Received: 29 January 2024 | Revised: 5 July 2024 | Accepted: 11 September 2024

DOI: 10.1002/ecy.4500

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Canopy complexity drives positive effects of tree diversity on productivity in two tree diversity experiments

Catherine Fahey[1] | **Dennis Choi**[2] | **Jianmin Wang**[2] | **Grant M. Domke**[3] | **Joseph D. Edwards**[4] | **Songlin Fei**[2] | **Stephanie N. Kivlin**[4] | **Elizabeth A. LaRue**[5] | **Melissa K. McCormick**[1] | **William J. McShea**[6] | **Richard P. Phillips**[7] | **Jamie Pullen**[1] | **John D. Parker**[1]

[1]Smithsonian Environmental Research Center, Edgewater, Maryland, USA

[2]Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana, USA

[3]Northern Research Station, USDA Forest Service, St. Paul, Minnesota, USA

[4]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Knoxville, Tennessee, USA

[5]Department of Biological Sciences, The University of Texas at El Paso, El Paso, Texas, USA

[6]Smithsonian's National Zoo Conservation Biology Institute, Front Royal, Virginia, USA

[7]Department of Biology, Indiana University, Bloomington, Indiana, USA

Correspondence
Catherine Fahey
Email: faheyc@si.edu

Funding information
Division of Environmental Biology, Grant/Award Numbers: 2044406, 2106014, 2106065, 2106096, 2106103

Handling Editor: Anthony W. D'Amato

Abstract

Forest canopy complexity (i.e., the three-dimensional structure of the canopy) is often associated with increased species diversity as well as high primary productivity across natural forests. However, canopy complexity, tree diversity, and productivity are often confounded in natural forests, and the mechanisms of these relationships remain unclear. Here, we used two large tree diversity experiments in North America to assess three hypotheses: (1) increasing tree diversity leads to increased canopy complexity, (2) canopy complexity is positively related to tree productivity, and (3) the relationship between tree diversity and tree productivity is indirect and driven by the positive effects of canopy complexity. We found that increasing tree diversity from monocultures to mixtures of 12 species increases canopy complexity and productivity by up to 71% and 73%, respectively. Moreover, structural equation modeling indicates that the effects of tree diversity on productivity are indirect and mediated primarily by changes in internal canopy complexity. Ultimately, we suggest that increasing canopy complexity can be a major mechanism by which tree diversity enhances productivity in young forests.

KEYWORDS

BiodiversiTREE, biodiversity-ecosystem functioning, forest structural complexity, LiDAR, productivity, tree diversity, TreeDivNet

INTRODUCTION

Forests play a pivotal role in sustaining life on Earth by providing essential ecosystem services that support both ecological and human well-being, making it critical to understand their functioning. Forest biodiversity-ecosystem functioning (BEF) experiments show that diverse tree stands often exhibit higher net primary productivity (Huang et al., 2018; Shovon et al., 2022; Urgoiti et al., 2022), support greater diversity at higher trophic levels (Wan et al., 2020), and confer resilience against environmental perturbations, pests, and diseases (Guo et al., 2019; Jactel et al., 2017). Moreover, it is increasingly recognized that forest structural complexity may be an important mediator of ecosystem function that could underlie many BEF relationships (Lang et al., 2023; LaRue et al., 2019). For example, the architecture of the forest canopy, including variation in tree heights, canopy gaps, and vertical stratification, can influence tree productivity by altering light acquisition among co-occurring species through increased canopy packing (LaRue, Fahey, et al., 2023). Thus, increases in structural diversity may be a key factor modulating the relationships between forest diversity and tree productivity.

Remote-sensing techniques capturing forest structure across large spatial scales have generated insights into the relationships among tree diversity, canopy complexity, and tree productivity across a variety of natural forests (Gough et al., 2019; LaRue, Knott, et al., 2023; Yi et al., 2022). However, it remains difficult to determine causation from these relationships, as canopy complexity is often conflated with site-level variables like soil fertility, water availability, and successional stage, all of which can also be associated with productivity (Coverdale et al., 2023; Ehbrecht et al., 2021; Reed et al., 2022). For example, a positive relationship between structural diversity and primary productivity exists across National Ecological Observatory Network (NEON) sites in the Eastern United States (Gough et al., 2019), but the relationship was negative across sites with varying disturbance regimes in southeastern China (Yi et al., 2022). A mechanistic understanding of the complexity-productivity relationship is needed to explain this variation.

Tree diversity-ecosystem function experiments provide an ideal opportunity to tease apart diversity-productivity relationships and their mechanisms. Diversity-driven increases in productivity can stem from a range of possible mechanisms, including above- or belowground resource partitioning, selection effects, facilitation, or trophic interactions. Previous studies suggest that forest canopy traits, particularly ones that increase canopy complexity, may play an important role in the diversity-productivity relationship (Ray et al., 2023). This relationship may be driven by complementarity in resource use among species, for example, through not only increased light capture and canopy packing, but also potential selection effects from size-asymmetric competition (Pretzsch, 2014).

In this study, we took advantage of two large-scale tree biodiversity-ecosystem function experiments in eastern North America colocated with NEON sites to address three hypotheses that are key to understanding the impacts of tree diversity on forest productivity: (1) increasing tree diversity leads to increased canopy complexity, (2) greater canopy complexity is positively related to tree productivity, and (3) canopy complexity indirectly influences the relationship between tree diversity and productivity.

METHODS

Study sites and experimental design

We examined growth and canopy structure across two forest diversity experiments in North America, BiodiversiTREE@SERC and BiodiversiTREE@SCBI, both of which are part of the TreeDivNet global network of tree diversity experiments (Grossman et al., 2018). BiodiversiTREE@SERC is located at the Smithsonian Environmental Research Center (SERC) near Edgewater, Maryland, USA (38.87 °N, 76.55 °W, elevation: 15 m, mean annual temperature [MAT]: 13.2°C, mean annual precipitation [MAP]: 1068 mm). In the spring of 2013, 17,850 1-year-old bareroot whips from 16 tree species were planted in monoculture plots ($n = 2$ plots per tree species, 32 total plots), 4-species polyculture plots ($n = 19$), and 12-species polyculture plots ($n = 19$). Each plot is 35 m by 35 m, with 2.4-m spacing between trees, with a total of 255 trees per plot planted in an equidistant hexagonal grid (Appendix S1: Figure S1A). All 16 tree species are native to mid-Atlantic forests and were selected to include the most common species in surrounding forests, including *Acer rubrum*, *Carpinus caroliniana*, *Carya tomentosa*, *Cayra glabra*, *Cornus florida*, *Fagus grandifolia*, *Fraxinus pennsylvanica*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Platanus occidentalis*, *Quercus alba*, *Quercus pagoda*, *Quercus rubra*, *Quercus velutina*, and *Ulmus americana*. The site is unfenced and, thus, accessible to common herbivores like white-tailed deer (*Odocoileus virginianus*). In 2019 and 2022, we measured tree dbh on 50 randomly selected "focal" trees out of the 110 total trees within the interior of each plot (excluding the outer three rows to reduce edge effects). All live stems with a height greater than 1.3 m were measured.

BiodiversiTREE@SCBI is located at the Smithsonian Conservation Biology Institute (SCBI) near Front Royal, Virginia, USA (38.89 °N, 78.16 °W, elevation: 350 m, MAT: 12.6°C, MAP: 1102 mm). In the spring of 2014, 10,000 1-year-old bareroot whips were planted from 16 tree species. Trees were planted in monoculture plots ($n = 2$ plots per tree species, 32 total plots), 4-species polyculture plots ($n = 10$), or 12-species polyculture plots ($n = 18$). Each plot is 35 m by 35 m, with 3 m between trees, with a total of 145 trees per plot planted in a diamond grid (Appendix S1: Figure S1B). The 16 tree species are all native to Mid-Atlantic forests, including *A. rubrum*, *C. glabra*, *Castanea dentata*, *Celtis occidentalis*, *Corylus americana*, *Diospyros virginiana*, *F. grandifolia*, *F. pennsylvanica*, *L. tulipifera*, *P. occidentalis*, *Prunus serotina*, *Q. alba*, *Quercus prinus*, *Q. rubra*, *Q. velutina*, and *Tilia americana*. Of the 16 species at each site, nine species are common between the two sites, and seven species are unique. The site is surrounded by a 2.5-m fence to reduce damage by white-tailed deer but did not prevent periodic damage from American black bear (*Ursus americana*) at SCBI. Tree dbh was measured for all live trees within the interior of each plot (65 trees/plot) in 2019 and 2022. Only the largest stem per tree with a height greater than 1.3 m was measured.

For both sites, aboveground biomass (AGB) was estimated from genus or species-specific allometric equations from dbh measurements using the *allodb* package in R (Gonzalez-Akre et al., 2023) (Appendix S1: Table S1). Aboveground production per individual per year (P) was calculated using the equation:

$$P = (\mathrm{AGB}_{2022} + \mathrm{mortality} - \mathrm{AGB}_{2019})/3\,\mathrm{years},$$

where AGB_{2022} and AGB_{2019} are the biomass of live stems in 2022 and 2019 respectively, and mortality is the biomass in 2019 of stems that died between 2019 and 2022 so that growth for stems that died is zero. Plot level values were calculated as the average production per individual of all the focal individuals per plot.

LiDAR measurements

Airborne light detection and ranging (LiDAR) data were collected during the growing season in 2016, 2017, 2019, 2021, and 2022 by the Airborne Observatory Platform (AOP) of the NEON at both sites (Appendix S1: Table S2) (NEON, 2023). To quantify the characteristics of vertical and horizontal canopy structure, we calculated five canopy complexity metrics derived from LiDAR data for each plot at each site including height, openness, exterior complexity (the canopy surface), and interior complexity (vertical canopy strata) (Appendix S1: Table S3) (Atkins et al., 2020). All complexity metrics were calculated after filtering out heights below 2 m to avoid detecting changes in vegetation from annual plot-cleaning. Plots where no trees attained greater than 2 m height during the experimental period were considered to have zero canopy complexity for all metrics, except rumple index which was set to its lowest value of 1. We generated a $1 \times 1\ \mathrm{m}^2$ canopy height model to derive the following metrics: mean outer canopy height (MOCH, mean value of canopy height model, in meters), canopy cover (1-deep gap fraction, proportion of canopy openings with heights less than 2 m, proportion), and canopy rumple index (surface roughness; ratio of canopy surface area to area of the 2D ground, ratio). Additionally, we calculated point-based canopy metrics, including the Gini coefficient (GC, unitless) index and foliage height diversity (FHD, unitless). All LiDAR data processing and analysis were performed using the *lidR* (Roussel et al., 2020) or *leafR* (de Almeida et al., 2021) packages.

Statistical analysis

All statistical analyses were performed in R version 4.3.1 (R Core Team, 2023). All five canopy structure variables were highly collinear ($R^2 = 0.60$–0.96), so we conducted models with each variable separately (Appendix S1: Figure S2). First, we conducted linear mixed-effects models testing for the fixed effects of tree diversity, year, site, and their interactions with each canopy structure metric with plot as a random effect. Because we found significant interactions between diversity and site, we then tested the same models for each site separately. Temporal autocorrelation was accounted for with a first-order autoregressive structure using the *nlme* package (Pinheiro et al., 2016). Individual pairwise contrasts among diversity levels by year were conducted using the *emmeans* package with Tukey adjustments (Lenth, 2023). To test whether the effects of tree diversity on productivity were direct or indirectly mediated by canopy complexity, we built structural equation models (SEMs) using the *piecewiseSEM* package (Lefcheck, 2016) for each site consisting of two linear models: (1) tree diversity effects on canopy complexity metrics in 2019 and (2) canopy complexity metrics and tree species diversity effects on log-transformed productivity between 2019 and 2022. This allowed us to assess the ability of canopy structure in 2019 to predict tree growth over the subsequent 3 years.

RESULTS

Diversity effects on structural complexity

We found positive effects of tree diversity on canopy structural metrics over time at both sites (Figure 1; Appendix S1: Figure S3, Tables S4 and S5). At SERC, a significant diversity effect on GC was observed as early as 2016 (1 vs. 12: $p = 0.047$), and at SCBI a significant diversity effect was first observed in 2019 (1 vs. 12: $p = 0.008$). By 2022, 9 years after planting at SERC, we observed significant diversity effects on both canopy complexity metrics. GC was 76% higher in 12 species mixtures compared with monocultures ($p < 0.001$), and 41% higher in 12 species mixtures versus four species mixtures ($p < 0.001$). FHD was 71% higher in 12 species mixtures compared with monocultures ($p < 0.001$).

By 2022, 8 years after planting, there were significant diversity effects for both internal canopy complexity metrics at SCBI. GC was 46% higher in four species

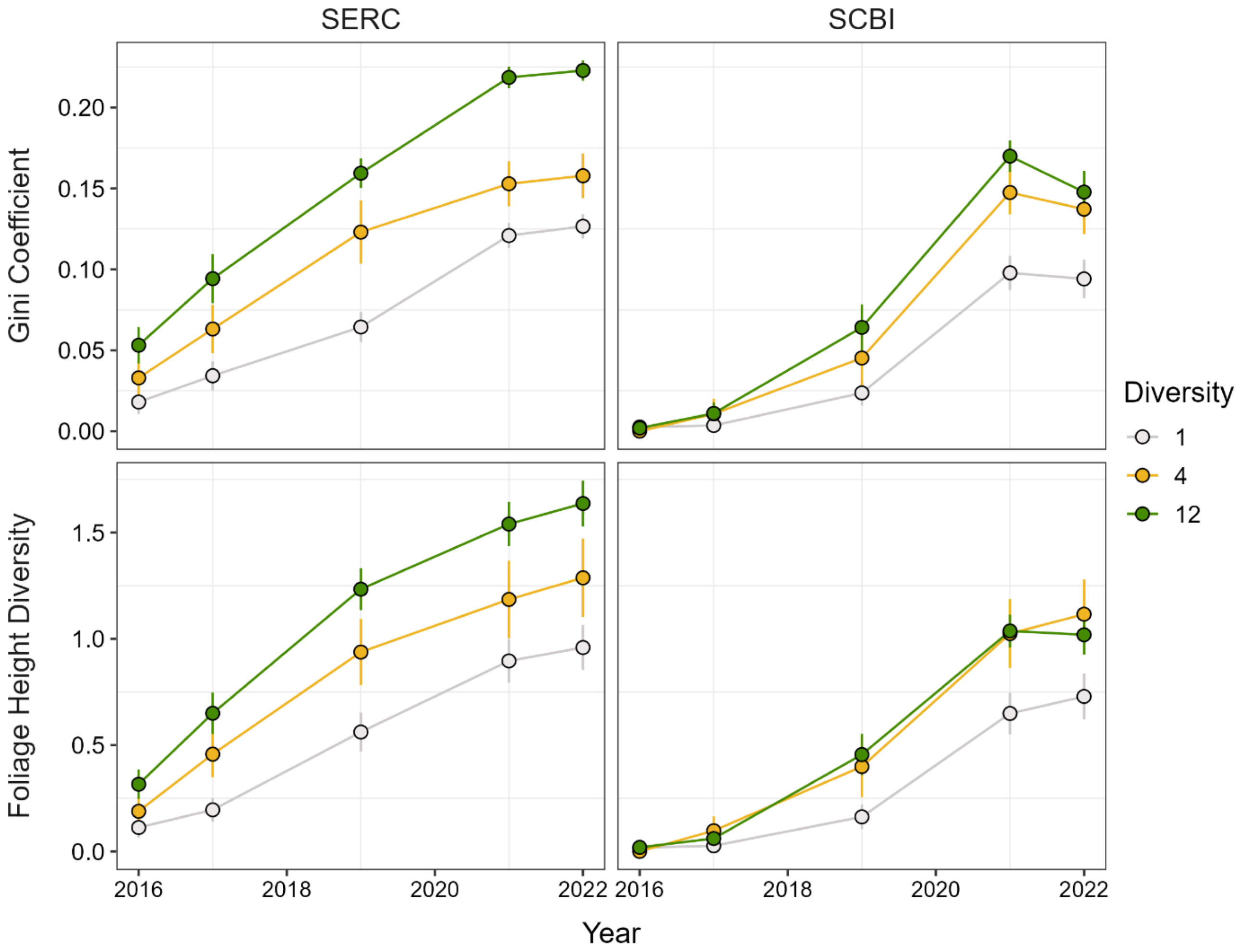

FIGURE 1 Light detection and ranging (LiDAR) metrics of canopy complexity, Gini coefficient, and foliage height diversity, for Smithsonian Environmental Research Center (SERC) and Smithsonian Conservation Biology Institute (SCBI) BiodiversiTREE sites over time between diversity treatments.

mixtures compared with monocultures ($p = 0.025$), and 57% higher in 12 species mixtures compared with monocultures ($p < 0.001$), but 4 and 12 species mixtures did not differ ($p = 0.818$). FHD was 53% higher in four species mixtures compared with monocultures ($p = 0.018$), and 40% higher in 12 species mixtures compared with monocultures ($p = 0.031$), but again did not differ between 4 and 12 species mixtures ($p = 0.794$), indicating a potential saturating relationship (Appendix S1: Figure S4).

Direct and indirect effects on productivity

At SERC, average productivity per year was 74% higher in 12 species mixtures compared with monocultures ($p = 0.002$) but not significantly different in 4 species mixtures than either monocultures or 12 species mixtures ($p > 0.1$; Appendix S1: Figure S5). At SCBI, productivity was marginally higher (65%) in 4 species mixtures ($p = 0.068$) but did not differ between 12 species mixtures and monocultures ($p = 0.121$). Across both sites, canopy complexity in 2019 was strongly related to productivity (Figure 2A; Appendix S1: Tables S6 and S7). SEMs further showed that both canopy complexity metrics were significant mediators of the diversity-productivity relationships across both sites. Diversity was positively related to GC (SERC: std. coef. = 0.53, $p < 0.001$; SCBI: std. coef. = 0.33, $p = 0.011$) and FHD (SERC: std. coef. =0.45, $p < 0.001$; SCBI: std. coef. = 0.32, $p = 0.013$), as was productivity and GC (SERC: std. coef. = 0.71, $p < 0.001$; SCBI: std. coef. = 0.59, $p < 0.001$) and FHD (SERC: std. coef. = 0.80, $p < 0.001$; SCBI: std. coef. = 0.58, $p < 0.001$), creating a positive indirect effect of diversity on productivity (Figure 2B; Appendix S1: Tables S6 and S7). In both SEMs, diversity had no direct effect on productivity ($p > 0.6$), and only an indirect effect on productivity via either of these internal canopy complexity metrics. At SERC, the FHD model in particular explained 66% of the

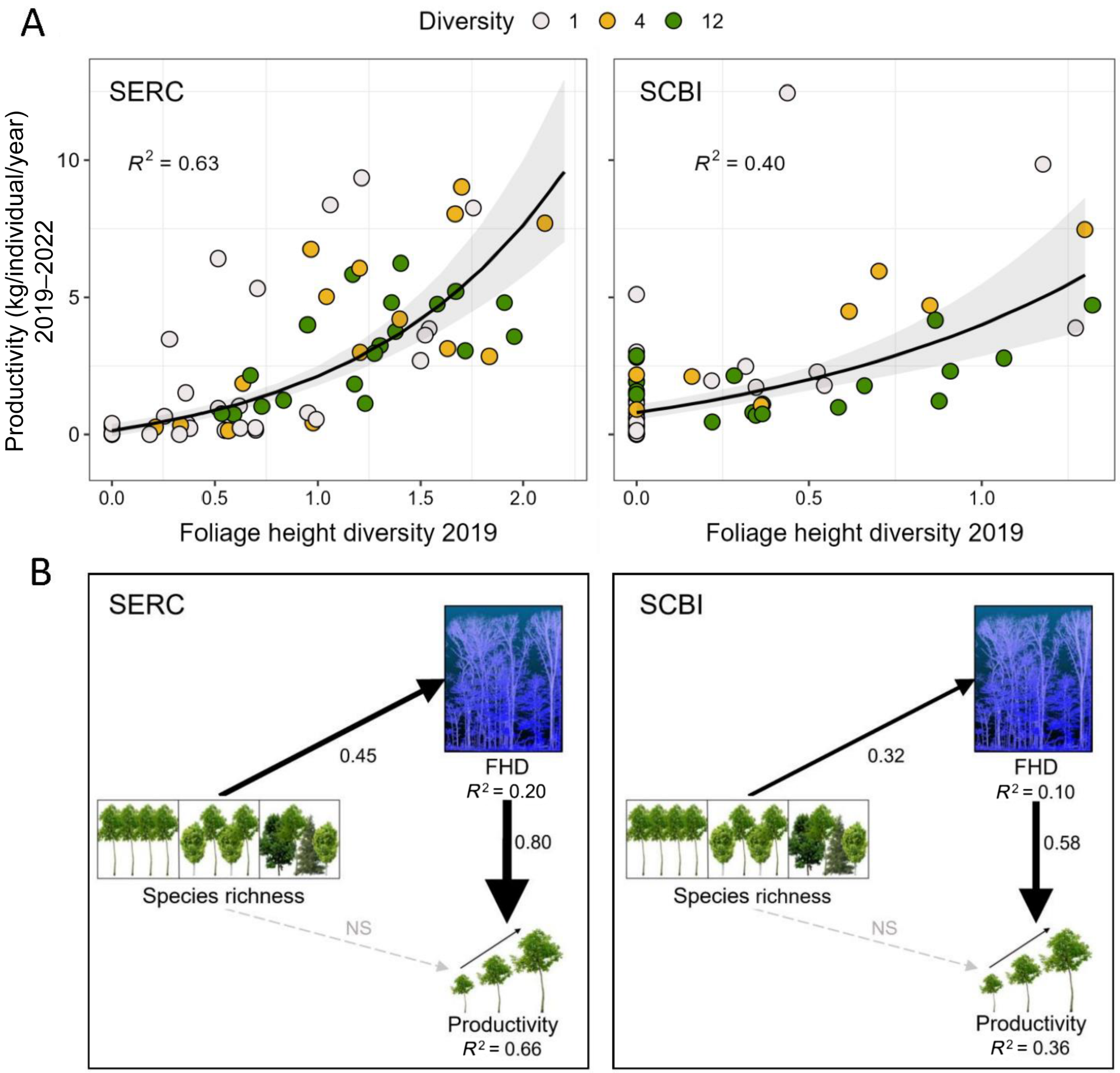

FIGURE 2 (A) Foliage height diversity (FDH) in 2019 versus tree productivity (in kilograms per individual per year) between 2019 and 2022 at Smithsonian Environmental Research Center (SERC) and Smithsonian Conservation Biology Institute (SCBI). (B) Structural equation models for the effect of tree richness on FDH (image credit: S. Fei) and productivity (log-transformed) at SERC and SCBI. Solid black arrows indicate significant paths and dashed gray arrows are nonsignificant paths. Standardized coefficients are displayed with corresponding path arrows and arrow size is proportional to the standardized coefficients. R^2 values for each component models are presented below corresponding response variables. White-tailed deer are excluded from plots at SCBI but open to browsing at SERC. All images licensed by Canva unless otherwise stated.

variation in productivity and 20% of the variation in FHD. At SCBI, the FHD model was similar but explained less variation compared with SERC, explaining 36% of variation in productivity and 10% of variation in FHD. Ultimately, across both sites, the two canopy complexity metrics played significant roles in driving positive diversity-productivity relationships. Additional canopy metrics are reported in Appendix S1: Figure S3, Tables S4 and S5.

DISCUSSION

We used LiDAR metrics to quantify canopy structural development over the course of 7 years across two tree diversity-ecosystem function experiments. In line with our hypotheses, we found that (1) increasing tree diversity led to increased canopy complexity, (2) canopy complexity showed a strong positive relationship to tree productivity, and (3) canopy complexity indirectly mediated the positive relationship between tree diversity and productivity at both sites. Thus, canopy complexity plays a primary role in driving the positive effects of tree diversity on tree productivity.

Diversity effects on canopy complexity

Diversity effects on canopy complexity emerged as quickly as 3–5 years after planting and became more pronounced over time at both sites. These early effects were likely driven by selection effects from fast growing early successional species and may shift to complementarity effects or trait dependent effects over time as has been observed for diversity-productivity relationships in forests (Urgoiti et al., 2022). Moreover, the shape of the diversity-complexity relationship provides further insight into the mechanisms that drive tree diversity-productivity relationships. Saturating relationships suggest functional redundancy between species, whereas linear relationships suggest more functional dissimilarity among species, and both have been observed in previous studies (Coverdale et al., 2023; Ehbrecht et al., 2017; Juchheim et al., 2020; Perles-Garcia et al., 2021). At SERC, canopy complexity metrics increased linearly across the diversity gradient and showed no signs of saturation, whereas at SCBI, increases in complexity saturated at four species mixtures. A more functionally dissimilar species pool at SERC seems unlikely given the taxonomically broad overlap in the species pools, but this is an area that deserves further attention as taxonomic and functional diversity are not perfectly correlated. Furthermore, environmental context can influence BEF relationships (Ratcliffe et al., 2017), though the level of environmental stress and species tolerance may interact resulting in species by environment interactions in functional complementarity among species. Topography and climate differ between the sites, where SCBI is higher elevation and has hilly terrain, whereas SERC has a coastal climate and minimal topography, so these differences could influence the strength and shape of the diversity effects on canopy complexity. Planting density is also lower at SCBI (145 trees per 35 × 35 m plot) compared with SERC (255 trees per 35 × 35 m plot) meaning light competition may be slower to develop at that site.

One prominent difference between the sites is the extent of browsing by white-tailed deer, which was greatly reduced by fencing at SCBI compared with SERC. The effects of browsing were clearly seen in the growth of *A. rubrum*, which because of extensive deer browsing at SERC were rarely able to reach dbh size (Cook-Patton et al., 2014; Devaney et al., 2020). Alternatively, *A. rubrum* was among the largest and fastest growing species at SCBI, where fencing prevented excessive deer browsing. Given the overall faster height growth at SERC, but with preferential browsing on some species, particularly in mixtures (Devaney et al., 2020), we suggest that early browsing on saplings could have suppressed the growth of palatable species and therefore initiated greater size asymmetry in canopy heights in mixtures at SERC (Reed et al., 2022). This is significant because the development of canopy structure during early forest succession can determine niche space for understory plants and wildlife populations resulting in differences in overall ecosystem function (Deere et al., 2020; LaRue et al., 2019; Rissanen et al., 2019). Further work is needed to investigate the influence of herbivore browsing as a potential moderating factor on the relationship between tree species diversity and structural complexity.

Diversity-canopy complexity-productivity relationship

Canopy complexity was strongly correlated with productivity. Interestingly, we demonstrated that diversity itself did not directly affect productivity, but internal canopy complexity mediated significant indirect effects of diversity on productivity at both sites. Greater canopy complexity can increase canopy space filling across canopy strata, thereby enhancing total light interception across space and time, for example with variation in sun angle (Dănescu et al., 2016; Jucker et al., 2015; Kunz et al., 2019; Mensah et al., 2018). Our results support findings from another tree-BEF experiment showing that stand structural complexity mediates a significant indirect effect of tree diversity on wood production and overyielding (Ray et al., 2023). However, our results contrast with the negative relationship observed between structural diversity and wood production across successional forests (Yi et al., 2022). Ultimately, despite varying strength in diversity-complexity and diversity-productivity relationships between sites, the indirect effect of diversity on productivity mediated by structural complexity was remarkably consistent. Therefore, we argue that increased canopy complexity is a primary mechanism driving diversity-productivity relationships in forests.

In summary, we highlight the positive impact of tree species diversity on forest canopy structural complexity and its relationship to productivity. The effect of tree diversity on canopy complexity was more pronounced at SERC than at SCBI, indicating the importance of considering site-specific conditions in understanding the dynamic progression of canopy complexity. Despite these differences, internal canopy complexity emerged as a key mediator between diversity and productivity across both sites, underscoring its crucial role in shaping the diversity effects observed in forest ecosystems. Furthermore, the strong correlation between internal canopy complexity and productivity across diversity treatments and species composition demonstrates that relatively easily obtained LiDAR data can predict forest productivity, at least in early successional forests. Ultimately, understanding the relationships among biodiversity, forest canopy structure, and productivity could inform forest management and conservation, particularly given recent calls to diversify planted forests to mitigate against global change scenarios (Messier et al., 2021).

ACKNOWLEDGMENTS

Funding was provided by NSF DEB No. 2106103 to Songlin Fei, Elizabeth LaRue, and Grant M. Domke; No. 2106096 to Richard P. Phillips; No. 2106065 to Stephanie Kivlin; and Nos. 2106014 and 2044406 to Catherine Fahey, John D. Parker, and Melissa K. McCormick. Janet Gingold, Steve Myers, Sam Newkirk, Shelley Bennett, and Grace Schilling contributed to dbh measurements at SERC and John Whitmoyer for maintaining plots at SCBI.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Fahey et al., 2024) are available in the Smithsonian Environmental Research Center's Figshare repository at https://doi.org/10.25573/serc.25106030.

ORCID

Catherine Fahey https://orcid.org/0000-0002-6987-0456
Dennis Choi https://orcid.org/0000-0002-4038-9204
Grant M. Domke https://orcid.org/0000-0003-0485-0355
Joseph D. Edwards https://orcid.org/0000-0002-0543-4233
Songlin Fei https://orcid.org/0000-0003-2772-0166
Stephanie N. Kivlin https://orcid.org/0000-0003-2442-7773
Elizabeth A. LaRue https://orcid.org/0000-0002-9535-0630
Melissa K. McCormick https://orcid.org/0000-0001-6564-7575
William J. McShea https://orcid.org/0000-0002-8102-0200
Richard P. Phillips https://orcid.org/0000-0002-1345-4138
Jamie Pullen https://orcid.org/0000-0001-5182-3662
John D. Parker https://orcid.org/0000-0002-3632-7625

REFERENCES

Atkins, J. W., B. Bond-Lamberty, R. T. Fahey, L. T. Haber, E. Stuart-Haëntjens, B. S. Hardiman, E. Larue, et al. 2020. "Application of Multidimensional Structural Characterization to Detect and Describe Moderate Forest Disturbance." *Ecosphere* 11: e03156.

Cook-Patton, S. C., M. LaForgia, and J. D. Parker. 2014. "Positive Interactions between Herbivores and Plant Diversity Shape Forest Regeneration." *Proceedings of the Royal Society B: Biological Sciences* 281(1783): 20140261.

Coverdale, T. C., A. B. Davies, and C. A. Silva. 2023. "Unravelling the Relationship between Plant Diversity and Vegetation Structural Complexity: A Review and Theoretical Framework." *Journal of Ecology* 111: 1378–95.

Dănescu, A., A. T. Albrecht, and J. Bauhus. 2016. "Structural Diversity Promotes Productivity of Mixed, Uneven-Aged Forests in Southwestern Germany." *Oecologia* 182: 319–333.

de Almeida, D. R. A., S. C. Stark, C. A. Silva, C. Hamamura, and R. Valbuena. 2021. "leafR: Calculates the Leaf Area Index (LAD) and Other Related Functions." version 0.3.5. CRAN. https://cran.r-project.org/web/packages/leafR/index.html.

Deere, N. J., G. Guillera-Arroita, T. Swinfield, D. T. Milodowski, D. A. Coomes, H. Bernard, G. Reynolds, Z. G. Davies, and M. J. Struebig. 2020. "Maximizing the Value of Forest Restoration for Tropical Mammals by Detecting Three-Dimensional Habitat Associations." *Proceedings of the National Academy of Sciences of the United States of America* 117: 26254–62.

Devaney, J. L., J. Pullen, S. C. Cook-Patton, K. T. Burghardt, and J. D. Parker. 2020. "Tree Diversity Promotes Growth of Late Successional Species despite Increasing Deer Damage in a Restored Forest." *Ecology* 101: e03063.

Ehbrecht, M., P. Schall, C. Ammer, and D. Seidel. 2017. "Quantifying Stand Structural Complexity and its Relationship with Forest Management, Tree Species Diversity and Microclimate." *Agricultural and Forest Meteorology* 242: 1–9.

Ehbrecht, M., D. Seidel, P. Annighöfer, H. Kreft, M. Köhler, D. C. Zemp, K. Puettmann, et al. 2021. "Global Patterns and Climatic Controls of Forest Structural Complexity." *Nature Communications* 12: 1–12.

Fahey, C., D. Choi, J. Wang, G. M. Domke, J. D. Edwards, S. Fei, S. N. Kivlin, et al. 2024. "Canopy Complexity Drives Positive Effects of Tree Diversity on Productivity in Two Tree Diversity Experiment." Smithsonian Environmental Research Center. Dataset. https://doi.org/10.25573/serc.25106030.v1.

Gonzalez-Akre, E., C. Piponiot, M. Lepore, and K. Anderson-Teixeira. 2023. "allodb: Tree Biomass Estimation at Extra-Tropical Forest Plots." version 0.1.9. https://github.com/ropensci/allodb.

Gough, C. M., J. W. Atkins, R. T. Fahey, and B. S. Hardiman. 2019. "High Rates of Primary Production in Structurally Complex Forests." *Ecology* 100: e02864.

Grossman, J. J., M. Vanhellemont, N. Barsoum, J. Bauhus, H. Bruelheide, B. Castagneyrol, J. Cavender-Bares, et al. 2018. "Synthesis and Future Research Directions Linking Tree Diversity to Growth, Survival, and Damage in a Global Network of Tree Diversity Experiments." *Environmental and Experimental Botany* 152: 68–89.

Guo, Q., S. Fei, K. M. Potter, A. M. Liebhold, and J. Wen. 2019. "Tree Diversity Regulates Forest Pest Invasion." *Proceedings of the National Academy of Sciences of the United States of America* 116: 7382–86.

Huang, Y., Y. Chen, N. Castro-Izaguirre, M. Baruffol, M. Brezzi, A. Lang, Y. Li, et al. 2018. "Impacts of Species Richness on Productivity in a Large-Scale Subtropical Forest Experiment." *Science* 362: 80–83.

Jactel, H., J. Bauhus, J. Boberg, D. Bonal, B. Castagneyrol, B. Gardiner, J. R. Gonzalez-Olabarria, J. Koricheva, N. Meurisse, and E. G. Brockerhoff. 2017. "Tree Diversity Drives Forest Stand Resistance to Natural Disturbances." *Current Forestry Reports* 3: 223–243.

Juchheim, J., M. Ehbrecht, P. Schall, C. Ammer, and D. Seidel. 2020. "Effect of Tree Species Mixing on Stand Structural Complexity." *Forestry: An International Journal of Forest Research* 93: 75–83.

Jucker, T., O. Bouriaud, and D. A. Coomes. 2015. "Crown Plasticity Enables Trees to Optimize Canopy Packing in Mixed-Species Forests." *Functional Ecology* 29: 1078–86.

Kunz, M., A. Fichtner, W. Härdtle, P. Raumonen, H. Bruelheide, and G. von Oheimb. 2019. "Neighbour Species Richness and Local Structural Variability Modulate Aboveground Allocation Patterns and Crown Morphology of Individual Trees." *Ecology Letters* 22: 2130–40.

Lang, A. K., E. A. LaRue, S. N. Kivlin, J. D. Edwards, R. P. Phillips, J. Gallion, N. Kong, et al. 2023. "Forest Structural Diversity Is Linked to Soil Microbial Diversity." *Ecosphere* 14: e4702.

LaRue, E. A., R. T. Fahey, B. C. Alveshere, J. W. Atkins, P. Bhatt, B. Buma, A. Chen, et al. 2023. "A Theoretical Framework for the Ecological Role of Three-Dimensional Structural Diversity." *Frontiers in Ecology and the Environment* 21: 4–13.

LaRue, E. A., B. S. Hardiman, J. M. Elliott, and S. Fei. 2019. "Structural Diversity as a Predictor of Ecosystem Function." *Environmental Research Letters* 14: 114011.

LaRue, E. A., J. A. Knott, G. M. Domke, H. Y. H. Chen, Q. Guo, M. Hisano, C. Oswalt, et al. 2023. "Structural Diversity as a Reliable and Novel Predictor for Ecosystem Productivity." *Frontiers in Ecology and the Environment* 21: 33–39.

Lefcheck, J. S. 2016. "piecewiseSEM: Piecewise Structural Equation Modelling in R for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7: 573–79.

Lenth, R. 2023. "emmeans: Estimated Marginal Means, aka Least-Squares Means." https://CRAN.R-project.org/package=emmeans.

Mensah, S., B. du Toit, and T. Seifert. 2018. "Diversity–Biomass Relationship across Forest Layers: Implications for Niche Complementarity and Selection Effects." *Oecologia* 187: 783–795.

Messier, C., J. Bauhus, R. Sousa-Silva, H. Auge, L. Baeten, N. Barsoum, H. Bruelheide, et al. 2021. "For the Sake of Resilience and Multifunctionality, Let's Diversify Planted Forests!" *Conservation Letters* 15(1): e12829.

National Ecological Observatory Network (NEON). 2023. *Discrete Return LiDAR Point Cloud (DP1.30003.001)*. https://doi.org/10.48443/xxby-5a18.

Perles-Garcia, M. D., M. Kunz, A. Fichtner, W. Härdtle, and G. von Oheimb. 2021. "Tree Species Richness Promotes an Early Increase of Stand Structural Complexity in Young Subtropical Plantations." *Journal of Applied Ecology* 58: 2305–14.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and The R Development Core Team. 2016. "nlme: Linear and nonlinear mixed effects models."

Pretzsch, H. 2014. "Canopy Space Filling and Tree Crown Morphology in Mixed-Species Stands Compared with Monocultures." *Forest Ecology and Management* 327: 251–264.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Ratcliffe, S., C. Wirth, T. Jucker, F. van der Plas, M. Scherer-Lorenzen, K. Verheyen, E. Allan, et al. 2017. "Biodiversity and Ecosystem Functioning Relations in European Forests Depend on Environmental Context." *Ecology Letters* 20: 1414–26.

Ray, T., B. M. Delory, R. Beugnon, H. Bruelheide, S. Cesarz, N. Eisenhauer, O. Ferlian, J. Quosh, G. von Oheimb, and A. Fichtner. 2023. "Tree Diversity Increases Productivity through Enhancing Structural Complexity across Mycorrhizal Types." *Science Advances* 9(40): eadi2362.

Reed, S. P., A. A. Royo, A. T. Fotis, K. S. Knight, C. E. Flower, and P. S. Curtis. 2022. "The Long-Term Impacts of Deer Herbivory in Determining Temperate Forest Stand and Canopy Structural Complexity." *Journal of Applied Ecology* 59: 812–821.

Rissanen, K., M. O. Martin-Guay, A. S. Riopel-Bouvier, and A. Paquette. 2019. "Light Interception in Experimental Forests Affected by Tree Diversity and Structural Complexity of Dominant Canopy." *Agricultural and Forest Meteorology* 278: 107655.

Roussel, J. R., D. Auty, N. C. Coops, P. Tompalski, T. R. H. Goodbody, A. S. Meador, J. F. Bourdon, F. de Boissieu, and A. Achim. 2020. "lidR: An R Package for Analysis of Airborne Laser Scanning (ALS) Data." *Remote Sensing of Environment* 251: 112061.

Shovon, T. A., S. Kang, M. Scherer-Lorenzen, and C. A. Nock. 2022. "Changes in the Direction of the Diversity–Productivity Relationship over 15 Years of Stand Development in a Planted Temperate Forest." *Journal of Ecology* 110: 1125–37.

Urgoiti, J., C. Messier, W. S. Keeton, P. B. Reich, D. Gravel, and A. Paquette. 2022. "No Complementarity No Gain—Net Diversity Effects on Tree Productivity Occur Once Complementarity Emerges during Early Stand Development." *Ecology Letters* 25: 851–862.

Wan, N. F., X. R. Zheng, L. W. Fu, L. P. Kiær, Z. Zhang, R. Chaplin-Kramer, M. Dainese, et al. 2020. "Global Synthesis of Effects of Plant Species Diversity on Trophic Groups and Interactions." *Nature Plants* 6: 503–510.

Yi, X., N. Wang, H. Ren, J. Yu, T. Hu, Y. Su, X. Mi, Q. Guo, and K. Ma. 2022. "From Canopy Complementarity to Asymmetric Competition: The Negative Relationship between Structural Diversity and Productivity during Succession." *Journal of Ecology* 110: 457–465.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Fahey, Catherine, Dennis Choi, Jianmin Wang, Grant M. Domke, Joseph D. Edwards, Songlin Fei, Stephanie N. Kivlin, et al. 2025. "Canopy Complexity Drives Positive Effects of Tree Diversity on Productivity in Two Tree Diversity Experiments." *Ecology* 106(1): e4500. https://doi.org/10.1002/ecy.4500