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Negative density dependence in the mortality and growth of tropical tree seedlings is strong, and primarily caused by fungal pathogens

Running Title

Natural enemies contribute to tree diversity

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Statement of Authorship

All authors formulated and designed the study, KH and HB established the experiment, all authors collected data, KH and CETP performed the data analysis, KH wrote the first draft and all authors contributed to the revisions.

Data Availability Statement

Should this manuscript be accepted, all data supporting these results will be archived in Dryad.

Abstract

1. Natural enemies have been implicated as agents of negative density dependence (NDD) in tropical forests, but their relative contributions to NDD, and thus to the maintenance of diversity, are largely unknown.

2. We monitored the rates of survival and relative growth rates on seedlings for ten years in tropical moist forest in Manu National Park, Peru. We then experimentally manipulated the plots to exclude fungal pathogens, insects, small mammals, and large mammals for an additional 31 months to assess the influence of these natural enemies on density-dependent interactions among tropical seedlings.

3. Fungal pathogens made the most important contribution to negative density dependence. The application of fungicide led to lower mortality rates, faster growth rates, and decreased species diversity. Other taxa of natural enemies had at most minor effects on seedling performance.

4. *Synthesis.* We conclude that fungal pathogens are the strongest contributors to the widely observed NDD that occurs among seedlings. Moreover, the presence of fungal pathogens augments the species diversity of seedlings, indicating their critical contribution to the maintenance of species coexistence and the structure of tropical tree communities.

Introduction

Negative density dependence (NDD) has received extensive empirical support as a key mechanism of species coexistence (Harms, Wright, Calderón, Hernández, & Herre, 2000; Liu et al., 2012; Wright, 2002; Zhu, Woodall, Monteiro, & Clark, 2015). NDD promotes coexistence by reducing individual performance at high conspecific density, thereby favouring rare species (Chesson, 2000).

Mechanisms that contribute NDD have been widely debated (Terborgh, 2012; Wright, 2002). NDD was once thought to be driven by competition among neighbouring plants for shared resources, but little evidence for competition among tropical rainforest seedlings has emerged (Paine, Harms, Schnitzer, & Carson, 2008; Svenning, Fabbro, & Wright, 2008). Multiple studies, on the other hand, have shown that natural enemies cause NDD by disproportionately preying upon locally common species (Bagchi et al., 2014; Bell, Freckleton, & Lewis, 2006; Jia et al., 2020; Packer & Clay, 2000; Paine, Beck, & Terborgh, 2016). Studies examining NDD focus on seedlings, as much of tree community structure is determined during the seedling stage, when mortality rates are high and non-random with respect to species (Green, Harms, & Connell, 2014).

We still know little about the relative importance of the taxa of natural enemies that contribute to NDD (Bagchi et al., 2014; Gripenberg et al., 2014; Jia et al., 2020; Paine et al., 2016). Bagchi et al. (2014) found both fungal pathogens and insect herbivores to cause NDD among seedlings in Belize, although only fungi affected species diversity. Their results are supported by those of Jia et al (2020), who additionally found that functional traits affected the severity of NDD in recruitment and survival. Paine et al. (2016) evaluated the contributions of mammals to NDD during seedling recruitment in Peru, finding that small and medium mammals, but not large mammals, affected mortality and diversity. We build upon these studies by evaluating the relative contributions of fungi, insects, small mammals, and large mammals to NDD in seedling mortality, growth, and species diversity. Each of the four taxa can contribute to NDD, as all consume seedlings (Packer & Clay, 2003; Paine et al., 2016).

The natural enemies most commonly implicated as drivers of NDD are pathogenic fungi or oomycota (referred to as fungal pathogens hereafter; Bell et al., 2006; Mangan et al., 2010). They are commonly highly host specific or have a limited host range (Gilbert, Magarey, Suiter, & Webb, 2012). Herbivorous insects can also cause NDD (Bagchi et al., 2014; Fricke, Tewksbury, & Rogers, 2014), though their contributions have been debated (Bagchi, Press, & Scholes, 2010; Gripenberg et al., 2014). Furthermore, small and large terrestrial mammals can also cause NDD (Beck, Snodgrass, & Thebpanya, 2013; Theimer, Gehring, Green, & Connell, 2011), although they appear to have limited consequences for diversity (Paine et al., 2016).

This study aims to determine the degree to which different taxa (fungi, insects and mammals) contribute to NDD and consequently maintain tree species diversity. We hypothesize that smaller natural enemies will make larger contributions to NDD (Bagchi et al., 2014), because they are far more abundant, and are more likely to be host specific (Gilbert et al., 2012), than are the larger-bodied taxa. We also hypothesize that the contributions of differing taxa of natural enemies to NDD will interact. For example, García-Guzman and Dirzo (2001) found that insect herbivores accelerated rates of pathogen infection by creating wounds through which pathogens attacked seedlings. To test this hypothesis, we experimentally combined exclusion treatments, expecting to find stronger effects on NDD in plots from which fungi, insects, or mammals were jointly excluded. We assess two aspects of seedling performance: mortality and relative growth rate (RGR). Because generalist natural enemies impact multiple species relatively mildly, we expect seedling RGR to be more strongly affected by generalist natural enemies such as insects and mammals (Beck et al., 2013; Novotny et al., 2002). We expect mortality, in contrast, to be more strongly driven by host specific enemies (Comita, Muller-Landau, Aguilar, & Hubbell, 2010), and we therefore expect fungi to contribute more to conspecific NDD in mortality (Bagchi et al., 2014; Gilbert et al., 2012).

Methods

Study site

This study was carried out at the Cocha Cashu Biological Station (CCBS). CCBS is located in Amazonian South-East Peru in lowland tropical rain forest, at 11°51’S, 71°19’W, 350 m elevation. This seasonal forest receives a mean of 2167 mm of rain annually, and mean daily temperatures vary between 21.8ºC and 24.2º over the course of a year (Paine, 2007). The site is in a highly diverse and remote area of Manu National Park, with over 350 tree species with a diameter ≥10 cm DBH. It has experienced minimal hunting, and no logging or mining, during the last century (Hazelwood et al., 2020).

Experimental design

Circular 1 m^2 experimental plots were established in a random blocked design throughout a 4 km^2 area of mature floodplain rain forest. 24 plots were spaced between 5 and 10 meters apart in each of 24 blocks, avoiding trails and newly fallen trees, for a total of 576 plots. Within each plot, all woody seedlings ≥10 cm and < 100 cm in stem height were identified and tagged over eight censuses between 2003 and 2017. Height was measured on all seedlings as the vertical distance from the soil to the apical meristem. All understory shrubs and lianas were excluded. Owing to the blocked design of the seedling plots, it was not feasible to identify the adult trees neighbouring them. Unfortunately, this precluded the assessment of adult competition on seedlings. Censuses were carried out 269 to 1566 days apart (see Paine & Harms, 2009 for details).

The experimental phase of the study began in October 2014, when we applied treatments to exclude fungi, insects, and mammals. Within each block, eight plots were randomly selected for the application of one of eight treatments: none (a control), fungi, insects, large mammals, all mammals, fungi and insects, all mammals and fungi, and all mammals and insects. The fungicide Amistar (Syngenta Ltd, active ingredient: azoxystrobin) provides a broad spectrum of protection against fungal attack, has low toxicity in non-target organisms, and was found to be effective by Bagchi et al. (2014). The insecticide Karate (Syngenta Ltd. active ingredient: lambda cyhalothrin), provides protection against a broad spectrum of insect herbivores, leaving low rates of residue and has low impact on non-target organisms. Pesticides were applied according to manufacturer’s instructions, mixing 1.25 ml of pesticide with 1 litre of water, and applying 50 ml of the mixture to 1 m^2 plot with spray bottles. Pesticides were applied to treatment plots every 10 to 14 days, in equal amounts over 31 months, with some treatment breaks when it was logistically impossible to apply treatments (max 1 month). Control plots were misted with an amount of water equivalent to that applied to pesticide plots.

We excluded mammals from the study plots using 2×2 m wire mesh exclosures. These were 150 cm high and included a 50 cm buffer around each plot to reduce potential germination bias from perching birds. The 'Large mammal' exclosures allowed the entry of small mammals through 15×15 cm holes cut into the base of the mesh. These were large enough to allow agoutis (*Dasyprocta* sp.) or smaller rodents to enter, but were too small for peccaries (*Pecari* and *Tayassu* spp.), deer (*Mazama americana*), or tapir (*Tapirus terrestris*). The 'All mammal' exclosures, on the other hand, were constructed flush to the ground and excluded all terrestrial mammals. Previous studies at the same site have shown this design of exclosures to be extremely effective at excluding terrestrial mammals (Beck et al., 2013; Paine et al., 2016).

No treatment was applied to the remaining 16 plots in each block. Seedling mortality and growth were modelled against conspecific and heterospecific neighbourhood density in control plots (where water was applied) and non-treatment plots (where no water was applied). No significant differences were found between control and non-treatment plots in any models ($P \geq 0.16$). Therefore, we combined control and non-treatment plots for all subsequent analyses.

Data analysis

In eight censuses conducted over 153 months, we monitored 10,557 seedlings from 638 unique species or morpho-species. Of these, 1,317 individuals were unidentified or identifiable only to family; they were excluded from all analyses. Evaluating the effects of conspecific crowding on very rare species was not possible. We therefore also excluded species that were represented by fewer than 10 seedlings, even if those species may be relatively abundant as adults. The resulting dataset consisted of 8,018 individuals representing 149 unique species and morpho-species, with 76.8% identified to species level and the remainder identified to genus level. Seedlings excluded from the dataset were counted among heterospecific neighbours.

Conspecific and heterospecific neighbourhood density, and the sizes of neighbouring seedlings, can impact mortality or RGR. We therefore calculated neighbourhood crowding indices (NCI) for each seedling per plot and census as: $NCI_k = \sum^{N} \frac{height_n}{height_k}$, where k is the focal individual, and n indexes over the N neighbouring seedlings. Because individual seedlings were not mapped within plots, distances among seedlings were not available. Indices were calculated separately for conspecific neighbours and heterospecific neighbours.

We first evaluated the extent to which density dependence shapes the rates of mortality and growth in this community. Mortality was predicted by heterospecific and conspecific crowding indices using a generalized linear mixed effect model with binomial errors. We included an offset of the log-transformed time between censuses to account for differing census intervals and to yield parameter estimates in units of years. We assessed the effects of crowding on RGR using a similarly structured linear mixed-effect model, in which relative growth rate was predicted by conspecific and heterospecific crowding indices. Seedling RGR was assumed to be exponential since growth rates do not slow until trees reach a height far exceeding 1 m.

In all models, species was included as a random intercept to account for differing rates of mortality or growth among species. We evaluated whether the effects of conspecific or heterospecific crowding differed among species by testing the support for models that included random slopes among species. Larger seedlings experience lower mortality risk (Green et al., 2014; Paine et al., 2012), therefore log-transformed seedling height was included as a fixed effect in all models. We evaluated the support for size dependent responses in models that included interactions between height and both crowding indices. Finally, location, coded as plots nested within blocks, was included as a random intercept, to account for spatial heterogeneity in the rates of mortality and growth across the study site.

Secondly, we assessed the effects of fungi, insects, and mammals as contributors of density-dependent mortality and growth. To do so, we included interactions between conspecific crowding and treatment, and between heterospecific crowding and treatment. The first assessment evaluated the effects of fungi, insects, large mammals and small mammals. The effects of fungi, insects, and large mammals were evaluated by comparing the mortality and growth of seedlings in control plots to their performance from which each taxon was excluded. The effects of small mammals was evaluated by comparing mortality and growth of seedling in plots from which large mammals were excluded against plots from which all mammals were excluded. These effects were tested using one-degree of freedom orthogonal contrasts.

To evaluate whether fungi, insects, and mammals make interactive contributions to density dependence, we built three further models: 1) fungi and insects: This model included the treatments fungicide, insecticide, fungicide and insecticide, and control; 2) fungi and mammals: including the treatments fungicide, all mammals, fungicide and all mammals, and control; and 3) mammals and insects, including the treatments all mammals, insecticide, all mammals and insecticide, and control. In each of these tests, we evaluated the support for a statistical interaction between the two main effects on seedling mortality and growth.

We assessed the effects of each experimental treatment on diversity using the exponent of the Shannon-Weiner diversity index for each plot at each census, which can be interpreted as the number of equally abundant species in a community (Jost, 2006). To assess the effects of each exclusion treatment on species diversity, and how the effects may change through time, diversity was predicted by the interaction of treatment and census period.

All analyses were performed in R 4.0.2 (R Core Team, 2020), using package lme4 (Bates, Mächler, Bolker, & Walker, 2012). All models were compared on an AIC basis. Model residuals were examined for overdispersion and heteroscedasticity using the DHARMa package (Hartig, 2020). No issues were identified. P values and confidence intervals were derived from non-parametric bootstrapping using 10,000 replicates.

Results

We estimated the effects of conspecific and heterospecific density on mortality and relative growth rate over the entire study period (2003-17). Across all seedlings, the estimated annual probability of mortality was 25.3% per year in the absence of crowding from neighbours. Mortality increased with conspecific crowding. An order-of-magnitude increase in conspecific crowding increased the mortality rate from 27.1% to 32.1% ($P < 0.001$, Fig. 1A). In contrast, heterospecific crowding did not affect the risk of mortality ($P = 0.10$, Fig. 1B).

Increasing seedling height consistently and significantly reduced mortality rates, but height did not interact significantly with crowding: large and small seedlings were similarly affected by crowding from neighbours. The estimated annual relative growth rate was 0.61 $mm \cdot cm^{-1} \cdot y^{-1}$ for median-sized seedlings (15 cm in height) in the absence of crowding from neighbours (Fig. 1C). However, there was great variation in growth rates, with many seedlings growing or shrinking, even in the absence of crowding from neighbours. There was a strong interaction between height and both conspecific and heterospecific crowding in RGR ($P < 0.0001$, Fig 1C &D). Growth among smaller seedlings increased with increasing conspecific and heterospecific crowding, whereas the opposite pattern was observed for larger seedlings, though the decline was stronger with heterospecific crowding (Fig. 1D).

Mortality

We assessed the contribution of each taxon of natural enemies to density dependent mortality during the experimental period of the study (2014-2017). The effect of conspecific crowding on mortality was significantly reduced by fungicide application ($P = 0.0476$, Fig. 2A). Fungicide application reduced mortality rate by 19% at a conspecific neighbourhood crowding index of 10, corresponding to a focal seedling in a plot with 10 conspecific seedlings of the same size as the focal. This result suggests that fungi are a major contributor to conspecific density dependence. In contrast, the application of insecticide and the use of mammal-excluding cages did not significantly interact with conspecific crowding ($P \geq 0.13$). The exclusion of small mammals led to a minor, though significant, decrease in mortality under high heterospecific crowding, whereas the application of fungicide increased seedling mortality under conditions of high heterospecific crowding (Fungicide: $P = 0.0001$;

Small mammals: $P = 0.046$, Fig 2B). The other treatments had no significant effects ($P \geq 0.13$). There was no significant interaction between the exclusion of insects, large mammals, or small mammals and conspecific crowding, suggesting that these taxa do not contribute in complementary manners to the effects of conspecific crowding on seedling mortality ($P \geq 0.30$, Figs. 2C, E, & G). The interactive contribution of fungicide and insecticide to heterospecific crowding were significant ($P = 0.0212$), but were intermediate between their independent effects (Fig. 2D). The combined application of fungicide and the exclusion of all mammals led to a significant increase in mortality in conditions of high heterospecific crowding ($P = 0.0001$, Fig 2F). Insecticide and the exclusion of all mammals had no interactive effects on mortality (Fig. 2H).

Relative growth rate

The application of fungicide led significantly increased relative growth rates under conditions of high conspecific crowding ($P = 0.0172$, Fig. 3A). In contrast, the application of insecticide significantly reduced growth rates ($P < 0.0001$), whereas the exclusion of large and small mammals had no significant effects. The interactive contributions of fungicide and insecticide to conspecific crowding significantly increased rates of growth in conditions of high conspecific crowding ($P = 0.0091$, Fig. 3C). Similarly, the interactive contributions of fungicide and the exclusion of all mammals also slightly but significantly, increased growth rates ($P = 0.0250$, Fig. 3E). Insecticide and the exclusion of all mammals had no interactive effects on growth (Fig. 3G). In contrast to the effects on conspecific crowding, no experimental treatment, or combination of treatments, influenced the growth response to heterospecific crowding ($P \geq 0.13$, Figs. 3B, D, F, H).

Diversity

The effect of exclusion treatments on diversity was assessed by monitoring the change in the exponent of Shannon-Weiner diversity since the experimental treatments were first applied in October 2014. The application of fungicide caused a rapid and significant decrease in diversity, which persisted over the experimental period (Fig. 4A). The application of insecticide, and the exclusion of large mammals, also reduced diversity, though these effects only became significant at the final census ($P \leq 0.006$, Fig. 4A). The exclusion of small mammals had no effect at any time ($P \geq 0.055$). When treatments were combined, their joint effects reduced diversity, at least by the final census, but their effects were intermediate between the relevant main effects in all cases (Fig. 4B, C, D).

Digging a bit deeper into the diversity data, we dissected the effects of each taxon of natural enemies on seedling species richness and evenness. The patterns observed in species diversity were mirrored by those of species richness. Patterns in species evenness, in contrast, were extremely minor, and divorced from those of diversity (Supplemental Figure 1). This indicates that natural enemies, particularly fungi, affect seedling diversity primarily though the local exclusion of species, rather than through effects on their relative abundance.

Discussion

The extent and causes of negative density dependence (NDD) in plant performance have long been investigated, owing to the fundamental importance of NDD in promoting the coexistence of species (Chesson, 2000; Wright, 2002). We examined the effects of NDD on mortality and growth in tropical tree seedlings using data from a 14-year period. The extensive dataset allows us to robustly conclude that conspecific crowding increases mortality rates, whereas crowding from heterospecific neighbours has much weaker effects (Fig. 1A, B). These patterns are broadly in accord with previous studies (Jia et al., 2020; Piao, Comita, Jin, & Kim, 2013; Terborgh, 2012; Wills et al., 2006). Conspecific crowding, and, to a lesser extent, heterospecific crowding increased the growth of small seedlings, but reduced the growth of larger ones (Fig. 1C, D). This result stands in contrast with previous studies, which found a purely negative effect on growth from conspecific neighbours. This delayed negative effect could arise through interspecific competition (Tanner, Teo, Coomes, & Midgley, 2005). However, competition among seedlings is unlikely, given their relative scarcity in the understory of closed-canopy tropical forests (Paine et al., 2008; Svenning et al., 2008). It should be noted that the stem density of seedlings at our study site (6.4 ± 4.8 stems m^{-2}; Harms, Powers, & Montgomery, 2004) is comparable to that found in other Neotropical rain forests (Paine et al., 2008). A stronger possibility is that the primary drivers of density dependent mortality and growth are natural enemies (Paine et al. 2016). Seedling germination and the initial survival of seedlings can be promoted in favourable microsites (Paine & Harms, 2009). Thereafter, natural enemies, including fungal pathogens, insects and mammals (Sedio & Ostling, 2013), would be attracted to high densities of host species, and their effects can be expected to accumulate over time to impact larger seedlings.

Studies of NDD have recently come under scrutiny for bias (Detto, Visser, Wright, & Pacala, 2019). Previous studies have over- and under-estimated the strengths of NDD because of their use of error-prone proxies. We believe that our conclusions are largely insulated from these biases. First, we assessed longitudinal data within a single life stage (seedlings), rather than transitions between life stages. This approach is not biased to detect NDD when none is present (Detto et al., 2019). Second, we used a similar analytical technique throughout the study. In other words, if bias taints our results, they should all be biased in a similar fashion. Thus, we are able to accurately assess the contribution of each taxon of natural enemies to NDD. Therefore, we are confident in the conclusions of this study.

Our primary conclusion, that fungi are the predominant contributor to NDD in seedling mortality and growth, confirms that of previous studies (Bagchi et al., 2014; Gripenberg et al., 2014; Packer & Clay, 2000; Paine et al., 2016). Our study builds upon this body of work in four ways: 1) We establish the baseline level of NDD over 14 years of observation, 2) We investigate the contributions of four key taxa of natural enemies to density-dependent performance using a consistent framework, 3) we examine the degree to which various taxa of natural enemies interact, and 4) we monitor both growth and survival. Despite the clear support for the leading role of fungi, all four taxa we investigated could plausibly have contributed to the NDD observed at this site (Fig. 1). Fungal pathogens and oomycota can negatively affect the performance of tropical tree seedlings (Augspurger, 1983; Bagchi, Swinfield, et al., 2010), even as mycorrhizal fungi are key to seedling establishment and growth. Similarly, many insect herbivores are host-specific or clade-specific (Forister et al., 2015; Novotny et al., 2002), and could therefore contribute to NDD.

We found that fungal pathogens contributed more to negative density dependence in mortality and growth than did insects or mammals, as the application of fungicide reduced rates of mortality and increased relative growth rates in conditions of high conspecific crowding (Figs. 2A & 3A). These results are consistent with studies that found strong associations between NDD and fungal pathogens (Bagchi et al., 2014; Bell et al., 2006; Jia et al., 2020; Packer & Clay, 2000), and validate a mechanism originally proposed by Janzen (1970) and Connell (1971). Given that the application of fungicide is likely to have reduced the abundance of both pathogenic and beneficial fungi, the strong positive effects of fungicide application on seedling performance lend further credence to our interpretation that pathogenic fungi are the key contributors to negative density dependence in this system, as they overcame countervailing positive effects from mycorrhizal fungi (Bagchi et al., 2014). Fungal pathogens are often highly host specific (Gilbert & Webb, 2007); it is this host-specificity that allows pathogens to pass between seedlings rapidly under high conspecific crowding. When we excluded fungi, mortality decreased and growth rates increased with conspecific density (Figs 2A & 3A). This indicates that, once released from the negative effects of fungal pathogens, the environmental conditions were favourable enough for high densities of conspecifics to thrive. This further supports the argument that intra-specific competition among seedlings is weak (Paine et al., 2008).

Moreover, the application of fungicide also reduced species diversity, suggesting that the depredations of fungal pathogens play a key role in maintaining diversity in this community (Fig. 4A). To a lesser degree, diversity was also promoted by insects and large mammals, but they appear to do so through non-NDD processes. Notably, fungi more strongly affected species richness than evenness (Supplemental Figure 1). This further suggests the role pathogenic fungi play in excluding seedling species, and thereby structuring the tree community.

In addition to fungi and insects, small mammals have been found to contribute to NDD at this site and in Corcovado National Park (CNP), Costa Rica (Demattia, Rathcke, & Curran, 2006; Paine et al., 2016). These two studies, however, focused on seed removal, rather than seedling growth or mortality, which may have led us to underestimate the contribution of small mammals to NDD. Beck et al. (2013) found, at the same study site, that large mammals also contributed to seedling mortality and abundance. However, we observed that White-lipped Peccaries (*Tayassu pecari*), which are major consumers of seeds and seedlings, occurred at unusually low densities at the site during the experimental phase of this study. We speculate that this may account for the contrast between our results and those of Beck et al. (2013). Moreover, none of the previous mammal-focused studies observed fungal pathogens or insects. Mammals can contribute to NDD in seedling recruitment, but their effects appear to occur during an earlier ontogenetic phase than that which we examined here.

If one taxon facilitates the consumption of another, then they could interactively affect the growth and eventually the mortality of seedlings. For example, insect herbivores can accelerate rates of pathogen infection (García-Guzmán & Dirzo, 2001). In the current study, interactions among taxa of natural enemies that intensified NDD were uncommon. Only the joint exclusions of fungi and insects, and fungi and mammals, increased growth rates in conditions of conspecific crowding (Fig. 3C, E). More frequently, the joint effect of excluding multiple taxa was intermediate between their independent effects, or was opposite to the pattern expected under NDD. This may be because perturbing multiple taxa of natural enemies simultaneously made the rates of mortality and growth more stochastic.

Overall, our results suggest that natural enemies are affecting NDD interactively, but rather that their effects are additive on the seedling community. This suggests that they are impacting different sections of the seedling community (Forister et al., 2015; Novotny et al., 2002), and provides evidence for differences among species in vulnerability to different types of natural enemies.

Multiple studies have examined mortality as an indicator of NDD in seedlings. Mortality, however, provides only a coarse indication of the strength of NDD, as it is a binary response, and can occur only once to any organism. RGR is a more sensitive detector of NDD, as it can vary at sub-lethal scales. RGR is also a noisy response variable, owing to the many factors unrelated to NDD that can cause it to vary (Zhu et al., 2015). Effects of heterospecific crowding on RGR, but not on mortality, implicate mechanisms that impact plant health but do not necessarily cause mortality, although a decline in health can result in death. Both competition and generalist natural enemies may have a slow but non-fatal impact on seedlings (Murrell, 2009; Theimer et al., 2011), and it is possible that these mechanisms reduced growth rates. In the current study, the insights provided by mortality, growth, and diversity were largely concurrent, together indicating that fungi are the predominant contributors to NDD in this system.

Conclusions

Our study demonstrates that fungal pathogens increase mortality rates, decrease growth rates, and promote species diversity in a highly diverse tropical moist forest. Insects and large mammals also promote diversity, but they appear to do so through non-NDD processes. Given the outsized importance of seedling recruitment in structuring tropical tree communities (Green et al., 2014; Harms et al., 2000), it is likely that the effects of fungi on seedlings persist throughout ontogeny. Although our results suggest that diversity is maintained by multiple drivers and should not be assigned a unique mechanism, we present strong evidence that fungal pathogens are uniquely important in shaping tropical tree communities, and are disproportionately important drivers of diversity in tropical forests.

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Figures

Figure 1

Predicted effects of conspecific and heterospecific neighbourhood crowding on mortality and relative growth rate between 2003 and 2017. Panels A) and B) display mortality, whereas C) and D) show relative growth rate. The three fitted lines on each panel represent the rates of mortality (A & B) or growth (C & D) for seedlings that began each census interval with heights of either 10, 20, or 50cm. Shaded areas represent 95% confidence intervals, derived from non-parametric bootstrapping. Histograms and right-hand vertical axes in panels A) and B) show the distribution of crowding experienced by seedlings that died (at bottom of panels) or survived between censuses (at top). Points in panels C) and D) represent the growth rates of seedlings. Many points are over-printed, either because crowding was zero, or because the observed rate of growth was zero. Note that all x-axes are log-transformed.

Figure 2

Probability of mortality predicted by conspecific crowding index (left column) or heterospecific crowding index (right column). Panels A) and B) show the change in mortality rates incurred by the exclusion of fungal pathogens, insects, large mammals, and small mammals. Panels C) and D) show the interacting effects of fungicide and insecticide with crowding. Panels E) and F) show the interacting effects of fungicide and all-mammal exclosures with crowding. Panels G) and H) show the interacting effects of all-mammal exclosures and insecticide with crowding. The P-values shown on each panel represent the significance of the interaction of each term with the crowding index (See Appendix 1 for complete statistical results).

Significant P-values represent effects that differ from the effects of crowding in control plots. Shaded areas represent 95% confidence intervals, derived from non-parametric bootstrapping. ns: not significant. Note that all x-axes are log-transformed.

Figure 3

Relative growth rate predicted by conspecific crowding index (left column) or heterospecific crowding index (right column). Panels A) and B) show the change in growth rate incurred by the exclusion of fungal pathogens, insects, large mammals, and small mammals. Panels C) and D) show the interacting effects of fungicide and insecticide with crowding. Panels E) and F) show the interacting effects of fungicide and all-mammal exclosures with crowding. Panels G) and H) show the interacting effects of all-mammal exclosures and insecticide with crowding. Formatting otherwise follows that of Figure 2.

Figure 4

Change in Shannon-Weiner Diversity index under the exclusion of A) fungal pathogens, insects, small mammals and large mammals. Panel B) shows the interacting effects of fungicide and insecticide on diversity, panel C) shows the interacting effects of fungicide and all-mammal exclosures, and panel D) shows the interacting effects of all-mammal exclosures and insecticide. Significant changes from the diversity level in September 2014 (just prior to the beginning of treatment application) are shown as filled dots. Error bars represent 95% confidence intervals, derived from non-parametric bootstrapping.

Supplemental Figures

Supplemental Figure 1

Change in species richness (A-D) and evenness (E-H) under the exclusion of A & E) fungal pathogens, insects, small mammals and large mammals. Panels B & F show the interacting effects of fungicide and insecticide on richness and evenness, panels C & G show the interacting effects of fungicide and all-mammal exclosures, and panels D & H show the interacting effects of all-mammal exclosures and insecticide. Significant changes from the levels of richness and evenness in September 2014 (just prior to the beginning of treatment application) are shown as filled dots. Error bars represent 95% confidence intervals, derived from non-parametric bootstrapping. Note the difference in scale on the Y axes of panels A-D and E-H.

Figure 1

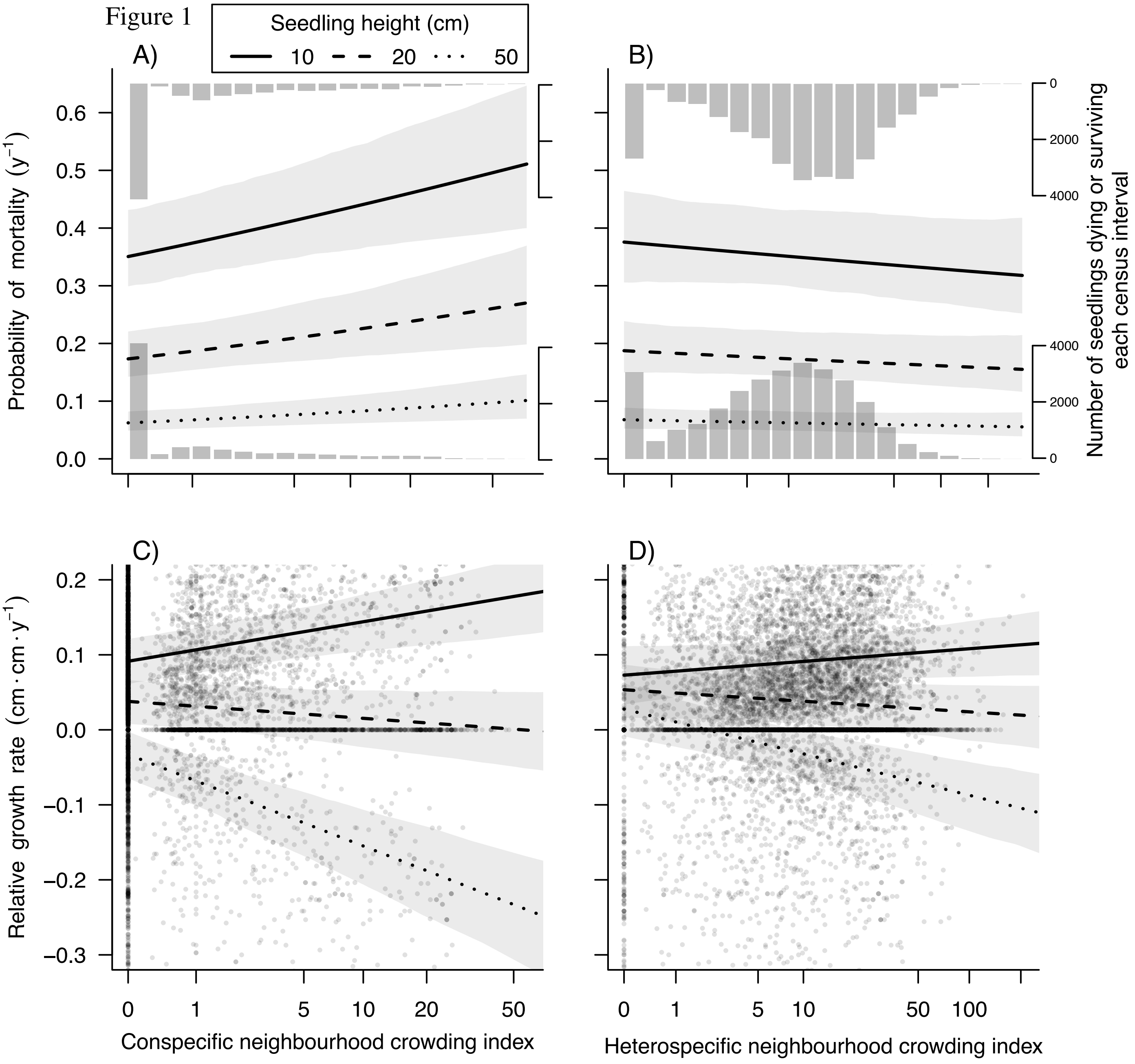

Seedling height (cm)
10
20
50
A)
B)
C)
D)
Probability of mortality (y^{-1})
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Number of seedlings dying or surviving each census interval
0
2000
4000
Relative growth rate ($cm \cdot cm \cdot y^{-1}$)
−0.3
−0.2
−0.1
0.0
0.1
0.2
0
1
5
10
20
50
100
Conspecific neighbourhood crowding index
Heterospecific neighbourhood crowding index

Figure 2

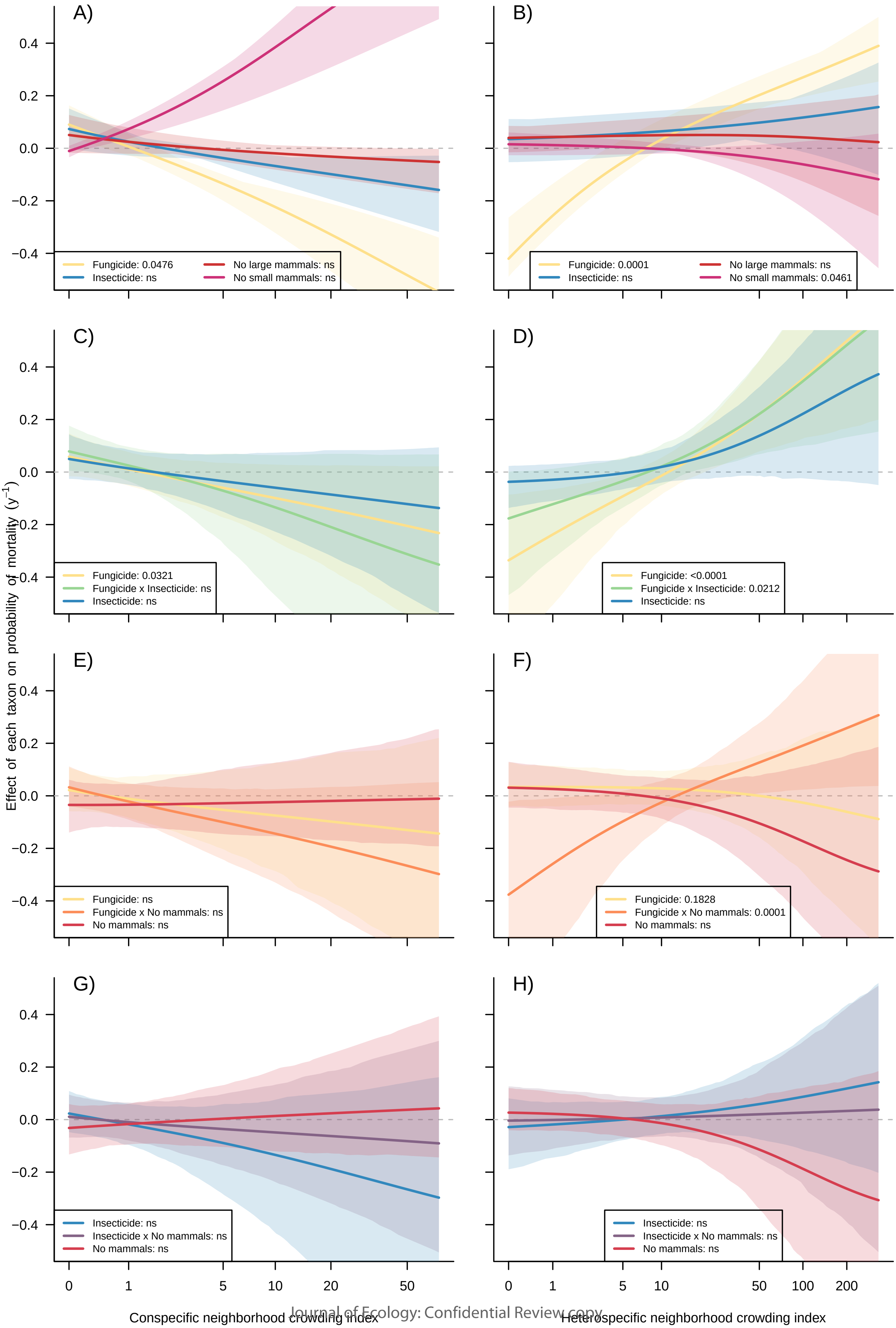

A)
Fungicide: 0.0476
Insecticide: ns
No large mammals: ns
No small mammals: ns
B)
Fungicide: 0.0001
Insecticide: ns
No large mammals: ns
No small mammals: 0.0461
C)
Fungicide: 0.0321
Fungicide x Insecticide: ns
Insecticide: ns
D)
Fungicide: <0.0001
Fungicide x Insecticide: 0.0212
Insecticide: ns
E)
Fungicide: ns
Fungicide x No mammals: ns
No mammals: ns
F)
Fungicide: 0.1828
Fungicide x No mammals: 0.0001
No mammals: ns
G)
Insecticide: ns
Insecticide x No mammals: ns
No mammals: ns
H)
Insecticide: ns
Insecticide x No mammals: ns
No mammals: ns
0.4
0.2
0.0
−0.2
−0.4
Effect of each taxon on probability of mortality (y^{-1})
0
1
5
10
20
50
0
1
5
10
50
100
200
Conspecific neighborhood crowding index
Heterospecific neighborhood crowding index

Figure 3

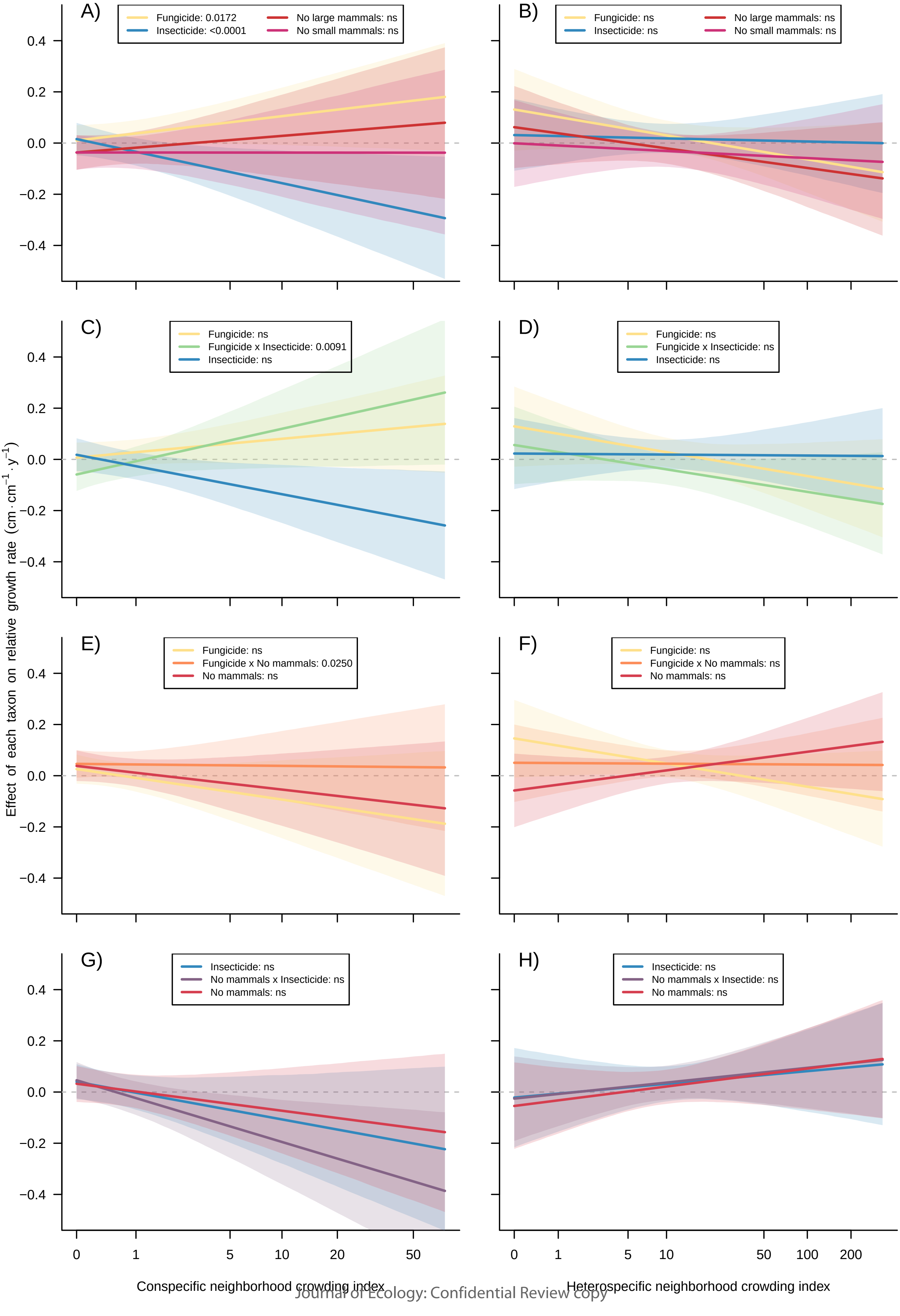
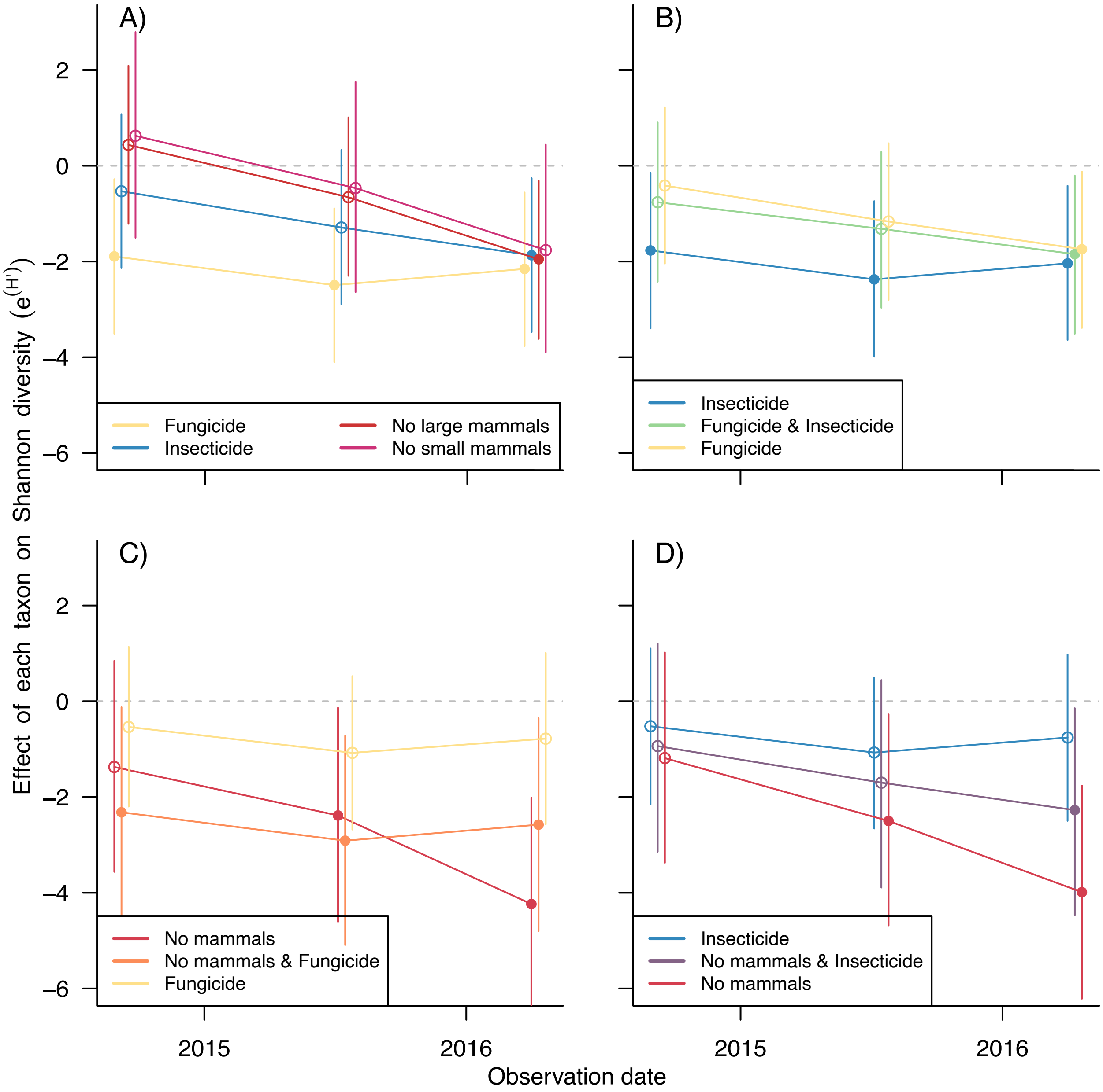
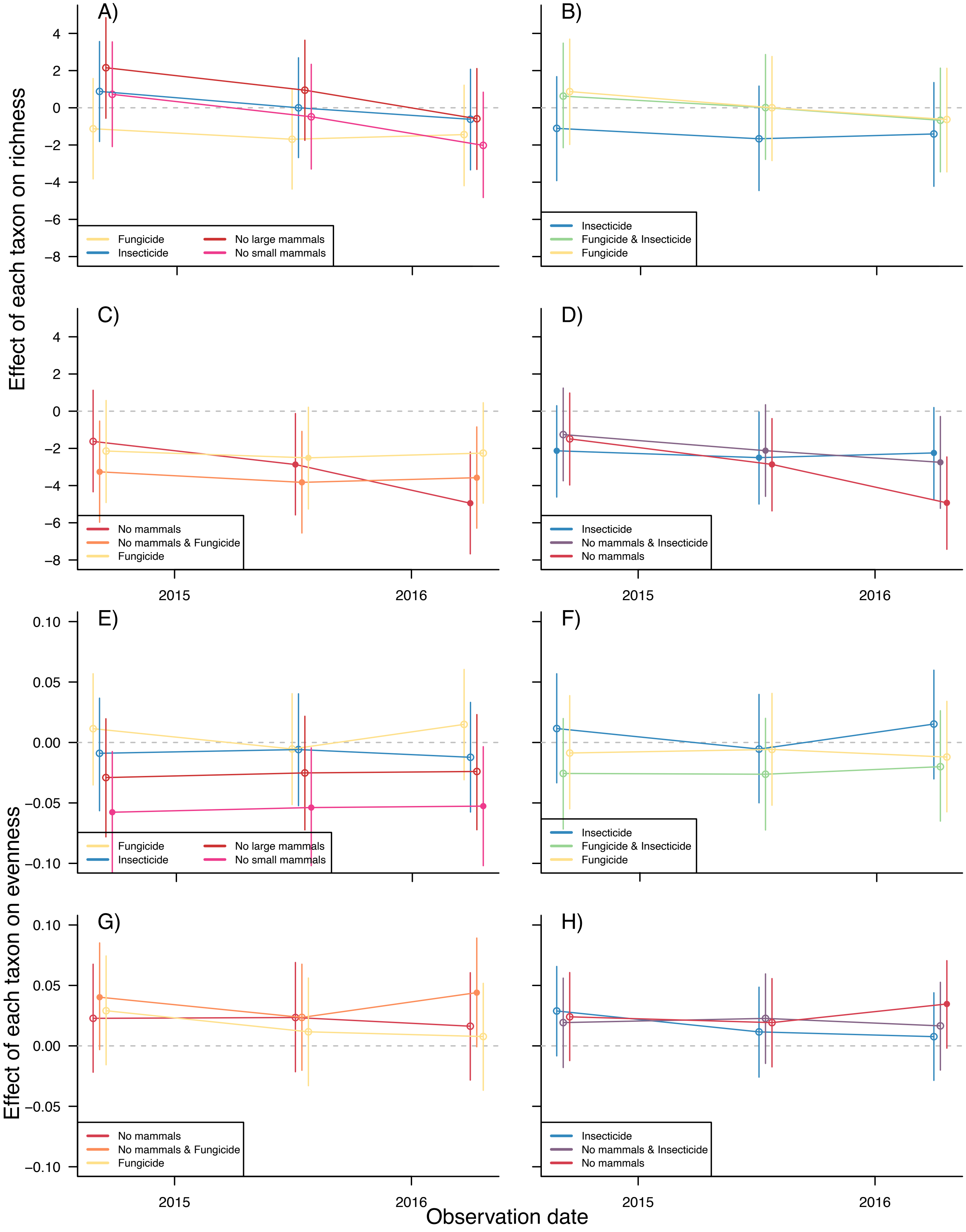

A)
Fungicide: 0.0172
Insecticide: <0.0001
No large mammals: ns
No small mammals: ns
B)
Fungicide: ns
Insecticide: ns
No large mammals: ns
No small mammals: ns
C)
Fungicide: ns
Fungicide x Insecticide: 0.0091
Insecticide: ns
D)
Fungicide: ns
Fungicide x Insecticide: ns
Insecticide: ns
E)
Fungicide: ns
Fungicide x No mammals: 0.0250
No mammals: ns
F)
Fungicide: ns
Fungicide x No mammals: ns
No mammals: ns
G)
Insecticide: ns
No mammals x Insecticide: ns
No mammals: ns
H)
Insecticide: ns
No mammals x Insectide: ns
No mammals: ns
0.4
0.2
0.0
−0.2
−0.4
Effect of each taxon on relative growth rate (cm · cm^{-1} · y^{-1})
0
1
5
10
20
50
0
1
5
10
50
100
200
Conspecific neighborhood crowding index
Heterospecific neighborhood crowding index

Figure 4


A)
B)
C)
D)
2
0
−2
−4
−6
Effect of each taxon on Shannon diversity $(e^{(H')})$
Fungicide
Insecticide
No large mammals
No small mammals
Insecticide
Fungicide & Insecticide
Fungicide
No mammals
No mammals & Fungicide
Fungicide
Insecticide
No mammals & Insecticide
No mammals
2015
2016
2015
2016
Observation date

Supplemental Figure 1



Appendix 1: Complete statistical output for all analyses

This document contains all the statistical output for the results presented in Hazelwood et al “Negative density dependence in the mortality and growth of tropical tree seedlings is strong, and primarily caused by fungal pathogens”

DENSITY DEPENDENCE (Figure 1)

Figure 1A & 1B

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
Offset: offset_time, Family: binomial  (cloglog)
event ~ consp.crowd.l + hetsp.crowd.l + ht.l + (1|trans/plot) + (1|Census) + (consp.crowd.l|Name) +
(hetsp.crowd.l|Name)

 AIC      BIC      logLik   deviance   df.resid
 15241.4  15340.1  -7607.7  15215.4    14594

Random effects:
 Groups     Name          Variance Std.Dev. Corr
 plot.trans (Intercept)   0.131053 0.36201
 Name       (Intercept)   0.255901 0.50587
            hetsp.crowd.l 0.012195 0.11043  -0.19
 Name.1     (Intercept)   0.170577 0.41301
            consp.crowd.l 0.031816 0.17837  -0.04
 trans      (Intercept)   0.007364 0.08581
 Census     (Intercept)   0.091562 0.30259
Number of obs: 14607, groups:  plot:trans, 516; Name, 143; trans, 24; Census, 11

Fixed effects:
              Estimate Std. Error z value P value
(Intercept)    1.96983    0.19904   9.897   0.000
consp.crowd.l  0.11740    0.03847   3.052   0.000
hetsp.crowd.l -0.03591    0.02981  -1.205   0.102
ht.l          -1.18234    0.04477 -26.412   0.000

R^2: Marginal 0.1393731, Conditional: 0.2997038
```

Figure 1C & 1D

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
rgr ~ (consp.crowd.l + hetsp.crowd.l)*ht.l + (1|trans/plot) + (1|Census) + (consp.crowd.l|Name) +
(hetsp.crowd.l|Name)
 AIC      BIC       logLik  deviance    df.resid
 -2038.3  -1923.4   1035.2  -2070.3     9697

Random effects:
 Groups     Name          Variance  Std.Dev. Corr
 plot.trans (Intercept)   0.0006340 0.02518
 Name       (Intercept)   0.0022570 0.04751
            hetsp.crowd.l 0.0004096 0.02024  -0.97
 Name.1     (Intercept)   0.0001903 0.01379
            consp.crowd.l 0.0005975 0.02444  -0.36
 trans      (Intercept)   0.0002024 0.01423
 Census     (Intercept)   0.0023253 0.04822
 Residual                 0.0459208 0.21429
Number of obs: 9713, groups:  plot:trans, 503; Name, 143; trans, 24; Census, 11

Fixed effects:
                    Estimate Std. Error t value P value
(Intercept)         0.137514   0.034871   3.944  0.0000
consp.crowd.l       0.126172   0.017359   7.268  0.0000
hetsp.crowd.l       0.054187   0.012259   4.420  0.0000
ht.l               -0.028064   0.009350  -3.001  0.0016
consp.crowd.l:ht.l -0.045262   0.006176  -7.329  0.0000
hetsp.crowd.l:ht.l -0.020219   0.004053  -4.988  0.0000

R^2: Marginal 0.07440856, Conditional: 0.1582671
```

MORTALITY (Figure 2)

Figure 2A & 2B

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
Offset: offset_time, Family: binomial (cloglog)
event ~ (consp.crowd.l + hetsp.crowd.l)*Trt + ht.l + (1|trans/plot) + (1|Census) + (1|Name)
  AIC      BIC      logLik   deviance   df.resid
  1117.1   1223.5   -538.6   1077.1     1488

Random effects:
 Groups     Name        Variance  Std.Dev.
 Name       (Intercept) 7.722e-01 0.878725
 plot:trans (Intercept) 4.731e-05 0.006878
 trans      (Intercept) 2.084e-01 0.456497
 Census     (Intercept) 2.128e-01 0.461341
Number of obs: 1508, groups:  Name, 105; plot:trans, 78; trans, 16; Census, 3

Fixed effects:
                                Estimate Std. Error z value P value
(Intercept)                      1.83847    0.98791   1.861  0.0030
consp.crowd.l                    0.14057    0.11424   1.230  0.1347
hetsp.crowd.l                    0.07311    0.14046   0.521  0.2513
TrtFungi                        -1.78587    0.65550  -2.724  0.0005
TrtInsects                       0.10104    0.70482   0.143  0.3760
TrtSmall Mammals                 0.40799    0.69468   0.587  0.1252
TrtLarge Mammals                 0.67241    0.87550   0.768  0.0429
ht.l                            -1.40947    0.23993  -5.874  0.0000
consp.crowd.l:TrtFungi          -0.27287    0.16668  -1.637  0.0476
consp.crowd.l:TrtInsects         0.11193    0.20983   0.533  0.3085
consp.crowd.l:TrtSmall Mammals   0.23218    0.31483   0.737  0.1663
consp.crowd.l:TrtLarge Mammals -0.31912    0.29724  -1.074  0.1289
hetsp.crowd.l:TrtFungi           0.68258    0.21693   3.147  0.0001
hetsp.crowd.l:TrtInsects         0.01507    0.23814   0.063  0.4715
hetsp.crowd.l:TrtSmall Mammals -0.15282    0.24061  -0.635  0.1342
hetsp.crowd.l:TrtLarge Mammals -0.24897    0.29509  -0.844  0.0461

R^2: Marginal 0.1297976, Conditional: 0.2760001
```

Figure 2C & 2D

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
event ~ (consp.crowd.l + hetsp.crowd.l)*Insecticide_trt*Fungicide_trt + ht.l + (1|trans/plot) + (1|Census) +
(1|Name)
Offset: offset_time, Family: binomial  (cloglog)
     AIC      BIC   logLik deviance df.resid
   919.7   1007.3   -442.8    885.7     1262

Random effects:
 Groups     Name        Variance  Std.Dev.
 Name       (Intercept) 5.967e-01 0.772472
 plot:trans (Intercept) 1.286e-06 0.001134
 trans      (Intercept) 1.925e-01 0.438730
 Census     (Intercept) 1.378e-01 0.371214
Number of obs: 1279, groups:  Name, 104; plot:trans, 64; trans, 16; Census, 3

Fixed effects:
                                                                  Estimate Std. Error z value P value
(Intercept)                                                        0.4691     1.3745   0.341  0.1735
consp.crowd.l                                                     -0.2561     0.2229  -1.149  0.1002
hetsp.crowd.l                                                      0.5824     0.3063   1.901  0.0016
Insecticide_trtInsecticide                                         0.6283     1.1860   0.530  0.1187
Fungicide_trtFungicide                                             2.4639     1.1185   2.203  0.0003
ht.l                                                              -1.3378     0.2644  -5.059  0.0000
consp.crowd.l:Insecticide_trtInsecticide                           0.3515     0.3190   1.102  0.1187
hetsp.crowd.l:Insecticide_trtInsecticide                          -0.3378     0.3905  -0.865  0.0514
consp.crowd.l:Fungicide_trtFungicide                               0.4943     0.2680   1.845  0.0321.
hetsp.crowd.l:Fungicide_trtFungicide                              -0.9904     0.3639  -2.722  0.0000
Insecticide_trtInsecticide:Fungicide_trtFungicide                 -1.4345     1.6066  -0.893  0.0217
consp.crowd.l:Insecticide_trtInsecticide:Fungicide_trtFungicide  -0.2623     0.4970  -0.528  0.3074
hetsp.crowd.l:Insecticide_trtInsecticide:Fungicide_trtFungicide   0.5513     0.5395   1.022  0.0212

R^2: Marginal 0.09758026, Conditional: 0.2120702
```

Figure 2E & 2F

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
event ~ (consp.crowd.l + hetsp.crowd.l)*Mammal_trt*Fungicide_trt + ht.l + (1|trans/plot) + (1|Census) + (1|Name)
Offset: offset_time, Family: binomial  (cloglog)
   AIC     BIC      logLik    deviance  df.resid
   935.0   1022.1   -450.5    901.0     1226

Random effects:
 Groups     Name        Variance  Std.Dev.
 Name       (Intercept) 0.8038940 0.89660
 plot:trans (Intercept) 0.0002498 0.01581
 trans      (Intercept) 0.0879335 0.29654
 Census     (Intercept) 0.1566762 0.39582
Number of obs: 1243, groups:  Name, 97; plot:trans, 63; trans, 16; Census, 3

Fixed effects:
                                                         Estimate Std. Error z value P value
(Intercept)                                               0.8503     1.2153   0.700   0.0936
consp.crowd.l                                            -0.3092     0.3858  -0.801   0.1320
hetsp.crowd.l                                             0.2676     0.2780   0.963   0.0732
Mammal_trtControl                                        -0.6413     1.1479  -0.559   0.1611
Fungicide_trtFungicide                                   -0.7333     1.2612  -0.581   0.1299
ht.l                                                     -1.2226     0.2652  -4.609   0.0000
consp.crowd.l:Mammal_trtControl                           0.0479     0.4419   0.108   0.4314
hetsp.crowd.l:Mammal_trtControl                           0.2895     0.3861   0.750   0.1063
consp.crowd.l:Fungicide_trtFungicide                      0.3461     0.5019   0.689   0.1828
hetsp.crowd.l:Fungicide_trtFungicide                      0.1946     0.4144   0.470   0.2003
Mammal_trtControl:Fungicide_trtFungicide                  3.2729     1.6584   1.974   0.0002
consp.crowd.l:Mammal_trtControl:Fungicide_trtFungicide    0.1991     0.5636   0.353   0.3248
hetsp.crowd.l:Mammal_trtControl:Fungicide_trtFungicide   -1.2164     0.5397  -2.254   0.0001

R^2: Marginal 0.0937560, Conditional: 0.2253659
```

Figure 2G & 2H

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
event ~ (consp.crowd.l + hetsp.crowd.l)*Mammal_trt*Insecticide_trt + ht.l + (1|trans/plot) + (1|Census) + (1|Name)
Offset: offset_time, Family: binomial (cloglog)
   AIC      BIC     logLik    deviance  df.resid
   827.6    913.2   -396.8    793.6     1119

Random effects:
 Groups     Name        Variance Std.Dev.
 Name       (Intercept) 0.65694  0.8105
 plot:trans (Intercept) 0.07534  0.2745
 trans      (Intercept) 0.05661  0.2379
 Census     (Intercept) 0.14863  0.3855
Number of obs: 1136, groups:  Name, 96; plot:trans, 63; trans, 16; Census, 3

Fixed effects:
                                                           Estimate Std. Error z value   P value
(Intercept)                                                 0.61495    1.20914   0.509    0.1599
consp.crowd.l                                              -0.16357    0.37649  -0.434    0.2620
hetsp.crowd.l                                               0.29223    0.28336   1.031    0.0933
Mammal_trtControl                                          -0.63457    1.18440  -0.536    0.1627
Insecticide_trtInsecticide                                  0.22666    1.28109   0.177    0.3172
ht.l                                                       -1.17708    0.26355  -4.466    0.0088
consp.crowd.l:Mammal_trtControl                            -0.15141    0.43841  -0.345    0.3442
hetsp.crowd.l:Mammal_trtControl                             0.30470    0.39639   0.769    0.1207
consp.crowd.l:Insecticide_trtInsecticide                    0.47073    0.45272   1.040    0.1139
hetsp.crowd.l:Insecticide_trtInsecticide                   -0.14945    0.42451  -0.352    0.2145
Mammal_trtControl:Insecticide_trtInsecticide                0.26369    1.75745   0.150    0.3012
consp.crowd.l:Mammal_trtControl:Insecticide_trtInsecticide -0.08393    0.55829  -0.150    0.4080
hetsp.crowd.l:Mammal_trtControl:Insecticide_trtInsecticide -0.13909    0.58052  -0.240    0.2510

R^2: Marginal 0.1023544, Conditional: 0.2161587
```

GROWTH (Figure 3)

Figure 3A & 3B

rgr ~ (consp.crowd.l + hetsp.crowd.l)*Trt + consp.crowd.l*ht.l + (1|trans/plot) + (1|Census) + (1|Name)

```
   AIC      BIC   logLik  deviance  df.resid
   -52.6    60.5  48.3    -96.6     1242

Random effects:
 Groups     Name        Variance  Std.Dev.
 Name       (Intercept) 0.0015318 0.03914
 plot:trans (Intercept) 0.0012265 0.03502
 trans      (Intercept) 0.0002194 0.01481
 Census     (Intercept) 0.0003325 0.01823
 Residual               0.0519215 0.22786
Number of obs: 1264, groups:  Name, 102; plot:trans, 76; trans, 16; Census, 3

Fixed effects:
                                Estimate Std. Error t value P value
(Intercept)                     0.244355   0.081453   3.000  0.0017
consp.crowd.l                   0.101088   0.062005   1.630  0.0537
hetsp.crowd.l                  -0.012587   0.012821  -0.982  0.1602
TrtFungi                        0.073079   0.053215   1.373  0.0890
TrtInsects                     -0.026165   0.045902  -0.570  0.2908
TrtSmall Mammals                0.004836   0.053745   0.090  0.4683
TrtLarge Mammals                0.010640   0.063735   0.167  0.4344
ht.l                           -0.049128   0.017825  -2.756  0.0037
consp.crowd.l:TrtFungi          0.035116   0.016359   2.147  0.0172
consp.crowd.l:TrtInsects       -0.076360   0.019952  -3.827  0.0000
consp.crowd.l:TrtSmall Mammals  0.022800   0.026255   0.868  0.1953
consp.crowd.l:TrtLarge Mammals  0.045617   0.028913   1.578  0.0615
hetsp.crowd.l:TrtFungi         -0.021176   0.018445  -1.148  0.1283
hetsp.crowd.l:TrtInsects        0.015326   0.017328   0.884  0.1940
hetsp.crowd.l:TrtSmall Mammals -0.013702   0.020557  -0.667  0.2542
hetsp.crowd.l:TrtLarge Mammals -0.015021   0.023958  -0.627  0.2642
consp.crowd.l:ht.l             -0.036686   0.022349  -1.642  0.0514

R^2: Marginal 0.04461308, Conditional: 0.1018705
```

Figure 3C & 3D

rgr ~ (consp.crowd.l+hetsp.crowd.l)*Insecticide_trt*Fungicide_trt + (1|trans/plot) + (1|Census)

```
   AIC      BIC   logLik deviance  df.resid
   -72.3    7.8   52.2   -104.3     1088

Random effects:
 Groups     Name        Variance  Std.Dev.
 plot:trans (Intercept) 1.322e-03 0.036361
 trans      (Intercept) 0.000e+00 0.000000
 Census     (Intercept) 5.363e-05 0.007323
 Residual               5.220e-02 0.228484
Number of obs: 1104, groups:  plot:trans, 63; trans, 16; Census, 3

Fixed effects:
                                                                  Estimate Std. Error t value P value
(Intercept)                                                       0.080709   0.051443   1.569  0.0603
consp.crowd.l                                                     0.007668   0.020344   0.377  0.3526
hetsp.crowd.l                                                    -0.009346   0.019814  -0.472  0.3136
Insecticide_trtInsecticide                                       -0.022885   0.070163  -0.326  0.3775
Fungicide_trtFungicide                                           -0.129339   0.078020  -1.658  0.0474
consp.crowd.l:Insecticide_trtInsecticide                          0.064706   0.028717   2.253  0.0118
hetsp.crowd.l:Insecticide_trtInsecticide                          0.001484   0.026950   0.055  0.4765
consp.crowd.l:Fungicide_trtFungicide                             -0.030602   0.024878  -1.230  0.1113
hetsp.crowd.l:Fungicide_trtFungicide                              0.041983   0.028113   1.493  0.0694
Insecticide_trtInsecticide:Fungicide_trtFungicide                 0.095869   0.107146   0.895  0.1827
consp.crowd.l:Insecticide_trtInsecticide:Fungicide_trtFungicide -0.107962   0.044959  -2.401  0.0091
hetsp.crowd.l:Insecticide_trtInsecticide:Fungicide_trtFungicide -0.003915   0.039177  -0.100  0.4534

R^2: Marginal 0.03257394, Conditional: 0.05741377
```

Figure 3E & 3F

rgr ~ (consp.crowd.l + hetsp.crowd.l)*Mammal_trt*Fungicide_trt + consp.crowd.l:ht.l + (1|trans/plot) + (1|Census)

```
  AIC      BIC     logLik  deviance   df.resid
  -177.2   -87.8   106.6   -213.2     1041

Random effects:
 Groups     Name        Variance  Std.Dev.
 plot:trans (Intercept) 6.587e-04 2.567e-02
 trans      (Intercept) 1.942e-19 4.407e-10
 Census     (Intercept) 0.000e+00 0.000e+00
 Residual               4.731e-02 2.175e-01
Number of obs: 1059, groups:  plot:trans, 62; trans, 16; Census, 3

Fixed effects:
                                                        Estimate Std. Error t value P value
(Intercept)                                             0.227055   0.093625   2.425  0.0078
consp.crowd.l                                           0.023428   0.068219   0.343  0.3696
hetsp.crowd.l                                          -0.001059   0.022765  -0.047  0.4854
Mammal_trtControl                                       0.058429   0.072988   0.801  0.2162
Fungicide_trtFungicide                                 -0.144450   0.077651  -1.860  0.0311
ht.l                                                   -0.044654   0.017977  -2.484  0.0058
consp.crowd.l:Mammal_trtControl                         0.038316   0.034057   1.125  0.1337
hetsp.crowd.l:Mammal_trtControl                        -0.032813   0.028098  -1.168  0.1225
consp.crowd.l:Fungicide_trtFungicide                    0.049489   0.035786   1.383  0.0838
hetsp.crowd.l:Fungicide_trtFungicide                    0.040594   0.028648   1.417  0.0800
Mammal_trtControl:Fungicide_trtFungicide                0.036149   0.105986   0.341  0.3584
consp.crowd.l:ht.l                                     -0.020407   0.021932  -0.930  0.1797
consp.crowd.l:Mammal_trtControl:Fungicide_trtFungicide -0.084653   0.042521  -1.991  0.0250
hetsp.crowd.l:Mammal_trtControl:Fungicide_trtFungicide -0.006426   0.038640  -0.166  0.4268

R^2: Marginal 0.03377294, Conditional: 0.04704284
```

Figure 3G & 3H

rgr ~ (consp.crowd.l + hetsp.crowd.l)*Mammal_trt*Insecticide_trt + consp.crowd.l:ht.l + (1|trans/plot) + (1|Census)

```
   AIC     BIC     logLik  deviance  df.resid
   77.8    165.8   -20.9   41.8      962

Random effects:
 Groups     Name        Variance Std.Dev.
 plot:trans (Intercept) 0.002101 0.04584
 trans      (Intercept) 0.000000 0.00000
 Census     (Intercept) 0.000000 0.00000
 Residual               0.059523 0.24397
Number of obs: 980, groups:  plot:trans, 62; trans, 16; Census, 3

Fixed effects:
                                                      Estimate Std. Error t value P value
(Intercept)                                           0.267508   0.108024   2.476  0.0092
consp.crowd.l                                        -0.015406   0.080412  -0.192  0.4277
hetsp.crowd.l                                        -0.007207   0.026495  -0.272  0.4052
Mammal_trtControl                                     0.055085   0.085367   0.645  0.2505
Insecticide_trtInsecticide                            0.021851   0.099334   0.220  0.4142
ht.l                                                 -0.053463   0.020602  -2.595  0.0073
consp.crowd.l:Mammal_trtControl                       0.044414   0.039175   1.134  0.1360
hetsp.crowd.l:Mammal_trtControl                      -0.031907   0.032913  -0.969  0.1625
consp.crowd.l:Insecticide_trtInsecticide              0.061138   0.041196   1.484  0.0731
hetsp.crowd.l:Insecticide_trtInsecticide             -0.022430   0.036204  -0.620  0.2670
Mammal_trtControl:Insecticide_trtInsecticide         -0.051828   0.125568  -0.413  0.3371
consp.crowd.l:ht.l                                   -0.007835   0.026019  -0.301  0.3767
consp.crowd.l:Mammal_trtControl:Insecticide_trtInsecticide -0.004998   0.051990  -0.096  0.4680
hetsp.crowd.l:Mammal_trtControl:Insecticide_trtInsecticide  0.028432   0.046730   0.608  0.2714

R^2: Marginal 0.0289217, Conditional: 0.06202766
```

DIVERSITY (Figure 4)

Figure 4A

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
diversity.shannon.exp ~ Trt * Census + (1|location)
     AIC      BIC   logLik deviance df.resid
  1013.9   1072.4   -490.0    979.9      213

Random effects:
 Groups   Name        Variance Std.Dev.
 location (Intercept) 10.34    3.215
 Residual              1.46    1.208
Number of obs: 230, groups:  location, 78

Fixed effects:
                          Estimate Std. Error t value P value
(Intercept)                5.64550    0.39082  14.445 0.0000
TrtFungi                  -1.35370    0.77144  -1.755 0.0379
TrtInsects                 0.01862    0.77144   0.024 0.4876
TrtSmall Mammals          -0.59626    0.77490  -0.769 0.2183
TrtLarge Mammals           0.36743    0.96045   0.383 0.3574
Census10                   0.83778    0.19714   4.250 0.0001
Census11                   1.31873    0.19705   6.692 0.0000
TrtFungi:Census10          0.23602    0.38520   0.613 0.2702
TrtInsects:Census10        0.08293    0.38520   0.215 0.4183
TrtSmall Mammals:Census10  0.23721    0.39209   0.605 0.2753
TrtLarge Mammals:Census10 -0.06968    0.48767  -0.143 0.4431
TrtFungi:Census11          1.05605    0.38516   2.742 0.0027
TrtInsects:Census11       -0.01793    0.38516  -0.047 0.4768
TrtSmall Mammals:Census11  1.04472    0.39205   2.665 0.0039
TrtLarge Mammals:Census11  0.03173    0.48735   0.065 0.4653
R^2: Marginal 0.0575303, Conditional: 0.883338
```

Figure 4B

diversity.shannon.exp ~ Insecticide_trt*Fungicide_trt*Census + (1|location)

```
   AIC      BIC    logLik  deviance df.resid
   875.1    920.6  -423.5  847.1    177

Random effects:
 Groups   Name        Variance Std.Dev.
 location (Intercept) 11.070   3.327
 Residual              1.845   1.358
Number of obs: 191, groups:  location, 64

Fixed effects:
                                                      Estimate Std. Error t value P value
(Intercept)                                           6.235201   0.904667   6.892  0.0000
Insecticide_trtInsecticide                           -0.608326   1.274994  -0.477  0.3166
Fungicide_trtFungicide                                0.763998   1.274994   0.599  0.0168
Census10                                              0.607132   0.491753   1.235  0.0105
Census11                                              0.280561   0.491753   0.571  0.2793
Insecticide_trtInsecticide:Fungicide_trtFungicide    -0.391900   1.799996  -0.218  0.1573
Insecticide_trtInsecticide:Census10                   0.147724   0.687319   0.215  0.3393
Insecticide_trtInsecticide:Census11                   1.056099   0.687319   1.537  0.0358
Fungicide_trtFungicide:Census10                      -0.005367   0.687319  -0.008  0.4612
Fungicide_trtFungicide:Census11                      -0.017885   0.687319  -0.026  0.4900
Insecticide_trtInsecticide:Fungicide_trtFungicide:Census10 -0.195037   0.966220  -0.202  0.3725
Insecticide_trtInsecticide:Fungicide_trtFungicide:Census11 -0.236325   0.966220  -0.245  0.3820

R^2: Marginal 0.02197799, Conditional: 0.8603057
```

Figure 4C

diversity.shannon.exp ~ Mammal_trt*Fungicide_trt*Census + (1|location)

```
   AIC      BIC    logLik  deviance  df.resid
   866.7    912.0  -419.3  838.7     174

Random effects:
 Groups   Name        Variance Std.Dev.
 location (Intercept) 9.904    3.147
 Residual             2.017    1.420
Number of obs: 188, groups:  location, 63

Fixed effects:
                                                   Estimate Std. Error t value P value
(Intercept)                                         4.67784    0.89148   5.247  0.0000
Mammal_trtControl                                   1.54807    1.24580   1.243  0.2564
Fungicide_trtFungicide                              1.37454    1.24088   1.108  0.1137
Census10                                            1.08705    0.51858   2.096  0.0130
Census11                                            2.38857    0.51858   4.606  0.0000
Mammal_trtControl:Fungicide_trtFungicide           -0.60125    1.74417  -0.345  0.3789
Mammal_trtControl:Census10                         -0.47063    0.73025  -0.644  0.1586
Mammal_trtControl:Census11                         -2.09872    0.73025  -2.874  0.0007
Fungicide_trtFungicide:Census10                    -0.07365    0.72183  -0.102  0.4558
Fungicide_trtFungicide:Census11                     0.47327    0.72183   0.656  0.2371
Mammal_trtControl:Fungicide_trtFungicide:Census10  0.05899    1.01858   0.058  0.4376
Mammal_trtControl:Fungicide_trtFungicide:Census11 -0.50045    1.01858  -0.491  0.3031

R^2: Marginal 0.07725853, Conditional: 0.843878
```

Figure 4D

diversity.shannon.exp ~ Insecticide_trt*Mammal_trt*Census + (1|location)

```
   AIC      BIC    logLik  deviance  df.resid
   820.8    866.1  -396.4  792.8     174

Random effects:
 Groups   Name        Variance Std.Dev.
 location (Intercept) 8.969    2.995
 Residual             1.478    1.216
Number of obs: 188, groups:  location, 63

Fixed effects:
                                                        Estimate Std. Error t value P value
(Intercept)                                              4.67784    0.83453   5.605  0.0000
Insecticide_trtInsecticide                               1.19449    1.16162   1.028  0.1428
Mammal_trtControl                                        1.55783    1.16549   1.337  0.2618
Census10                                                 1.08705    0.44393   2.449  0.0064
Census11                                                 2.38857    0.44393   5.380  0.0000
Insecticide_trtInsecticide:Mammal_trtControl           -1.80328    1.63223  -1.105  0.2762
Insecticide_trtInsecticide:Census10                      0.22410    0.61793   0.363  0.3448
Insecticide_trtInsecticide:Census11                      0.41220    0.61793   0.667  0.2450
Mammal_trtControl:Census10                             -0.48039    0.62517  -0.768  0.1358
Mammal_trtControl:Census11                             -2.10848    0.62517  -3.373  0.0001
Insecticide_trtInsecticide:Mammal_trtControl:Census10 -0.07591    0.87198  -0.087  0.4864
Insecticide_trtInsecticide:Mammal_trtControl:Census11  0.64437    0.87198   0.739  0.2013

R^2: Marginal 0.08041946, Conditional: 0.8698903
```