**ARTICLE**

**Vegetation Ecology**

# Pawpaws prevent predictability: A locally dominant tree alters understory beta-diversity and community assembly

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**Abstract**

While dominant species are known to be important in ecosystem functioning and community assembly, biodiversity responses to the presence of dominant species can be highly variable. Dominant species can increase the importance of deterministic community assembly by competitively excluding species in a consistent way across local communities, resulting in low site-to-site variation in community composition (beta-diversity) and nonrandom community structure. In contrast, dominant species could increase the importance of stochastic community assembly by reducing the total number of individuals in local communities (community size), resulting in high beta-diversity and more random community structure. We tested these hypotheses in a large, temperate oak-hickory forest plot containing a locally dominant tree species, pawpaw (*Asimina triloba*; Annonaceae), an understory tree species that occurs in dense, clonal patches in forests throughout the east-central United States. We determined how the presence of pawpaw influences local species diversity, community size, and beta-diversity by measuring the abundance of all vascular plant species in 1 × 1-m plots both inside and outside pawpaw patches. To test whether the presence of pawpaw influences local assembly processes, we compared observed patterns of beta-diversity inside and outside patches to a null model in which communities were assembled at random with respect to species identity. We found lower local species diversity, lower community size, and higher observed beta-diversity inside pawpaw patches than outside pawpaw patches. Moreover, standardized effect sizes of beta-diversity from the null model were lower inside pawpaw patches than outside pawpaw patches, indicating more random species composition inside pawpaw patches. Together these results suggest that pawpaw increases the importance of stochastic relative to deterministic community assembly at local scales, likely by decreasing overall numbers of individuals and increasing random local extinctions inside patches. Our findings provide insights into the ecological processes by which locally dominant tree species shape the assembly and diversity of understory plant communities at different spatial scales.

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## INTRODUCTION

Highly abundant species within communities can have strong effects on biodiversity and ecosystem functioning (Avolio et al., 2019; Gaston, 2011; Grime, 1998). Species that have high abundance relative to other species in a community and proportionate effects on environmental conditions, community diversity, and/or ecosystem functioning are considered "dominant species" (Avolio et al., 2019). Dominant species can determine nutrient cycling and primary productivity (Ellison, 2019; Grime, 1998), increase resistance or resilience of ecosystems to environmental change (Avolio et al., 2019), add physical structure to a habitat (Altieri & Witman, 2014; Dayton, 1972), and modify the abiotic environment in ways that create more harsh conditions or conversely ameliorate abiotic stress for other species (Gavilán & Callaway, 2017; Hughes, 2010; Lustenhouwer et al., 2012). Although the loss of dominant species can have cascading effects on communities and ecosystems, their effects on patterns of species diversity can be highly variable (Avolio et al., 2019; Ellison et al., 2019; Elsberry & Bracken, 2021; Gavilán & Callaway, 2017; Hughes, 2010; Myers & Harms, 2009). This variation potentially reflects multiple ecological processes through which dominant species affect community assembly, but the relative roles of these processes remain understudied.

Dominant species can affect community assembly through deterministic or stochastic processes. Deterministic processes include abiotic filtering and biotic interactions such as competition and facilitation that reflect niche differences among species in a community (Chase & Myers, 2011; Leibold & Chase, 2017; Vellend, 2010). Dominant species can increase the importance of interspecific competition when they limit space or resources for other species (e.g., Lustenhouwer et al., 2012), resulting in competitive exclusion (Ellison et al., 2015; Konno, 2002; Segre et al., 2014). Alternatively, dominant species can facilitate the survival of certain species by lowering abiotic stress (e.g., Gavilán & Callaway, 2017). Dominant species can also increase the importance of stochastic community assembly by decreasing the total number of individuals in a local community (local community size) (Powell et al., 2013). As local community size decreases, more species in the community may become rare, thereby increasing demographic stochasticity and random

changes in species' relative abundances (ecological drift; Hubbell, 2001; MacArthur & Wilson, 1967; Orrock & Watling, 2010). At the community level, these demographic processes can create patterns of community composition that are random with respect to species identity (Vellend, 2016; Vellend et al., 2014). In addition, amelioration of stressful conditions by dominant species can lead to more random assembly of nondominant species (Arnillas & Cadotte, 2019). The effects of dominant species on deterministic and stochastic processes are expected to increase when dominant species are also of large stature, that is, when size asymmetries among competing species or guilds are large (Keddy & Shipley, 1989; Myers & Harms, 2009).

Despite widespread interest in the role of dominant species in communities and ecosystems (Avolio et al., 2019; Ellison et al., 2005; Gilbert et al., 2009), their relative effects on deterministic and stochastic community assembly remain unresolved. First, previous studies have largely focused on how dominant species influence species diversity at local spatial scales (e.g., alpha diversity), but similar patterns of local species diversity could reflect different assembly processes. For example, low species richness can result from either competitive exclusion by dominant species (Ellison et al., 2015; Konno, 2002; Segre et al., 2014) or random local extinctions in small communities with few individuals (Powell et al., 2013). Most dominant-species removal experiments in plant communities have focused on changes in local species richness or diversity, finding a mix of positive (Avolio et al., 2019; Ellison et al., 2015; Konno, 2002; Segre et al., 2014), negative (Altieri & Witman, 2014; Gavilán & Callaway, 2017; Hughes, 2010), or no clear response (Gilbert et al., 2009; Myers & Harms, 2009) to the removal of dominant plant species. Second, relatively few studies have examined how dominant species influence site-to-site variation in community composition (beta-diversity). Patterns of beta-diversity can help elucidate the relative importance of deterministic and stochastic processes (Anderson et al., 2011; Chase & Myers, 2011). For example, deterministic exclusion of inferior competitors by dominant species should cause local communities to converge in composition (i.e., low beta-diversity), whereas random local extinctions in small communities should cause local communities to diverge in composition (i.e., high beta-diversity). Finally, observed

## (a) Inside Plot

## (b) Outside Plot



**FIGURE 1** Examples of understory plant communities (a) inside a pawpaw (*Asimina triloba*) patch ("inside plot") and (b) outside a pawpaw patch at least 10 m away from the patch edge ("outside plot"). White squares show $1 \times 1$-m plots. Photo credit: Anna C. Wassel.

changes in beta-diversity can be compared to a null model of random community assembly to further assess the relative roles of deterministic and stochastic processes (Catano et al., 2017; Chase, 2007). Therefore, patterns of diversity at different scales can provide key insights into the ecological roles of dominant species in community assembly and ecosystem functioning.

In this study, we examined the effect of a locally dominant tree species, pawpaw (*Asimina triloba*; Annonaceae), on the diversity and assembly of understory plant communities in a temperate forest-dynamics plot (Figure 1). Our focal species, pawpaw, is a widely distributed understory tree species that occurs in dense, clonal patches in forests throughout the east-central United States. Pawpaw has been shown to be a dominant species in temperate forests with high local abundance (Appendix S1: Figure S1) and strong effects on the diversity of other tree species (Baumer & Runkle, 2010). While the assembly of forest tree communities is fairly well studied (e.g., Condit et al., 2000, 2002; Ellison et al., 2019), the assembly of forest herb communities has received less attention, despite a large and growing body of literature on herbaceous plant community ecology in temperate forests (Bray & Curtis, 1957; Gilliam, 2014; Whittaker, 1956) and the disproportionate contribution of herbaceous plant species to temperate forest diversity (Gilliam, 2007; Spicer et al., 2020). We therefore examined the effect of pawpaw on both the total

understory community (woody and herbaceous species combined) and herbaceous species only.

We tested two nonmutually exclusive hypotheses. First, we tested the hypothesis that pawpaw increases the relative role of deterministic assembly through interspecific competition (hereafter the deterministic assembly hypothesis). Second, we tested the hypothesis that pawpaw increases the relative role of stochastic assembly by decreasing local community size (hereafter the stochastic assembly hypothesis). The deterministic assembly hypothesis predicts that the presence of dominant species (1) decreases local species diversity due to competitive exclusion, (2) decreases beta-diversity among local communities by selecting for a limited subset of species that can co-occur with dominant species, and (3) results in lower beta-diversity than expected from sampling of the species pool at random with respect to species identity. In contrast, the stochastic assembly hypothesis predicts that the presence of dominant species (1) decreases local species diversity, but (2) increases beta-diversity among local communities, due to random local extinctions, and (3) results in beta-diversity that is more similar to random sampling of the species pool. We tested these predictions by comparing observed patterns of local species diversity, local community size, and beta-diversity among paired groups of understory plant communities located inside and outside pawpaw patches. We then compared observed

patterns of beta-diversity to a null model that simulated the assembly of local communities from the species pool at random with respect to species identity.

## METHODS

### Study site and focal species

We conducted this study at Washington University in St. Louis' environmental field station, Tyson Research Center, located approximately 40 kilometers from St. Louis, Missouri. The 800-ha site is located on the edge of the Ozark highlands, dominated by late-successional, deciduous oak-hickory forest, and contains a topographically heterogeneous landscape characterized by silty loam and silty clay soils that develop from shale and cherty limestone (Zimmerman & Wagner, 1979). In the oak-hickory forests at our study site, local plant communities are strongly delineated by three general habitat types: (1) valleys with wet-to-mesic soils and high soil pH and nutrient availability, (2) east- and north-facing slopes with mesic soils and intermediate soil pH and nutrient availability, and (3) west- and south-facing slopes with drier soils and low soil pH and nutrient availability (Figure 2a,c; Myers et al., 2013; Reu et al., 2022; Spasojevic et al., 2014; Zimmerman & Wagner, 1979). Our study was conducted in one of these habitat types (valleys) in the Tyson Research Center Forest Dynamics Plot, a large (20.16 ha; $480 \times 420$ m), stem-mapped forest plot that is part of the Forest Global Earth Observatory (ForestGEO) network (Anderson-Teixeira et al., 2015). The 20-ha plot includes more than 1600 stems of pawpaw at least 1 cm
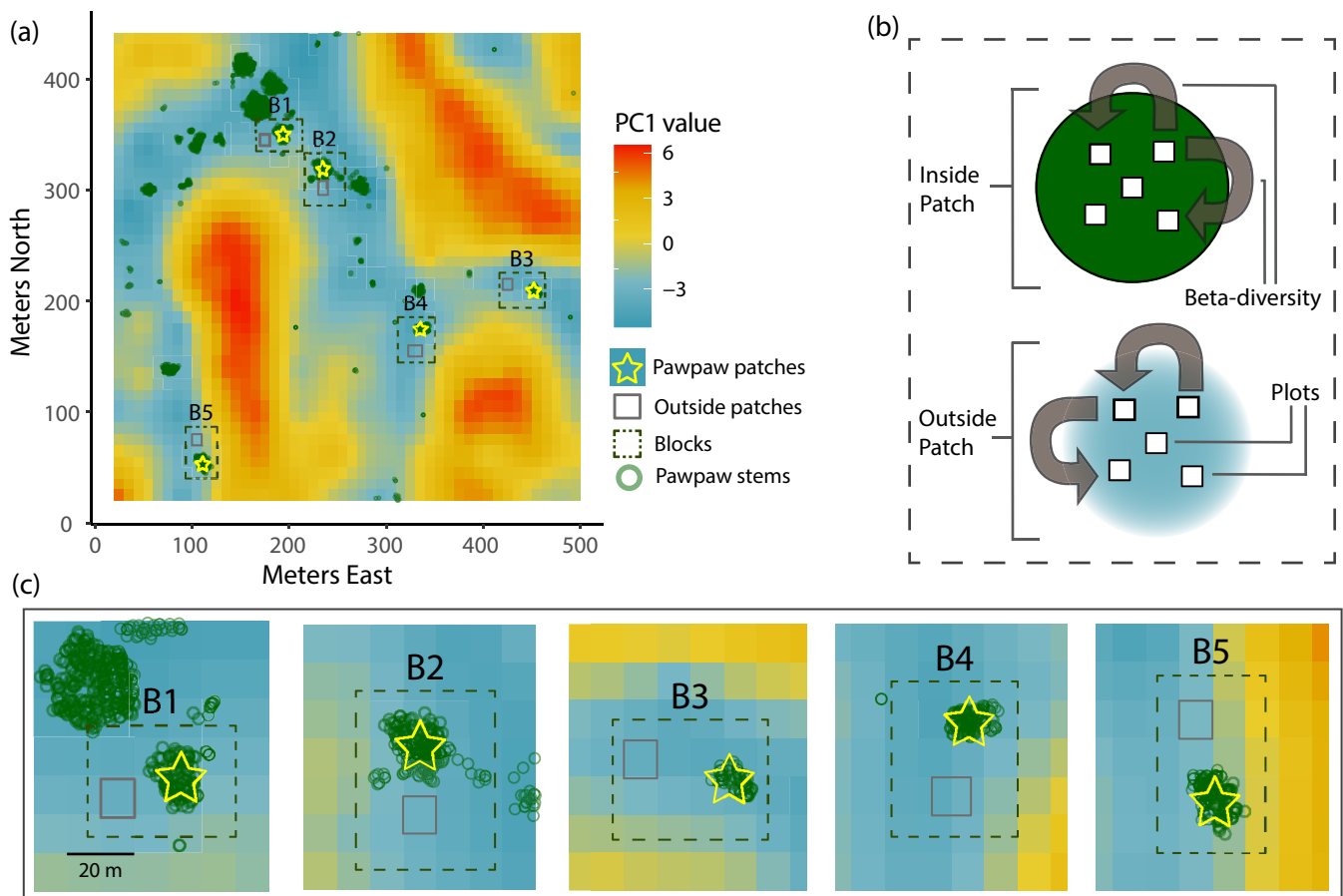


**FIGURE 2** Sampling design within the Tyson Research Center Forest Global Earth Observatory (ForestGEO) Plot, Missouri. (a) Abiotic conditions (soil resources and topography) represented by the first axis of a principal components analysis (PCA) including 17 environmental variables at the $10 \times 10$-m scale (Appendix S1: Figure S2), mapped locations of all pawpaw stems ≥1 cm in dbh, and selected sampling blocks. Blue values represent areas of lower elevation, higher soil nutrient availability, and higher soil pH, whereas red values represent higher elevation, lower nutrient availability, and more acidic soils. (b) For each block, the pawpaw patch edge was defined and five $1 \times 1$-m plots were placed inside or outside the patch. Gray arrows represent how beta-diversity was calculated within each of the two patch types (inside and outside plots). (c) Each block is shown enlarged to illustrate the environmental conditions and relative location for both the inside patches and outside patches.

in dbh, most of which occur in 18 patches ranging in area from 5 to 1028 m$^2$.

Our focal dominant species for this study is the pawpaw tree, *A. triloba* (Annonaceae) (hereafter pawpaw). Pawpaw is distributed widely throughout the east-central United States and parts of southern Canada (Sullivan, 1993), making it the northernmost member of the otherwise tropical family Annonaceae. It primarily occurs in moist valleys and mesic hillsides (Immel & Anderson, 2001). Pawpaw can reproduce both sexually and asexually, forming dense, discrete clonal patches (Hosaka et al., 2005). While not the most abundant species in temperate forests at larger spatial scales due to its patchy distribution, at our study site, it is frequently the most abundant species at the 10 × 10-m scale when it is present (Appendix S1: Figure S1), making it a locally dominant species. The local dominance and discrete patch structure of this species make it an ideal study system for investigating how the presence or absence of a dominant species affects community assembly processes.

## Sampling design

We selected five blocks located in the same general habitat type (valleys) to contain a pawpaw patch and an adjacent area without pawpaws, referred to as "inside" and "outside" patches, respectively (Figures 1 and 2). The five inside (pawpaw) patches ranged from 58 to 435 m$^2$ in size (mean = 189 m$^2$). The paired outside patches were selected to have abiotic (soil and topographic) conditions similar to those inside the pawpaw patch and were 10–20 m from the edge of the pawpaw patch (Figure 2a,c). We determined the similarity of soil and topographic conditions between the inside and outside patches through a principal components analysis (PCA) on 17 soil and topographic variables (Appendix S1: Figure S2). The values were estimated for each 10 × 10-m subplot in the 20-ha ForestGEO plot based on measurements taken in 2013 (detailed in LaManna et al., 2016; Spasojevic et al., 2016). The outside patches were chosen to have a similar PC1 score as the pawpaw patches. Thus, our sampling design minimized differences in abiotic conditions (soils and topography) among blocks and among plots located inside and outside pawpaw patches (Figure 2a,c; elevation: 195.6 m ± 11.1 m [mean ± 1 SD]; PC1 score of soil and topographic variables: −3.1 ± 0.6).

For each patch type in each of the five blocks, five 1 × 1-m plots were sampled for plant community composition (*n* = 25 inside plots, *n* = 25 outside plots, *n* = 50 plots total; Figure 2b). Within each pawpaw patch, we placed the first plot in the center of the patch. We then placed the other four plots at least 1 m away from the center plot with the additional constraints that they could not be within 2 m of the edge of the pawpaw patch and could not contain larger woody stems over 1 m tall. Given the high density of pawpaw stems, this greatly limited the availability of potential locations for plot placement. Therefore, plot locations were stratified within the central area of each pawpaw patch to minimize edge effects, maintain similar inter-plot distances within and among blocks, and avoid locations physically dominated by large trees to standardize the amount of available ground area available for understory plants.

We recorded the identity and estimated the abundance of all understory vascular plant species, that is, herbaceous plants including ferns, and woody plants and vines. In each 1 × 1-m plot, we estimated abundance (number of stems per species) as the number of 10 × 10-cm cells that contained rooted stems of the given species. For most clonal species, it is not possible to determine whether a rooted stem is a ramet or genet in the field. While this metric may overestimate abundances of clonal species and local community size, it is less likely to confound abundance with individual plant size compared to other metrics such as percent cover. In addition, for species that had more than one rooted stem (ramet or genet) in a given 10 × 10-cm cell, this method conservatively assigns an abundance value of one for that cell. In cases when individuals could not be identified to species in the field, they were identified to genus or assigned a morphospecies and photos were uploaded to iNaturalist for future assistance with identification; 8% of stems were considered morphospecies for analyses. We estimated local community size by summing the abundances of all species in each plot. Sampling was conducted during the peak growing season from July to September of 2021. Due to the different life stages and biology of young woody seedlings compared to the adult herbaceous plants, we conducted two separate analyses for (1) herbaceous and woody plant species combined (hereafter total understory community) and (2) herbaceous species only.

## Analyses

We analyzed local species diversity, community size, and beta-diversity using linear mixed-effects models in R (package "nlme"; Pinheiro et al., 2023). All models included patch type (inside or outside) as a fixed effect and block as a random effect. When necessary, we log-transformed response variables to meet the assumptions of homogeneous variances between patch types and normality of model residuals. When transformation did not improve homogeneity of variances, we used a heterogeneous variance model ("varIdent"

function). We describe the analyses for each response variable below.

To test our first prediction, we calculated local species diversity using the inverse Simpson's index (Oksanen et al., 2024; Simpson, 1949), a scale-independent diversity measure of the effective number of species that is insensitive to differences in numbers of individuals (Chase et al., 2018). For the model testing local diversity of the total understory community, we log-transformed the inverse-Simpson's values to meet the assumption of homogeneous variances. For the model testing local diversity of herbaceous species only, we used a heterogeneous variance model and excluded the two plots with no species.

To test our second prediction, we calculated observed beta-diversity as the compositional dissimilarity among plots using the Bray–Curtis index. We analyzed beta-diversity based on distance-to-centroid values (Anderson, 2006; Kraft et al., 2011) using the "betadisper" function in the R vegan package (Oksanen et al., 2024), where each value represents the distance (compositional dissimilarity) from an individual plot to the centroid of the group of all 25 plots within each patch type (Figure 2b). When analyzing beta-diversity of herbaceous species only, we excluded two inside plots from Block 5 that contained no herbaceous plants.

To test our third prediction, we used a null model to simulate the compositional dissimilarity expected when local communities are assembled at random with respect to species identity (Kraft et al., 2011; LaManna et al., 2021; Myers et al., 2013). First, we defined the species pool as all species recorded during the study across all inside and outside plots combined. We estimated the total abundance of each species (number of stems) in the species pool by summing its frequencies (number of $10 \times 10$-cm cells in which a rooted stem was recorded) across all plots. By including all species recorded in all plots within the same general habitat type (valleys) and abiotic conditions (soils and topography; Figure 2), this definition includes only species that can potentially disperse to and persist in the environmental conditions of the focal habitat type, also known as a "filtered pool," a commonly used approach to define species pools in ecological studies (Cornell & Harrison, 2014). An important advantage of this definition is that it allows for potential differences in the strength of biotic filtering among pawpaw patches at the landscape scale to influence local community composition. In turn, deviations of the empirical data from the null model (standardized effect sizes; described below) reflect the degree to which variation in species composition inside and outside pawpaw patches is higher or lower than expected from sampling at random with respect to species identity from an abiotically filtered species pool. Second, in each of 2000 iterations of the null model, we simulated community assembly

in each plot by sampling stems from the species pool at random with respect to species identity, while keeping constant the empirically observed total number of stems in each plot (local community size) and total abundance of each species in the species pool. Third, we calculated the mean simulated beta-diversity for each plot by averaging the Bray–Curtis distance-to-centroid values from the 2000 null-model iterations. Fourth, we calculated the standardized effect size as the difference between the observed beta-diversity (distance-to-centroid) and mean simulated values for each plot, divided by the SD of simulated values for each plot. A standardized effect size of zero indicates that observed beta-diversity does not differ from sampling of the species pool at random with respect to species identity, a positive value indicates higher beta-diversity than expected from random sampling (i.e., high spatial aggregation of species across local communities), and a negative value indicates lower beta-diversity than expected from random sampling (i.e., low spatial aggregation of species across local communities). We tested median standardized effect sizes of each patch type against the null expectation of zero with one-sample two-sided Wilcoxon tests.

To explore whether overall species composition differed among blocks and patch types, we performed a permutational ANOVA (PERMANOVA) of the total understory community (herbaceous and woody plant species) using the "adonis2" function in the R vegan package (Oksanen et al., 2024). This model included Bray–Curtis dissimilarity calculated using fourth-root transformed abundances as the response variable (Anderson, 2001; Borcard et al., 2018), and block and patch type nested within block as categorical predictor variables. We used nonmetric multidimensional scaling (NMDS; "metaMDS" function in R) to generate a two-dimensional ordination showing differences in species composition among blocks and patch types. In addition, we tested whether blocks differed with respect to variation in species composition (dispersion) using a permutational multivariate analysis of dispersion (Anderson, 2006) with Bray–Curtis distance-to-centroids calculated using fourth-root transformed abundances as the response variable, and block as a categorical predictor variable. All analyses were conducted in R (R Core Team, 2022).

## RESULTS

Overall, we observed a total of 79 plant species and morphospecies (hereafter species) in this study, including 52 herbaceous plant species and 27 woody plant species (Appendix S1: Tables S1–S3). Only six species were unique to inside patches, while there were 29 species unique to outside patches. Of the 52 herbaceous plant species,

24 occurred inside pawpaw patches and 47 occurred in outside patches. Of the 27 woody plant species, 12 occurred inside pawpaw patches and 26 occurred in outside patches. Of the 37 herbaceous and woody species (excluding pawpaw) that occurred in both patch types (inside and outside), most had a lower total abundance inside pawpaw patches (Appendix S1: Figure S3; Tables S1–S3). Among the 27 shared species with ≥3 stems inside or outside a pawpaw patch, the median local abundance per 1 × 1-m plot was 66% lower inside pawpaw patches (Appendix S1: Tables S1–S3). Among taxa identified to the species level (nonmorphospecies, Appendix S1: Tables S1 and S2), herbaceous species were more abundant than woody species outside pawpaw patches (68.4% of the total estimated number of stems), but less abundant than woody species inside pawpaw patches (39.9% of the total estimated number of stems).

## Local species diversity and community size

Local species diversity and community size were significantly lower inside than outside pawpaw patches (Figure 3; Appendix S1: Table S4). For herbaceous species only, median local diversity was 49% lower inside than outside pawpaw patches (Figure 3a). Median community size (total estimated number of rooted stems of all species in a plot) for herbaceous species was 76% lower inside than outside pawpaw patches (Figure 3b). Similar patterns were observed for the total understory community (herbaceous and woody species combined). For the total understory community, median local diversity was 29% lower inside than outside pawpaw patches (Figure 3a), and median community size was 67% lower inside than outside pawpaw patches (Figure 3b).

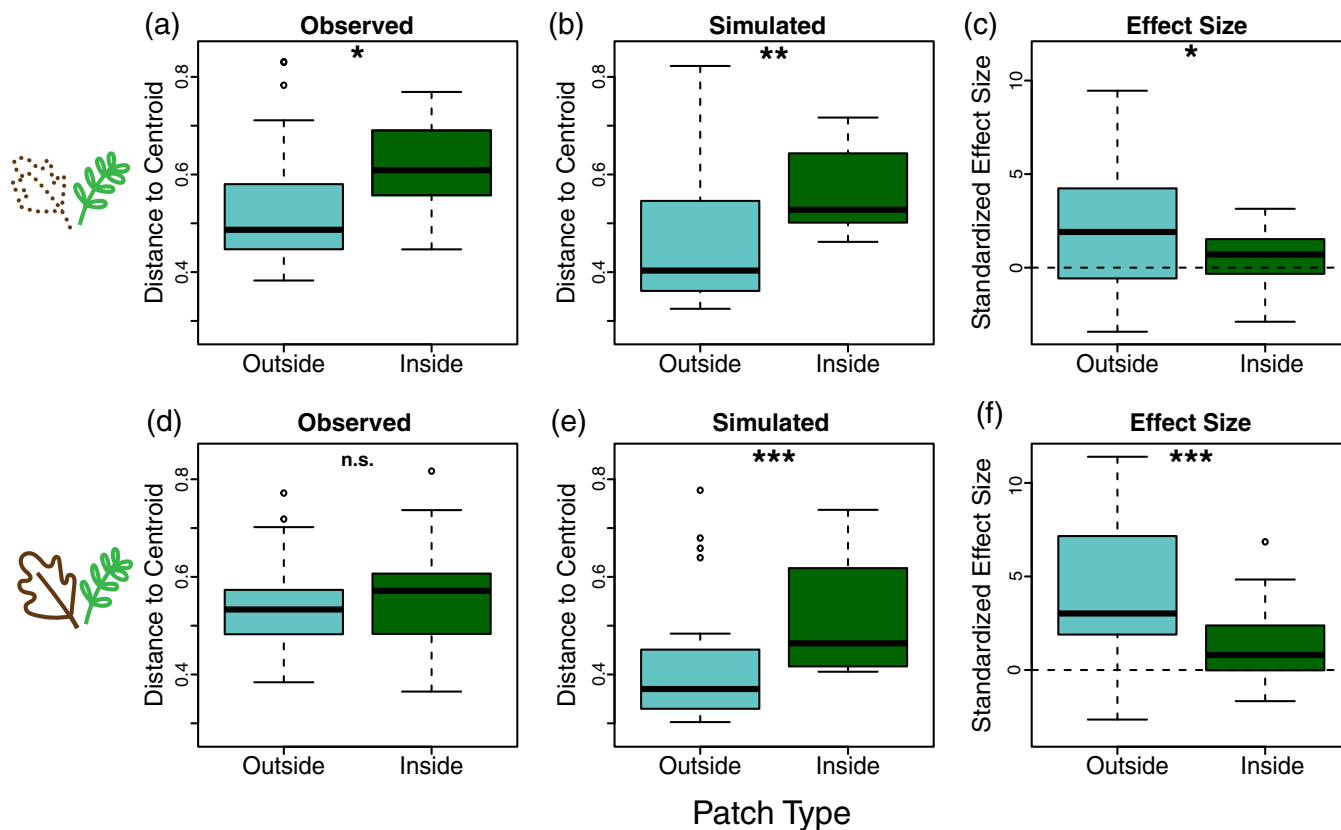## Observed, simulated, and standardized effect sizes of beta-diversity

Observed, simulated, and standardized effect sizes of beta-diversity differed significantly inside and outside pawpaw patches for herbaceous species only (Figure 4a–c; Appendix S1: Table S4). Observed beta-diversity was 25% higher inside than outside pawpaw patches (Figure 4a; absolute difference in median distance-to-centroids: 0.12). Simulated beta-diversity was 30% higher inside than outside pawpaw patches (Figure 4b; absolute difference in median distance-to-centroids: 0.12). In contrast, standardized effect sizes of beta-diversity were 61% lower inside than outside pawpaw patches (Figure 4c; absolute difference in median standardized effect sizes: 1.15). Median standardized effect sizes inside and outside pawpaw
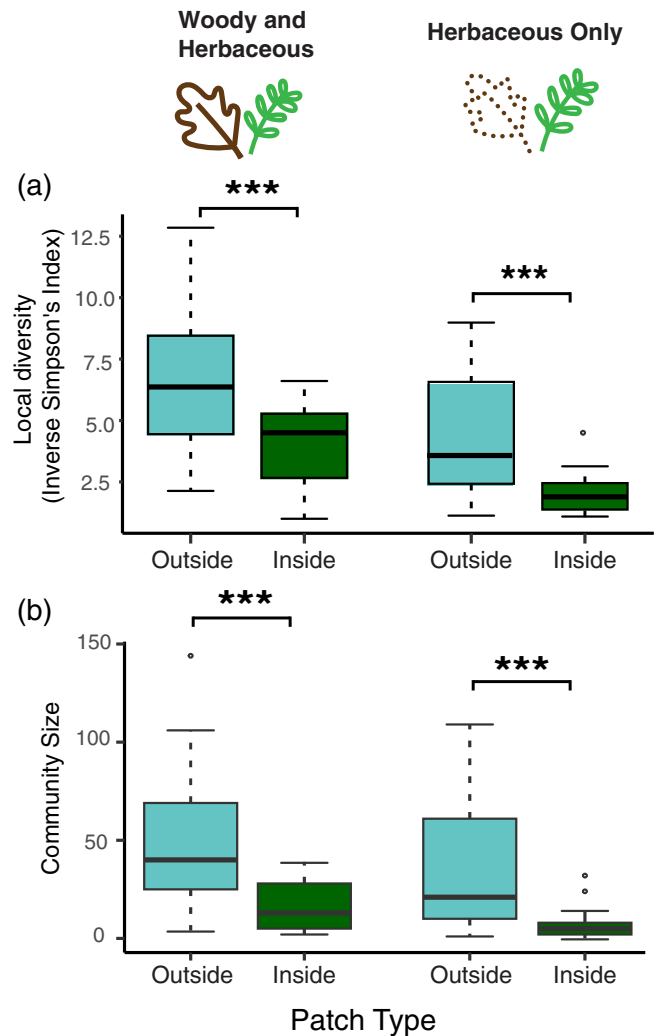


**FIGURE 3** Local plant species diversity and community size are lower inside than outside pawpaw patches. (a) Local species diversity (inverse Simpson's index) outside and inside plots for the total understory community (herbaceous and woody plant species) ($N = 25$ for inside and outside plots) and herbaceous species only ($N = 23$ for inside plots, $N = 25$ for outside plots). (b) Local community size for the total understory community and herbaceous species only ($N = 25$ for inside and outside plots). Community size was estimated as the total number of rooted stems of all species in each plot. Boxes represent the median and 25th/75th percentile, whiskers extend to the largest value up to 1.5 times the interquartile range, and dots represent outlier data points (***$p < 0.001$).

patches were both positive and differed significantly from zero, although the difference was less significant inside pawpaw patches (Figure 4c; Appendix S1: Table S5; $p = 0.044$ inside patches; $p = 0.001$ outside patches). Similar patterns were observed for the total understory community, with the exception of observed beta-diversity, which showed no significant difference between patch types. Standardized effect sizes differed more between

**FIGURE 4** Variation in species composition (beta-diversity) differs inside and outside pawpaw patches. (a) Observed beta-diversity of herbaceous plant species in plots outside ($N = 25$) and inside ($N = 23$) pawpaw patches. (b) Simulated beta-diversity expected from a null model of random assembly. (c) Standardized effect size of beta-diversity. Panels (d), (e), and (f) show the same results including herbaceous and woody species. The dashed line at zero represents the null expectation. Boxes represent the median and 25th/75th percentile, whiskers extend to the largest value up to 1.5 times the interquartile range, and dots represent outlier data points (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). n.s., not significant.

patch types for the total understory community (Figure 4f) compared to herbaceous species only (Figure 4c), due to larger standardized effect sizes for the total understory community outside pawpaw patches. For the total understory community, standardized effect sizes were 73% lower inside than outside pawpaw patches (Figure 4f; absolute difference in median standardized effect sizes: 2.30). Median standardized effect sizes of the total understory community inside and outside pawpaw patches both differed significantly from zero (Appendix S1: Table S4; $p = 0.013$ inside patches; $p < 0.001$ outside patches).
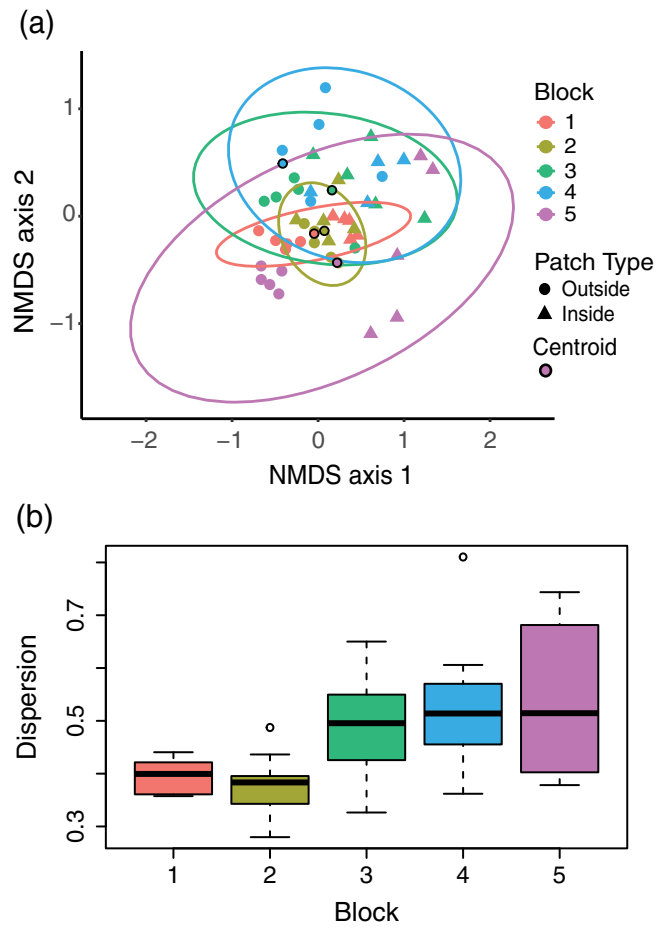
## Overall species composition

Species composition of the total understory community differed significantly among blocks and between patch types within blocks (Figure 5; Appendix S1: Table S6). Block and patch type each explained less than 25% of the variation in species composition, and patch type explained slightly more variation in species composition than block

(PERMANOVA: $R^2 = 0.23$ for patch type, $R^2 = 0.20$ for block; Appendix S1: Table S6). Blocks exhibited high overlap in species composition based on their centroids (Figure 5a), but differed in terms of their overall variation in community composition based on their dispersion (Figure 5b; permutational multivariate analysis of dispersion on average distance-to-centroids: df = 4; $F = 5.84$, $p = 0.0015$).

## DISCUSSION

Overall, our results support the stochastic assembly hypothesis. The lower local species diversity, lower community size, and more random variation in species composition found within pawpaw patches all support predictions of this hypothesis. Beta-diversity was higher than expected from sampling at random with respect to species identity inside and outside pawpaw patches, but patterns of beta-diversity inside pawpaw patches more closely resembled the null expectation of random

## (a)



## (b)



**FIGURE 5** Overall differences in species composition among blocks and patch types (inside or outside pawpaw patches). (a) Ordination of species composition of the total understory community (Bray–Curtis dissimilarity calculated using fourth-root transformed abundances) derived from nonmetric multidimensional scaling (NMDS; stress = 0.16). Points close together in ordination space indicate plots with similar species composition. Ellipses represent the total variation in species composition within each block, and centroids for each block are shown by colored circles with a black outline. For ease of visualization, one outlier plot in Block 4 is not shown; see Appendix S1: Figure S4 for a figure including this plot. (b) Boxplots of distance-to-centroid values (Bray–Curtis dissimilarity using fourth-root transformed abundances) showing dispersion of species composition within each block ($N = 10$ plots per block). Boxes represent the median and 25th/75th percentile, whiskers extend to the largest value up to 1.5 times the interquartile range, and dots represent outlier data points.

sampling. These findings suggest that both deterministic and stochastic assembly processes are important in shaping the understory plant community, but that local communities in different patch types are not assembled the same way, with stochastic processes being relatively more important than deterministic processes in patches dominated by pawpaw.

Observed beta-diversity of herbaceous species was higher inside than outside pawpaw patches, supporting the second prediction of the stochastic assembly hypothesis (Figure 4a). Higher beta-diversity among plots inside pawpaw patches is in line with the findings of other studies that observed the presence of dominant woody species increases beta-diversity (Ellison et al., 2015, 2019) or decreases local relative to regional diversity (Powell et al., 2013). However, previous studies have often focused on how dominant tree species affect other tree species, without explicit consideration of their effects on herbaceous species. In our study, the difference in observed beta-diversity of herbaceous species inside and outside pawpaw patches (Figure 4a) became weaker and nonsignificant when considering the total understory community of herbaceous and woody species together (Figure 4d). This indicates that abundances of woody species are consistent enough across the patch types to reduce overall differences in community composition. This could be due to several factors. First, woody species are generally less dispersal-limited than herbaceous species (Turnbull et al., 2000). In our study, for example, the most-common species of woody seedlings present inside pawpaw patches was northern spicebush (*Lindera benzoin*) (Appendix S1: Table S1), a bird-dispersed shrub with high adult abundance at our site. With increased dispersal, we expect decreased beta-diversity (Germain et al., 2017; Leibold & Chase, 2017; Ron et al., 2018; Thompson et al., 2020). Second, the woody seedlings are at a life stage that experiences higher mortality and is generally less diverse than the adult tree community (Green et al., 2014; Ramachandran et al., 2023). Seedling communities have been shown to have lower beta-diversity than adult tree communities (Ramachandran et al., 2023), presumably due to these ontogenetic differences in the importance of different assembly mechanisms (Cavender-Bares & Bazzaz, 2000; Comita et al., 2007; Green et al., 2014; Spasojevic et al., 2014). Meanwhile, the herbaceous community largely contains diverse adult assemblages that survived past the seedling stage. Lastly, most of the plant species diversity in temperate forests comprised herbaceous species, many of which are rare in the understory (Gilliam, 2007; Spicer et al., 2020), such that including more common woody species will inherently shift the composition towards being more similar. These results illustrate the need to further investigate how herbaceous communities assemble in forests, as differences in functional diversity and life-stages between herbaceous and woody species can elucidate different assembly processes in the understory (Spicer et al., 2022).

Patterns of beta-diversity inside pawpaw patches more closely resembled the null model (Figure 4c,f), supporting the third prediction of the stochastic assembly hypothesis. The smaller effect sizes inside pawpaw patches could reflect

several ecological processes. First, theory (Hubbell, 2001; Orrock & Watling, 2010; Vellend, 2016) and empirical studies (e.g., Fodelianakis et al., 2021; Gilbert & Levine, 2017; Siqueira et al., 2020) show that decreases in community size cause random changes in species relative abundances (ecological drift), thereby increasing compositional variation among local communities. In our study, community size was 67%–76% lower inside than outside pawpaw patches (Figure 3b), and of the species present in both patch types, most had much lower abundance inside pawpaw patches (Appendix S1: Figure S3), likely making local populations within pawpaw patches more prone to demographic stochasticity. Second, simulation models exploring the interplay between selection and ecological drift show that high beta-diversity can emerge when niche-based processes exacerbate the effects of neutral processes (Latombe et al., 2015). For example, Gilbert and Levine (2017) demonstrated that the presence of a dominant competitor can deterministically lower other species' relative abundances to a point where stochasticity has an even greater effect, causing higher variation in species composition among experimental plots with the smallest community sizes. In addition to smaller community size, more homogeneous light conditions under pawpaw patches could reduce fitness differences among co-occurring species and increase the relative importance of ecological drift (Beck et al., 2022; Hubbell, 2006). Third, while our study focused on patterns of species composition, the trait and phylogenetic composition of communities may exhibit more nonrandom responses to abiotic and biotic drivers of community assembly, particularly when communities are dominated by species with functionally redundant traits that are phylogenetically clustered or overdispersed (Cavender-Bares et al., 2009; Webb et al., 2002). Lastly, larger null-model deviations outside pawpaw patches can reflect more deterministic processes such as fine-scale environmental heterogeneity, local plant–soil and plant–plant interactions, and species-specific differences in dispersal ability (Bauer et al., 2017; Condit et al., 2002; Germain et al., 2017; Thompson et al., 2020). Collectively, these processes likely contribute to the nonrandom patterns of beta-diversity observed inside and outside pawpaw patches, as well as the relatively stronger nonrandom patterns observed outside pawpaw patches.

We also found that local species diversity was consistently lower inside than outside pawpaw patches (Figure 3a). Previous studies have found that dominant plant species can decrease local diversity (e.g., Eckberg et al., 2023; Ellison et al., 2015; Hejda et al., 2019; Hernández et al., 2022; McCain et al., 2010; Myers & Harms, 2009), but the underlying ecological processes remain unresolved. Although our study cannot discern

the degree to which low species diversity inside patches reflects dispersal limitation, nonrandom competitive exclusion, or ecological drift, lower community size may increase the role of ecological drift inside pawpaw patches. The effects of community size and dispersal limitation may be further exacerbated in larger pawpaw patches, where dispersal from source populations located outside patches may be less likely to balance local extinctions of dispersal-limited herbs inside pawpaw patches. Additionally, our findings are in contrast to studies that found that some dominant species facilitated species diversity by mitigating harsh conditions, often at the edge of subordinate species' range (Dayton, 1972; Elsberry & Bracken, 2021; Gavilán & Callaway, 2017; Pellissier et al., 2010).

Several abiotic and biotic factors may explain the lower community size, lower local species diversity, and more random patterns of beta-diversity within pawpaw patches. First, above and below ground abiotic conditions may be altered by pawpaw trees. Pawpaws have been shown to be strong competitors for light which could decrease the abundances of otherwise shade-tolerant understory plants (Cole & Weltzin, 2005). High pawpaw stem densities and clonal growth may also increase belowground competition for soil nutrients and water (Baumer & Runkle, 2010). While interference competition through allelopathy has been suggested for pawpaw, the current evidence for allelopathy in pawpaw is weak (McEwan et al., 2010; Pavliuchenko et al., 2018) to negative (Cole & Weltzin, 2005). Second, to the extent that clonal plant species are less common inside pawpaw patches than nonclonal plant species, lower community size (estimated as the summed frequencies of rooted stems) and higher simulated beta-diversity could also reflect lower overall densities of ramets, but not necessarily individuals (genets), inside pawpaw patches. Third, pawpaw's interaction with a dominant herbivore, white-tailed deer (*Odocoileus virginianus*), may explain patterns of diversity. Pawpaw is unpalatable to deer, leading deer to selectively browse other species (Jenkins et al., 2015; Shelton et al., 2014; Slater & Anderson, 2014). If deer are selectively browsing the herbaceous layer in pawpaw communities to avoid the unpalatable pawpaw leaves, this could decrease community size, decrease local species diversity, and increase beta-diversity within pawpaw patches. Alternatively, if deer avoid pawpaw patches altogether due to their inedibility, this could potentially decrease seed dispersal by deer via endozoochory and epizoochory of new propagules into pawpaw patches (e.g., Blyth et al., 2013; Guiden, 2017; Myers et al., 2004). Finally, a combination of suboptimal niche conditions and medium to high dispersal rates may make local communities within pawpaw patches subject to source-sink

dynamics, with pawpaw patches harboring "sink" populations (Pulliam, 1988).

At the landscape scale, we also found that overall species composition differed among blocks, as well as between patch types within blocks (Figure 5a). Moreover, the difference in species composition among blocks appeared to be mostly driven by differences with respect to variation in species composition (dispersion), rather than their average composition (centroids). This result suggests a role for ecological processes in shaping variation in community composition at larger spatial scales across this forest landscape. For example, higher variation in species composition (dispersion) in a locality (e.g., block) could reflect higher seed dispersal limitation or higher species sorting in more heterogeneous environments (Burton et al., 2011; Gilbert & Lechowicz, 2004). While our sampling design minimized differences in abiotic conditions (soils and topography) among blocks and among plots located inside and outside pawpaw patches (Figure 2), other environmental factors such as variation in understory disturbance and microtopography, light availability, and microclimate may contribute to spatial variation in species sorting (Anderson et al., 1969; Beatty, 1984; Struik & Curtis, 1962). Higher variation in species composition in a locality could also result from differences in the relative strength of deterministic and stochastic processes among patches, if, for example, ecological drift is especially strong within a pawpaw patch and deterministic assembly is especially strong outside a pawpaw patch. Regardless of the underlying mechanisms, our results underscore the importance of understanding how the relative importance of deterministic and stochastic processes vary and interact across spatial scales within the same landscape (Beck et al., 2022; Chase, 2014; Chase & Myers, 2011; Spasojevic et al., 2016).

Our study highlights several avenues for future research on the mechanisms by which pawpaw shapes forest community assembly. Future studies can use seed-addition experiments to test the degree to which low species diversity (Myers & Harms, 2009) and high beta-diversity (Germain et al., 2017) of herbaceous species are caused by dispersal limitation within pawpaw patches. Pawpaw-removal experiments can be used to disentangle the effects of pawpaw from potentially confounding or associated biotic and abiotic factors, including herbivory, light availability, microclimate and microtopography, and soil conditions. Future studies can also explore how pawpaw patch characteristics such as patch size, age, and demography affect the strength of deterministic and stochastic assembly processes and biodiversity patterns. While our study investigated these processes using observational data from one field census, long-term studies of plant demography (recruitment, growth, survival) and changes in community composition over time can be used to test complementary demographic and temporal predictions of various assembly processes (Vellend, 2016; Vellend et al., 2014) inside and outside pawpaw patches, and elucidate how pawpaws may affect forest regeneration (Baumer & Runkle, 2010; Hochwender et al., 2016) or invasive species spread (Cole & Weltzin, 2005). Further understanding the biology and ecology of this and other locally dominant tree species will provide key insights into how species interactions drive the assembly, diversity, and dynamics of understory plant communities at varying spatial scales.

## CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT
Data (Wassel & Myers, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.14183437.

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## REFERENCES
Altieri, A. H., and J. D. Witman. 2014. "Modular Mobile Foundation Species as Reservoirs of Biodiversity." *Ecosphere* 5: 124.

Anderson, A. R. C., O. L. Loucks, and A. M. Swain. 1969. "Herbaceous Response to Canopy Cover, Light Intensity, and Throughfall Precipitation in Coniferous Forests." *Ecology* 50: 255–263.

Anderson, M. J. 2001. "A New Method for Non-Parametric Multivariate Analysis of Variance." *Austral Ecology* 26: 32–46.

Anderson, M. J. 2006. "Distance-Based Tests for Homogeneity of Multivariate Dispersions." *Biometrics* 62: 245–253.

Anderson, M. J., T. O. Crist, J. M. Chase, M. Velland, B. D. Inouye, A. L. Freestone, N. J. Sanders, et al. 2011. "Navigating the Multiple Meanings of β Diversity: A Roadmap for the Practicing Ecologist." *Ecology Letters* 14: 19–28.

Anderson-Teixeira, K. J., S. J. Davies, A. C. Bennett, E. B. Gonzalez-Akre, H. C. Muller-Landau, S. J. Wright, K. Abu Salim, et al. 2015. "CTFS-ForestGEO: A Worldwide Network Monitoring Forests in an Era of Global Change." *Global Change Biology* 21: 528–549.

Arnillas, C. A., and M. W. Cadotte. 2019. "Experimental Dominant Plant Removal Results in Contrasting Assembly for Dominant and Non-Dominant Plants." *Ecology Letters* 22: 1233–42.

Avolio, M. L., E. J. Forrestel, C. C. Chang, K. J. La Pierre, K. T. Burghardt, and M. D. Smith. 2019. "Demystifying Dominant Species." *New Phytologist* 223: 1106–26.

Bauer, J. T., N. Blumenthal, A. J. Miller, J. K. Ferguson, and H. L. Reynolds. 2017. "Effects of Between-Site Variation in Soil Microbial Communities and Plant–Soil Feedbacks on the Productivity and Composition of Plant Communities." *Journal of Applied Ecology* 54: 1028–39.

Baumer, M., and J. R. Runkle. 2010. "Tree Seedling Establishment under the Native Shrub, *Asimina triloba*." *Castanea* 75: 421–432.

Beatty, S. W. 1984. "Influence of Microtopography and Canopy Species on Spatial Patterns of Forest Understory Plants." *Ecology* 65: 1406–19.

Beck, J. J., D. Li, S. E. Johnson, D. Rogers, K. M. Cameron, K. J. Sytsma, T. J. Givnish, and D. M. Waller. 2022. "Functional Traits Mediate Individualistic Species-Environment Distributions at Broad Spatial Scales while Fine-Scale Species Associations Remain Unpredictable." *American Journal of Botany* 109: 1991–2005.

Blyth, L. H., L. J. Ouborg, D. M. Johnson, and L. J. Anderson. 2013. "The Short-Term Germination and Establishment Success of Deer-Dispersed Seeds in Mesic Temperate Forests." *The Journal of the Torrey Botanical Society* 140: 334–348.

Borcard, D., F. Gillet, and P. Legendre. 2018. *Numerical Ecology with R*, 2nd ed. Cham: Springer International Publishing.

Bray, J. R., and J. T. Curtis. 1957. "An Ordination of the Upland Forest Communities of Southern Wisconsin." *Ecological Monographs* 27: 326–349.

Burton, J. I., D. J. Mladenoff, M. K. Clayton, and J. A. Forrester. 2011. "The Roles of Environmental Filtering and Colonization in the Fine-Scale Spatial Patterning of Ground-Layer Plant Communities in North Temperate Deciduous Forests." *Journal of Ecology* 99: 764–776.

Catano, C. P., T. L. Dickson, and J. A. Myers. 2017. "Dispersal and Neutral Sampling Mediate Contingent Effects of Disturbance on Plant Beta-Diversity: A Meta-Analysis." *Ecology Letters* 20: 347–356.

Cavender-Bares, J., and F. A. Bazzaz. 2000. "Changes in Drought Response Strategies with Ontogeny in *Quercus rubra*: Implications for Scaling from Seedlings to Mature Trees." *Oecologia* 124: 8–18.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. "The Merging of Community Ecology and Phylogenetic Biology." *Ecology Letters* 12: 693–715.

Chase, J. M. 2007. "Drought Mediates the Importance of Stochastic Community Assembly." *Proceedings of the National Academy of Sciences of the United States of America* 104: 17430–34.

Chase, J. M. 2014. "Spatial Scale Resolves the Niche Versus Neutral Theory Debate." *Journal of Vegetation Science* 25: 319–322.

Chase, J. M., B. J. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, O. Purschke, and N. J. Gotelli. 2018. "Embracing Scale-Dependence to Achieve a Deeper Understanding of Biodiversity and its Change across Communities." *Ecology Letters* 21: 1737–51.

Chase, J. M., and J. A. Myers. 2011. "Disentangling the Importance of Ecological Niches from Stochastic Processes across Scales." *Philosophical Transactions of the Royal Society B* 366: 2351–63.

Cole, P. G., and J. F. Weltzin. 2005. "Light Limitation Creates Patchy Distribution of an Invasive Grass in Eastern Deciduous Forests." *Biological Invasions* 7: 477–488.

Comita, L. S., R. Condit, and S. P. Hubbell. 2007. "Developmental Changes in Habitat Associations of Tropical Trees." *Journal of Ecology* 95: 482–492.

Condit, R., P. S. Ashton, P. Baker, S. Bunyavejchewin, S. Gunatilleke, N. Gunatilleke, S. P. Hubbell, et al. 2000. "Spatial Patterns in the Distribution of Tropical Tree Species." *Science* 288: 1414–18.

Condit, R., N. Pitman, E. G. Leigh, Jr., J. Chave, J. Terborgh, R. B. Foster, P. Núñez, et al. 2002. "Beta-Diversity in Tropical Forest Trees." *Science* 295: 666–69.

Cornell, H. V., and S. P. Harrison. 2014. "What Are Species Pools and when Are they Important?" *Annual Review of Ecology, Evolution, and Systematics* 45: 45–67.

Dayton, P. K. 1972. "Toward an Understanding of Community Resilience and the Potential Effects of Enrichments of the Benthos at McMurdo Sound, Antarctica." In *Proceedings of the Colloquium on Conservation Problems in Antarctica*, edited by B. C. Parker, 81–96. Lawrence, KS: Allen Press.

Eckberg, J. N., A. Hubbard, E. T. Schwarz, E. T. Smith, and N. J. Sanders. 2023. "The Dominant Plant Species *Solidago canadensis* Structures Multiple Trophic Levels in an Old-Field Ecosystem." *Ecosphere* 14: e4393.

Ellison, A. M. 2019. "Foundation Species, Non-Trophic Interactions, and the Value of Being Common." *iScience* 13: 254–268.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, et al. 2005. "Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems." *Frontiers in Ecology and the Environment* 3: 479–486.

Ellison, A. M., A. A. Barker Plotkin, and S. Khalid. 2015. "Foundation Species Loss and Biodiversity of the Herbaceous Layer in New England Forests." *Forests* 7: 9.

Ellison, A. M., H. L. Buckley, B. S. Case, D. Cardenas, Á. J. Duque, J. A. Lutz, J. A. Myers, D. A. Orwig, and J. K. Zimmerman. 2019. "Species Diversity Associated with Foundation Species in Temperate and Tropical Forests." *Forests* 10: 128.

Elsberry, L. A., and M. E. S. Bracken. 2021. "Functional Redundancy Buffers Mobile Invertebrates against the Loss of Foundation Species on Rocky Shores." *Marine Ecology Progress Series* 673: 43–54.

Fodelianakis, S., A. Valenzuela-Cuevas, A. Barozzi, and D. Daffonchio. 2021. "Direct Quantification of Ecological Drift at the Population Level in Synthetic Bacterial Communities." *The ISME Journal* 15: 55–66.

Gaston, K. J. 2011. "Common Ecology." *BioScience* 61: 354–362.

Gavilán, R. G., and R. M. Callaway. 2017. "Effects of Foundation Species above and below Tree Line." *Plant Biosystems* 151: 665–672.

Germain, R. M., S. Y. Strauss, and B. Gilbert. 2017. "Experimental Dispersal Reveals Characteristic Scales of Biodiversity in a Natural Landscape." *Proceedings of the National Academy of Sciences of the United States of America* 114: 4447–52.

Gilbert, B., and M. J. Lechowicz. 2004. "Neutrality, Niches, and Dispersal in a Temperate Forest Understory." *Proceedings of the National Academy of Sciences of the United States of America* 101: 7651–56.

Gilbert, B., and J. M. Levine. 2017. "Ecological Drift and the Distribution of Species Diversity." *Proceedings of the Royal Society of London B: Biological Sciences* 284: 20170507.

Gilbert, B., R. Turkington, and D. S. Srivastava. 2009. "Dominant Species and Diversity: Linking Relative Abundance to Controls of Species Establishment." *The American Naturalist* 174: 850–862.

Gilliam, F. S. 2007. "The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems." *BioScience* 57: 845–858.

Gilliam, F. S., ed. 2014. *The Herbaceous Layer in Forests of Eastern North America*. Oxford: Oxford University Press.

Green, P. T., K. E. Harms, and J. H. Connell. 2014. "Nonrandom, Diversifying Processes Are Disproportionately Strong in the Smallest Size Classes of a Tropical Forest." *Proceedings of the National Academy of Sciences of the United States of America* 111: 18649–54.

Grime, J. P. 1998. "Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects." *Journal of Ecology* 86: 902–910.

Guiden, P. W. 2017. "Spatial Heterogeneity in White-Tailed Deer Activity Increases Seed Dispersal of Shade-Intolerant Plants near Forest Edges in Fragmented Forests." *The Journal of the Torrey Botanical Society* 144: 371–78.

Hejda, M., K. Štajerová, J. Pergl, and P. Pyšek. 2019. "Impacts of Dominant Plant Species on Trait Composition of Communities: Comparison between the Native and Invaded Ranges." *Ecosphere* 10: e02880.

Hernández, D. L., A. Antia, and M. J. McKone. 2022. "The Ecosystem Impacts of Dominant Species Exclusion in a Prairie Restoration." *Ecological Applications* 32: e2592.

Hochwender, C. G., A. Nunn, M. Sonnenberger, and M. Roberts. 2016. "Tree Regeneration in a Southwestern Indiana Forest: Implications of Long-Term Browsing by Deer." *Proceedings of the Indiana Academy of Sciences* 125: 103–113.

Hosaka, N., S. Gómez, N. Kachi, J. F. Stuefer, and D. F. Whigham. 2005. "The Ecological Significance of Clonal Growth in the Understory Tree, Pawpaw (*Asimina triloba*)." *Northeastern Naturalist* 12: 11–22.

Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.

Hubbell, S. P. 2006. "Neutral Theory and the Evolution of Ecological Equivalence." *Ecology* 87: 1387–98.

Hughes, B. B. 2010. "Variable Effects of a Kelp Foundation Species on Rocky Intertidal Diversity and Species Interactions in Central California." *Journal of Experimental Marine Biology and Ecology* 393: 90–99.

Immel, D. L., and M. K. Anderson. 2001. *Pawpaw: Asimina Triloba (L.) Dunal*. Fort Collins, CO: U.S. Department of Agriculture Natural Resources Conservation Service.

Jenkins, L. H., B. D. Murray, and M. A. Jenkins. 2015. "Woody Regeneration Response to over a Decade of Deer Population Reductions in Indiana State Parks." *The Journal of the Torrey Botanical Society* 142: 205–219.

Keddy, P. A., and B. Shipley. 1989. "Competitive Hierarchies in Herbaceous Plant Communities." *Oikos* 54: 234–241.

Konno, Y. 2002. "Effects of Competitive Exclusion by the Dominant *Sasa tsuboiana* on Associate Species." *Vegetation Science* 19: 1–10.

Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, et al. 2011. "Disentangling the Drivers of β Diversity along Latitudinal and Elevational Gradients." *Science* 333: 1755–58.

LaManna, J. A., L. A. Burkle, R. T. Belote, and J. A. Myers. 2021. "Biotic and Abiotic Drivers of Plant–Pollinator Community Assembly across Wildfire Gradients." *Journal of Ecology* 109: 1000–1013.

LaManna, J. A., M. L. Walton, B. L. Turner, and J. A. Myers. 2016. "Negative Density Dependence Is Stronger in Resource-Rich Environments and Diversifies Communities when Stronger for Common but Not Rare Species." *Ecology Letters* 19: 657–667.

Latombe, G., C. Hui, and M. A. McGeoch. 2015. "Beyond the Continuum: A Multi-Dimensional Phase Space for Neutral-Niche Community Assembly." *Proceedings of the Royal Society of London B* 282: 20152417.

Leibold, M. A., and J. M. Chase. 2017. *Metacommunity Ecology*. Princeton, NJ: Princeton University Press.

Lustenhouwer, M. N., L. Nicoll, and A. M. Ellison. 2012. "Microclimatic Effects of the Loss of a Foundation Species from New England Forests." *Ecosphere* 3(3): 26.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

McCain, K. N. S., S. G. Baer, J. M. Blair, and G. W. T. Wilson. 2010. "Dominant Grasses Suppress Local Diversity in Restored Tallgrass Prairie." *Restoration Ecology* 18: 40–49.

McEwan, R. W., L. G. Arthur-Paratley, L. K. Rieske, and M. A. Arthur. 2010. "A Multi-Assay Comparison of Seed Germination Inhibition by *Lonicera maackii* and Co-Occurring Native Shrubs." *Flora* 205: 475–483.

Myers, J. A., J. M. Chase, I. Jiménez, P. M. Jørgensen, A. Araujo-Murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. "Beta-Diversity in Temperate and Tropical Forests Reflects Dissimilar Mechanisms of Community Assembly." *Ecology Letters* 16: 151–57.

Myers, J. A., and K. E. Harms. 2009. "Local Immigration, Competition from Dominant Guilds, and the Ecological Assembly of High-Diversity Pine Savannas." *Ecology* 90: 2745–54.

Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. "Seed Dispersal by White-Tailed Deer: Implications for Long-Distance Dispersal, Invasion, and Migration of Plants in Eastern North America." *Oecologia* 139: 35–44.

Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, et al. 2024. "vegan: Community Ecology Package." R Package Version 2.6-6.1.

Orrock, J. L., and J. I. Watling. 2010. "Local Community Size Mediates Ecological Drift and Competition in Metacommunities." *Proceedings of the Royal Society of London B* 277: 2185–91.

Pavliuchenko, N. A., K. Svitlana, D. Vitaliy, and K. Sergiy. 2018. "Allelopathic and Biochemical Characteristics of the Root

Environment of *Asimina triloba* (L.) Dunal." *Agrobiodiversity for Improving Nutrition, Health and Life Quality* 2018: 62–68.

Pellissier, L., K. Anne Bråthen, J. Pottier, C. F. Randin, P. Vittoz, A. Dubuis, N. G. Yoccoz, T. Alm, N. E. Zimmermann, and A. Guisan. 2010. "Species Distribution Models Reveal Apparent Competitive and Facilitative Effects of a Dominant Species on the Distribution of Tundra Plants." *Ecography* 33: 1004–14.

Pinheiro, J., D. Bates, and R Core Team. 2023. "nlme: Linear and Nonlinear Mixed Effects Models." R Package Version 3.1-164.

Powell, K. I., J. M. Chase, and T. M. Knight. 2013. "Invasive Plants Have Scale-Dependent Effects on Diversity by Altering Species-Area Relationships." *Science* 339: 316–18.

Pulliam, H. R. 1988. "Sources, Sinks, and Population Regulation." *The American Naturalist* 132: 652–661.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramachandran, A., J. D. Huxley, S. McFaul, L. Schauer, J. Diez, R. Boone, T. Madsen-Hepp, et al. 2023. "Integrating Ontogeny and Ontogenetic Dependency into Community Assembly." *Journal of Ecology* 111: 1561–74.

Reu, J. C., C. P. Catano, M. J. Spasojevic, and J. A. Myers. 2022. "Beta Diversity as a Driver of Forest Biomass across Spatial Scales." *Ecology* 103(10): e3774.

Ron, R., O. Fragman-Sapir, and R. Kadmon. 2018. "Dispersal Increases Ecological Selection by Increasing Effective Community Size." *Proceedings of the National Academy of Sciences of the United States of America* 115(44): 11280–85.

Segre, H., R. Ron, N. De Malach, Z. Henkin, M. Mandel, and R. Kadmon. 2014. "Competitive Exclusion, Beta Diversity, and Deterministic Vs. Stochastic Drivers of Community Assembly." *Ecology Letters* 17: 1400–1408.

Shelton, A. L., J. A. Henning, P. Schultz, and K. Clay. 2014. "Effects of Abundant White-Tailed Deer on Vegetation, Animals, Mycorrhizal Fungi, and Soils." *Forest Ecology and Management* 320: 39–49.

Simpson, E. H. 1949. "Measurement of Diversity." *Nature* 163: 688.

Siqueira, T., V. S. Saito, L. M. Bini, A. S. Melo, D. K. Petsch, V. L. Landeiro, K. T. Tolonen, J. Jyrkänkallio-Mikkola, J. Soininen, and J. Heino. 2020. "Community Size Can Affect the Signals of Ecological Drift and Niche Selection on Biodiversity." *Ecology* 101(6): e03014.

Slater, M. A., and R. C. Anderson. 2014. "Intensive Selective Deer Browsing Favors Success of *Asimina triloba* (Paw Paw) a Native Tree Species." *Natural Areas Journal* 34: 178–187.

Spasojevic, M. J., B. L. Turner, and J. A. Myers. 2016. "When Does Intraspecific Trait Variation Contribute to Functional Beta-Diversity?" *Journal of Ecology* 104: 487–496.

Spasojevic, M. J., E. A. Yablon, B. Oberle, and J. A. Myers. 2014. "Ontogenetic Trait Variation Influences Tree Community Assembly across Environmental Gradients." *Ecosphere* 5(10): 129.

Spicer, M. E., H. Mellor, and W. P. Carson. 2020. "Seeing beyond the Trees: A Comparison of Tropical and Temperate Plant Growth Forms and Their Vertical Distribution." *Ecology* 101(4): e02974.

Spicer, M. E., H. V. N. Radhamoni, M. C. Duguid, S. A. Queenborough, and L. S. Comita. 2022. "Herbaceous Plant Diversity in Forest Ecosystems: Patterns, Mechanisms, and Threats." *Plant Ecology* 223(2): 117–129.

Struik, G. J., and J. T. Curtis. 1962. "Herb Distributions in an *Acer saccharum* Forest." *American Midland Naturalist* 68: 285–296.

Sullivan, J. 1993. "*Asimina triloba*." Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, https://www.fs.usda.gov/database/feis/plants/tree/asitri/all.html.

Thompson, P. L., L. M. Guzman, L. De Meester, Z. Horváth, R. Ptacnik, B. Vanschoenwinkel, D. S. Viana, et al. 2020. "A Process-Based Metacommunity Framework Linking Local and Regional Scale Community Ecology." *Ecology Letters* 23: 1314–29.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. "Are Plant Populations Seed-Limited? A Review of Seed Sowing Experiments." *Oikos* 88: 225–238.

Vellend, M. 2010. "Conceptual Synthesis in Community Ecology." *The Quarterly Review of Biology* 85: 183–206.

Vellend, M. 2016. *The Theory of Ecological Communities*. Princeton, NJ: Princeton University Press.

Vellend, M., D. S. Srivastava, K. M. Anderson, C. D. Brown, J. E. Jankowski, E. J. Kleynhans, N. J. B. Kraft, et al. 2014. "Assessing the Relative Importance of Neutral Stochasticity in Ecological Communities." *Oikos* 123: 1420–30.

Wassel, A., and J. A. Myers. 2024. "Pawpaws Prevent Predictability: A Locally Dominant Tree Alters Understory Beta-Diversity and Community Assembly." Dataset. Zenodo. https://doi.org/10.5281/zenodo.14183437.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. "Phylogenies and Community Ecology." *Annual Review of Ecology, Evolution, and Systematics* 33: 475–505.

Whittaker, R. H. 1956. "Vegetation of the Great Smoky Mountains." *Ecological Monographs* 26: 1–80.

Zimmerman, M., and W. L. Wagner. 1979. "A Description of the Woody Vegetation of Oak-Hickory Forest in the Northern Ozark Highlands." *Bulletin of the Torrey Botanical Club* 106: 117–122.

## SUPPORTING INFORMATION

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

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