

1 **Ecosphere**

2 Article

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

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11 Open research statement: The data underlying this article will be made freely available and
12 permanently archived in Dryad or Zenodo if accepted for publication. Code used for this study is
13 not novel: R packages used are cited in the body of the paper and code for the null model is
14 provided in previous papers Kraft et al. 2011; LaManna et al. 2021).

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16 Key words: *Asimina triloba*; beta-diversity; community assembly; community size; competition;
17 dominant species; ecological drift; forest herbs; null model; species interactions; stochasticity;
18 temperate forest

19 **Abstract –**

20 While dominant species are known to be important in ecosystem functioning and community
21 assembly, biodiversity responses to the presence of dominant species can be highly variable.
22 Dominant species can increase the importance of deterministic community assembly by
23 competitively excluding species in a consistent way across local communities, resulting in low
24 site-to-site variation in community composition (beta-diversity) and non-random community
25 structure. In contrast, dominant species could increase the importance of stochastic community
26 assembly by reducing the total number of individuals in local communities (community size),
27 resulting in high beta-diversity and more random community structure. We tested these
28 hypotheses in a large, temperate oak-hickory forest plot containing a locally-dominant tree
29 species, pawpaw (*Asimina triloba*; Annonaceae), an understory tree species that occurs in dense,
30 clonal patches in forests throughout the east-central United States. We determined how the
31 presence of pawpaw influences local species diversity, community size, and beta-diversity by
32 measuring the abundance of all vascular plant species in 1x1-m plots both inside and outside
33 pawpaw patches. To test whether the presence of pawpaw influences local assembly processes,
34 we compared observed patterns of beta-diversity inside and outside patches to a null model of
35 random assembly. We found lower local species diversity, lower community size, and higher
36 observed beta-diversity inside pawpaw patches than outside pawpaw patches. Moreover,
37 standardized effect sizes of beta-diversity from the null model were lower inside pawpaw
38 patches than outside pawpaw patches, indicating more random community composition inside
39 pawpaw patches. Together these results suggest that pawpaw increases the importance of
40 stochastic relative to deterministic community assembly at local scales, likely by decreasing
41 overall numbers of individuals, and increasing random local extinctions inside patches. Our

- 42 findings provide insights into the ecological processes by which locally-dominant tree species
- 43 shape the assembly and diversity of understory plant communities at different spatial scales.

44 **Introduction**

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

60 Dominant species can affect community assembly through deterministic or stochastic
61 processes. Deterministic processes include abiotic filtering and biotic interactions such as
62 competition and facilitation that reflect niche differences among species in a community
63 (Vellend 2010, Chase and Myers 2011, Leibold and Chase 2017). Dominant species can increase
64 the importance of interspecific competition when they limit space or resources for other species
65 (e.g. Lustenhouwer et al. 2012), resulting in competitive exclusion (Konno 2002, Segre et al.
66 2014, Ellison et al. 2015). Alternatively, dominant species can facilitate the survival of certain

67 species by lowering abiotic stress (e.g. Gavlán and Callaway 2017). Dominant species can also
68 increase the importance of stochastic community assembly by decreasing the total number of
69 individuals in a local community (local community size) (Powell et al. 2013). As local
70 community size decreases, more species in the community may become rare, thereby increasing
71 demographic stochasticity and random changes in species' relative abundances (ecological drift;
72 MacArthur and Wilson 1967, Hubbell 2001, Orrock and Watling 2010). In addition, amelioration
73 of stressful conditions by dominant species can lead to more random assembly of nondominant
74 species (Arnillas and Cadotte 2019). The effects of dominant species on deterministic and
75 stochastic processes are expected to increase when dominant species are also of large stature, i.e.,
76 when size asymmetries among competing species or guilds are large (Keddy and Shipley 1989,
77 Myers and Harms 2009).

78 Despite widespread interest in the role of dominant species in communities and
79 ecosystems (Ellison et al. 2005, Gilbert et al. 2009, Avolio et al. 2019), their relative effects on
80 deterministic and stochastic community assembly remain unresolved. First, previous studies have
81 largely focused on how dominant species influence species diversity at local spatial scales (e.g.,
82 alpha diversity), but similar patterns of local species diversity could reflect different assembly
83 processes. For example, low species richness can result from either competitive exclusion by
84 dominant species (Konno 2002, Segre et al. 2014, Ellison et al. 2015) or random local
85 extinctions in small communities with few individuals (Powell et al. 2013). Most dominant-
86 species removal experiments in plant communities have focused on changes in local species
87 richness or diversity, finding a mix of positive (Konno 2002, Segre et al. 2014, Ellison et al.
88 2015, Avolio et al. 2019), negative (Hughes 2010, Altieri and Witman 2014, Gavlán and
89 Callaway 2017), or no clear response (Myers and Harms 2009, Gilbert et al. 2009) to the

90 removal of dominant plant species. Second, relatively few studies have examined how dominant
91 species influence site-to-site variation in community composition (beta-diversity). Patterns
92 of beta-diversity can help elucidate the relative importance of deterministic and stochastic
93 processes (Anderson et al. 2011, Chase and Myers 2011). For example, deterministic exclusion
94 of inferior competitors by dominant species should cause local communities to converge in
95 composition (i.e., low beta-diversity), whereas random local extinctions in small communities
96 should cause local communities to diverge in composition (i.e., high beta-diversity). Finally,
97 observed changes in beta-diversity can be compared to a null model of random community
98 assembly to further assess the relative roles of deterministic and stochastic processes (Chase
99 2007, Catano et al. 2017). Therefore, patterns of diversity at different scales can provide key
100 insights into the ecological roles of dominant species in community assembly and ecosystem
101 functioning.

102 In this study, we examined the effect of a locally-dominant tree species, pawpaw
103 (*Asimina triloba*; Annonaceae), on the diversity and assembly of understory plant communities
104 in a temperate forest-dynamics plot. Our focal species, pawpaw, is a widely-distributed
105 understory tree species that occurs in dense, clonal patches in forests throughout the east-central
106 United States. Pawpaw has been shown to be a dominant species in temperate forests with high
107 local abundance (Appendix S1: Fig. S1) and strong effects on the diversity of other tree species
108 (Baumer and Runkle 2010). While the assembly of forest tree communities is fairly well studied
109 (e.g. Condit et al. 2000, Condit et al. 2002, Ellison et al. 2019), the assembly of forest herb
110 communities has received less attention, despite the disproportionate contribution of herbaceous
111 plant species to temperate forest diversity (Gilliam 2007, Spicer et al. 2020). We therefore

112 examined the effect of pawpaw on both the total understory community (woody and herbaceous
113 species combined) and herbaceous species only.

114 We tested two non-mutually exclusive hypotheses. First, we tested the hypothesis that
115 pawpaw increases the relative role of deterministic assembly through interspecific competition
116 (hereafter the deterministic assembly hypothesis). Second, we tested the hypothesis that pawpaw
117 increases the relative role of stochastic assembly by decreasing local community size (hereafter
118 the stochastic assembly hypothesis). The deterministic assembly hypothesis predicts that the
119 presence of dominant species 1) decreases local species diversity due to competitive exclusion,
120 2) decreases beta-diversity among local communities by selecting for a limited subset of species
121 that can co-occur with dominant species, and 3) results in lower beta-diversity than expected by
122 random assembly from the species pool. In contrast, the stochastic assembly hypothesis predicts
123 that the presence of dominant species 1) decreases local species diversity, but 2) increases beta-
124 diversity among local communities, due to random local extinctions, and 3) results in beta-
125 diversity that is more similar to patterns expected under random assembly from the species pool.
126 We tested these predictions by comparing observed patterns of local species diversity, local
127 community size, and beta-diversity among paired groups of understory plant communities
128 located inside and outside of pawpaw patches. We then compared observed patterns of beta-
129 diversity to a null model that simulated random assembly of local communities from the species
130 pool.

131 **Methods**

132 *Study site and focal species*

133 We conducted this study at Washington University in St. Louis' environmental field
134 station, Tyson Research Center, located 25 miles from St. Louis, Missouri. The 800-ha site is

135 located on the edge of the Ozark highlands, dominated by late-successional, deciduous oak-
136 hickory forest, and contains a topographically heterogeneous landscape characterized by silty
137 loam and silty clay soils that develop from shale and cherty limestone (Zimmerman and Wagner
138 1979). Our study was conducted within the Tyson Research Center Forest Dynamics Plot, a large
139 (20.16 ha; 480 x 420 m), stem-mapped forest plot that is part of the Forest Global Earth
140 Observatory (ForestGEO) network (Anderson-Teixeira et al. 2015). The 20-ha plot includes
141 more than 1,600 stems of pawpaw at least 1 cm in diameter at breast height (DBH), most of
142 which occur in 18 patches ranging in area from 5-1028 m².

143 Our focal dominant species for this study is the pawpaw tree, *Asimina triloba*
144 (Annonaceae) (hereafter pawpaw). Pawpaw is distributed widely throughout the east-central
145 United States and parts of southern Canada (Sullivan 1993), making it the northernmost member
146 of the otherwise tropical family Annonaceae. It primarily occurs in moist valleys and mesic
147 hillsides (Immel and Anderson 2001). Pawpaw can reproduce both sexually and asexually,
148 forming dense, discrete clonal patches (Hosaka et al. 2005). While not the most abundant species
149 in temperate forests at larger spatial scales due to its patchy distribution, at our study site it is
150 frequently the most abundant species at the 10x10 m scale when it is present (Appendix S1: Fig.
151 S1), making it a *locally* dominant species. The local dominance and discrete patch structure of
152 this species make it an ideal study system for investigating how the presence or absence of a
153 dominant species affects community assembly processes.

154 *Sampling design*

155 We selected five blocks to contain a pawpaw patch and an adjacent area without
156 pawpaws, referred to as “inside” and “outside” patches, respectively (Fig. 1, Fig. 2). The inside
157 (pawpaw) patches selected ranged from 58-435 m² in size (mean = 189 m²). The paired outside

158 patches were selected to have abiotic (soil and topographic) conditions similar to those inside the
159 pawpaw patch and were 10 to 20 m from the edge of the pawpaw patch (Fig. 2a, 2c). We
160 determined the similarity of soil and topographic conditions between the inside and outside
161 patches through a Principal Component Analysis (PCA) on 17 soil and topographic variables
162 (Appendix S1: Fig. S2). The values were estimated for each 10 × 10-m subplot in the 20-ha
163 ForestGEO plot based on measurements taken in 2013 (detailed in Spasojevic et al. 2014,
164 LaManna et al. 2016). The outside patches were chosen to have a similar PC1 score as the
165 pawpaw patches.

166 For each patch type in each of the five blocks, five 1x1-m plots were sampled for plant
167 community composition (n=25 inside plots, n=25 outside plots, n=50 plots total; Fig. 2b). Each
168 plot was at least two m within the edge of the pawpaw patch but did not contain any woody
169 stems over 1 cm DBH. Woody stems over 1 cm DBH were excluded to keep standard the
170 amount of available ground area available for understory plants. We recorded the identity and
171 estimated the abundance of all understory vascular plant species, i.e. herbaceous plants including
172 ferns, and woody plants and vines. We estimated abundance (number of stems per species) as the
173 number of 10x10-cm cells that contained rooted stems of the given species. In cases when
174 individuals could not be identified to species in the field, they were identified to genus or
175 assigned a morphospecies and photos were uploaded to iNaturalist for future assistance with
176 identification; 8% of stems were considered morphospecies for analyses. We estimated local
177 community size by summing the abundances of all species in each plot. Sampling was conducted
178 during the peak growing season from July to September of 2021. Due to the different life stages
179 and biology of young woody seedlings compared to the adult herbaceous plants, we conducted

180 two separate analyses for: 1) herbaceous and woody plant species combined (hereafter total
181 understory community); and 2) herbaceous species only.

182

183 *Analyses*

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

191 To test our first prediction, we calculated local species diversity using the inverse
192 Simpson’s index (Simpson 1949, Oksanen et al. 2022); a scale-independent diversity measure of
193 the effective number of species that is insensitive to differences in numbers of individuals (Chase
194 et al. 2018). For the model testing local diversity of the total understory community, we log-
195 transformed the inverse-Simpson’s values to meet the assumption of homogeneous variances.
196 For the model testing local diversity of herbaceous species only, we used a heterogeneous
197 variance model and excluded the two plots with no species.

198 To test our second prediction, we calculated observed beta-diversity as the compositional
199 dissimilarity among plots using the Bray-Curtis index. We analyzed beta-diversity based on
200 distance-to-centroid values (Anderson 2006, Kraft et al. 2011) using the ‘betadisper’ function in
201 the R vegan package (Oksanen et al. 2022), where each value represents the distance
202 (compositional dissimilarity) from an individual plot to the centroid of the group of all 25 plots

203 within each patch type (Fig. 2b). When analyzing beta-diversity of herbaceous species only, we
204 excluded two inside plots from block 5 that contained no herbaceous plants.

205 To test our third prediction, we used a null model to simulate the compositional
206 dissimilarity expected by random community assembly (Kraft et al. 2011, Myers et al. 2013,
207 LaManna et al. 2021). First, we defined the species pool as all species recorded during the study
208 across all inside and outside plots combined. We estimated the total abundance of each species
209 (number of stems) in the species pool by summing its frequencies (number of 10x10-cm cells in
210 which a rooted stem was recorded) across all plots. Second, in each of 2000 iterations of the null
211 model, we simulated community assembly in each plot by randomly sampling stems from the
212 species pool, while keeping constant the empirically observed total number of stems in each plot
213 (local community size) and total abundance of each species in the species pool. Third, we
214 calculated the mean simulated beta-diversity for each plot by averaging the Bray-Curtis distance-
215 to-centroid values from the 2000 null-model iterations. Fourth, we calculated the standardized
216 effect size as the difference between the observed beta-diversity (distance-to-centroid) and mean
217 simulated values for each plot, divided by the standard deviation of simulated values for each
218 plot. A standardized effect size of zero indicates that observed beta-diversity does not differ from
219 random sampling of the species pool, a positive value indicates higher beta-diversity than
220 expected by chance, and a negative value indicates lower beta-diversity than expected by chance.
221 We tested median standardized effect sizes of each patch type against the null expectation of
222 zero with one-sample two-sided Wilcoxon tests. All analyses were conducted in R (R Core Team
223 2022).

224 **Results**

225 Overall, we observed a total of 79 plant species and morphospecies (hereafter species) in this
226 study, including 52 herbaceous plant species and 27 woody plant species (Appendix S1: Table
227 S1, S2, S3). Only 6 species were unique to inside patches while there were 29 species unique to
228 outside patches. Of the 52 herbaceous plant species, 24 occurred inside pawpaw patches and 47
229 occurred in outside patches. Of the 27 woody plant species, 12 occurred inside pawpaw patches
230 and 26 occurred in outside patches. Of the species that occurred in both patch types (inside and
231 outside), most had lower abundance inside pawpaw patches (Appendix S1: Fig. S3). Among taxa
232 identified to the species level (non-morphospecies, Appendix S1: Table S1, S2), herbaceous
233 species were more abundant than woody species outside of pawpaw patches (68.4% of the total
234 estimated number of stems), but less abundant than woody species inside pawpaw patches
235 (39.9% of the total estimated number of stems).

236 **Local species diversity and community size**

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

245 **Observed, simulated, and standardized effect sizes of beta-diversity**

246 Observed, simulated, and standardized effect sizes of beta-diversity differed significantly
247 inside and outside pawpaw patches for herbaceous species only (Fig. 4a-c; Appendix S1: Table
248 S4). Observed and simulated beta-diversity was higher inside than outside pawpaw patches (Fig.
249 4a-b). In contrast, standardized effect sizes of beta-diversity were significantly lower inside than
250 outside pawpaw patches (Fig. 4c). Median standardized effect sizes inside and outside of
251 pawpaw patches were both positive and differed significantly from zero, though the difference
252 was less significant inside pawpaw patches (Fig. 4c; Appendix S1: Table S5; $P = 0.044$ inside
253 patches; $P = 0.001$ outside patches). Similar patterns were observed for the total understory
254 community, with the exception of observed beta-diversity, which showed no significant
255 difference between patch types. Median standardized effect sizes differed more between patch
256 types, due to larger standardized effect sizes outside of pawpaw patches for the total understory
257 community (Fig. 4f) compared to herbaceous species only (Fig. 4c). For the total understory
258 community (Fig. 4f), median standardized effect sizes inside and outside pawpaw patches both
259 differed significantly from zero (Table S4; $P = 0.013$ inside patches; $P < 0.001$ outside patches).

260

261 **Discussion**

262 Overall, our results support the stochastic assembly hypothesis. The lower local species
263 diversity, lower community size, and more random variation in species composition found within
264 pawpaw patches all support predictions of the stochastic assembly hypothesis. Beta-diversity was
265 higher than expected by chance both inside and outside of pawpaw patches, but patterns of beta-
266 diversity inside pawpaw patches more closely resembled the null expectation of random
267 community assembly. These findings suggest that both deterministic and stochastic assembly
268 processes are important in shaping the understory plant community, but that local communities

269 in different patch types are not assembled the same way, with stochastic processes being
270 relatively more important than deterministic processes in patches dominated by pawpaw.

271 Observed beta-diversity of herbaceous species was higher inside than outside of pawpaw
272 patches, supporting the second prediction of the stochastic assembly hypothesis (Fig. 4a). Higher
273 beta-diversity among plots inside pawpaw patches is in line with the findings of other studies
274 that observed the presence of dominant woody species increases beta-diversity (Ellison et al.
275 2015, Ellison et al. 2019,) or decreases local relative to regional diversity (Powell et al. 2013).
276 However, previous studies have often focused on how dominant tree species affect other tree
277 species, without explicit consideration of their effects on herbaceous species. In our study, the
278 difference in observed beta-diversity of herbaceous species inside and outside of pawpaw
279 patches (Fig. 4a) became weaker and non-significant when considering the total understory
280 community of herbaceous and woody species together (Fig. 4d). This indicates that abundances
281 of woody species are consistent enough across the patch types to reduce overall differences in
282 community composition. This could be due to several factors. First, woody species are generally
283 less dispersal-limited than herbaceous species (Turnbull et al. 2000). In our study, for example,
284 the most-common species of woody seedlings present inside pawpaw patches was northern
285 spicebush (*Lindera benzoin*) (Appendix S1: Table S1), a bird-dispersed shrub with high adult
286 abundance at our site. With increased dispersal, we expect decreased beta-diversity (Leibold and
287 Chase 2017, Germain et al. 2017, Ron et al. 2018, Thompson et al. 2020). Second, the woody
288 seedlings are at a life stage that experiences higher mortality and is generally less diverse than
289 the adult tree community (Green et al. 2014, Ramachandran et al. 2023). Seedling communities
290 have been shown to have lower beta-diversity than adult tree communities (Ramachandran et al.
291 2023), presumably due to these ontogenetic differences in the importance of different assembly

292 mechanisms (Cavender-Bares and Bazzaz 2000, Comita et al. 2007, Green et al. 2014,
293 Spasojevic et al. 2014). Meanwhile, the herbaceous community largely contains diverse adult
294 assemblages that survived past the seedling stage. Lastly, most of the plant species diversity in
295 temperate forests is comprised of herbaceous species, many of which are rare in the understory
296 (Gilliam 2007, Spicer et al. 2020), such that including more common woody species will
297 inherently shift the composition towards being more similar. These results illustrate the need to
298 further investigate how herbaceous communities assemble in forests, as differences in functional
299 diversity and life-stages between herbaceous and woody species can elucidate different assembly
300 processes in the understory (Spicer et al. 2022).

301 Patterns of beta-diversity inside pawpaw patches more closely resembled the null
302 expectation of random assembly (Fig. 4c, f), supporting the third prediction of the stochastic
303 assembly hypothesis. . The smaller effect sizes inside pawpaw patches could reflect several
304 ecological processes. First, theory (Hubbell 2001, Orrock and Watling 2010, Vellend 2016) and
305 empirical studies (e.g. Gilbert and Levine 2017, Siqueira et al. 2020, Fodelianakis et al. 2021)
306 show that decreases in community size causes random changes in species relative abundances
307 (ecological drift), thereby increasing compositional variation among local communities. In our
308 study, community size was 49–76% lower inside than outside pawpaw patches (Fig. 3b), and of
309 the species present in both patch types, most had much lower abundance inside pawpaw patches
310 (Appendix S1: Fig. S3), likely making local populations within pawpaw patches more prone to
311 demographic stochasticity. Second, simulation models exploring the interplay between selection
312 and ecological drift show that high beta-diversity can emerge when niche-based processes
313 exacerbate the effects of neutral processes (Latombe et al. 2015). For example, Gilbert and
314 Levine (2017) demonstrated that the presence of a dominant competitor can deterministically

315 lower other species' relative abundances to a point where stochasticity has an even greater effect,
316 causing very high species turnover among their plots with the smallest overall community sizes.
317 Third, larger null-model deviations outside of pawpaw patches can reflect more deterministic
318 processes such as fine-scale environmental heterogeneity, local plant-soil and plant-plant
319 interactions, and species-specific differences in dispersal ability (Condit et al. 2002, Bauer et al.
320 2017, Germain et al. 2017, Thompson et al. 2020). These deterministic processes likely
321 contribute to the non-random patterns of beta-diversity observed inside and outside pawpaw
322 patches, as well as the relatively stronger non-random patterns observed outside pawpaw
323 patches.

324 We also found that local species diversity was consistently lower inside than outside
325 pawpaw patches (Fig. 3a). Previous studies have found that dominant plant species can decrease
326 local diversity (e.g. Myers and Harms 2009, McCain et al. 2010, Ellison et al. 2015, Hejda et al.
327 2019, Hernández et al. 2022, Eckberg et al. 2023), but the underlying ecological processes
328 remain unresolved. Although our study cannot discern the degree to which low species diversity
329 inside patches reflects dispersal limitation, non-random competitive exclusion, or ecological
330 drift, lower community size may increase the role of ecological drift inside pawpaw patches. The
331 effects of community size and dispersal limitation may be further exacerbated in larger pawpaw
332 patches, where dispersal from source populations located outside patches may be less likely to
333 balance local extinctions of dispersal-limited herbs inside pawpaw patches. Additionally, our
334 findings are in contrast to studies that found that some dominant species facilitated species
335 diversity by mitigating harsh conditions, often at the edge of subordinate species' range (Dayton
336 1972, Pellissier et al. 2010, Gavilán and Callaway 2017, Elsberry and Bracken 2021).

337 Several abiotic and biotic factors may explain the lower community size, lower local
338 species diversity, and more random patterns of beta-diversity within pawpaw patches. First,
339 above and below ground abiotic conditions may be altered by pawpaw trees. Pawpaws have been
340 shown to be strong competitors for light which could decrease the abundances of otherwise
341 shade-tolerant understory plants (Cole and Weltzin 2005). In addition, high pawpaw stem
342 densities and clonal growth may increase belowground competition for soil nutrients and water
343 (Baumer and Runkle 2010). Second, pawpaw may be allelopathic (McEwan et al. 2010,
344 Pavliuchenko 2018). In our study ecosystem, sites invaded by the allelopathic shrub, bush
345 honeysuckle (*Lonicera mackii*), have low diversity of native plant species (Powell et al. 2013),
346 making this a particularly intriguing hypothesis. However, the current evidence for allelopathy in
347 pawpaws is weak (McEwan et al. 2010, Pavliuchenko 2018) to negative (Cole and Weltzin
348 2005). Third, pawpaw's interaction with a dominant herbivore, white-tailed deer (*Odocoileus*
349 *virginianus*), may explain patterns of diversity. Pawpaw is unpalatable to deer, leading deer to
350 selectively browse other species (Slater and Anderson 2014, Shelton et al. 2014, Jenkins et al.
351 2015). If deer are selectively browsing the herbaceous layer in pawpaw communities to avoid the
352 unpalatable pawpaw leaves, this could decrease community size, decrease local species diversity,
353 and increase beta-diversity within pawpaw patches. Alternatively, if deer avoid pawpaw patches
354 altogether due to their inedibility, this could potentially decrease seed dispersal by deer via
355 endozoochory and epizoochory of new propagules into pawpaw patches (e.g. Myers et al. 2004,
356 Blyth et al. 2013, Guiden 2017). Finally, a combination of suboptimal niche conditions and
357 medium to high dispersal rates may make local communities within pawpaw patches subject to
358 source-sink dynamics, with pawpaw patches harboring "sink" populations (Pulliam 1988).

359 Our study highlights several avenues for future research on the mechanisms by which
360 pawpaw shapes forest community assembly. Future studies can use seed-addition experiments to
361 test the degree to which low species diversity (Myers and Harms 2009) and high beta-diversity
362 (Germain et al. 2017) of herbaceous species are caused by dispersal limitation within pawpaw
363 patches. Similarly, investigating the degree to which micro-habitat variation in light and soil
364 conditions inside and outside pawpaw patches determine community composition can help
365 further differentiate between deterministic and stochastic assembly processes. Future studies can
366 also explore how pawpaw patch characteristics such as patch size, age, and demography affect
367 the strength of these processes and biodiversity patterns. Long-term studies of woody plant
368 recruitment, growth, and survival inside and outside of pawpaw patches can elucidate how
369 pawpaws may affect forest regeneration (Baumer and Runkle 2010, Hochwender et al. 2016) or
370 invasive species spread (Cole and Weltzin 2005). Further understanding the biology and ecology
371 of this and other locally-dominant tree species will provide key insights into how species
372 interactions drive the assembly, diversity, and dynamics of understory plant communities at
373 varying spatial scales.

374

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389

390 **Conflict of Interest:**

391 The authors report no conflict of interest.

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624 **Figure Captions**

625 Fig. 1. Examples of understory plant communities (a) inside a pawpaw (*Asimina triloba*) patch
626 (“inside plot”) and (b) outside a pawpaw patch at least 10 m away from the patch edge (“outside
627 plot”). White squares show 1x1-m plots. Photos by Anna C. Wassel.

628

629 Fig. 2. Sampling design within the Tyson Research Center ForestGEO Plot, Missouri. (a)
630 Abiotic conditions (soil resources & topography) represented by the first axis of a principal
631 component analysis (PCA) including 17 environmental variables at the 10x10-m scale
632 (Appendix S1: Fig. S2), mapped locations of all pawpaw stems ≥ 1 cm in diameter at breast
633 height (DBH), and selected sampling blocks. Blue values represent areas of lower elevation,
634 higher soil-nutrient availability, and higher soil pH, whereas red values represent higher
635 elevation, lower nutrient availability, and more acidic soils. (b) For each block, the pawpaw
636 patch edge was defined and five 1x1-m plots were placed inside or outside the patch. Gray
637 arrows represent how beta-diversity was calculated within each of the two patch types (inside
638 and outside plots). (c) Each block is shown zoomed in to illustrate the environmental conditions
639 and relative location for both the inside patches (yellow stars over pawpaw stems) and outside
640 patches represented by gray rectangles.

641

642 Fig. 3. Local plant species diversity and community size are lower inside than outside of pawpaw
643 patches. (a) Local species diversity (inverse Simpson’s index) outside ($N = 25$) and inside plots
644 ($N = 25$) for the total understory community (herbaceous and woody plant species), and
645 herbaceous species only. (b) Local community size for the total understory community, and
646 herbaceous species only. Community size was estimated as the total number of rooted stems of

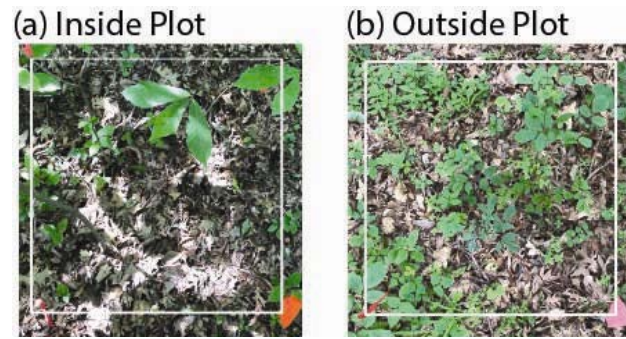
647 all species in each plot. Boxes represent the median and 25th/75th percentile, whiskers extend to
648 the largest value up to 1.5 times the interquartile range, and dots represent outlier data points.

649 (***) = $P < 0.001$)

650

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

659 **Figures**

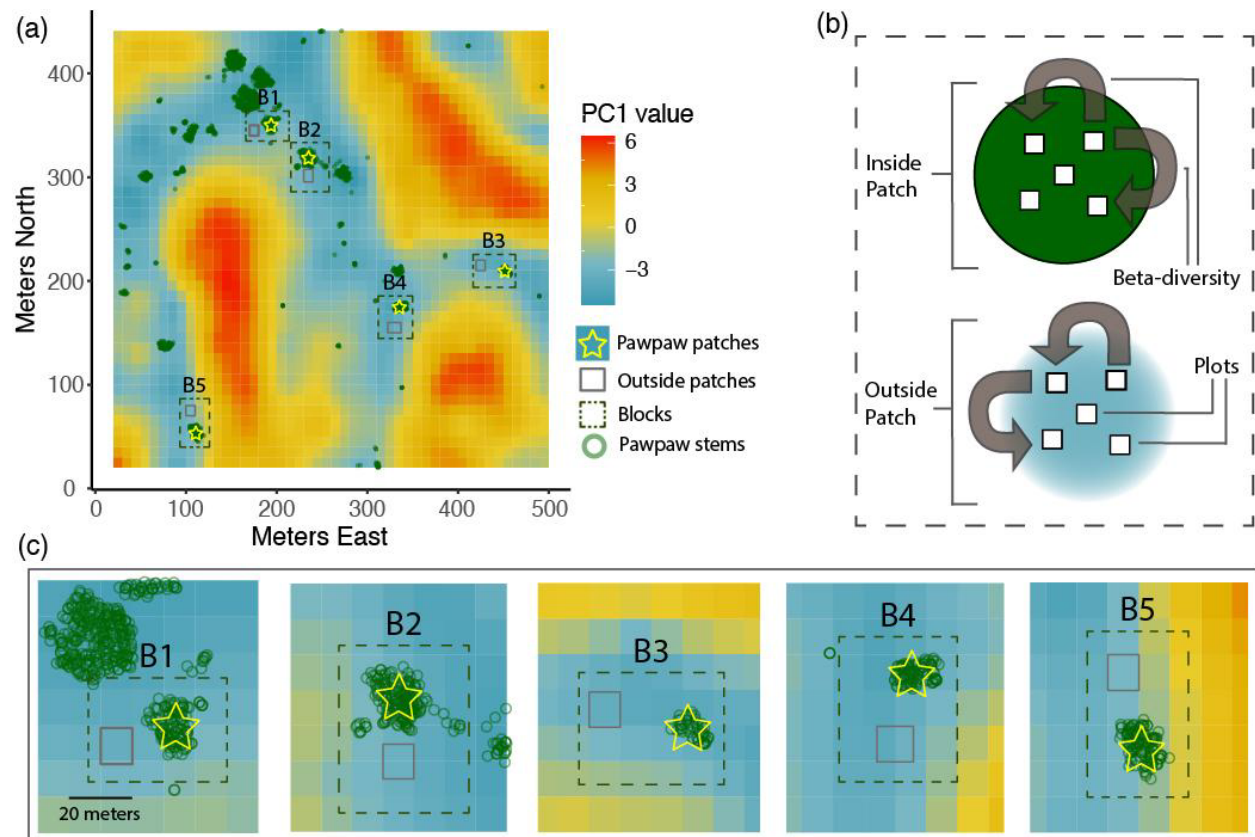


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662 **Figure 1.**

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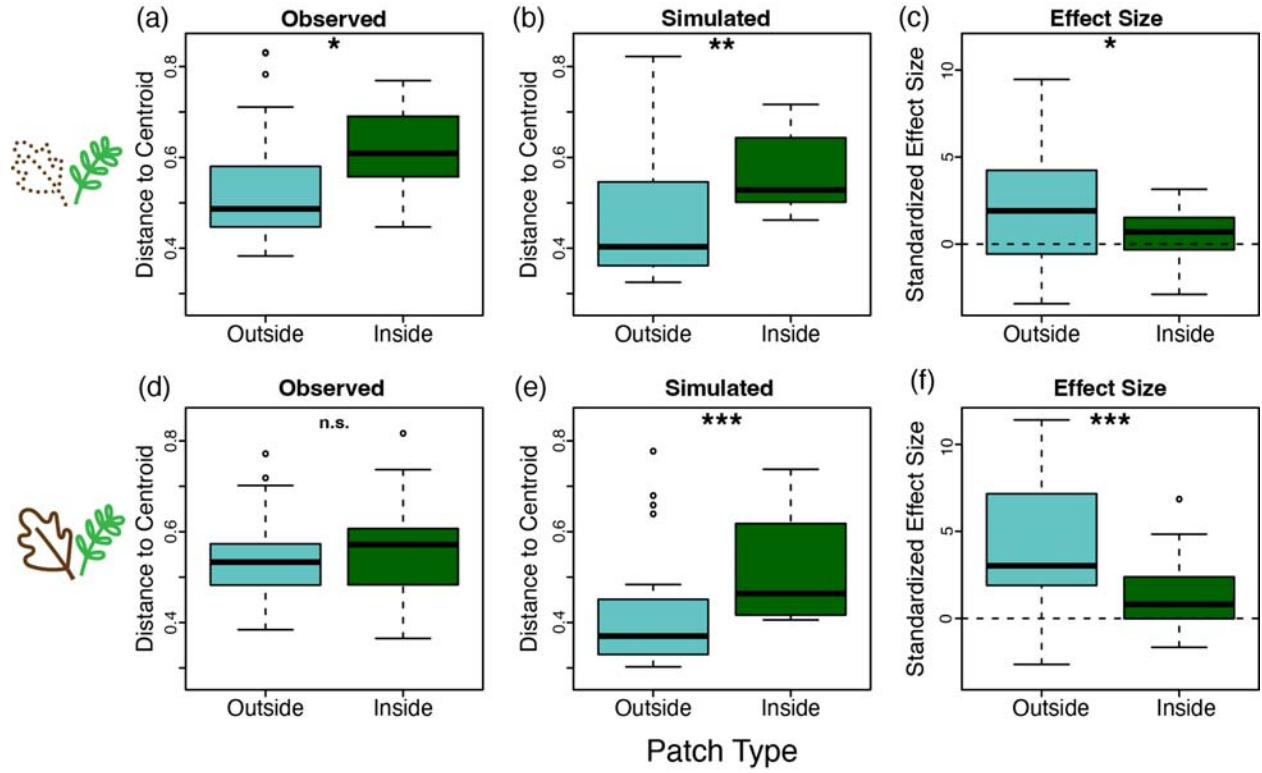


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Figure 2.



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668 **Figure 3**



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670 **Figure 4**