Received: 20 March 2023 | Revised: 17 May 2023 | Accepted: 25 May 2023

DOI: 10.1002/ecy.4116

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Positive tree diversity effects on arboreal spider abundance are tied to canopy cover in a forest experiment

Elizabeth M. Butz[1] | **Lauren M. Schmitt**[1] | **John D. Parker**[2] | **Karin T. Burghardt**[1,2]

[1]Department of Entomology, University of Maryland, College Park, Maryland, USA

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

Correspondence
Karin T. Burghardt
Email: kburghar@umd.edu

Funding information
National Science Foundation, Grant/Award Numbers: DEB-2044361, DEB-2044406, DEB-2106014, REU-1659668, REU-1950656; U.S. Department of Agriculture, Grant/Award Numbers: MD-ENTM-19001, MD-ENTM-19932

Handling Editor: Kirsten M. Prior

Abstract

Human actions are decreasing the diversity and complexity of forests, and a mechanistic understanding of how these changes affect predators is needed to maintain ecosystem services, including pest regulation. Using a large-scale tree diversity experiment, we investigate how spiders respond to trees growing in plots of single or mixed species combinations (4 or 12) by repeatedly sampling 540 trees spanning 15 species. In 2019 (6 years post-establishment), spider responses to tree diversity varied by tree species. By 2021, diversity had a more consistently positive effect, with trees in 4- or 12-species plots supporting 23% or 50% more spiders, respectively, compared to conspecifics in monocultures. Spiders showed stronger tree species preferences in late summer, and the positive impact of plot diversity doubled. In early summer, the positive diversity effect was tied to higher canopy cover in diverse plots, leading to higher spider densities. This indirect path strengthened in late summer, with an additional direct effect of plot diversity on spiders. Prey availability was higher in diverse plots but was not tied to spider density. Overall, diverse plots supported more predators, partly by increasing available habitat. Adopting planting strategies focused on species mixtures may better maintain higher trophic levels and ecosystem functions.

KEYWORDS

arthropods, biodiversity-ecosystem functioning, predator, tree architecture, tree diversity, trophic interactions

INTRODUCTION

A central question in community ecology is how diversity at lower trophic levels, such as primary producers, shapes populations or functions in higher trophic levels. These patterns need better resolution in forest ecosystems, where 80% of the world's terrestrial biomass and 50% of biodiversity resides (Shvidenko & Gonzalez, 2005). Humans are reducing diversity and complexity in forests through deforestation and degradation while adding millions of trees through afforestation and reforestation (Yao et al., 2019). As humans reshape forest diversity and structure, it is urgent to understand how these changes will impact forest function, including support for higher trophic levels (Holl & Brancalion, 2020).

Biodiversity-ecosystem function (BEF) experiments interrogate the relationship between biodiversity and ecosystem function, such as the abundance and composition

of upper trophic levels that may contribute to pest regulation (Siemann et al., 1998). Initial terrestrial BEF experiments were conducted primarily in grasslands and found a positive relationship between plant diversity and predator abundance (Haddad et al., 2001, 2009). Whether this relationship is the same in forests garnered recent attention. A 2020 meta-analysis that included seven predator abundance studies in forests found high variability in predator responses to tree diversity. This suggests context-dependence, perhaps predator-guild or site-driven, requiring additional studies to resolve this question (Wan et al., 2020). More recently, a separate meta-analysis found that tree diversity was more positively linked with natural enemy abundance and diversity in the tropics compared to temperate areas (Stemmelen et al., 2022). However, the temperate studies of arthropod predators mainly occurred in Eurasia, with just one study in temperate North America quantifying predation rates (Nixon & Roland, 2012) and none quantifying abundance. Predation rates and abundances are generally positively correlated, but their relationship can be mediated by other factors, including plant architecture (Pearson, 2009). While climatically similar and composed of functionally similar species, European forests contain fewer tree species than eastern North American forests (Ordonez & Svenning, 2018); these differences in tree richness could alter the relationship between tree diversity and predator abundance. Thus, how North American arthropod predators respond to forest diversity remains to be determined.

Further, the relative importance of the mechanistic pathways by which tree diversity alters predator abundance remains unresolved across ecosystems (Staab & Schuldt, 2020). Higher-order arthropods in forests are diverse, abundant, and interconnected by complex food webs. Spiders are critical predators in forests (Turnbull, 1973), consuming 400–800 million tons of primarily insect and collembolan prey annually—equivalent to ~1% of global terrestrial net primary production (Nyffeler & Birkhofer, 2017). Spiders shape herbivore communities directly through consumption and indirectly by changing behavior (Schmitz et al., 1997), often collectively resulting in an indirect positive effect on plants. This top-down control forms the basis of the classical "enemies hypothesis," which predicts that plant diversity will increase herbivore diversity and, thus, predator diversity and abundance (Letourneau, 1987). Empirical tests of the enemies hypothesis in forests have found mixed results, perhaps because even low-diversity forests provide structural diversity (Staab & Schuldt, 2020).

However, emerging evidence suggests that forest diversity also modifies habitat characteristics such as tree architecture, thus indirectly affecting spiders. Spiders prefer complex habitat when it correlates with prey abundance or provides refuge from vertebrate or invertebrate predators (Halaj et al., 1998; Langellotto & Denno, 2004). Structural characteristics such as tree height, canopy closure, and foliage density are aspects of habitat complexity influencing spider distribution (Uetz, 1991), with denser foliage supporting more arboreal species (De Souza & Martins, 2005; Hatley & Macmahon, 1980). Higher levels of tree diversity can also alter tree morphology and allometry and, thus, canopy cover experienced by spiders (Guillemot et al., 2020; Williams et al., 2021), providing a diversity-driven mechanism underlying spider tree use in forests. The importance of trees as habitat may also vary seasonally, with more arboreal spiders observed in hotter months (Hatley & Macmahon, 1980; Hsieh & Linsenmair, 2012), possibly due to the cooling effects of shading on spider temperature, which affects development and behavior (Opell et al., 2007; Romero et al., 2022).

Here, we focused on how tree diversity shapes spider abundance by leveraging a large-scale forest diversity experiment. Specifically, we ask:

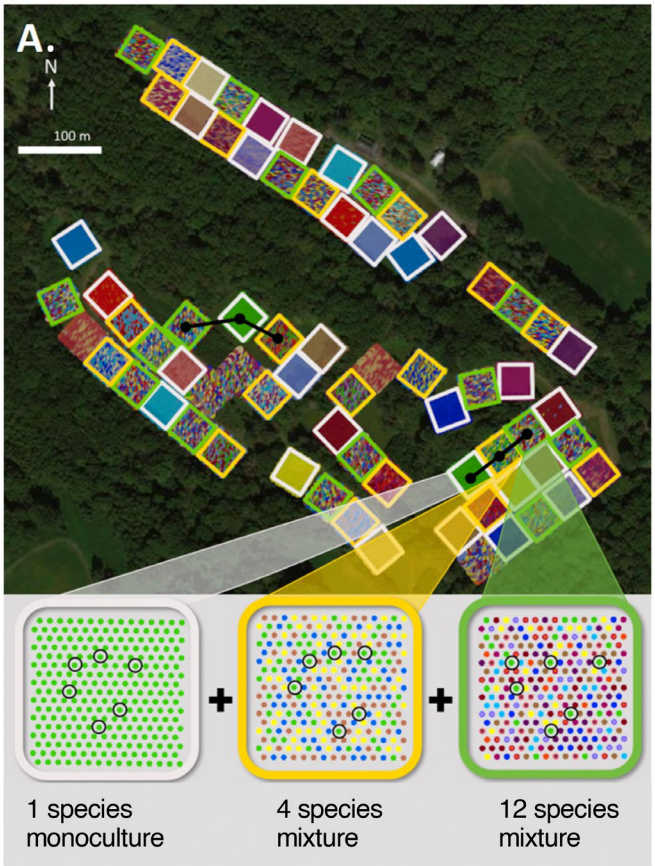
1. How tree-dwelling spiders respond to plot diversity and tree species identity;
2. Whether the importance of plot diversity for spiders shifts seasonally; and
3. Whether tree architecture or prey availability explains diversity-driven differences in spider abundances.

As spider abundance often increases with vegetation complexity, we predicted that trees in more diverse experimental plots would support more spiders. We also predicted that spiders would use trees at higher rates in late summer when shelter from high temperatures may be more critical. Last, we expected spider abundance to correlate with prey item availability and that taller trees with greater canopy cover would support higher spider densities.

METHODS

Site details

This study was conducted in 2019 and 2021 at the "BiodiversiTREE" experiment at the Smithsonian Environmental Research Center in Edgewater, Maryland, USA (38°52′ N 76°33′ W). In 2013, the site was reforested from corn agriculture into a classic BEF design with 75 plots measuring 35 × 35 m (Figure 1A) planted with 255 trees each, spaced 2.5 m apart. Diversity manipulations of 1, 4, or 12 tree species were drawn from 16 common species native to Maryland (Figure 1B; for more site



B.

Scientific Name	Common Name	Species Code
Acer rubrum	Red maple	ACRU
Carpinus caroliniana	American hornbeam	CACA
**Carya glabra*	*Pignut hickory	*CAGL
Carya tomentosa	Mockernut hickory	CATO
Cornus florida	Dogwood	COFL
Fagus grandifolia	Beech	FAGR
Fraxinus pennsylvanica	Green ash	FRPE
Liriodendron tulipifera	Tulip poplar	LITU
Liquidambar styraciflua	Sweetgum	LIST
Nyssa sylvatica	Blackgum	NYSY
Platanus occidentalis	Sycamore	PLOC
Quercus alba	White oak	QUAL
Quercus pagoda	Cherrybark oak	QUPA
Quercus rubra	Red oak	QURU
Quercus velutina	Black oak	QUVE
Ulmus americana	American elm	ULAM

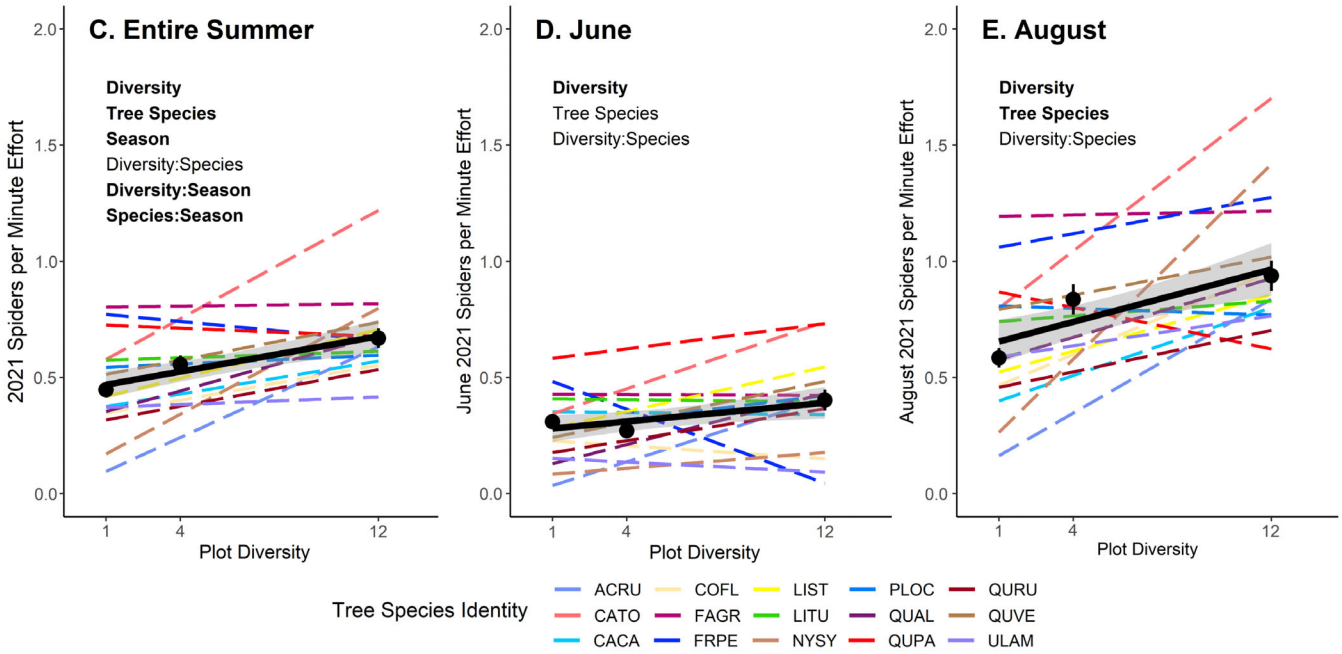


FIGURE 1 Map of the BiodiversiTREE experiment (A). The plot-level diversity treatment is indicated by the outline color of each plot (1 = gray, 4 = yellow, or 12 = green), while each dot represents a single tree. For 15 of the 16 tree species planted in the experiment (B), we sampled spiders from 2 replicates of 6 individual trees in the same spatial arrangement in 1-, 4-, and 12-species plots, all containing that focal species. Each grouping of 18 trees is termed a "triplet." Here, we illustrate this design for LITU; an identical approach was used for the other 14 species. We sampled two triplets for each species, one in each spatial block, equaling 540 focal trees. Species codes are the first two letters of the genus and species. *Carya glabra* is in the experiment but not sampled due to low survival. Spiders found per minute effort across 15 tree species, each growing in plots of three different levels of tree diversity treatments (1, 4, or 12 species) in 2021 across both summer samples (C), only June (D), or only August (E). Lines shown are regression lines for each tree species separately (dashed, colored) and the overall raw means with standard error bars (black, solid). Fixed effects from LMM models are bolded where significant ($p < 0.05$).

description, see Griffin et al., 2019 and Devaney et al., 2020). This is a young successional forest, with dynamic changes in tree size. The mean tree height was 2.36 m in 2019 and 3.08 m by 2021. Abiotic conditions at the site were recorded using the Vaisala Weather Transmitter model WXT536 on a 120′ tower (36.6 m).

Experimental design

We selected 540 focal trees for repeated sampling from 15 of the 16 tree species in the experiment. We used a paired focal tree sampling design to examine how plot diversity alters spiders' use of individual focal trees. For each tree species, we sampled trees in a triplet design, where we paired one monoculture with the nearest 4- and 12-species plot containing the focal species (Figure 1A). In each plot within a triplet, we sampled six trees of the focal species. Focal trees were evenly spaced in the plot interior to minimize edge effects (Figure 1A). We repeated this for a second monoculture, creating two spatial blocks of paired treatments per tree species (Figure 1A). In sum, we sampled spiders from three diversity treatments × 15 tree species × 2 blocks/triplets × 6 trees = 540 trees. In 2019, we sampled one block in June ($n = 270$) and one in August ($n = 270$). In 2021, both blocks were sampled during June ($n = 540$) and again in August ($n = 540$ trees). Between 2019 and 2021, 35 focal trees had no accessible foliage or had died; here, we switched the focal tree to the nearest conspecific tree with accessible foliage.

Spider sampling

We sampled spiders from ~8:00 AM to 3:00 PM in dry weather. To minimize temporal and observer variation, the same set of observers searched all 18 trees within a triplet (species nested in block) on the same day. For this study, we consider "spiders" to include the two large-bodied arboreal Arachnida predator groups found at the site: members of the orders Araneae and Opiliones. Using a timed visual search technique with standardized effort, we sampled living spiders non-destructively to avoid impacts on other long-term trophic measurements in the experiment. For each tree, we searched all foliage and branches within reach, tallying spiders found over 4 min of sampling effort split across observers. Our methodology accurately captured spider density but limited our ability to quantify diversity simultaneously; thus, we focus here on abundance. In rare cases, we exhaustively sampled all leaves before time elapsed. Here, the search ended early. Total search time was used for effort standardization by dividing spider number by total time sampled and comparing equivalent effort across trees (i.e., spiders per minute effort, a metric of spider density). We excluded one focal tree from the 2019 analysis containing a recently hatched spider egg sac as these individuals had not yet made individual dispersal or habitat choices.

Prey availability sampling

During each spider sampling visit, trees were also visually searched for the same duration (target = 4 min) for caterpillar prey items—any herbivorous larvae belonging to the order Lepidoptera (moths and butterflies) or the suborder Symphyta (sawflies) within the order Hymenoptera. We used the abundance of caterpillars per minute sampling effort for each sample date as a proxy for focal tree prey availability for spiders.

Tree architecture measurements

We quantified tree architecture in two ways. First, in winter of 2021, we measured tree height (in centimeters) with a measuring tape, or when trees were taller than 2 m, a rangefinder (Bosch GLM400c Blaze Laser Measure). These measurements were not available for the subset of 35 trees that were substituted into the sample in June 2021 when the foliage of some original 2019 focal trees became inaccessible for sampling. Second, in July 2021, we used the Canopeo application (Patrignani & Ochsner, 2015) to quantify the canopy cover of each focal tree. To capture this across variably sized trees, we used a multi-pronged approach. When crown height, or the height of the first branch on the trunk, was >1 m, we took upward-facing photos 1 m from the trunk and off the ground. When crown height was ≤1 m, we took photos at crown height. We considered focal trees without side branches and without taller neighbors to have a canopy cover of zero. For each image, we manually adjusted the hue threshold in Canopeo to calculate the percent canopy cover. We excluded all trees ($n = 40$) from the analysis where relocation or image quality issues decreased metric accuracy.

Statistical methods

Analyses were done in R version 4.2.1 (R Core Team, 2021). We used the "lme4" package to run a series of linear mixed models (Bates et al., 2022) with a log-transformed response variable of spiders per minute search effort to achieve normally distributed model

residuals. We included a random intercept for "triplet" ($n = 30$) accounting for the spatially blocked and tree species-matched sampling design (Figure 1A). We used anova() from the "lmerTest" package to perform F-tests with Type III Sums of Squares using Satterthwaite approximation for degrees of freedom (Kuznetsova et al., 2017).

Preliminary 2019 spider response to treatments model

We first built a model to determine if spider abundance was explained by the fixed effects of plot diversity, focal tree species identity, or if the impact of diversity depended on tree species, as follows: spiders per minute ~ tree species + plot diversity + tree species × plot diversity + (1|triplet).

2021 Spider response to treatments model

In 2021, we visited each tree in June and August. We added a fixed effect of season and an interaction between season and both plot diversity and tree species to test if the effect of diversity or species changed over the summer using the model structure: spiders per minute ~ tree species + diversity + season + season × diversity + season × tree species + tree species × plot diversity + (1|triplet). As both two-way interactions involving season were significant, we ran an additional simplified model for each season individually using the same structure, but without season as an individual or interactive fixed effect. We used these simplified models to aid in interpreting the interactive effects.

2021 Path analysis with focal tree attributes

Last, we performed a confirmatory path analysis to test if our data support a causal model where plot diversity alters spider abundance by changing attributes of individual focal trees. A local estimation approach was chosen to allow the specification of nested random effects in the structural equation model (SEM). We used the "piecewise" package (Lefcheck, 2016) to specify an a priori candidate model with one direct path from plot diversity to spider density and three indirect paths from plot diversity to spider response through (1) tree canopy cover, (2) tree height, and (3) prey availability. We also included direct paths from tree height to tree canopy cover as we would expect taller trees to have more vertical space for the foliage to fill and one between tree height and prey availability, as adult insects often select taller, more apparent trees for oviposition (Castagneyrol et al., 2013). We ran a separate SEM for each season, including all trees with a complete set of attribute measurements (June = 467 trees; August = 470 trees). All piecewise mixed models were fit using the lme() command in the "nlme" package with the fixed effects specified by the paths above and a random intercept for tree species nested within block. The global fit of the data to the model structure was tested using Fisher's C derived from Shipley's test of directed separation. A p-value >0.05 indicates that the data adequately fit the model structure. If our data fit the overall model, we interpreted the standardized coefficients and significance tests for individual paths.

RESULTS

In 2019, we sampled 499 trees (230 in June and 269 in August) and tallied 677 spiders, with a mean of 0.398 (±0.023, SE) per minute sampling effort per tree. In 2021, we sampled 526 trees in June and 529 trees in August and counted 1995 total spiders, with a mean of 0.554 (±0.021, SE) per minute sampling effort per tree. Common spiders included web- and orb-building, ambush, and active hunting spiders and harvestmen species (Burghardt et al., 2023).

2019 Spider response to treatments

Tree species and plot diversity interactively shaped spider abundance ($F_{14,450} = 1.76$, $p = 0.04$), with higher plot diversity resulting in more spiders on some but not all tree species (overall model goodness of fit—$R^2_m = 0.12$; $R^2_c = 0.17$; Appendix S1). While both were part of a significant interaction, neither plot diversity ($F_{1,450} = 2.75$, $p = 0.10$) nor tree species was significant ($F_{14,36} = 1.19$, $p = 0.32$) as an individual fixed effect.

2021 Spider response to treatments

Unlike in 2019, there was no interaction between tree species and plot diversity ($F_{14,993} = 1.31$, $p = 0.20$). Instead, spider abundance was consistently higher on trees in diverse plots ($F_{1,996} = 25.37$, $p < 0.001$). The fewest spiders were on focal trees in monoculture plots (0.45 ± 0.03), with 23% and 50% more in 4-species plots (0.55 ± 0.04) and 12-species plots (0.67 ± 0.04), respectively. Spider abundances differed across tree species ($F_{14,28} = 2.50$, $p = 0.02$) and were higher later in the season ($F_{1,993} = 46.77$, $p < 0.001$) (Figure 1C), with more spiders per minute in August (0.784 ± 0.034) than in

June (0.327 ± 0.021). However, the impact of plot diversity on spiders varied by season (season × plot diversity; $F_{1,993} = 5.74$, $p = 0.02$), as did the effect of tree species (season × tree species; $F_{14,993} = 1.99$, $p = 0.02$; overall goodness of fit for the model—$R^2_m = 0.24$; $R^2_c = 0.29$).

Seasonality

Parameter estimates from the full and separate seasonal models clarify the seasonal interactions. Specifically, the season by diversity interaction in the full model is not driven by a pattern reversal between seasons but by a more substantial positive impact of plot diversity in late summer (August; $F_{1,485} = 22.83$, $p < 0.001$; coefficient = 0.03 ± 0.01; Figure 1E) versus June ($F_{1,484} = 3.99$, $p = 0.046$, coefficient = 0.02 ± 0.01; Figure 1D). The tree species by season interaction is due to spider abundances only differing among tree species in August ($F_{14,33} = 2.07$, $p = 0.043$, Figure 1E) but not in June ($F_{14,37} = 1.50$, $p = 0.159$, Figure 1D).

2021 SEM using focal tree attributes

Measured data adequately fit the model for June ($C_2 = 2.98$; $p = 0.23$) and August ($C_2 = 1.52$; $p = 0.47$). All independence claims, unspecified but possible paths such as canopy cover to caterpillar abundance, were supported at $p > 0.05$. In June, plot diversity indirectly increases spider abundance through changes in focal tree canopy cover (Figure 2A). While plot diversity and tree height increase prey availability, there is no subsequent effect on spiders. Focal tree height did not directly mediate spider density but did contribute to higher canopy cover. August's data support a similar model structure with two crucial distinctions (Figure 2B). The relative importance of focal tree canopy cover for explaining spider density triples compared to other variables, and we find an additional direct positive path between plot diversity and spider density.

DISCUSSION

Overall, our study documents that spider predators use trees planted in mixed plots more than conspecific trees growing in monocultures. This diversity effect appears to be strengthening as the tree diversity experiment ages. Plot diversity was more important for spiders in late summer, which coincided with preferences by spiders for particular tree species and, overall, more spiders using experimental trees (Figure 1). In early summer, higher spider abundances on trees in diverse plots were tied to differences in focal tree canopy cover rather than tree height or prey availability. In late summer, diversity-driven differences in canopy cover were even more important to spiders. We also detected a potential unidentified mediator of the diversity effect, not encompassed by our measured variables suggesting that additional emergent properties of diverse plots (e.g., canopy packing and/or stability in prey availability) increase their attractiveness to spiders (Figure 2). This is one of the first experiments in temperate North America documenting tree diversity effects on arthropod predator abundance. Further, we identify changes in tree canopy cover as a key mechanism by which tree diversity shapes spider densities.

Six years after planting (2019), plot diversity had altered how spiders used some of the tree species, but we did not have the replication needed to see which tree species were driving the positive diversity response. Two years later, tree diversity had a more substantial, consistently positive effect on spiders across tree species. Previous studies of tree diversity and spiders also found a positive effect of tree species richness on arboreal spider species richness. However, they noted more substantial impacts of tree identity and composition (Matevski & Schuldt, 2021). The lack of a species by diversity interaction 2 years later, even with increased replication, indicates that in this 8-year-old experiment, our results are not primarily driven by compositional differences (i.e., the presence of attractive neighboring tree species in mixed plots) but by emergent effects of tree richness. Our results align with a tropical study containing similarly-sized trees that found positive effects of tree diversity on spider abundance (Esquivel-Gómez et al., 2017). Trees compete for light in this young forest, resulting in variable canopy closure across and within plots (J. D. Parker, unpublished data). Between 2019 and 2021, spiders shifted from preferring to use some tree species in mixed plots and others in single species plots toward a more consistent preference for trees in mixed plots regardless of species. As trees grow larger across the experiment and physically interact more with neighboring trees, the positive impact of higher tree diversity may extend to a greater proportion of surrounding trees and tree species.

Compared to single-species plots, the higher spider densities in 12-species plots increased from a 30% difference in June to a 61% difference by August (Figure 1D,E), and twice as many spiders used the focal trees. Interestingly, the abundance of spiders in the 4-species plots more closely resembled the single-species plots in June but was more similar to the 12-species plots in August. We suggest two non-mutually exclusive explanations. First, spiders may need time in the spring to

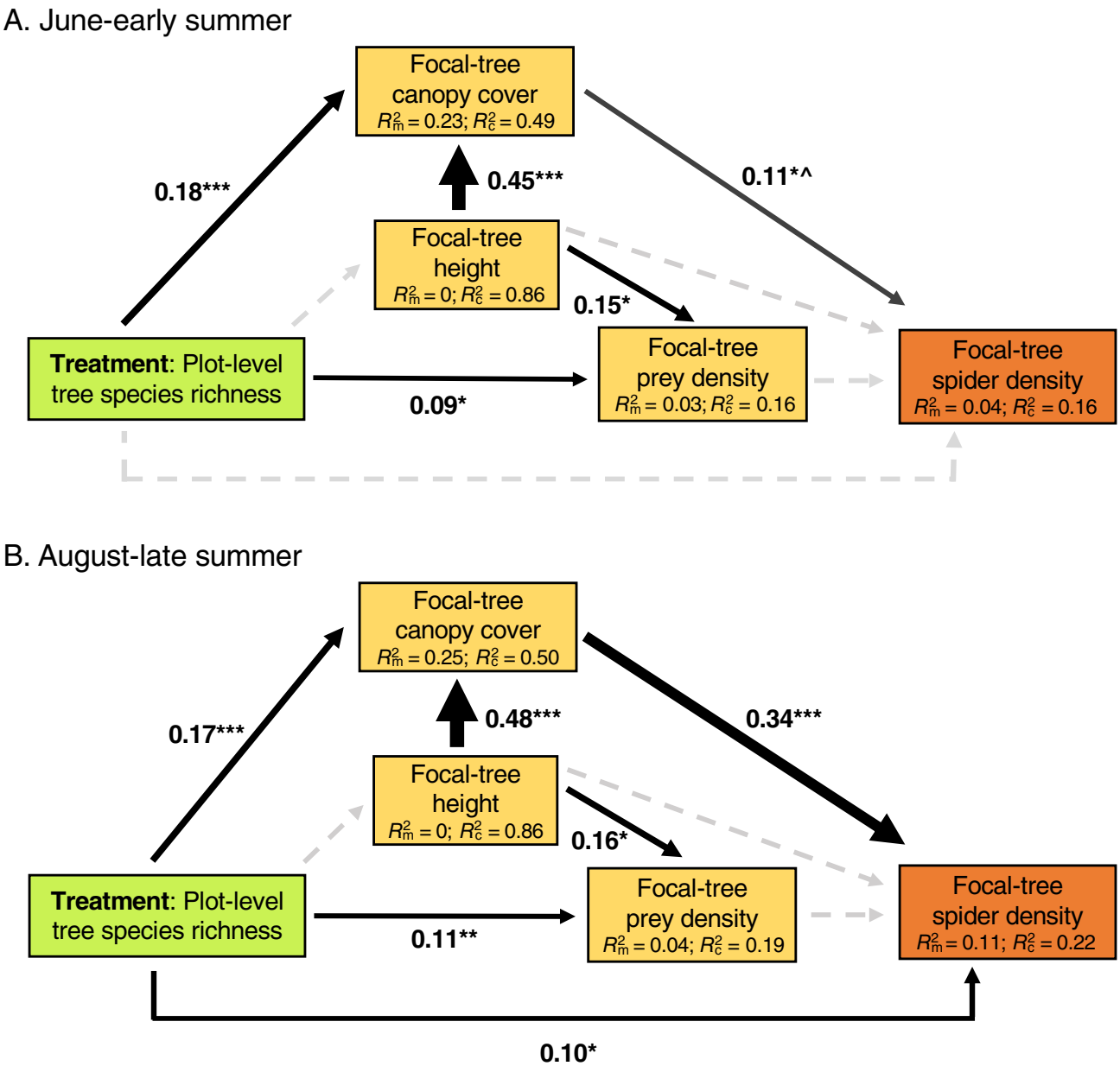


FIGURE 2 Structural Equation Models (SEM) of hypothesized causal relationships (arrows) by which focal tree attributes (yellow boxes) may mediate the relationship between tree species richness (green box; 1, 4, or 12 species) and spider densities (orange box). The measured data adequately fit the model for (A). June ($C_2 = 2.95$; $p = 0.23$) and (B). August ($C_2 = 1.52$; $p = 0.47$). Black arrows with the width scaled to standardized path coefficients represent strong evidence of important individual paths (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). A dark gray arrow marks a single path with weaker evidence of importance (*^$p = 0.051$). Dashed, light gray arrows represent unimportant paths ($p > 0.1$). Marginal (fixed effects) and conditional (fixed + random effects) R^2 are reported in the box of each component response variable.

disperse into the experimental plots or trees from nearby overwintering or aestivation sites (Arango et al., 2000; Hsieh & Linsenmair, 2012), resulting in a transient or incomplete community in June. Our study design does not allow us to determine whether spiders spend their entire lifecycle in diverse plots; however, they preferentially use trees in diverse plots in the summer months when insect herbivores are most active. Second, canopy cover could moderate the microclimate experienced by spiders. Air temperatures at our site are, on average, 1.7°C warmer in August compared to June, with relative humidity 5.8% higher. Therefore, habitat with reduced air temperature or lower relative humidity, such as might occur with the increased canopy cover, could be essential shelter for spiders later in the season even if they use other habitats (e.g., duff layer or herbaceous vegetation)

within a plot to seek mates or nest during cooler periods (Draney, 1997). Determining which habitat elements change in diverse plots will require additional work measuring fine-scale microclimate information at the focal-tree level.

Another potential mechanism increasing the attractiveness of trees in diverse plots may be differences in the tree architecture of focal trees and neighbors in mixtures compared to single species plots (Kunz et al., 2019). We were not able to manipulate canopy cover. Still, we provide strong evidence of an association between spider abundance and higher canopy cover in diverse plots in August, consistent with dense canopies and foliage biomass being preferred spider habitat (De Souza & Martins, 2005; Halaj et al., 1998). Complex tree structure—here, trees with more closed crowns—may offer refugia through protection from predators, such as birds (Gunnarsson, 1996), or increased branching, which results in more places to build a web (Moore, 1977). As diversity-driven changes in canopy cover alone did not fully account for the positive effect of tree diversity on spider abundance in August, other unmeasured architectural elements should be explored.

While the abundance of a likely spider prey item, caterpillars, increased in response to plot planting diversity in both early and late summer, we found no evidence that this increased abundance was associated with spider densities on focal trees (Figure 2). This is surprising given the well-established importance of arboreal spiders as predators and previous results of a meta-analysis of eight forest studies which found predator abundances in diverse plots correlate with fewer herbivores indicating herbivore suppression (Wan et al., 2020). There are at least two possible explanations for this discrepancy. First, even though we anecdotally observed spiders feeding on caterpillars during our observation periods, spiders may respond more strongly to other prey groups, such as hemipterans or flying insects. Alternatively, as these other studies did not simultaneously assess both habitat attributes and prey availability, physiological limits such as thermal tolerance or refugia from spider predators may be a more limiting factor in some forests than prey availability. This might be particularly true in a young forest where trees living in plots without canopy closure receive full sun conditions.

Moving forward, we suggest focusing on spatial differences in spider communities (e.g., ground-dwelling spiders [Wise, 2004]), or temporally distinct communities (e.g., nocturnal [Green, 1999], seasonal [Hsieh & Linsenmair, 2012]), and determining which guilds of spiders are driving the positive diversity response. Additional potential biotic mediators to explore include spider hunting methods, shelter availability, and temporal consistency in prey availability (Arango et al., 2000; De Souza & Martins, 2005; Gunnarsson, 1996; Halaj et al., 1998). Spider activity may also be essential to elucidate the types and strength of interactions between spiders, their habitat, and their prey (Stemmelen et al., 2022).

Spiders are critical predators in forest ecosystems providing ecosystem services such as pest regulation (Nyffeler & Birkhofer, 2017; Turnbull, 1973). Here, we highlight how tree diversity in a North American forest benefits higher trophic levels, specifically spiders. Plot diversity has an increasingly positive effect on spider abundances across the years studied as the forest grows and across a single season, moving from cooler spring to hotter summer conditions. This effect is partially, but not entirely, explained by diversity-driven differences in focal tree canopy cover, suggesting additional emergent mechanisms underlying spider abundances in diverse forests. As forest restoration, reforestation, and carbon capture efforts through tree-planting increase, our work stresses the importance of planting mixed stands to enhance habitat for higher trophic levels and ultimately maintain or enhance ecosystem function and services.

ACKNOWLEDGMENTS

We thank W. Lamp, Hamby and Gruner lab group members, and two anonymous reviewers for feedback on this manuscript. J. Pullen and many volunteers and interns help to maintain the BiodiversiTREE experiment. E. Perry, B. Randall, M. Ferlauto, K. Jayd, and K. McGurrin contributed to field sampling. This work was supported by NSF DEB Nos. 2044361, 2044406, and 2106014, NSF REU Nos. 1659668 and 1950656, USDA MD-ENTM-19932 and MD-ENTM-19001, and a generous gift from John and Ann Ryan.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Burghardt et al., 2023) are available in Figshare: https://doi.org/10.6084/m9.figshare.20997910.v1.

ORCID

Elizabeth M. Butz https://orcid.org/0000-0002-0189-4291
Lauren M. Schmitt https://orcid.org/0000-0002-8145-3583
Karin T. Burghardt https://orcid.org/0000-0002-9302-6802

REFERENCES

Arango, A. M., V. Rico-Gray, and V. Parra-Tabla. 2000. "Population Structure, Seasonality, and Habitat Use by the Green Lynx

Spider *Peucetia viridans* (Oxyopidae) Inhabiting Cnidoscolus Aconitifolius (Euphorbiaceae)." *The Journal of Arachnology* 28(2): 185–94.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, et al. 2022. "Lme4: Linear Mixed-Effects Models Using 'Eigen' and S4." https://CRAN.R-project.org/package=lme4.

Burghardt, K., E. Butz, L. Schmitt, and J. Parker. 2023. "Spider and Caterpillar Abundance, Tree Size, and Canopy Closure Metrics in a Tree Diversity Experiment." Figshare. https://doi.org/10.6084/m9.figshare.20997910.v1.

Castagneyrol, B., B. Giffard, C. Péré, and H. Jactel. 2013. "Plant Apparency, an Overlooked Driver of Associational Resistance to Insect Herbivory." *Journal of Ecology* 101(2): 418–29.

De Souza, A. L. T., and R. P. Martins. 2005. "Foliage Density of Branches and Distribution of Plant-Dwelling Spiders." *Biotropica* 37(3): 416–20.

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(8): e03063.

Draney, M. L. 1997. "Ground-Layer Spiders (Araneae) of a Georgia Piedmont Floodplain Agroecosystem: Species List, Phenology and Habitat Selection." *The Journal of Arachnology* 25(3): 333–51.

Esquivel-Gómez, L., L. Abdala-Roberts, M. Pinkus-Rendón, and V. Parra-Tabla. 2017. "Effects of Tree Species Diversity on a Community of Weaver Spiders in a Tropical Forest Plantation." *Biotropica* 49(1): 63–70.

Green, J. 1999. "Sampling Method and Time Determines Composition of Spider Collections." *The Journal of Arachnology* 27(1): 176–82.

Griffin, E. A., J. G. Harrison, M. K. McCormick, K. T. Burghardt, and J. D. Parker. 2019. "Tree Diversity Reduces Fungal Endophyte Richness and Diversity in a Large-Scale Temperate Forest Experiment." *Diversity* 11(12): 234.

Guillemot, J., M. Kunz, F. Schnabel, A. Fichtner, C. P. Madsen, T. Gebauer, W. Härdtle, G. Oheimb, and C. Potvin. 2020. "Neighbourhood-Mediated Shifts in Tree Biomass Allocation Drive Overyielding in Tropical Species Mixtures." *New Phytologist* 228(4): 1256–68.

Gunnarsson, B. 1996. "Bird Predation and Vegetation Structure Affecting Spruce-Living Arthropods in a Temperate Forest." *Journal of Animal Ecology* 65(3): 389–97.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. "Plant Species Loss Decreases Arthropod Diversity and Shifts Trophic Structure." *Ecology Letters* 12(10): 1029–39.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. H. Knops. 2001. "Contrasting Effects of Plant Richness and Composition on Insect Communities: A Field Experiment." *The American Naturalist* 158(1): 17–35.

Halaj, J., D. W. Ross, and A. R. Moldenke. 1998. "Habitat Structure and Prey Availability as Predictors of the Abundance and Community Organization of Spiders in Western Oregon Forest Canopies." *The Journal of Arachnology* 26(2): 203–20.

Hatley, C. L., and J. A. Macmahon. 1980. "Spider Community Organization: Seasonal Variation and the Role of Vegetation Architecture." *Environmental Entomology* 9(5): 632–9.

Holl, K. D., and P. H. S. Brancalion. 2020. "Tree Planting Is Not a Simple Solution." *Science* 368(6491): 580–1.

Hsieh, Y., and K. E. Linsenmair. 2012. "Seasonal Dynamics of Arboreal Spider Diversity in a Temperate Forest." *Ecology and Evolution* 2(4): 768–77.

Kunz, M., A. Fichtner, W. Härdtle, P. Raumonen, H. Bruelheide, and G. Oheimb. 2019. "Neighbour Species Richness and Local Structural Variability Modulate Aboveground Allocation Patterns and Crown Morphology of Individual Trees." *Ecology Letters* 22(12): 2130–40.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "LmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82(13): 1–26.

Langellotto, G. A., and R. F. Denno. 2004. "Responses of Invertebrate Natural Enemies to Complex-Structured Habitats: A Meta-Analytical Synthesis." *Oecologia* 139(1): 1–10.

Lefcheck, J. S. 2016. "PiecewiseSEM: Piecewise Structural Equation Modelling in r for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7(5): 573–9.

Letourneau, D. K. 1987. "The Enemies Hypothesis: Tritrophic Interactions and Vegetational Diversity in Tropical Agroecosystems." *Ecology* 68(6): 1616–22.

Matevski, D., and A. Schuldt. 2021. "Tree Species Richness, Tree Identity and Non-Native Tree Proportion Affect Arboreal Spider Diversity, Abundance and Biomass." *Forest Ecology and Management* 483(3): 118775.

Moore, C. W. 1977. "The Life Cycle, Habitat and Variation in Selected Web Parameters in the Spider, Nephila Clavipes Koch (Araneidae)." *The American Midland Naturalist* 98(1): 95–108.

Nixon, A. E., and J. Roland. 2012. "Generalist Predation on Forest Tent Caterpillar Varies with Forest Stand Composition: An Experimental Study across Multiple Life Stages." *Ecological Entomology* 37(1): 13–23.

Nyffeler, M., and K. Birkhofer. 2017. "An Estimated 400–800 Million Tons of Prey Are Annually Killed by the Global Spider Community." *The Science of Nature* 12: 30.

Opell, B. D., A. M. Berger, and R. S. Shaffer. 2007. "The Body Size of the New Zealand Orb-Weaving Spider Waitkera Waitakerensis (Uloboridae) Is Directly Related to Temperature and Affects Fecundity." *Invertebrate Biology* 126(2): 183–90.

Ordonez, A., and J. Svenning. 2018. "Greater Tree Species Richness in Eastern North America Compared to Europe Is Coupled to Denser, more Clustered Functional Trait Space Filling, Not to Trait Space Expansion." *Global Ecology and Biogeography* 27(11): 1288–99.

Patrignani, A., and T. E. Ochsner. 2015. "Canopeo: A Powerful New Tool for Measuring Fractional Green Canopy Cover." *Agronomy Journal* 107(6): 2312–20.

Pearson, D. E. 2009. "Invasive Plant Architecture Alters Trophic Interactions by Changing Predator Abundance and Behavior." *Oecologia* 159(3): 549–58.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Romero, G. Q., T. Gonçalves-Souza, T. Roslin, R. J. Marquis, N. A. C. Marino, V. Novotny, T. Cornelissen, et al. 2022. "Climate Variability and Aridity Modulate the Role of Leaf Shelters for Arthropods: A Global Experiment." *Global Change Biology* 28(11): 3694–710.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. "Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions." *Ecology* 78(5): 1388–99.

Shvidenko, A., and P. Gonzalez. 2005. "Ecosystems and Human Well-Being." In *Europes Ecological Backbone*, edited by W. A. Sarukhán, 587–614. Washington: Island Press.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. "Experimental Tests of the Dependence of Arthropod Diversity on Plant Diversity." *The American Naturalist* 152(5): 738–50.

Staab, M., and A. Schuldt. 2020. "The Influence of Tree Diversity on Natural Enemies—A Review of the "Enemies" Hypothesis in Forests." *Current Forestry Reports* 6(4): 243–59.

Stemmelen, A., H. Jactel, E. Brockerhoff, and B. Castagneyrol. 2022. "Meta-Analysis of Tree Diversity Effects on the Abundance, Diversity and Activity of Herbivores' Enemies." *Basic and Applied Ecology* 58(February): 130–8.

Turnbull, A. L. 1973. "Ecology of the True Spiders (Araneomorphae)." *Annual Review of Entomology* 18(1): 305–48.

Uetz, G. W. 1991. "Habitat Structure and Spider Foraging." In *Habitat Structure: The Physical Arrangement of Objects in Space*. Population and Community Biology Series, edited by S. S. Bell, E. D. McCoy, and H. R. Mushinsky, 325–48. Dordrecht: Springer.

Wan, N., 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(5): 503–10.

Williams, L. J., E. E. Butler, J. Cavender-Bares, A. Stefanski, K. E. Rice, C. Messier, A. Paquette, and P. B. Reich. 2021. "Enhanced Light Interception and Light Use Efficiency Explain Overyielding in Young Tree Communities." *Ecology Letters* 24(5): 996–1006.

Wise, D. H. 2004. "Wandering Spiders Limit Densities of a Major Microbi-Detritivore in the Forest-Floor Food Web." *Pedobiologia* 48(2): 181–8.

Yao, N., C. C. Konijnendijk van den Bosch, J. Yang, T. Devisscher, Z. Wirtz, L. Jia, J. Duan, and L. Ma. 2019. "Beijing's 50 Million New Urban Trees: Strategic Governance for Large-Scale Urban Afforestation." *Urban Forestry & Urban Greening* 44: 126392.

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: Butz, Elizabeth M., Lauren M. Schmitt, John D. Parker, and Karin T. Burghardt. 2023. "Positive Tree Diversity Effects on Arboreal Spider Abundance are Tied to Canopy Cover in a Forest Experiment." *Ecology* 104(8): e4116. https://doi.org/10.1002/ecy.4116