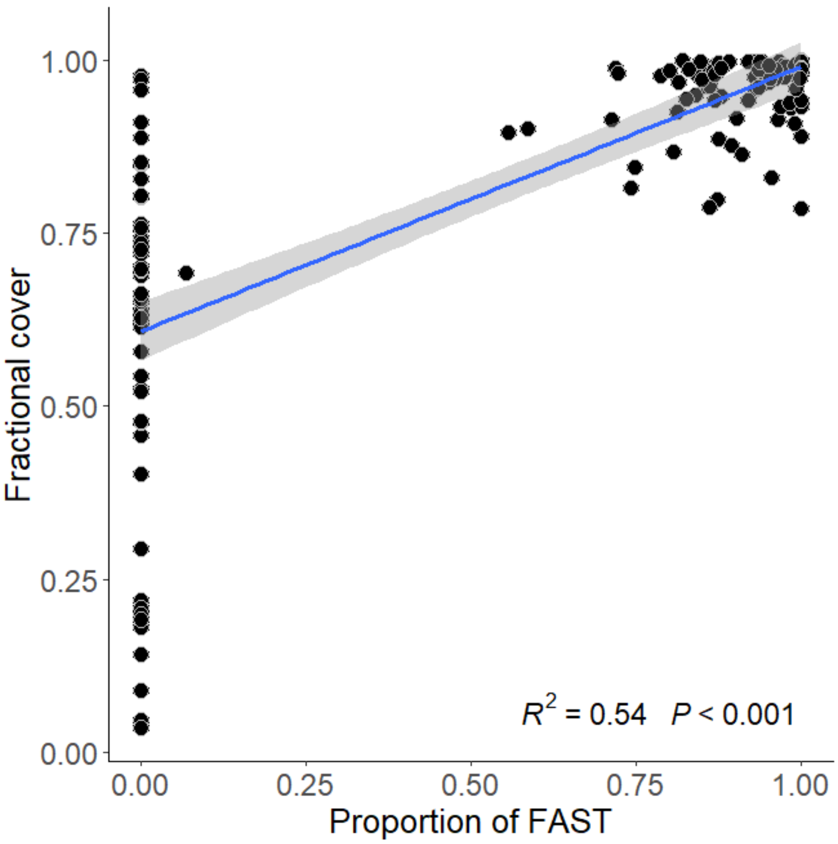


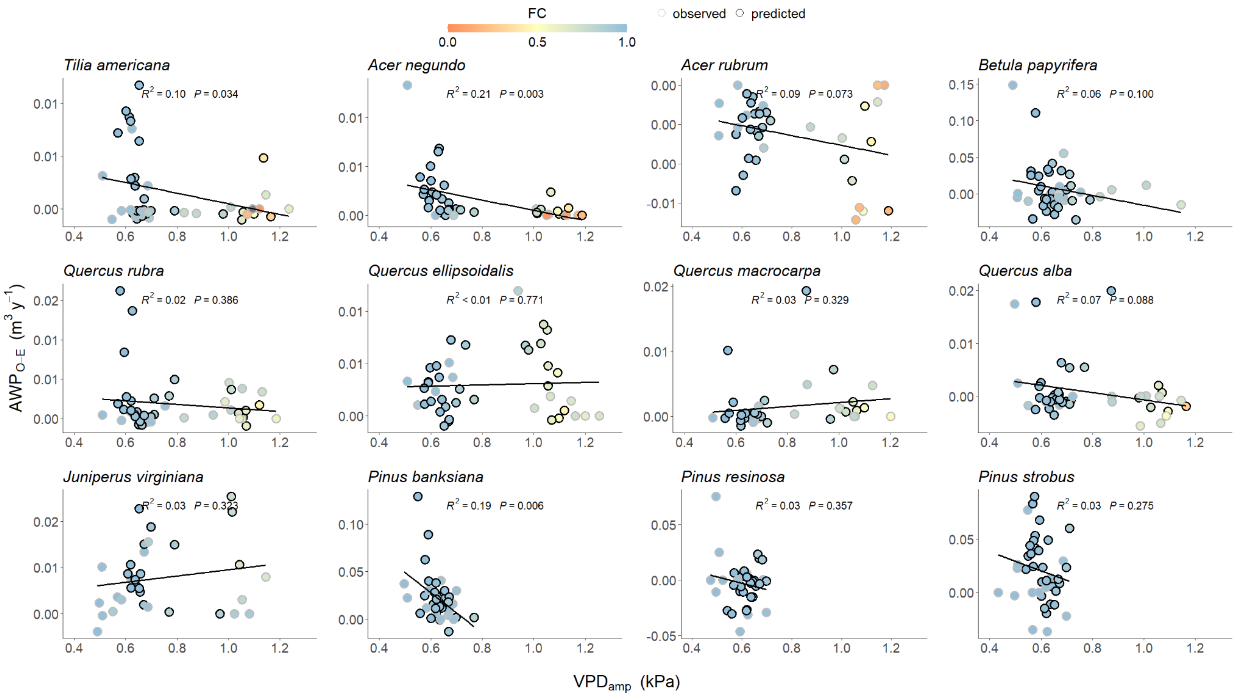
Figure 5. Relationships between micro-environmental metrics and leaf physiology of four focal species. To understand how environmental changes in the forest plots influenced tree physiology, we selected four species to study in-depth: *Acer rubrum, Quercus alba, Quercus rubra,* and *Tilia americana*. Black regression lines show significant regressions ($p < 0.01$) between variables for all four species combined across plots representing different diversity and composition treatments. Displayed R^2 and p values correspond to these regression lines. Individual colored

lines are linear regressions of each species and are included for relationships in which $p < 0.1$. Environmental variables VWC and VPD were measured at the plot level. VWC is expressed as % water volume per unit volume of soil. All of the remaining physiological variables are species averages per plot. Leaf-level water content (WC) is the relative water content in a fresh leaf by mass (%). Carter Miller Stress Index (CMS) is a unitless ratio. Avg LMA refers to average leaf mass per area, Avg A refers to average photosynthetic gas exchange of a leaf (µmol m^{-2} s^{-1}), and Avg g_{sw} refers to average stomatal conductance to water of a leaf (mol m^{-2} s^{-1}). Leaf lignin content is estimated as % dry mass. Significant regressions across plots ($p < 0.01$) include: VPD_{amp} and leaf water content, leaf water content and CMS, VPD_{amp} and LMA, LMA and leaf lignin, leaf lignin and CMS, LMA and photosynthesis, and stomatal conductance and photosynthesis.

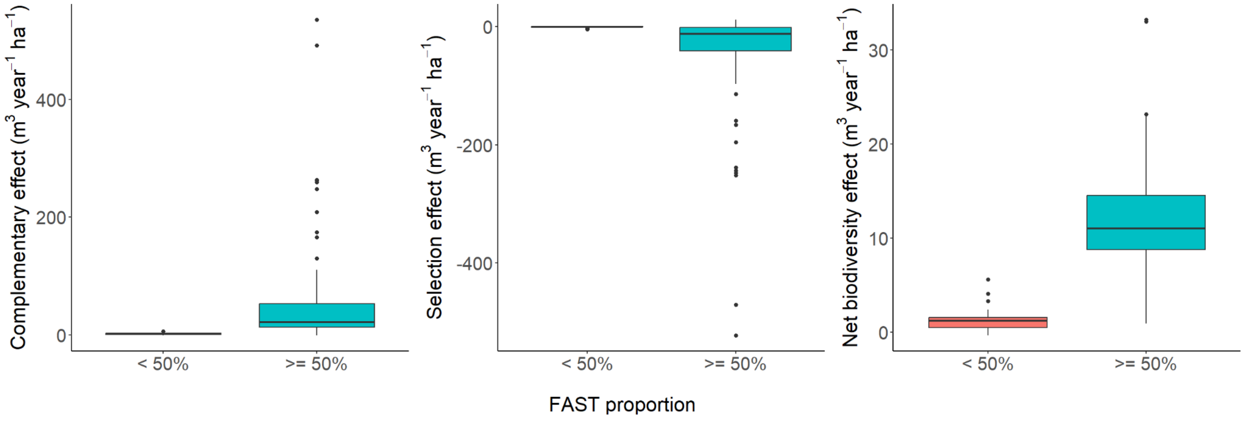
SUPPLEMENTARY MATERIALS



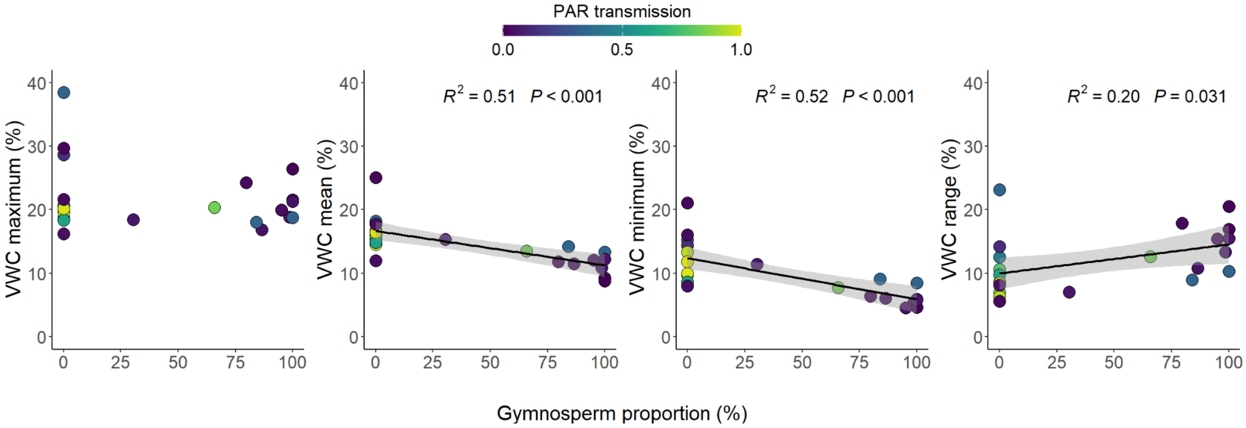
Supplementary Figure 1. The FAST proportion was significantly correlated with fractional cover in a forest plot ($p < 0.001$). When FAST species had high abundance in a plot, they contributed a substantial proportion of the plot wood volume, leading to the split in data observed in this graph.



Supplementary Figure 2. Increases in VPD_{amp} significantly decreased the annual wood production (AWP_{O-E}) of tree species that were shade tolerant and/or water limited, including *T. americana, A. negundo,* and *P. banksiana*. Each point represents a forest plot. Plots with more fractional cover (FC) were generally associated with reduced VPD_{amp}. A multiple linear regression model was developed to predict VPD_{amp} for plots in which this metric was not measured (Equation 2). Plots in which $VPD_{amp}$was observed are encircled in grey, and plots for which VPD_{amp} was predicted are encircled in black.



Supplementary Figure 3. Overall trends in overyielding (net biodiversity effect) were driven by complementarity effects. Plots in which FAST species composed 50% or more of the wood volume displayed greater complementary ($p < 0.01$), less selection ($p < 0.05$) and more overyielding ($p < 0.001$) than plots with less than 50% FAST proportion.



Supplementary Figure 4. The proportion of gymnosperms significantly influenced the mean, minimum, and range of volumetric water content (VWC), but not the maximum VWC, in forest plots. PAR transmission was moderately correlated with the range of VWC ($p < 0.1$).

Acknowledging that VPD_{amp} and $\text{VWC}_{\text{range}}$ were not measured on the same timescales, we found that the two variables were largely decoupled in this system. Given that the proportion of gymnosperms did not significantly influence the maximum VWC but significantly lowered the mean and minimum VWC in plots, the relationship between gymnosperms and $\mathrm{VWC}_{\mathrm{range}}$ may have been driven by increased water uptake by the well-established gymnosperm roots in the shallow rooting zone (Bond 1989). The aboveground wood volume of gymnosperm species in the experiment was substantial, suggesting that belowground root volume was similarly sizable (Annighöfer et al. 2022).

Supplementary Table 1. The table describes the experimental design of this study. Microclimate and soil moisture monitoring sensors were distributed in plots that spanned large gradients of the different diversity metrics considered in FAB2. Plots in which sensors were installed are noted with "1", and the total number of plots are summed at the bottom of the table. One control plot, an unplanted, unmown open area, was included in the experimental design for quality control purposes but was not included in the analyses presented in this paper. The gymnosperm-angiosperm ratio was used as a rough estimate of gymnosperm proportion based on the original planting ratios (i.e. 1 gymnosperm species out of 4 total species in a plot = 0.25 gymnosperm-angiosperm ratio).

Supplementary Table 2. The table explains how volumetric water content (VWC) calibration curves were fit to two soil moisture sensors used in the experiment. In 2023, soil from an unplanted section of the FAB2 experiment was harvested and placed in a drying oven. After the soil was completely dry, the soil was placed in a large bucket. Water was incrementally added to the soil in known quantities and thoroughly mixed. Two different sensors (GS1, Teros 10) were placed in the soil at regular intervals to obtain voltage readings. VWC was calculated as the volume of water divided by the total volume of soil. The volume of soil was calculated as the area of the bucket base ($\pi d^2/4$) multiplied by the height of the soil. Linear regression lines were fitted in R v. 4.3.1 to obtain coefficients that could be used to convert voltage readings into VWC for each sensor (R Core Team 2023).

Appendix 1. We used predicted models on full-range reflectance spectra (350–2500 nm) measurements to derive two leaf traits: lignin and water content. These models were constructed on pair measurements of traits and reflectance spectra (lignin: n = 117, and water content: n = 357) of samples collected on woody species across central Minnesota using Partial Least Square Regressions within a machine learning framework. This framework involves methods for model calibration and validation as described in Burnett et al. 2021. Data were split using a stratified sampling according to the distribution of a trait in a histogram to randomly select 60% samples for model calibration and the remaining 40% for independent model validation. On the calibration samples, 1000 repeated PLSR were applied using 80% of the samples each time. These repeated models were used to identify the optimal numbers of components required to avoid underfitting and overfitting for predictions (i.e., lignin = 6; water content = 8). Using the optimal number of components, PLSR coefficients were extracted and used to compute leaf traits. These models were assessed using R^2 and relative root mean squared error (rRMSE) between measurements and predictions on validation datasets (lignin: $R^2 = 0.65$, rRMSE = 0.26; water content: $R^2 = 0.6$, rRMSE = 0.15). All statistical analyses for these models were performed in R v. 3.6.3 (R Core Team 2020) using the package pls v. 2.7.1 (Mevik and Wehrens 2007) for PLSR modelling.