

**Title:** Contrasting effects of nutrients and consumers on tree colonization and growth during secondary succession

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**Data accessibility:** Upon acceptance, data will be archived in the Dryad Digital Repository.

## 1 **Abstract**

2           For succession to proceed from herbaceous to woody dominance, trees must colonize  
3 herbaceous communities and grow. Success across these two phases of succession might result  
4 from different interactions with the herbaceous community. First, colonizing trees must compete  
5 against larger, established herbs, while subsequent growth occurs among similarly sized or  
6 smaller herbs. This shift from colonization to growth may cause three drivers of secondary  
7 succession— nutrients, consumers, and herbaceous diversity—to differentially affect tree  
8 colonization and growth. Initially, these drivers should favor larger, established herbs, reducing  
9 colonization. Later, when established trees can better compete with herbs, these drivers should  
10 benefit trees and increase their growth. In a four-year study, we added nutrients to, excluded  
11 aboveground consumers from, and manipulated initial richness of, the herbaceous community,  
12 then allowed trees to naturally colonize these communities (from intact seedbanks or as seed-  
13 rain) and grow. Nutrients and consumers had opposing effects on tree colonization and growth:  
14 adding nutrients and excluding consumers reduced tree colonization, but later increased  
15 established tree growth (height, basal diameter). Together, this shows stage-specific impacts of  
16 nutrients and consumers that may improve predictions of the rate and trajectory of succession:  
17 factors that initially limited tree colonization later helped established trees to grow.

18

19 **Keywords:** community assembly; diversity-invasibility; fertilization; insect herbivory; loblolly  
20 pine; old fields; *Pinus taeda*; plant pathogens; top-down, bottom-up; tree establishment

## 21 **Introduction**

22 For succession to proceed, trees must first colonize, then grow in herbaceous  
23 communities (Oosting 1942, Keever 1950, Wright and Fridley 2010, Fridley and Wright 2018).  
24 Success in transitioning from colonization to growth may result from changes in the interactions  
25 between trees and herbs (HilleRisLambers et al. 2012): colonizing trees must compete against  
26 larger, established herbs, while established trees experience limited size-based disadvantages as  
27 they continue to grow. These changing interactions may alter the responses of successional  
28 systems to other biotic and abiotic factors. For instance, recent work also suggests that soil  
29 nutrients and plant consumers (i.e., herbivores and pathogens) may independently and  
30 interactively alter early stages of succession (e.g., Fridley and Wright 2012, Meiners et al. 2015,  
31 Wilfahrt et al. 2020). Yet, few studies have explored whether nutrients and consumers exert  
32 differing impacts on different stages of succession. Importantly, this implies that the same factors  
33 that inhibit tree colonization can increase the growth of established trees later in succession,  
34 hampering the ability to predict how biotic and abiotic drivers will affect the speed of succession.

35 Changes in tree-herb interactions between the colonization and growth stages of  
36 succession are key for understanding how nutrients and consumers will impact succession. When  
37 trees first colonize herbaceous communities, they have a large size-based competitive  
38 disadvantage. This interaction may change with soil nutrient availability and consumer pressure  
39 (Tilman 2004). High nutrient availability often increases productivity and litter accumulation,  
40 reducing light availability (Hautier et al. 2009, Borer et al. 2014, Wilfahrt et al. 2020), and  
41 potentially limiting tree colonization (Sarneel et al. 2016). Consumers can reduce the size of  
42 resident plant populations and the performance of individuals (Alexander 2010), which may  
43 enhance tree colonization. Nutrients and consumers may also jointly alter tree colonization:

44 increased nutrient supply can shift communities toward species and individuals that allocate little  
45 to defense against herbivores and pathogens (Hahn and Maron 2016, Heckman et al. 2019),  
46 leading to higher rates of herbivory and disease (Veresoglou et al. 2013, Heckman et al. 2016). If  
47 consumers are excluded from nutrient-rich habitats, where consumer impacts are highest, the  
48 resident community exploit high nutrient supply without experiencing the negative impacts of  
49 consumers (Mattson 1980, Heckman et al. 2016); this could drastically reduce tree colonization.

50 As trees establish, their size-based disadvantage against herbs should decline over time,  
51 making competition more symmetric (Schwinning and Weiner 1998), and allowing coexistence  
52 when trees and herbs occupy different niches (Chesson 2000). Niche overlap may decline  
53 because trees can capture resources unavailable to herbs by developing deeper roots and taller  
54 stems and may share few pathogens and herbivores with herbs (Gilbert and Webb 2007, Chesson  
55 and Kuang 2008, Craine and Dybzinski 2013). Ultimately, trees will outcompete herbs for light,  
56 which is often limiting in nutrient-rich environments (Hautier et al. 2009). As such, factors like  
57 high nutrient availability and low consumer pressure, which favored the herbaceous community  
58 earlier and slowed succession, could benefit established trees later and accelerate succession.

59 Nutrient- and consumer-mediated interactions between herbs and trees may also change  
60 with herbaceous diversity. More diverse communities often exhibit lower light and soil nutrient  
61 availability, less disease and herbivory, and higher productivity (Loreau and Hector 2001,  
62 Tilman 2004, Maron et al. 2011, Halliday et al. 2019). This may further enhance the competitive  
63 advantage of established herbs over tree seedlings in diverse communities and reduce  
64 colonization (Mattingly and Reynolds 2014, Heckman et al. 2017, Wilfahrt et al. 2020). But as  
65 trees establish and grow, their competitive disadvantage against herbs should decline, allowing

66 trees and herbs exhibiting sufficiently large niche differences to coexist (Chesson 2000) and  
67 reducing the influence of herbaceous diversity on the growth of established trees.

68 Ultimately, the speed of succession results from the ability of trees to establish and grow  
69 within herbaceous communities, which is determined by the abiotic and biotic conditions in the  
70 community (Fridley and Wright 2018, Wilfahrt et al. 2020). In this study we examine whether  
71 nutrients, consumers, and initial plant community richness interact to influence tree colonization  
72 in an old field community. Among established individuals of a dominant early successional tree,  
73 we further examine whether these factors interactively influence tree growth.

## 74 **Methods**

75 We performed this study at Widener Farm, an old field in Duke Forest Research and  
76 Teaching Lab (Orange County, NC, USA) that produced row crops until 1996. Since 1996, the  
77 site has been mowed to maintain herbaceous dominance by native species common in North  
78 Carolina Piedmont old fields (Oosting 1942) and several exotic species (Heckman et al. 2016).

79 The study employed a randomized complete block design with three factorial treatments:  
80 we manipulated native herbaceous plant richness with multiple community compositions at each  
81 level of richness; access by foliar fungal pathogens and insect herbivores; and soil nutrient  
82 supply. This yielded a study that comprised 240 plots (5 replicate blocks  $\times$  2 nutrient supply  
83 levels  $\times$  2 consumer access levels  $\times$  2 richness levels  $\times$  6 native community compositions).

### 84 *Plant composition and species richness*

85 In May 2011, we established five spatial blocks, each containing 48 1 m<sup>2</sup> plots with 1 m  
86 aisles. We first applied glyphosate herbicide (Riverdale<sup>®</sup> Razor<sup>®</sup> Pro, Nufarm Americas Inc, Burr  
87 Ridge, IL) to each plot, removed all dead vegetation, and covered plots with landscape fabric,  
88 while avoiding disturbance to the existing seed bank. We assigned each plot to one of two

89 richness levels, monoculture or five-species polyculture. From a pool of six native herbaceous  
90 perennial species, we assembled twelve planted communities: six monocultures and six five-  
91 species polycultures, where one species was excluded from each community. All species were  
92 already present locally, and included three grasses—*Andropogon virginicus*, *Setaria parviflora*,  
93 *Tridens flavus*, and three forbs—*Packera anonyma*, *Scutellaria integrifolia*, *Solidago pinetorum*.

94 We propagated all species in the greenhouse at the University of North Carolina at  
95 Chapel Hill. Each species was planted between June and September 2011 in 1-2 days when  
96 seedlings were large enough to survive transplant stress. In early summer 2012, we replaced all  
97 individuals that had died. To minimize recruitment from the seedbank while establishing the  
98 species richness treatment, seedlings were planted into small holes in the landscape fabric  
99 covering the plot. Plots contained 41 individuals, each spaced ~10 cm from its nearest neighbors  
100 in a checkerboard pattern. Polycultures contained 9 individuals of one randomly chosen species  
101 and 8 individuals of the other 4 species. In July 2012, we removed landscape fabric from plots  
102 and weeded non-planted individuals by hand. We then allowed natural colonization for the  
103 duration of the study. Thus, the species richness treatments represent initial conditions.

#### 104 *Nutrient supply and consumer access treatments*

105 We began consumer access and nutrient supply treatments in July 2012. To manipulate  
106 access by foliar fungal pathogens and insect herbivores, each plot was assigned to one of two  
107 treatments (sprayed with fungicide and insecticide vs. not sprayed). From July 2012 through  
108 September 2015, we sprayed non-systemic broad-spectrum biocides on all aboveground biomass  
109 every two to three weeks during the main growing season (April-October). Neither the fungicide  
110 (mancozeb, Dithane<sup>®</sup> DF, Dow AgroSciences, Indianapolis, IN) nor the insecticide (es-  
111 fenvalerate, Asana<sup>®</sup> XL, Dupont, Wilmington, DE) had any non-target effects on plant growth

112 under greenhouse conditions (Heckman et al. 2016). Similarly, this fungicide has no adverse  
113 effects on mycorrhizal fungi when used as recommended (Parker and Gilbert 2007). Together,  
114 these biocides reduced foliar damage in this study by >55% (Heckman et al. 2017).

115 To manipulate soil nutrient supply, each plot was assigned to one of two treatments  
116 (fertilized with 10 g N m<sup>-2</sup> yr<sup>-1</sup> as slow-release urea, 10 g P m<sup>-2</sup> yr<sup>-1</sup> as triple super phosphate, and  
117 10 g K m<sup>-2</sup> yr<sup>-1</sup> as potassium sulphate vs. not fertilized). This level of fertilization has been  
118 shown to alleviate limitation by N, P, and K across a range of grassland habitats (Fay et al.  
119 2015). In 2012, we fertilized plots in July, and in subsequent years, we fertilized in early May.

#### 120 *Tree colonization and growth*

121 To examine tree colonization, we identified all plant species in a marked 0.75 × 0.75 m  
122 subplot in the center of each plot in September 2012 – 2015 (Wilfahrt et al. 2020); 11 tree  
123 species had colonized one or more plots (*Acer rubrum*, *Celtis laevigata*, *Cercis canadensis*,  
124 *Cornus florida*, *Fraxinus* sp., *Juniperus virginiana*, *Liquidambar styraciflua*, *Liriodendron*  
125 *tulipifera*, *Pinus taeda*, *Sassafras albidum*, and *Ulmus alata*). To examine the growth of  
126 established trees, in May 2016, we measured the height and basal diameter of each *P. taeda*  
127 individual. We focused on *P. taeda* because it is the most abundant early successional tree in the  
128 region and within this study (Oosting 1942, Wright and Fridley 2010).

#### 129 *Data analysis*

130 We took two approaches to examine the effects of treatments on tree dynamics:  
131 evaluating the presence of trees across all plots and evaluating tree presence and performance  
132 only in plots containing trees. Modeling tree presence in all plots allowed us to understand  
133 overall treatment effects, but did not account for stochasticity in natural seed rain. In contrast,  
134 modeling tree growth and colonization time only in plots containing trees allowed us to evaluate

135 treatment effects while greatly reducing stochasticity in natural seed rain. We analyzed all data in  
136 R version 3.5.3 (R Foundation for Statistical Computing, Vienna 2019).

137 To model the independent and interactive effects of initial richness, fertilization, and  
138 spraying on tree colonization across all plots (i.e., the presence of trees in a plot), we used the  
139 glmmTMB package for generalized linear mixed models (Brooks et al. 2017) with binomial  
140 errors and a logit link. This model also included year of observation as a continuous fixed effect,  
141 which could interact with treatment effects. We assessed model significance with Wald tests  
142 using the `Anova` function in the car package (Fox and Weisberg 2018). To evaluate how initial  
143 richness, fertilization, and spraying independently and interactively influenced tree growth and  
144 colonization time in plots containing trees, we analyzed three responses using the `lme` function  
145 in the nlme package (Pinheiro et al. 2016): the height and basal diameter of *P. taeda* in spring  
146 2016 and the earliest year (fall 2012-2015) in which trees had colonized a plot. In all models,  
147 fertilization, spraying, initial richness, and their interactions were categorical fixed effects.  
148 Following Schmid et al. (2002), planted community composition was a random effect; plot was  
149 nested within composition to account for repeated sampling in the tree colonization GLMM. We  
150 simplified fixed effects following Zuur et al. (2009).

## 151 **Results**

152 As expected in an old field undergoing succession, the presence of trees increased over  
153 time (Time:  $P = 0.027$ ; Table S1) and this effect was interactively altered by nutrients and  
154 consumers (Nutrients  $\times$  Consumers  $\times$  Time:  $P < 0.001$ ; Table S1; Figure 1). Spraying and  
155 fertilization each reduced the rate at which trees colonized plots relative to controls ( $P < 0.001$   
156 for each contrast), but spraying did not significantly change the colonization rate in fertilized  
157 plots ( $P = 0.07$ ). Among plots containing trees, spraying and fertilization also interactively

158 altered the timing of establishment (Nutrients  $\times$  Consumers:  $P = 0.02$ ; Table S2; Figure S1).  
159 Spraying advanced the average colonization date by 0.91 years in unfertilized plots ( $P = 0.01$ ),  
160 but did not affect colonization time in fertilized plots ( $P = 0.91$ ). Similarly, fertilization advanced  
161 the average colonization date by 0.92 years in unsprayed plots ( $P = 0.018$ ), but did not affect  
162 colonization time in sprayed plots ( $P = 0.91$ ). Initial richness did not influence either response  
163 (Table S1; Table S2). This indicates that trees colonized sprayed and fertilized plots less  
164 frequently, but trees that colonized sprayed and fertilized plots did so earlier.

165         Whereas fertilization and spraying reduced tree colonization, these treatments had the  
166 opposite effect on growth of the focal species, *P. taeda*. Specifically, after four years of  
167 treatments, nutrients and consumers interactively altered two measures of *P. taeda* growth: basal  
168 diameter and height (Basal diameter, Nutrients  $\times$  Consumers:  $P = 0.002$ ; Height, Nutrients  $\times$   
169 Consumers:  $P = 0.002$ ; Table S3; Figure 2a, 2b). Spraying increased basal diameter by 105% and  
170 height by 81% in unfertilized plots (Basal diameter:  $P = 0.002$ ; Height:  $P = 0.001$ ), but not in  
171 fertilized plots (Basal diameter:  $P = 0.60$ ; Height:  $P = 0.67$ ), while fertilization increased basal  
172 diameter by 84% and height by 55% in unsprayed plots (Basal diameter:  $P = 0.031$ ; Height:  $P =$   
173  $0.055$ ), but not in sprayed plots (Basal diameter:  $P = 0.21$ ; Height:  $P = 0.13$ ). Similar to tree  
174 establishment, initial richness had no effect on *P. taeda* growth (Table S3).

175         Together, these results reveal contrasting effects of nutrients and consumers on tree  
176 colonization and growth. Fertilization and spraying hindered tree colonization after the first year  
177 of the study, possibly because these treatments disproportionately benefitted the herbaceous  
178 community. But when trees established, fertilization and spraying enhanced their growth.

## 179 **Discussion**

180           These results provide evidence for contrasting effects of nutrients and consumers on two  
181 early stages of secondary succession, tree colonization and growth. These contrasting effects are  
182 likely driven by a change in the role of the herbaceous community during succession (Pickett et  
183 al. 1987, Meiners et al. 2015): herbaceous residents can be critical for hindering colonization and  
184 establishment (Smit and Olf 1998, Rebele 2013), but established trees might outcompete, or  
185 avoid competing with, herbs. Thus, factors like high nutrient supply and low consumer pressure  
186 largely prevented tree colonization by benefiting the herbaceous community (Sarneel et al. 2016,  
187 Heckman et al. 2017), while later promoting growth among the trees that did establish.  
188 Contrasting effects of competitors, consumers, and nutrients on colonization and growth could  
189 help explain some of the conflicting results seen in earlier studies of the drivers of secondary  
190 succession (e.g., Gill and Marks 1991, Rebele 2013, Fridley and Wright 2018).

191           As predicted, nutrient addition and consumer exclusion each reduced tree colonization,  
192 potentially by several mechanisms. Adding nutrients and excluding consumers reduced light  
193 availability (Wilfahrt et al. 2020), which was a key driver of herbaceous colonization in another  
194 study at this site (R.W. Heckman *unpublished data*) and for community assembly broadly  
195 (Hautier et al. 2009, Harpole et al. 2017). Moreover, because herbs were at a higher density than  
196 colonizing trees, they likely experienced stronger negative consumer impacts through high  
197 density-dependent consumer pressure (Chesson and Kuang 2008, Mordecai 2011). Thus,  
198 excluding consumers likely reduced tree colonization by favoring the herbaceous community.  
199 Together, this suggests that the larger size and higher density of herbs relative to trees allowed  
200 them to exploit the more favorable conditions of adding nutrients and excluding consumers.

201           Whereas adding nutrients and excluding consumers reduced tree colonization, these  
202 factors increased the growth of established trees, which we measured using the focal tree species,

203 *P. taeda*. Several processes likely contributed to this effect. First, *P. taeda* individuals could  
204 occupy a niche distinct enough from the herbaceous community to largely avoid competition  
205 (Chesson 2000). This could have occurred because *P. taeda* is phylogenetically and functionally  
206 distinct from the herbaceous community (Mayfield and Levine 2010). By exploiting this niche  
207 difference, *P. taeda* would benefit from increased nutrient supply and release from consumers  
208 without experiencing increased competition intensity (Chesson and Kuang 2008). Second, once  
209 *P. taeda* established, and reached the herbaceous canopy, these trees may have been released  
210 from competition for light and become more apparent to plant consumers, resulting in stronger  
211 competition for soil nutrients and stronger regulation by consumers (Schwinning and Weiner  
212 1998, Chesson and Kuang 2008, Mordecai 2011). Finally, *P. taeda* may have outcompeted the  
213 herbaceous community. Conditions promoting strong competition for light, like nutrient  
214 addition, favor tall *P. taeda* individuals over short herbs (Hautier et al. 2009, Craine and  
215 Dybzinski 2013). Importantly, even if *P. taeda* successfully exploited a niche difference, its  
216 superior ability to compete for light will, in the absence of disturbance, drive its herbaceous  
217 competitors to low abundance or local extinction (Craine and Dybzinski 2013).

218 This study demonstrates the importance of nutrients and consumers in driving early  
219 succession but has several limitations. First, we did not measure damage on *P. taeda* or any other  
220 tree in this study. However, past research has shown that our spraying approach effectively  
221 reduces damage to numerous species without having biotoxic or biostimulatory effects  
222 (Heckman et al. 2016, Heckman et al. 2017). Second, our five-year study did not cover the  
223 entire, decades-long duration of succession. However, succession in southern US old fields  
224 proceeds rapidly (Oosting 1942, Keever 1950, Fridley and Wright 2018, Wilfahrt et al. 2020),  
225 and our study captured the critical early stages of old field succession, which determine the

226 trajectory of forest development (Fridley and Wright 2018). Finally, because the field  
227 surrounding this experiment was maintained by mowing, very few trees in the field were large  
228 enough to produce seeds. Consequently, most trees colonized plots from the forest edge or  
229 resident seedbank, resulting in stochastic colonization and establishment—by the end of the  
230 study, even *P. taeda*, the most successful early successional tree, had only established in ~ 25%  
231 of plots. Future experiments could overcome this limitation by adding seeds or seedlings.

232 Our results suggest that competition with resident herbs is an important driver of tree  
233 colonization and growth during secondary succession; yet, counterintuitively, neither tree  
234 colonization nor growth were affected by initial richness of the herbaceous community. This  
235 raises an important question: if competition with resident herbs was so important for tree  
236 colonization or growth, why were no effects of initial herbaceous richness detected? One  
237 possible explanation for this result is that increasing niche complementarity, which is often  
238 associated with reduced invasion or increased stability in more diverse communities, was not  
239 necessary to inhibit colonization or impact tree growth (Shea and Chesson 2002, Seabloom  
240 2007). This may occur because trees and herbs were competing primarily for an asymmetric  
241 resource, light. In old fields, where most species are shade intolerant, there is limited opportunity  
242 to partition light in a way that promotes coexistence. Rather, when vegetation is dense enough to  
243 create a closed canopy, taller individuals gain a considerable competitive advantage irrespective  
244 of niche differentiation (Westoby 1998). Moreover, because we did not maintain richness  
245 treatments beyond July 2012, any richness effect declined over time (Halliday et al. 2019,  
246 Wilfahrt et al. 2020).

247 Our results indicate that the same drivers can affect each stage of early succession  
248 differently, potentially resolving idiosyncrasies in previous studies. Within a site, many studies

249 have shown that nutrient supply and consumer pressure are important drivers of succession  
250 (Pickett et al. 1987, Meiners et al. 2015), but the strength and direction of these effects often  
251 differed (Gill and Marks 1991, Rebele 2013). Many of these results are seen as supporting  
252 different models of succession. For instance, the succession models of Connell and Slatyer  
253 (1977) describe three possible outcomes: inhibition, tolerance, and facilitation. In our study, the  
254 earliest stages of succession—when the herbaceous community prevented tree colonization—  
255 were consistent with the inhibition model. Later, when established trees responded positively to  
256 nutrient addition and consumer exclusion, herbs and trees may have exhibited more neutral  
257 interactions, consistent with the tolerance model. However, when studies do not account for  
258 changing interactions between herbs and trees, these differences may be obscured. Thus,  
259 discrepancies in the importance of nutrients and consumers among past studies may have  
260 resulted from testing colonization and growth together instead of considering each separately.

## 261 *Conclusions*

262 In this study, two early stages of succession from herbaceous to woody dominance were  
263 influenced by nutrients and consumers in contrasting ways, suggesting an important shift in the  
264 ecological drivers of secondary succession. Nutrient addition and consumer exclusion limited  
265 tree colonization, likely through an indirect route mediated by the herbaceous community.  
266 Unlike establishment, growth of the focal tree, *P. taeda* increased with nutrient addition and  
267 consumer exclusion, perhaps because trees overcame competition for light with the herbaceous  
268 community. Thus, these two factors, which are so critical to many aspects of community ecology  
269 (HilleRisLambers et al. 2012), had contrasting effects on different stages of succession. As large  
270 tracts of former farmland are abandoned and undergo secondary succession (Wright and Fridley  
271 2010), the speed of this process, and the carbon that it sequesters, may be determined to a large

272 extent by consumers and nutrient availability.

273

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282

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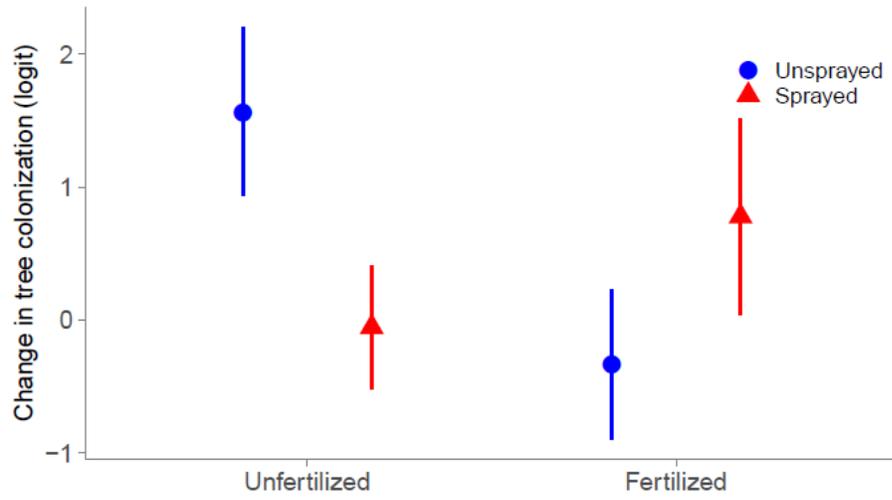
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## Figure legends

**Figure 1** Effects of nutrient supply (unfertilized, fertilized with NPK) and consumer access (unsprayed, sprayed with aboveground fungicide and insecticide) on logit change in colonization of plots (presence/absence) by all tree species between the beginning of the study in 2012 and 2015 (N = 240 plots; mean  $\pm$  95% confidence intervals), calculated using a generalized linear mixed model with binomial errors and a logit link. Error bars overlapping 0 denote no change in the rate at which trees colonized plots over the course of the study; positive values indicate that the rate at which trees colonized plots increased over the course of the study

**Figure 2** Effects of nutrient supply (unfertilized, fertilized with NPK) and consumer access (unsprayed, sprayed with aboveground fungicide and insecticide) on performance of *Pinus taeda* (basal diameter and height) in spring 2016 (N = 63 plots; mean  $\pm$  95% confidence intervals), after four growing seasons of experimental treatments, calculated using linear mixed models with restricted maximum likelihood estimation

**Figure 1**



**Figure 2**

