

Insect herbivores increase mortality and reduce tree seedling growth of some species in temperate forest canopy gaps

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Insect herbivores are thought to have relatively weak impacts on tree seedling dynamics in temperate forests despite having considerable influence in grasslands and other systems. Relatively few studies, however, have experimentally manipulated forest insect abundance and tracked impacts over multiple years. We conducted a three-year experiment (2012-2014) deterring insect herbivores from seedlings in new treefall gaps in deciduous hardwood forests in Maryland. During this study, we tracked recruitment of all tree seedlings, as well as survivorship and growth of 889 individual seedlings from five tree species: *Acer rubrum*, *Fagus grandifolia*, *Fraxinus* spp., *Liriodendron tulipifera*, and *Liquidambar styraciflua*. Insect herbivores had little effect on recruitment of any tree species, although there was a weak indication that recruitment of *A. rubrum* was higher in the presence of herbivores. Insect herbivores reduced survivorship of *L. tulipifera*, but had no significant effects on *A. rubrum*, *Fraxinus* spp., *F. grandifolia*, or *L. styraciflua*. Additionally, insects reduced growth rates of early pioneer species *A. rubrum*, *L. tulipifera*, and *L. styraciflua*, but had little effect on more shade-tolerant species *F. grandifolia* and *Fraxinus* spp. Overall, by negatively impacting growth and survivorship of early pioneer species, forest insects may play an important but relatively cryptic role in forest gap dynamics, with potentially interesting impacts on the overall maintenance of diversity.

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28 Introduction

29 Insect herbivores can directly and indirectly influence plant community composition by
30 reducing the growth and abundance of individual plant species (Maron and Crone 2006; Kim et
31 al. 2013). In old fields, for example, insect herbivores can indirectly increase the cover of
32 subdominant plant species by reducing the growth of competitively superior species (Brown and
33 Gange 1992; Davidson 1993; La Pierre et al. 2015). In forests, the most well-documented and
34 obvious impacts of insects come from outbreaks of pest species like mountain pine beetles,
35 which can reduce standing biomass via widespread mortality of dominant tree species (Romme
36 et al. 1986). In contrast, we know relatively little about the role of insects in forests in non-
37 outbreak scenarios (Maron and Crone 2006), probably because there have been relatively few
38 experimental manipulations of non-outbreaking insect herbivores in natural forest settings.

39 Recent evidence suggests that non-outbreaking insect herbivores may have significant,
40 albeit cryptic, impacts on forest dynamics through differential impacts on seedlings, the most
41 vulnerable tree life-history stage. Norghauer & Newbery (2013, 2014) for example,
42 demonstrated that herbivorous insects significantly alter forest community composition through
43 selective predation on particular seedling species (Norghauer & Newbery, 2013, 2014). Such
44 selective predation can allow for coexistence of competitively inferior seedlings by reducing
45 growth rates of competitively superior species (Fine et al. 2004; Fine et al. 2006). This
46 mechanism is thought to be at least partly responsible for the maintenance of forest diversity
47 (Swamy and Terborgh 2010; Terborgh 2012; Bagchi et al. 2014). Insect herbivores can also
48 cause immediate plant death, tripling normal seedling mortality rates (Prittinen et al. 2003),
49 whereas in other cases insect-caused seedling mortality may occur up to several years
50 following initial defoliation (Eichhorn et al. 2010). Similarly, chronic foliar damage can
51 exacerbate competition-induced mortality among seedlings (Meiners and Handel 2000),

52 highlighting the need for relatively long-term studies of insect impacts on tree seedling
53 dynamics.

54 The effects of insects on tree seedlings might be particularly strong within treefall gaps.
55 Treefall gaps maintain forest diversity by increasing light availability and nitrogen mineralization
56 rates (Denslow 1987; Mladenoff 1987; Hubbell et al. 1999), leading to abundant germination
57 and recruitment of a diverse assemblage of tree species (Denslow 1987). In addition, insect
58 herbivores are attracted to the warmth and light in treefall gaps, increasing local abundances
59 and thus their potential impacts on seedling growth and mortality (Richards and Windsor 2007;
60 Norghauer and Newbery 2013). Moreover, early successional plant species are generally
61 thought to possess high growth rates at the expense of anti-herbivore defenses, which might
62 make them particularly susceptible to insect herbivory (Coley et al. 1985; Shure and Wilson
63 1993). Thus, recruitment in forest gaps may be partially mediated by insect herbivore
64 consumption of palatable new seedlings, but little information exists regarding the role of insect
65 herbivores in forest regeneration in treefall gaps.

66 Here, we conducted a three-year experiment to assess the influence of insect herbivores
67 on community dynamics within treefall gaps in a temperate forest in the eastern United States.
68 We used a paired design, where each treefall gap consisted of two plots: a control plot and a
69 plot sprayed with pesticide to remove insect herbivores. We then tracked seedling recruitment,
70 mortality, and growth in each plot for three years. We hypothesized that herbivory by insects
71 would decrease seedling growth, increase mortality, and decrease recruitment and that these
72 effects would vary among species.

73

74 **Materials and Methods**

75 We conducted this experiment in an intensively studied forest at the Smithsonian
76 Environmental Research Center (SERC; Edgewater, Maryland USA. 38°53' N, 76°33'W). SERC

77 comprises a 2650 acre protected research facility encompassing a variety of early-, mid-, and
78 late-successional forests. Most forests at SERC, including those in this study, are mid-
79 successional forests 75-120 years old that have been federally protected since the 1960s
80 (Parker et al. 2010). This forest was typical of those in the mid-Atlantic United States, dominated
81 by *Carya* spp., *Fagus grandifolia*, *Fraxinus* spp., *Liquidambar styraciflua*, *Liriodendron tulipifera*,
82 and *Quercus* spp. In May 2012, we surveyed the forest for new treefall gaps. We only recorded
83 gaps that appeared during the previous winter, restricting our experiment to new forest
84 regeneration. We found six new treefall gaps large enough to include two 1.5 x 1.5 m
85 experimental plots. In May 2013, we added one additional gap that opened during the winter of
86 2012-2013, resulting in seven total gaps. All gaps were interspersed within a forest area of
87 approximately 16 ha.

88 In each gap we established two 2.25 m² plots surrounded by 1 m high chicken wire to
89 exclude deer, as we were solely interested in the impacts of insects in this experiment. Previous
90 experiments at SERC have used identical plot designs to successfully eliminate deer browsing,
91 where deer densities are low (3-8 individuals km⁻²) compared to many parts of the United States
92 (Cook-Patton et al. 2014), and no evidence of deer browsing was observed in any plot over the
93 course of this experiment. Plots within each gap were located at least 5 m apart, minimizing the
94 possibility of pesticide spray drifting between plots. Plots were not cleared or weeded in order to
95 leave all natural vegetation intact. Within each gap, one plot was randomly designated as the
96 'Control' treatment and the other was designated as a 'Pesticide' treatment. 'Pesticide' plots
97 were sprayed every 2-3 weeks with 0.5 L of ASANA XL (DuPont) pesticide, diluted to a
98 concentration of 40 µL/L . ASANA XL is an esfenvalerate insecticide that contains very little
99 nitrogen, such that fertilization effects on plant growth should be minimal. It is therefore
100 commonly used to examine the effects of insect herbivory on plant communities (Heath et al.
101 2014). Control plots were sprayed with an equivalent amount of water to control for possible
102 watering effects. Pesticide applications began each year in May and continued through October,

103 encompassing the entire growing season. Pesticide was applied for three years, beginning in
104 2012 and ending in 2014. We sprayed the entirety of each plot, including ground cover, in order
105 to judge how insects affect recruitment. To judge the efficacy of the pesticide treatment, we
106 surveyed each seedling in each plot for insect damage at the end of the 2012 growing season.
107 We examined the top four leaves of each seedling, categorizing damage as 0%, 25%, 50%,
108 75%, or 100% damage and then averaged the values over all seedlings in each plot (Palmer
109 and Brody 2013; Johnson et al. 2016).

110 In May of each year, each seedling was identified, measured for initial height, and
111 tagged with a unique identification number. In October of each year, plots were censused again
112 to record seedling final height, mortality, and recruitment over the growing season. Seedlings
113 were only recorded as dead if an empty tag was found within the plot. New seedlings without
114 tags were recorded as new recruits in both May and October, although only recruitment over the
115 growing season (*i.e.* recruits appearing in October) was examined here, as recruits over the
116 winter were not exposed to pesticide treatment. Seedlings were considered dead if they had no
117 measurements for at least two consecutive census periods and did not reappear in the plot at a
118 later date. In total, we tagged and measured 1,173 seedlings over the course of the experiment.

119

120 *Data Analysis*

121 We examined herbivore effects only on seedlings ≤ 15 cm in height because these were
122 the newest recruits and thus the most likely to experience mortality from herbivory. The term
123 seedling has a broad and inconsistent usage, referring to plants anywhere between 0 – 4 years
124 old (Hanley et al. 2004), but we use seedling to refer any individual ≤ 15 cm in height. Of the
125 original dataset, 924 individuals (78%) met this criterion. We further restricted our analyses to
126 the five most common species that occurred in enough plots to provide reasonable replication at
127 the species level: *Acer rubrum*, *Fagus grandifolia*, *Fraxinus* spp., *Liriodendron tulipifera*, and
128 *Liquidambar styraciflua* (Table 1). These five species comprised 82% of observed seedlings

129 (76% of all tagged individuals) and are dominant species in the eastern United States (Parker et
130 al. 1989).

131 We conducted all analyses using Bayesian methods, which allowed us to incorporate
132 prior information that prevented us from overestimating effect sizes. Small sample sizes, as
133 used here ($n = 7$ gaps), often lead to overestimates of the true effect sizes when using
134 traditional analytical methods. Such overestimates have been a persistent problem in biological
135 research (Button et al. 2013). Bayesian methods allowed us to place weakly informative priors
136 $N(0, 1)$ on all parameters, which shrink parameter estimates towards 0 and help prevent
137 overestimating effect sizes during the analysis of small sample sizes (Kruschke 2010; Button et
138 al. 2013).

139 We analyzed total recruitment using Bayesian hierarchical Poisson regression, with
140 species as random effects (Appendix 1). We calculated the total number of new recruits for
141 each of the five species in each plot to yield total number of recruits observed for each species
142 over the entire experimental duration.

143 We used a hierarchical Bayesian model to examine the influence of pesticide treatment
144 and gap age on seedling mortality. We analyzed mortality rate using logistic regression that
145 included pesticide treatment, gap age, and the interactions of these two categorical variables as
146 predictors (Appendix 1). We did not use a paired model because not all species were present in
147 all gaps during each year, yielding an unbalanced design. Species were random effects, with
148 species-level coefficients varying around overall coefficients. Overall coefficients describe the
149 aggregate influence of insect herbivores and gap age on overall seedling mortality. The
150 correlation matrix between species-level parameters was given an uninformative Wishart prior.
151 Variances of mortality rate were allowed to differ among species, relaxing the assumption of
152 homogenous variances among species.

153 We analyzed relative growth rate [$100 * (\text{Height}_{\text{end}} - \text{Height}_{\text{start}}) / \text{Height}_{\text{start}}$] using a similar
154 hierarchical Bayesian model as described above (Appendix 1). To account for the fact that

155 individual seedlings were not independent within a plot, growth of individual seedlings within a
156 plot varied around the mean growth of their respective species in that particular plot and year.
157 The plot-level means were a function of pesticide treatment, gap age, and their interactions
158 (Appendix 1). Species-level coefficients varied around the overall coefficients as described
159 above..

160 Posterior distributions for all parameters were constructed using 5,000 ‘burn-in’ iterations
161 that were discarded followed by 5,000 sampling iterations for each chain, saving every 10th
162 posterior draw (4 chains, 2,000 estimates per parameter). Response variables, except total
163 recruitment, were standardized prior to analyses by subtracting the mean from each observation
164 and dividing by the standard deviation in order to allow the use of weakly informative priors as
165 described above. We examined model assumptions and fit using standardized residual plots.
166 We report all statistics as probability of an effect (Pr), where higher probabilities denote more
167 certainty regarding the importance of an effect. For example, Pr = 0.95 indicates that 95% of a
168 coefficient’s posterior distribution lay above or below zero. There is therefore a 95% chance that
169 the coefficient is either negative or positive and therefore important. In contrast, Pr = 0.50
170 indicates that a coefficient is equally likely to be either positive or negative and therefore
171 unimportant. To facilitate interpretation of probabilities, we provide effect sizes and 95% credible
172 intervals for all effects. Credible intervals were calculated as the interval between the 2.5% and
173 97.5% quantiles for each posterior distribution (all posterior distributions were normal and
174 symmetric). All analyses were conducted in Python v2.7. Bayesian models were built using
175 STAN accessed via Pystan (Stan Development Team 2015).

176

177 **Results**

178 At the beginning of the experiment in May 2012, plots contained an average of 20
179 seedlings each (range: 9 to 163 seedlings per plot). The five common species analyzed here

180 accounted for ~80% of all initially tagged seedlings, with *L. tulipifera* being the most common
181 (36.3%) followed by *Fraxinus* spp. (15.8%), *F. grandifolia* (15.1%), *L. styraciflua* (8.5%), and *A.*
182 *rubrum* (8.5%) (Table 1). Pesticide application reduced foliar damage by approximately half.
183 Percent of leaf area removed in 'Control' plots was $7.38 \pm 0.83\%$, whereas leaf area removal in
184 'Pesticide' plots was $4.27 \pm 0.76\%$ ($\text{Pr}(\text{Control} > \text{Pesticide}) = 0.99$). *Fagus grandifolia* suffered
185 the highest insect damage ($16.5 \pm 5.7\%$), followed by *A. rubrum* ($9.7 \pm 5.9\%$), *L. styraciflua* (5.6
186 $\pm 2.7\%$), *Fraxinus* spp. ($3.7 \pm 3.7\%$), and *L. tulipifera* ($0.64 \pm 0.34\%$).

187

188 *Recruitment*

189 In general, recruitment over the duration of the experiment was relatively low. Most
190 species averaged fewer than two recruits during the growing season per plot over the duration
191 of the experiment. *Liriodendron tulipifera* had the most recruits of any species, with plots
192 averaging > 10 new recruits over the entire three years (Fig. 1). Surprisingly, long-term
193 recruitment of two species, *A. rubrum* and *Fraxinus* spp., was higher in control plots exposed to
194 herbivores compared to plots sprayed with pesticide ($\text{Pr}(\text{Control} > \text{Pesticide}) \geq 0.95$ for both
195 species) (Fig. 1, Table 2). Insect herbivores did not affect the recruitment of the other three
196 species ($\text{Pr}(\text{Control} < \text{Pesticide}) < 0.84$ for all species) (Fig. 1, Table 2).

197

198 *Mortality*

199 Insect herbivores had negligible effects on seedling mortality averaged across all
200 species ($\text{Pr}(\text{Control} > \text{Pesticide}) = 0.66$). However, species varied in their responses to
201 pesticide. Herbivory did not alter mortality rates of *A. rubrum*, *F. grandifolia*, *Fraxinus* spp., or *L.*
202 *styraciflua* ($\text{Pr}(\text{Control} > \text{Pesticide}) \leq 0.79$ for all four species, Fig. 2, Table 3). In contrast,
203 herbivorous insects marginally increased mortality for *L. tulipifera* ($\text{Pr}(\text{Control} > \text{Pesticide}) =$
204 0.93) (Fig. 2, Table 3). Mortality of *L. tulipifera* was 33.1% higher in plots without pesticide
205 compared to control plots ($\text{CI}_{95} = 9.9\%$ lower – 76.3% higher). Weak interaction coefficients

206 suggest that herbivore effects were consistent across all years for all species (Table 3). Insect
207 herbivores therefore marginally decreased survival of one common, temperate tree species, *L.*
208 *tulipifera*.

209 Overall, total seedling mortality declined between the one and three year old gaps
210 ($\text{Pr}(\text{Year 3} < \text{Year 1}) = 1.0$), and this effect was consistent across all species except *L.*
211 *styraciflua* (Table 3). Mortality of *F. grandifolia* and *L. styraciflua* marginally declined as gaps
212 aged (Table 3). *Fraxinus* spp. mortality significantly decreased between one and three year old
213 gaps ($\text{Pr}(\text{Year 3} < \text{Year 1}) = 0.98$, Table 3). Mortality of *A. rubrum* and *L. tulipifera* declined
214 rapidly between the first and second year (Table 3, Fig. 2) and between the second and third
215 year for *L. tulipifera* ($\text{Pr}(\text{Year 3} < \text{Year 1}) = 1.00$). Mortality did not decline further between two
216 and three year old gaps for *A. rubrum* ($\text{Pr}(\text{Year 3} < \text{Year 2}) = 0.88$) (Fig. 2).

217

218 *Relative Growth Rates*

219 Insect herbivory slightly decreased overall relative growth rates of seedlings ($\text{Pr}(\text{Control}$
220 $< \text{Pesticide}) = 0.91$), and this effect also varied among species (Table 4). *Acer rubrum* grew
221 23.7% faster ($\text{CI}_{95} = 4.1\% - 45.6\%$) in one-year-old gaps in the absence of herbivores
222 ($\text{Pr}(\text{Control} < \text{Pesticide}) = 0.99$, Fig. 3). However, pesticide did not affect *A. rubrum* growth rates
223 in either two or three year old gaps ($\text{Pr}(\text{Control} < \text{Pesticide}) < 0.69$ for both years, Fig. 3, Table
224 4). Herbivory had little effect on relative growth rates of *F. grandifolia* ($\text{Pr}(\text{Control} < \text{Pesticide}) <$
225 0.80 for all years) or *Fraxinus* spp. ($\text{Pr}(\text{Control} < \text{Pesticide}) < 0.85$ for all years) (Fig. 3, Table 4).
226 *Liriodendron tulipifera* growth increased markedly in two year old gaps ($\text{Pr}(\text{Year 2} > \text{Year 1}) =$
227 1.00) but was unaffected by insect herbivores ($\text{Pr}(\text{Control} < \text{Pesticide}) < 0.85$ for all years, Fig.
228 3, Table 4). Insect herbivores suppressed growth of *L. styraciflua* by 19.3% ($\text{CI}_{95} = 1.3\% -$
229 38.2%) in one year old gaps ($\text{Pr}(\text{Control} < \text{Pesticide}) = 0.998$) but had no effect in two or three
230 year old gaps ($\text{Pr}(\text{Control} < \text{Pesticide}) < 0.80$ for both years) (Fig. 3, Table 4).

231

232 **Discussion**

233 Insects can kill > 50% of canopy trees during outbreak years (Romme et al. 1986). Even
234 during non-outbreak years, insect herbivores play important roles in forest ecosystem function.
235 For example, over one quarter of annual nitrogen deposition in tropical forests derives from
236 insect frass (Metcalf et al. 2014). Insect herbivores can also govern community composition on
237 decadal time scales by changing the abundance and diversity of tree seedling recruits in tropical
238 forests (Dyer et al. 2010; Swamy and Terborgh 2010; Terborgh 2012; Bagchi et al. 2014).
239 Despite a comparatively large body of literature documenting the impact of insect herbivores in
240 tropical forests, we know relatively little about their role in temperate forests. Our study
241 demonstrates that insects play a relatively minor role in structuring temperate forest
242 communities. Most seedling species were resistant or tolerant of insect herbivores, as insects
243 decreased growth of only three early pioneer tree species (*A. rubrum*, *L. styraciflua*, *L. tulipifera*)
244 and decreased survival of only *L. tulipifera* during the initial phase of forest regeneration in
245 temperate treefall gaps.

246 We found relatively weak effects of insect herbivores on cumulative recruitment
247 throughout the study period. Recruitment of most species (*F. grandifolia*, *L. tulipifera*, and *L.*
248 *styraciflua*) was unaffected by insects. Surprisingly, insect herbivores appeared to stimulate
249 recruitment of both *A. rubrum* and *Fraxinus* spp, albeit weakly. These patterns are similar to
250 those reported by Meiners *et al.* (2000), where the presence of insect herbivores occasionally
251 resulted in higher germination rates of *A. rubrum*. In our study, increased cumulative recruitment
252 of *A. rubrum* exposed to herbivores was largely driven by recruitment during the last year, in
253 which two plots contained 13 new recruits, 57% of the total number of *A. rubrum* recruits
254 observed over the entire study duration. We therefore cannot discount the possibility that our
255 results are driven by abnormally high recruitment in two plots independent of insect presence.

256 Indeed, insect herbivores exerted only weak, if any, effects on recruitment for both *A. rubrum*
257 and *Fraxinus* spp., as herbivores increased recruitment by ~ 1 individual over the course of
258 three years for both species. Taken together, these results and others suggest that insect
259 herbivores may have little influence on the recruitment of the tree species studied in this forest.

260 Although several studies have characterized the effects of insect herbivores on seedling
261 growth and mortality in treefall gaps (Norghauer and Newbery 2014), few track the effects of
262 insects over multiple years. Interannual studies are especially important given yearly
263 fluctuations in herbivore abundances, temperature, and rainfall (Burt et al. 2014; Norghauer and
264 Newbery 2014). In our study, gap age was a more important predictor of seedling growth and
265 mortality than insect herbivory, as the impact of insect herbivory on seedling growth of *A.*
266 *rubrum*, *L. tulipifera*, and *L. styraciflua* and mortality of *L. tulipifera* declined as gaps and
267 seedlings aged. The declining effects of insects over time might be attributed to changes in
268 herbivore abundance over time or, more likely, increased tolerance to herbivory by older
269 seedlings. Indeed, seedlings alter their resource allocation patterns to maximize survival at any
270 given demographic stage (Zhang and Jiang 2002); seedlings invest in growth, rather than
271 defenses, to avoid competition with other seedlings, while older juvenile plants increase
272 concentrations of secondary defenses to offset the negative effects of herbivory (Boege and
273 Marquis 2005). As a consequence, herbivores often prefer younger seedlings to mature plants
274 (Fenner et al. 1999; Fritz et al. 2001), likely because older seedlings are more resistant and
275 tolerant to herbivory (Fritz et al. 2001; Warner and Cushman 2002). Furthermore, herbivore
276 damage causes high mortality in vulnerable seedlings, while older plants have the carbohydrate
277 reserves necessary to withstand loss of photosynthetic tissue (Hanley et al. 1995). Thus,
278 physiological changes in plant chemistry likely mediate the declining impact of insect herbivores
279 as gaps and seedlings age and might be responsible for the overriding effects of gap age on
280 seedling growth and mortality.

281 Importantly, our study examines the youngest life stage of tree seedlings (<15 cm tall),
282 whereas many other studies of insect herbivores on tree seedlings use older, well-established
283 seedlings that can withstand defoliation and loss of photosynthetic capacity (e.g. Myster &
284 McCarthy, 1989). Despite our examination of a younger and more vulnerable life stage, most
285 seedling species were tolerant of herbivory. Our results support previous observations that
286 insect herbivores have little effect on the survival of many temperate forest species, like *A.*
287 *rubrum*, *Fraxinus* spp., and *F. grandifolia* (Meiners et al. 2000; Siemann and Rogers 2003).
288 Many other temperate tree species, like *Quercus* spp. or *Prunus serotina*, are also resistant to
289 insect herbivory or pathogens unless simultaneously subject to high densities of conspecific
290 neighbors and, as a result, intense intraspecific competition (Packer and Clay 2000; Bell et al.
291 2006; Burt et al. 2014). Seedling density is therefore likely an important predictor of herbivore-
292 driven mortality (Paine et al. 2012). Indeed, insect herbivores increased the mortality of only one
293 species, *L. tulipifera*, which had the highest seedling densities of any species examined here
294 and suffered the greatest increase in mortality rates due to insect herbivory. In our study, *L.*
295 *tulipifera* averaged 11.35 individuals m⁻², substantially lower than the densities of seedlings
296 observed in either Burt et al. (2014) or Bell et al., (2006) (10 – 80 or 100 – 1000 individuals m⁻²,
297 respectively) but similar to densities of *P. serotina* recorded by Packer & Clay (2000) (1 – 15
298 individuals m⁻²). Our results therefore suggest that insect herbivores slightly reduce seedling
299 survival of *L. tulipifera* and that seedling densities need not reach exceedingly high levels to
300 yield density-dependent mortality.

301 Plant life-history strategy appears to be an important determinant of the effects of insect
302 herbivory. Early pioneer species, like *A. rubrum*, *L. tulipifera*, and *L. styraciflua*, all suffered
303 reduced growth rates in the presence of insect herbivores. Herbivory may therefore help
304 maintain forest diversity by decreasing the survival and growth of abundant, fast-growing
305 seedlings: although *L. tulipifera* and *A. rubrum* comprised 36.3% and 8.5% of all tagged
306 seedlings, the adult community is more diverse; *A. rubrum* and *L. tulipifera* comprise only 7.71%

307 and 0.34% of adult trees in this study system (Parker et al. 1989). In contrast, *F. grandifolia* is a
308 slow-growing, shade-tolerant, late-successional species that accounts for 20.77% of adult trees
309 in our forest (Parker et al. 1989). In our study, *F. grandifolia* was tolerant of herbivory,
310 suggesting that species that resist or tolerate insect herbivory during the seedling stage can
311 become dominant members of the overstory community. Variable susceptibility to insect
312 herbivores among seedlings of temperate tree species therefore indicates that insects might
313 influence trajectories of temperate forest succession by selectively preying on seedlings of
314 specific species; abundant but palatable seedlings comprise less of the forest overstorey than
315 do abundant, non-palatable seedling species.

316 Insect herbivores increased mortality of *L. tulipifera* and decreased seedling relative
317 growth rates of a select subset of temperate forest tree species during forest regeneration in
318 treefall gaps. However, the relatively weak effects of insect herbivores on seedling survival and
319 growth reported here suggest that any effects of insect herbivore on forest succession are likely
320 due to increased mortality of a single, dominant species: *L. tulipifera*. Long-term studies should
321 examine whether or not insect herbivores can increase forest diversity by reducing the
322 abundance of such competitively dominant tree species in temperate forests.

323

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328

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Figure 1

Number of recruits of five tree species in plots exposed to and protected from insect herbivores at the Smithsonian Environmental Research Center (Edgewater, MD) from 2012-2014.

Points show means \pm 1 SE. Data were pooled by each plot ($n = 7$ plots per treatment) prior to calculating treatment means and standard errors.

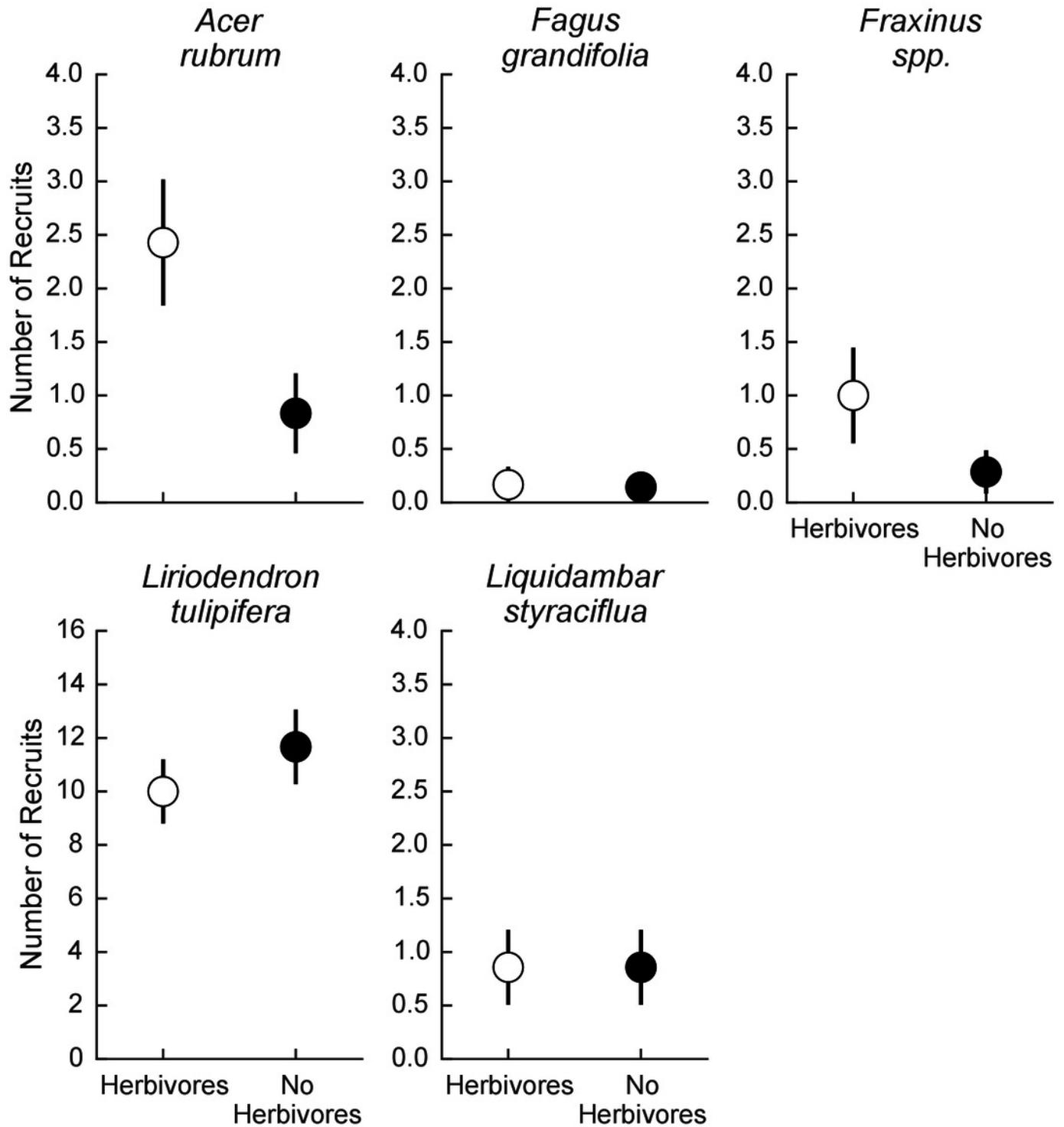


Figure 2

Mortality rate of five tree species in plots exposed to and protected from insect herbivores at the Smithsonian Environmental Research Center (Edgewater, MD) from 2012-2014.

Points show means \pm 1 SE. We calculated the proportion of mortality of each species in each plot ($n = 7$ plots per treatment) prior to calculating treatment means and standard errors.

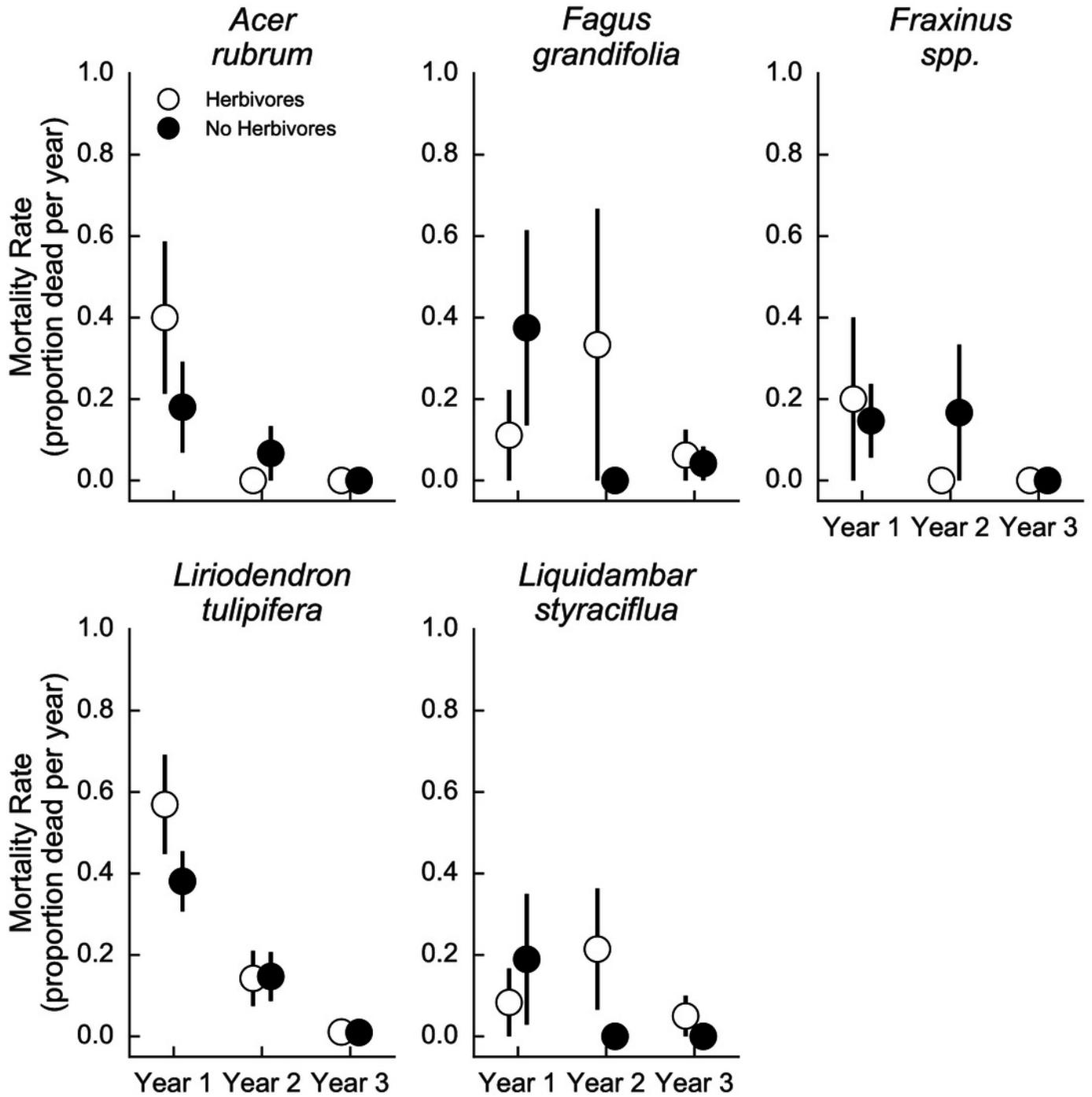


Figure 3

Relative growth rates of five tree species in plots exposed to and protected from insect herbivores at the Smithsonian Environmental Research Center (Edgewater, MD) from 2012-2014.

We calculated mean growth rate of each species within each plot ($n = 7$ plots per treatment) prior to calculating treatment means and standard errors.

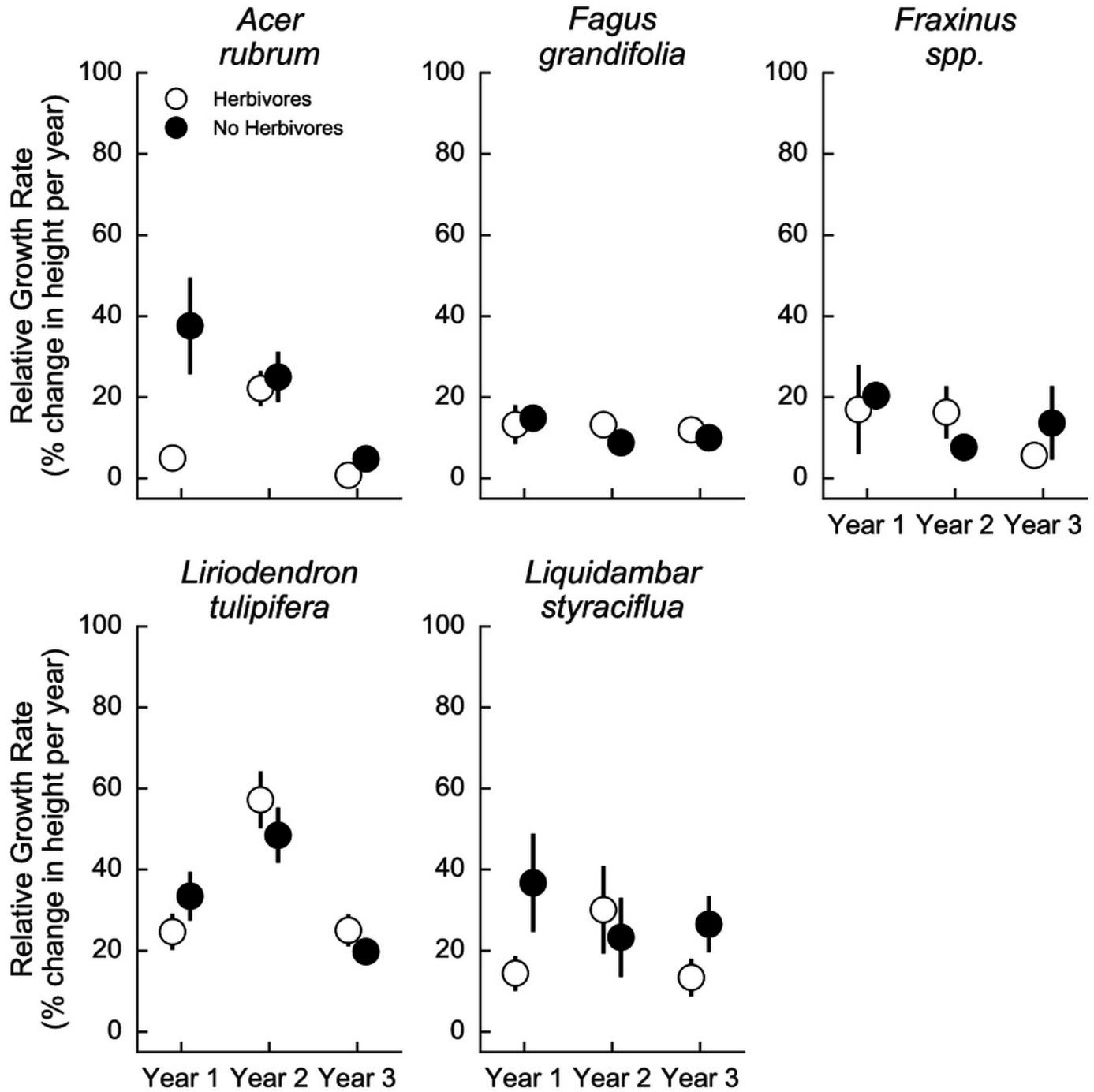


Table 1 (on next page)

Table 1. Numbers of seedlings (individuals < 15 cm tall) observed for each species during each year for each of the five focal species at the Smithsonian Environmental Research Center.

1
2

Species	Year 1 2012	Year 2 2013	Year 3 2014
<i>Acer rubrum</i>	29	23	22
<i>Fagus grandifolia</i>	22	24	30
<i>Fraxinus</i> spp.	42	41	28
<i>Liriodendron tulipifera</i>	332	278	191
<i>Liquidambar styraciflua</i>	55	51	14

3

Table 2 (on next page)

Probability that each recruitment coefficient is greater or less than zero for each of the five species analyzed here.

Probabilities denote $\max[\Pr(\text{coefficient}) > 0, \Pr(\text{coefficient}) < 0]$, such that sign of the coefficient was ignored and the probabilities simply represent the probability of the coefficient being important in the model. Bold denotes $\Pr(\text{coefficient}) \geq 0.90$.

1
2

Recruitment Coefficient	<i>Acer rubrum</i>	<i>Fagus grandifolia</i>	<i>Fraxinus spp.</i>	<i>Liriodendron tulipifera</i>	<i>Liquidambar styraciflua</i>
Pesticide	0.99	0.74	0.95	0.82	0.58

3
4

Table 3 (on next page)

Probability that each mortality coefficient is greater or less than zero for each of the five species analyzed here.

Probabilities denote $\max[\Pr(\text{coefficient}) > 0, \Pr(\text{coefficient}) < 0]$, such that sign of the coefficient was ignored and the probabilities simply represent the probability of the coefficient being important in the model. Bold denotes $\Pr(\text{coefficient}) \geq 0.90$.

1

Mortality Coefficient	<i>Acer rubrum</i>	<i>Fagus grandifolia</i>	<i>Fraxinus spp.</i>	<i>Liriodendron tulipifera</i>	<i>Liquidambar styraciflua</i>
Pesticide	0.79	0.68	0.65	0.93	0.56
Year 2	0.99	0.93	0.97	1.00	0.91
Year 3	0.99	0.93	0.98	1.00	0.87
Pesticide x Year 2	0.63	0.84	0.71	0.78	0.85
Pesticide x Year 3	0.66	0.63	0.72	0.59	0.70

2

3

Table 4(on next page)

Probability that each growth coefficient is greater or less than zero for each of the five species analyzed here.

Probabilities denote $\max[\Pr(\text{coefficient}) > 0, \Pr(\text{coefficient}) < 0]$, such that sign of the coefficient was ignored and the probabilities simply represent the probability of the coefficient being important in the model. Bold denotes $\Pr(\text{coefficient}) \geq 0.90$.

1

Growth Coefficient	<i>Acer rubrum</i>	<i>Fagus grandifolia</i>	<i>Fraxinus spp.</i>	<i>Liriodendron tulipifera</i>	<i>Liquidambar styraciflua</i>
Pesticide	0.99	0.77	0.84	0.84	0.98
Year 2	0.87	0.76	0.71	0.99	0.93
Year 3	0.79	0.51	0.67	0.54	0.58
Pesticide x Year 2	0.94	0.91	0.94	0.92	0.97
Pesticide x Year 3	0.90	0.75	0.67	0.84	0.72

2