The effect of biotic interactions on latitudinal range expansion of plant species in response to climate change

by

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DEDICATION

For Liz Walker, who showed that even the most visionary goals are attainable when approached with creativity, fortitude, and plenty of hard work.

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ABSTRACT

As climates warm, plant species distributions are expected to shift poleward. When plants colonize new areas, they will interact with new suites of organisms and the resulting biotic interactions may differ from those within the plants' original range. Large net differences in biotic interactions with natural enemies could affect plant performance and therefore colonization success and range expansion dynamics. Despite the potential importance of herbivores and pathogens to plant performance, few studies have quantified how interactions between plants and their natural enemies vary across range edges. I explored the potential for foliar herbivores and pathogens to influence plant range expansion using a combination of meta-analysis and field experiments. First, I investigated the effects of invertebrate herbivores on plant populations using a meta-regression approach, and found that herbivory often played important roles in reducing plant population growth rates, corroborating the potential importance of invertebrate herbivores to range expansion dynamics. In my next two chapters, I planted ten plant species along a latitudinal gradient that contained the range edges of some of these species. I then monitored seedling foliar herbivory and disease, providing some of the first empirical evidence on how above-ground interactions with natural enemies vary across latitudinal range edges. Four out of five species experienced less foliar disease when planted beyond their ranges. The amount of enemy escape was coarsely predicted by distance dependent dynamics within species ranges. However, the species included in this study did not benefit substantially from enemy escape; common levels of foliar damage had only minor effects on seedling survival. This suggests that the biotic interactions considered in this study are unlikely to have a major effect on colonization success for these particular species. Even so, this study provides insight

into what conditions are likely to result in enemy release beyond range edges and the scenarios in which this may lead to increased performance during range expansion.

Chapter I:

INTRODUCTION

Climate change is expected to result in shifts in species distributions as plants and animals track changing temperatures and precipitation (Parmesan and Yohe 2003, Hickling et al. 2006, Crimmins et al. 2011). There is some empirical evidence that tree species are already experiencing this distributional shift along latitudinal gradients in North America (Woodall et al. 2009, Murphy et al. 2010, Boisvert-Marsh et al. 2014, Desprez et al. 2014; but see Zhu et al. 2012). Although paleo-reconstructions of changes in vegetation composition during previous periods of climate change give some insight into plant range shifts (Davis 1983, Graumlich and Davis 1993, Jackson and Overpeck 2000, Petit et al. 2002, Williams et al. 2004), much remains unknown about how contemporary latitudinal range expansion will proceed.

Poleward shifts in species distributions will depend upon the success of individuals on the expanding range front. These individuals, hereafter referred to as migrants, will interact with different suites of organisms beyond their range edges. If the resulting biotic interactions systematically differ from those experienced within that species' original range, there could be effects on plant performance and therefore colonization success and range expansion dynamics (Moorcroft et al. 2006, Engelkes et al. 2008, Phillips et al. 2010b, Van der Putten et al. 2010b). Few models of species range shifts explicitly incorporate biotic interactions, and so differences in biotic interactions across range edges would cast doubt on their forecasts (Araújo and Luoto

2007, Boulangeat et al. 2012, Godsoe and Harmon 2012, Urban et al. 2013). An increasing number of researchers have called attention to this knowledge gap and have emphasized that biotic interactions are a major component missing from our understanding of how species ranges will shift in response to warming temperatures (Morriën et al. 2010, Van der Putten et al. 2010b, van der Putten 2011, Zarnetske et al. 2012, HilleRisLambers et al. 2013, Renwick and Rocca 2015). Recently, several investigations have quantified net changes in plant-soil feedback across latitudinal range edges (van Grunsven et al. 2010, Stanton-Geddes and Anderson 2011, Mccarthy-Neumann and Ibáñez 2012). However, to my knowledge, no studies have yet tested how interactions between plants and above ground natural enemies vary across latitudinal range edges. In my dissertation, I use meta-analysis and a series of field experiments to investigate whether biotic interactions between temperate trees and their natural enemies will affect range expansion dynamics.

Invertebrate herbivores and plant populations

The potential importance of natural enemies to range expansion dynamics is prefaced on the belief that herbivores and pathogens affect plant population dynamics. Although invertebrate herbivory undeniably has strong effects on individual plant survival, growth, and fecundity (Hawkes and Sullivan 2001, Morris et al. 2007, Zvereva et al. 2010, Stephens and Westoby 2015), assessing its effects on plant population growth rates is less straightforward. Indeed, at one point, it was debated whether the effects of herbivory on individuals would even scale up to the population level (e.g., Crawley 1989). An updated understanding of the effects of invertebrate herbivores on plant populations is needed to provide the context for whether herbivory could affect range expansion dynamics.

Over the last several decades, an increasing number of studies have quantified relationships between herbivory and plant population dynamics (Maron and Crone 2006) using stage-structured (Caswell 1989) or integral projection (Easterling et al. 2000) population models. These models can be used to calculate population growth rates for plants growing under ambient herbivory vs. reduced herbivory. In **Chapter II**, I synthesized the results of experiments that compared plant population growth rates with and without invertebrate herbivory. I found that invertebrate herbivores do frequently reduce plant population growth rates, often when the potential for growth is highest. However, I also found that measured herbivory rates are a poor proxy for the population level effects of herbivores.

Differences in biotic interactions across latitudinal range edges

There is both theoretical and empirical evidence suggesting that biotic interactions will vary across range edges. First, migrants are likely to leave their specialist enemies behind, as populations at the edge of an expanding range occur at low densities and often go through repeated founder events (Phillips et al. 2010). Empirical support for natural enemy escape at range edges can be seen in several taxa (Alexander et al. 2007, Menéndez et al. 2008, Phillips et al. 2010b, Tsai and Manos 2010). Conversely, there are some mechanisms by which generalist natural enemies in new communities could have stronger effects on migrants (Verhoeven et al. 2009) and generalist natural enemy community composition could also vary between regions. Still, the net change in biotic interactions across latitudinal range edges has not yet been measured and several researchers have emphasized that in situ field experiments are required to address this gap (Morriën et al. 2010, Van der Putten et al. 2010b, Renwick and Rocca 2015).

In **Chapter III**, I initiated a field experiment to determine whether biotic interactions varied across range edges. Seven species of trees were planted along a 450-km latitudinal gradient that crossed the edges of five of these species current distributional ranges and I monitored foliar herbivory and disease over five years. Foliar herbivory and disease were analyzed as a function of distance to, and density of, conspecific and congeneric trees at several spatial scales as well as environmental variables (light, soil moisture, and soil nutrients). Within species ranges foliar disease was lower for seedlings that were farther from conspecific adults for several species, and for these same species enemy release was even stronger beyond range edges. The species that did not show signs of enemy release within their ranges also did not generally experience strong enemy release beyond their ranges. Patterns of distance dependent herbivory across spatial scales was generally weak and in some cases was negative (i.e., seedlings further from conspecific adults had more herbivory), possibly because of mutualistic tri-trophic interactions.

This experiment provides some of the first empirical evidence that above-ground interactions with natural enemies vary across latitudinal range edges. Moreover, my approach revealed that the amount of disease experienced beyond ranges can be understood and potentially predicted for other species using the framework of distance dependence.

The effects of biotic interactions on plant performance

In **Chapter IV**, I investigated how damage caused by foliar pathogens and herbivores affected seedling survival. Strong effects could allow migrant species that escape from disease to outcompete native plants, facilitating colonization success locally and increasing overall rates of range expansion (Moorcroft et al. 2006). Conversely, weak effects could indicate that these biotic interactions will not affect range expansion dynamics.

To test whether differences in biotic interactions across range edges were strong enough to affect plant performance, I measured seedling survival in the field experiment described above as well as on three other species. I also applied a pesticide treatment to reduce herbivory and validate my observational findings. After accounting for other variables, including environmental conditions and vertebrate herbivory, I found that foliar disease and herbivory resulted in differences in survival that were statistically significant for six species but the effect size was uniformly small. The minor effects of measured leaf herbivory on survival are corroborated by the pesticide treatment only having small effects on seedling survival.

These results show that common levels of foliar herbivory and disease on seedlings are unlikely to play a major role in the range expansion dynamics of at least these tree species. It is possible that other life stages will be more sensitive to aboveground herbivores and pathogens, but there are several reasons to expect their largest effects to be on post-dispersal recruitment success. First, migrant seedlings are especially likely to experience the marginal environments that they are least well equipped for (e.g., Castro et al. 2004, Cairns and Moen 2004, Arrieta and Suarez 2006). Second, smaller life stages are close to carbon compensation points; even small perturbations can have important consequences for seedlings (Poorter and Kitajima 2007, Myers and Kitajima 2007). A lack of carbon reserves means that seedlings are much more susceptible to environmental stresses than larger stages (Anderson and Tomlinson 1998, Nunn et al. 2005, Vargas et al. 2009, Niinemets 2010) and smaller plants also tend to have weaker chemical defenses (Barton and Koricheva 2010, Boege et al. 2011, Massad 2013). Finally, several empirical studies demonstrate that density dependent forces often disproportionately affect younger life stages (Green et al. 2014, Zhu et al. 2015 but see Piao et al. 2013). Various researchers have found evidence of habitat filtering at the seedling stage driven by both biotic (HilleRisLambers et al. 2002, Fine et al. 2006, Andersen et al. 2014) and abiotic variables (Kullman 1993, 2002). Thus, while the effects of natural enemies on other demographic rates (e.g., seed production) are still of potential importance to plant populations and deserve investigation (Angert and Schemske 2005), the seedling stage is the best place to start.

Contributions to understanding latitudinal range expansion

A large number of studies and predictive models have focused on range shifts of plants in response to climate change. One of the major obstacles to understanding contemporary response of plant distributions is a lack of knowledge of how biotic interactions will affect range expansion dynamics (Van der Putten et al. 2010b, Zarnetske et al. 2012, HilleRisLambers et al. 2013, Renwick and Rocca 2015). My field experiments are some of the first to quantify how interactions with above ground natural enemies vary across latitudinal range edges. My results demonstrated that biotic interactions with natural enemies vary across range edges, but show that the damage they cause has only minor effects on survival for these species. Based on the inter-system variability in the effects of invertebrate herbivores on plant populations that I found in my meta-analysis, this is not unexpected. As I conclude in **Chapter V**, what is more important is that my dissertation provides a basis for understanding the circumstances in which biotic interactions are likely to have an important effect on range expansion. Specifically, I documented that plant species that experience strong distance/density dependent biotic interactions that affect plant performance within their range are likely to escape from natural enemies on and beyond their range edges, a trend that has been previously hypothesized but that has not been empirically demonstrated until now. This deeper understanding of how biotic interactions may affect plant performance will help us better assess colonization success and range expansion dynamics.

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Chapter II:

THE EFFECTS OF INVERTEBRATE HERBIVORES ON PLANT POPULATION GROWTH: A META-REGRESSION ANALYSIS

ABSTRACT

Although the importance of herbivory to individual plants has been well studied, less is known about the effects of herbivory on plant populations. Over the last two decades, an increasing number of studies have quantified the effects of herbivory on plant populations using stage-structured population models and integrated projection models, allowing for the calculation of plant population growth rates (λ) with and without herbivory. So far, there has not been a comprehensive quantitative analysis of the effects of invertebrate herbivores on plant populations. In this paper, I assembled 27 studies and conducted a meta-regression to determine the importance of invertebrate herbivores to λ and how that varied as a function of measured herbivory and the type of herbivory (general herbivory vs. seed predation). I also tested if herbivores stabilized plant population growth (i.e., whether herbivores reduced population growth more when there was the potential for rapid population growth, or if the effects of herbivores were unrelated to potential population growth rates). I found that invertebrate herbivory often induced important reductions in plant population growth rates, although this relationship was stronger for general herbivory than for seed predation, except when seed predation rates were very high. Even so, measured herbivory was a poor predictor of the population level effects of herbivory, which strongly cautions against using measured herbivory rates as a proxy for the impact of herbivores. Finally, herbivory reduced plant population growth rates substantially more when potential growth rates were high, which demonstrates how

important invertebrate herbivores are in preventing plant populations from reaching high growth rates.

INTRODUCTION

It has been estimated that herbivores consume roughly 10-20% of annual net primary production in terrestrial ecosystems (Hartley and Jones 1997) and foliar herbivory rates average around 5% of leaf area a year (Turcotte et al. 2014). Although herbivory undeniably has strong effects on individual plant survival, growth, and fecundity (Hawkes and Sullivan 2001, Morris et al. 2007, Zvereva et al. 2010, Stephens and Westoby 2015), assessing its effects on plant population growth rates is less straightforward. Indeed, at one point, it was debated whether the effects of herbivory on individuals would even scale up to the population level (e.g., Crawley 1989). Since then, an increasing number of studies have quantified relationships between herbivory and plant population dynamics (Maron and Crone 2006). In most cases, this has been accomplished with stage-structured population models (Caswell 1989) or with integral projection models (IPM; Easterling et al. 2000). These models respectively divide populations into either discrete categories or continuous variables along the gradients of size, age, or stage in the life cycle. Demographic transition rates are then parameterized and can be used to calculate population growth rates (λ). Separate models can be constructed using parameter estimates that were derived from plants growing under ambient herbivory vs. reduced herbivory. Parameter estimates for reduced herbivory can either be determined by experimentally reducing herbivory (e.g., applying pesticides or constructing herbivore exclosures) or observationally (e.g., measuring seed predation rates and then using seed sowing experiments to see how much the loss of seeds reduced λ). In both cases, plant population growth rates can be calculated both with and without herbivory; any differences in λ can then be attributed to herbivores.

These studies give unique opportunities to answer important questions. First, these studies can show what the range of responses to invertebrate herbivores is at the population level, and whether it varies by type of herbivory. Studies of λ can also be used to assess how good of a proxy measured herbivory rates are for actual population growth. Many studies have used measurements of herbivory to make inferences about population level phenomena (e.g., tests of the enemy release hypothesis), and so would benefit from knowing the strength of the association between measured herbivory and population growth rates. Finally, studies assessing the effects of invertebrate herbivores on plant populations may provide the opportunity to check whether herbivores stabilize population growth rates by preventing plant populations from reaching high growth rates. Specifically, these data can be used to test whether herbivores decrease plant population growth more when it has the potential to be high or if the effects of herbivores are constant across the range of plant population growth rates.

Even though these are important questions, and the studies that have investigated the impacts of herbivory on λ tend to report disparate results that are frequently discussed, there has not yet been a meta-analysis of this body of literature (but see an insightful semi-quantitative review by Maron and Crone 2006). This may, in part, be due to the difficulty of the task; formal meta-analysis generally requires the variance of reported estimates and the sample size of each study (Hedges et al. 1999, Gurevitch and Hedges 2001, Koricheva et al. 2013), but these data are frequently not available or are not easily applied to comparisons of plant population growth rates (Crone et al. 2011). First, one of the key issues is that most plant population growth rates are calculated in a deterministic framework, and as such produce a single estimate of λ, without an estimate of variance (Crone et al. 2011), even though ways to estimate variance are available (e.g., Pascarella and Horvitz 1998; Zuidema and Franco 2001). Second, comparing the sample size for different studies is not straight forward; separate experiments are often used to calculate the demographic rates that enter a population model and it is not infrequent for a study to use methodologically separate experiments or estimates from the literature for a particular demographic transition rate. Moreover, it is not clear if it would be truly acceptable to equally weight different life stages (e.g., a comparison of 100 seeds vs. 100 adults). These issues present serious challenges to the usage of traditional meta-analyses on these studies but the insight that they could provide is too large for the topic to go unaddressed. Moreover, a cohesive analysis at this point could prompt future studies to include data or use methodologies that will fill gaps in our understanding while providing the metadata required for future syntheses. Fortunately, increasing numbers of studies are providing examples of innovative ways to approach meta-analyses when datasets are incomplete or heterogeneous (e.g., Ogle et al. 2014; Ibáñez et al. 2014).

In this study, I compiled the results of experiments that compared plant population growth rates with and without invertebrate herbivory. I included studies that either estimated the effect of herbivory on plant demography by experimentally reducing herbivory or by observing the reductions in demographic rates caused by herbivory. I then used this dataset to conduct a meta-regression analysis to answer several questions: 1) What is the overall effect of herbivory on plant population growth rates? 2) Is measured herbivory a good indicator for the effects of herbivores on plant population growth rates? 3) Does herbivory have stronger effects on plant populations that have the potential for rapid growth? The answers to these questions provide a better understanding of how invertebrate herbivores affect plant population growth rates.

METHODS

In November 2013, I searched for papers that reported the impacts of invertebrate herbivores on plant population growth rates through the Institute for Scientific Information Web of Science using the following terms in the "Topic" category: (*plant*) AND (*population growth*) AND (*insect herbiv**) OR (*mollus* herbiv**); this returned 860 publications. I selected publications that reported plant population growth rates (λ) at naturally occurring amounts of herbivory (λ_{+H}) or with reduced invertebrate herbivory (λ_{-H}). These are respectively referred to as actual population growth and potential population growth rate throughout this paper. I also selected studies that were conducted in natural environments or common gardens, but greenhouse experiments were excluded because they lack ecological complexity that could affect plant and herbivore population dynamics. To ensure that no studies were overlooked, I also systematically searched through the references of the selected publications and through studies that had cited each selected publication. Of the articles retrieved, I only kept those that used field estimates of demographic rates to track the impacts of invertebrate herbivore(s) on host plant λ. If parameter estimates for the importance of herbivory to plant populations were taken from other systems or places and then extrapolated to the study system, then the study was excluded. However, I did include studies which borrowed parameter estimates for other demographic transition rates from the literature. Following these criteria, I included a total of 29 studies from 26 publications (study is defined here as an investigation of a particular plant species using a particular methodology; separate experiments assessing seed herbivores and general herbivores reported within the same publication are counted as separate studies). Of these studies, nine reported estimates in multiple years and 10 reported estimates in multiple locations, which resulted in a total of 168 data points. One data point was excluded from all analyses as an outlier because the population growth rates reported was approximately an order of magnitude more than other observations and the standard deviation was correspondingly large (λ_{+H} = 20.4 ± 6.8, λ_{-H} = 20.3 ± 6.9).

For each study, I collected information about the estimates of plant population growth rates both with and without herbivory and their associated variance. I also collected information on the study system, the plant, the herbivore(s), the type of the study (experimental vs. observational), and the amount of herbivory experienced. When data were reported in figures but not in the text or in tables, the information was extracted using Plot Digitizer (Huwaldt and Steinhorst 2013). In most studies, herbivory was quantified as a percentage of leaf area removed or as the percentage of seeds attacked. However, in one study (Miller et al. 2009), herbivory measurements were not reported as a percentage of plant area impacted; in order to standardize herbivory measurements for this study, I divided all herbivory measurements by the maximum amount of herbivory observed, scaling it to a maximum of 1. I calculated the difference in measured herbivory between the control and the treatment ($_{\Delta}H = H_{control} - H_{treatment}$).

Statistical analysis

Plant population growth rate data present several challenges for meta-analysis, including missing data on variation in λ and incomparable or misleading sample sizes. In the face of these difficulties, it would be difficult to answer this study's research questions with a traditional meta-analysis. I therefore conducted a Bayesian meta-regression analysis; the statistical approaches and their justifications are described below.

The most common effect size used to compare the means of two continuous outcomes in meta-analysis is a standardized mean difference effect size, such as Hedges’ D (Gurevitch and Hedges 2001). However, Hedges’ D is calculated in part based on sample variance. This presents a problem because the calculated effect size can be very large for studies that have small differences in means between treatments, but even smaller variances. For example, in one observation included in this analysis, the population growth rates (mean and standard deviation) were estimated very precisely (λ_{+H} = 1.0000 ± 0.0001, λ_{-H} = 1.1600 ± 0.0014), which resulted in a very small variance and an enormous effect size (Hedges' D: 159.76). While this is effective for showing that there was very little chance that the means of the two treatments were the same, the main questions posed in this meta-regression focus on the size of the effect rather than on whether the differences in means are significant. I therefore used response ratios, which are a useful alternative (Hedges et al. 1999), and have been widely used for meta-analyses in ecology (Koricheva et al. 2013). I calculated the response ratio for each observation as $R = \frac{\lambda_{-H}}{\lambda_{+H}}$; for example, an R of 2 would mean that population growth rates were twice as high in the herbivory reduction treatment. I then took the natural log of R, lnR, which has several useful statistical properties, including a non-skewed distribution, so differences in lnR are directly comparable (Koricheva et al. 2013).

Relatively few studies of plant population growth report variation in λ (Halpern and Underwood 2006, Nelson et al. 2010); of the observations included in this study, only 28 of 168 did so. One of the only other meta-analyses of plant population growth rates used variability between sites and years to calculate variance in λ (Schmidt et al. 2011). However, among other potential problems, aggregating information based on site or year prevents the usage of data taken at the finest resolution (e.g., averaging across years prevents the analysis of yearly herbivory measurements). I therefore used multiple imputation methods (Lajeunesse 2013) to estimate missing values. Specifically, I estimated missing variance values using the observed range of reported variance for other types of herbivory: SD ~ Uniform(0 – 1.45) and seed predation: SD ~ Uniform(0 – 0.86). Next, to calculate the effect size, lnR, I drew 10,000 pairs of random numbers from the distributions of λ_{+H} and λ_{-H}, and divided one by the other and then took the natural log of the quotient. The distribution of λ_{+H} and of λ_{-H} for each observation was assumed to be normally distributed around their measured mean and with a standard deviation that was either extracted from the paper or that was drawn from the uniform distributions described above. As such, the distribution of lnR for each observation incorporates both the variance associated with λ_{+H} and λ_{-H}, and, when data were missing, the range of uncertainty associated with missing data. This approach for estimating unreported standard deviations leads to highly conservative estimates of the effect size, and therefore the significance of the results, because observed standard deviations are positively skewed (Supporting Information 2.A: Observed Standard Deviations).

I then performed a hierarchical Bayesian meta-regression to analyze how reduced herbivory treatments and other covariates affected population growth rates. Several different models were explored (e.g., quadratic effects for herbivory) and I selected the model with the lowest DIC (Deviance Information Criterion; Spiegelhalter et al. 2002) that allowed the questions to be addressed. I performed separate analyses for observations that focused on seed predation and for observations that measured other types of herbivory (synonymously referred to as general herbivory).

The final models included two covariates, the difference in measured herbivory between the control and the herbivory reduction treatment, $_{\Delta}H$, (continuous, ranging from -0.007 – 0.92) and the potential population growth rate without herbivory, λ_{-H}, (continuous, ranging from 0.06 – 5.20). For observations where $_{\Delta}H$ was not reported (80), I drew it from a non-informative distribution, $_{\Delta}H \sim \mathrm{Uniform}(-0.007, 0.92)$. The models also included random effects for each study, *j*, which were drawn from a normal distribution with a mean of μ: $\gamma_{study\ j} \sim N(\mu, \sigma^2_{study})$; μ was in turn drawn from a non-informative normal distribution, $\mu \sim N(0, 1000)$. The effect size for each observation *i*, $\ln R_i$, was centered around a normal distribution with a mean of θ_i and the reported or simulated standard deviation σ_i associated with the effect size:

$$\ln R_i \sim N(\theta_i, \sigma_i^2)$$

$$\theta_i = \beta_1 * {}_{\Delta}H_i + \kappa * \lambda_{-H\ i} + \gamma_{study\ j(i)}$$

The model for studies that focused on seed predation was the same, except a quadratic term was added for the effect of herbivory (models using an exponential function instead of a quadratic function did not converge):

$$\ln R_i \sim N(\theta_i, \sigma_i^2)$$

$$\theta_i = \beta_1 * {}_{\Delta}H_i + \beta_2 * {}_{\Delta}H_i^2 + \kappa * \lambda_{-H\ i} + \gamma_{study\ j\ (i)}$$

I then simulated θ across the range of $_{\Delta}H$, while holding λ_{-H} at its mean value (1.28) to visualize the model results. Similarly, I simulated θ across the range of λ_{-H}, while holding $_{\Delta}H$ at its mean value (34%).

For these analyses, posterior densities of the parameters were obtained by Gibbs sampling (Geman and Geman 1984) using JAGS 3.4 (Plummer 2003) via the rjags package in R (Plummer 2014). Convergence occurred after 1,000 to 5,000 iterations and chains were inspected visually. Each model was run for 50,000 iterations and posterior parameter values were based on postconvergence results. Fixed effects coefficients were considered statistically significant when their 95% credible intervals (CI) did not overlap with zero.

I also conducted a traditional random effects meta-analysis that weighted each study by the reported variance associated with ${}_{\Delta}\lambda$. Relatively few observations reported variance in λ (27), so I used inter-annual and inter-site differences to calculate variances for other studies. Combined, this resulted in a total of 54 observations from 14 studies. Although the variance in these extra observations reflects both inter-annual variability as well as uncertainty in parameter estimates, many of the studies that did report variation were themselves parameterized over multiple years and also used year to year differences to estimate variability (e.g., Ehrlén 1995). I also used lnR for this analysis, but the variance was calculated in the traditional way (Hedges et al. 1999). I then used the metafor package to conduct a random effects meta-analysis with study random effects (Viechtbauer 2010).

The distribution of effect sizes was not depressed around zero suggesting a lack of publication bias against publishing non-significant results (Greenland 1987). In order to further assess the possibility of publication bias, I calculated a failsafe number (Orwin 1983) and created funnel plots (both are available in Supporting Information 2.B: Funnel plots and publication bias). All analyses were conducted using R (R Core Team 2013). Visualization was conducted using the ggplot2 package in R (Wickham 2009).

RESULTS

Summary of selected studies

The selected publications (Supporting Information 2.C: Selected Publications) included studies where fieldwork was carried out between 1982 and 2010 and were conducted in temperate forests (7) and tropical forests (3), grasslands (14), mountains (3), and a desert (1). Of the observations, the parameterization time period ranged from 1–11 years (average = 1.4), although if data were reported separately for each year, they are reported as such here.

The plants studied included woody or herbaceous perennials (158 observations from 26 species), perennial grasses (7 observations from 1 species), and herbaceous annuals (3 observations from 2 species). Most plants were native (159 observations from 23 species) but some were exotic (9 observations from 6 species) and most of the herbivores were native (165) but a few were exotic (3), although herbivores were assumed to be native unless otherwise specified. Of the data points, 120 were collected using observational techniques, whereas 48 were derived from experimentally manipulating herbivory using pesticides (46) or in one case insect exclusion cages (1). Herbivory was reported on flowers (11), seeds (122), juveniles (39), and adults (46); in some cases, herbivory was quantified on a specific subset of life stages or plant tissues. Of those studies that reported host specificity of the herbivores, most observations were of specialists (49) but several were of generalists (4); many studies reported damage caused by invertebrate herbivore communities (46 observations from 14 studies) and the rest focused on particular invertebrates (122 observations from 16 studies).

Of the 167 data points from native plants, lnR was positive in most cases (145), although in some cases it was exactly zero (14) or negative (8) (Fig. 2.1). The average value of λ including herbivory was λ_{+H}: 1.08 (SD = 0.36) and the average value of λ without herbivory was λ_{-H}: 1.28 (SD = 0.58). There were 67 observations of plant populations that had decreasing population growth rates, $\lambda_{+H} < 1$, in control conditions; in 20 of these observations, the population growth rate was > 1 in the reduced herbivory treatment, λ_{-H}.

Measured herbivory was extracted for approximately half of all observations (87), from a total of 22 studies (some studies either did not measure herbivory or did not report it in a form that could be linked to particular observations). The amount of herbivory in controls ranged from 0 – 98% with a mean of 41% whereas in reduced herbivory treatments, herbivory ranged from 0% –56% with a mean of 3%. The effectiveness of the herbivory reduction treatments also varied widely; the difference in measured herbivory ($_{\Delta}$H) between controls and the reduced herbivory treatment ranged from -1% to 92% with a mean of 34%.

Model results

Herbivores significantly reduced plant population growth rates, as shown by the mean value and 95% CI for θ (Fig. 2.2). The estimated values of θ were generally higher for studies of general herbivores than for seed predators, except for at very high levels of seed predation (Fig. 2.2). For studies of general herbivores, the amount of herbivory measured did not have a significant effect in studies of general herbivory, as can be seen by the almost flat line in Fig. 2.2, although studies with very low levels of herbivory had very small effect sizes (β_1: mean = 0.01, 95% CI: -0.01 – 0.03). In contrast, in studies of seed predation, there were relatively strong responses to the amount of herbivory measured; seed predation studies that had higher herbivory rates experienced greater losses in population growth rates (β_1 mean = -1.24, 95% CI: -2.51 – 0.22 and β_2 mean =1.64, 95% CI: -0.04 – 3.07, Fig. 2.2).

Herbivores had larger effects on plant populations that had the potential for high growth rates; herbivores generally prevented plants from achieving high $\lambda_{\text{-H}}$. This was true for both studies of general herbivory (κ: mean = 0.26, 95% CI: 0.21 – 0.31) and for seed predation studies (κ: mean = 0.20, 95% CI: 0.03 – 0.39; Fig. 2.3). For seed predation studies this was in part because the largest proportions of seeds were eaten in cases where there was high $\lambda_{\text{-H}}$ (Fig. 2.3 and Supporting Information 2.D: Seed predation and $\lambda_{\text{-H}}$). The R^2 for the model of general types of herbivory was 0.09 and for seed predation it was 0.74; parameter estimates are given in Supporting Information 2.E: Parameter estimates.

Traditional meta-analysis results

The traditional random effects meta-analysis with study level effects showed wide variability in the effect of herbivores on plant populations across and within studies (Fig. 2.4: Traditional random effects meta-analysis). Even so, the overall effect was significant (mean = 0.37, 95% CI: 0.07 – 0.67, $p < 0.05$).

DISCUSSION

This quantitative synthesis demonstrates that invertebrate herbivores often cause substantial reductions in plant population growth rates. While there is extensive variability in the population effects of herbivores across and within study systems, these results contradict the once tenable perspective that invertebrate herbivores do not have strong effects on plant populations (Crawley 1989). However, the results show that across systems measured herbivory rates are a very poor proxy for the importance of herbivory to that population. The compiled evidence from these studies also emphasizes that herbivores are effective at preventing plants from attaining high population growth rates.

Measured herbivory is a poor proxy for impacts on populations

Measured herbivory was significantly correlated with its effect on population growth rates for studies that focused on seed predation, but the variability was high and there was not a significant relationship for studies that investigated other types of herbivory. Thus, when comparing across study systems, years, or sites, it was not uncommon for the population with lower measured herbivory to be more affected by herbivores (e.g., Ehrlén 1995a, 1996, 2002). This synthesis therefore confirms that damage rates do not always reflect the true importance of herbivory to plant population growth rates (Crawley 1989, Ehrlén 2003, Maron and Crone 2006) and goes one step further by showing the strength of the relationship. There are several reasons why herbivory rates are a poor proxy for population growth. First, a population's sensitivity to the impacted demographic rate(s) can vary considerably over ontogeny, space, and time (Ehrlén 1996, 2002, Dauer et al. 2012, Euler et al. 2014). Second, herbivory recorded is not necessarily a good indicator of total herbivory experienced; herbivory is almost never monitored in every single plant organ over every single life stage. Indeed, not a single study that I reviewed measured below ground herbivory, which is very important to individual plants and entire communities (Van der Putten 2003). These results reiterate the problematic nature of using damage rates or even single demographic rates to test the importance of the enemy release hypothesis or the Janzen-Connell hypothesis (Chun et al. 2010, Comita et al. 2014).

Herbivores stabilize population growth rates

Invertebrate herbivores had proportionately larger effects when potential population growth rates were high (Fig. 2.3). This could be caused by the potential population growth rate determining the relative importance of different life stages, such as the ones affected by herbivory in a particular study. For example, in "good" years (i.e., years with high survival and growth rates), population growth rates are relatively sensitive to seeds and seedlings, because these early life stages are likely to reach reproductive stages; herbivory on seeds and seedlings in these cases could have large effects on population growth. In contrast, in "bad" years, early demographic stages are less likely to reach reproductive stages, and so herbivory on seeds and seedlings is less important to population growth rates, which would depend more on other rates, such as survival of adults. While the phenomenon of high sensitivity to the demographic rates of propagules at high population growth rates is well documented empirically (e.g., Silvertown et al. 1993; Ehrlén 2002; Euler et al. 2014), it is not clearly connected with density dependence.

Another plausible explanations relates to density dependence; seed predation rates were the highest for observations with high λ_{-H}. This relationship could result from seed predators being attracted to high concentrations of resources or because of the effects of seed availability on seed predator populations. There is support for density dependent seed predation (i.e., seed density, not necessarily density of adults) in the literature; for example, several researchers have noted higher seed predation rates for individual plants or plants in plots that produce more seeds (e.g., Ehrlén 1996; Ehrlén 2002; Egan and Irwin 2008; Euler et al. 2014). In a review, it was noted that for small-seeded species, seed predation tends to be density dependent (Hulme 1998). Similar mechanisms may also apply to other types of herbivory; there may be higher general herbivory in cases where plants have higher reproductive capacity. For example, in one study it was observed that larger plants were more likely to have higher herbivore loads (Rose et al. 2005). Although potential population growth rates only explain a small part of the variation in measured herbivory (general and seed), even weak density dependent effects on demography can still be effective at regulating populations (Fowler 1995), and in these studies the observations with the highest potential population growth rates all were strongly affected by herbivores. Regardless of mechanism, the results of these studies show that herbivory prevents plant populations from attaining high population growth rates, therefore stabilizing herbivore populations.

General herbivory vs seed predation

Studies that focused exclusively on seed predation reported smaller effects of herbivores on population growth rates. These results are also corroborated by the literature; seed predation reduces fecundity, which is generally one of the less important demographic rates for perennial plants (Silvertown et al. 1993). Thus, it stands to reason that seed predation has less of an impact than other types of herbivory. However, it should be noted that studies that focused on seed predators were also more likely to be observational than experimental, and were more likely to focus on only one species of herbivore.

Existing natural populations are unlikely to experience extreme herbivory

The plant demography studies selected for this meta-analysis show that established plant populations experience a wide range of effects from herbivory, but herbivores can be even more important when they prevent a plant population from establishing in the first place. In established plant populations, one would not expect to find many examples of extreme effects of herbivory; in cases where a plant population was severely impacted by herbivory, it would soon be extirpated and therefore unavailable to study. There are many examples of herbivores preventing their host plants from colonizing particular habitats, such as serpentine soils (Fine et al. 2004, 2006, Lau et al. 2008), well-lit areas (Louda and Rodman 1996), or particular elevation zones (Parker and Root 1981, Rand 2002). While population matrices were not calculated in these cases, the absence of the plant species from an area into which its propagules disperse, combined with evidence that herbivory is the limiting factor, strongly suggest that herbivores are effectively preventing population establishment and growth. Further support can be seen in the invasion biology literature, where there are numerous examples of native herbivores preventing non-native species from invading or reaching high abundances in new regions (Levine et al. 2004). Thus, a focus on existing plant populations and their herbivores systematically underrepresents the potential for herbivory to effect plant populations.

Knowledge gaps

This synthesis has documented that invertebrate herbivores can and often do have large impacts on plant populations, but the extent to which herbivory regulates plant populations remains unknown. Although a few studies reported information on changes in plant density and herbivory rates over time or over space (e.g., Fagan and Bishop 2000; Fröborg and Eriksson 2003; Rose et al. 2011), most did not. Density dependence is only infrequently included in plant population growth models that quantify the impacts of herbivory (Halpern and Underwood 2006, Ramula and Buckley 2009). By including plant and herbivore density and damage rates (Halpern and Underwood 2006), future studies may be able to more directly connect herbivores to plant population regulation.

It should also be noted that particular systems remain understudied; of the studies reviewed, only two focused on annual plants, none studied trees, and only three studied exotic herbivores. While phylogeny has not been found to be a strong driver of population growth rates (Buckley et al. 2010), additional studies on underrepresented functional groups will help to fill in gaps.

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Figure 2.1. Plant population growth rate with and without herbivory

The effects of herbivory on plant population growth rates with ambient herbivory (λ_{+H}) and with reduced herbivory (λ_{-H}) for all observations from native plants. Values above the one:one line indicate that reducing herbivory had a positive effect on plant population growth rates; standard deviations are included when available. The inset provides an enlarged view of the box to the left.

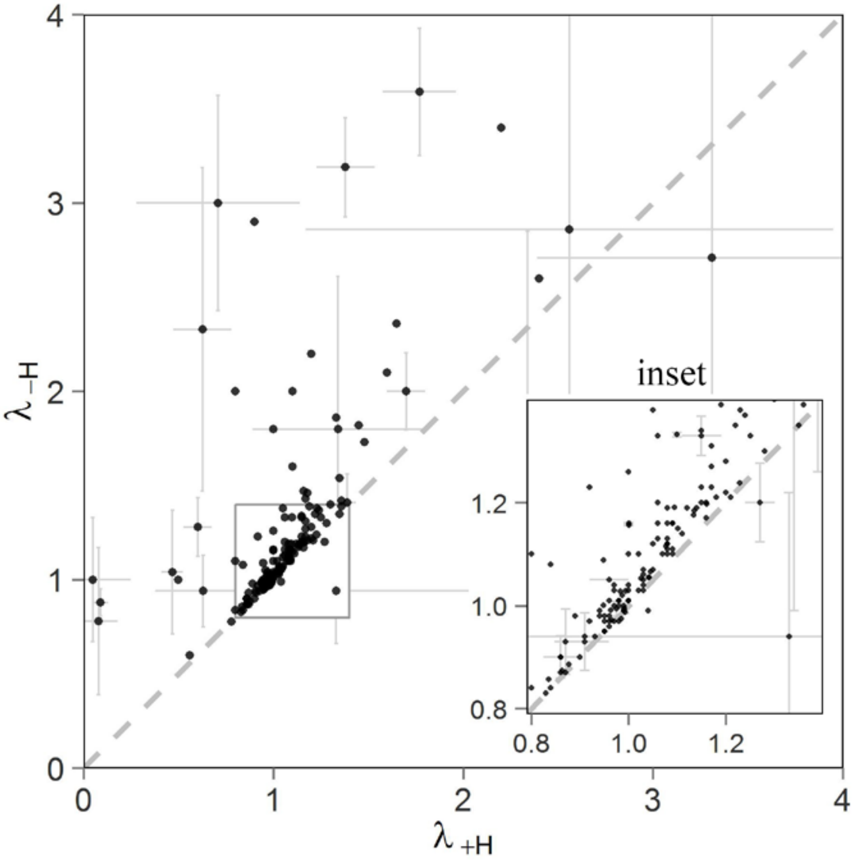


Figure 2.2. Population level effects of herbivores as a function of measured herbivory

The estimated effect of herbivory reduction treatments on population growth rate (θ) across the observed range of measured herbivory values ($_{\Delta}$H), simulated at the average levels of λ_{-H} for observations of other types of herbivory (1.57) and seed predation (1.18). Mean modeled values are shown (solid lines) as are 95 % CIs (dotted lines). Raw data (circles and triangles) from observations that measured herbivory are plotted for comparison. The fit of the model for other types of herbivory was $R^2 = 0.10$ and for seed predation it was $R^2 = 0.75$.

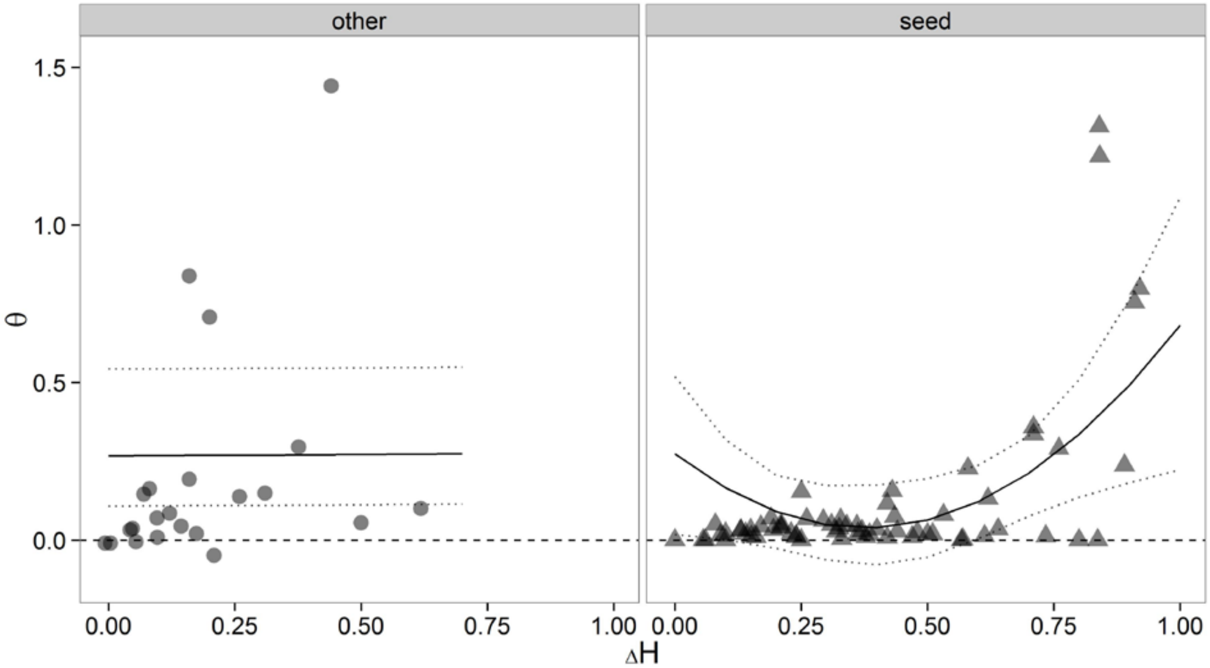


Figure 2.3. Population level effects of herbivores as a function of potential population growth rate

The estimated effect of herbivory reduction treatments on population growth rate (θ) across the observed range of potential population growth rates (λ_{-H}), simulated at the average levels of $_{\Delta}H$ for other types of herbivory (19%) and seed predation (40%). Mean modeled values are shown (solid lines) as are 95 % CIs (dotted lines). Raw data (circles and triangles) are plotted for comparison and if herbivory was measured, it is depicted by shading.

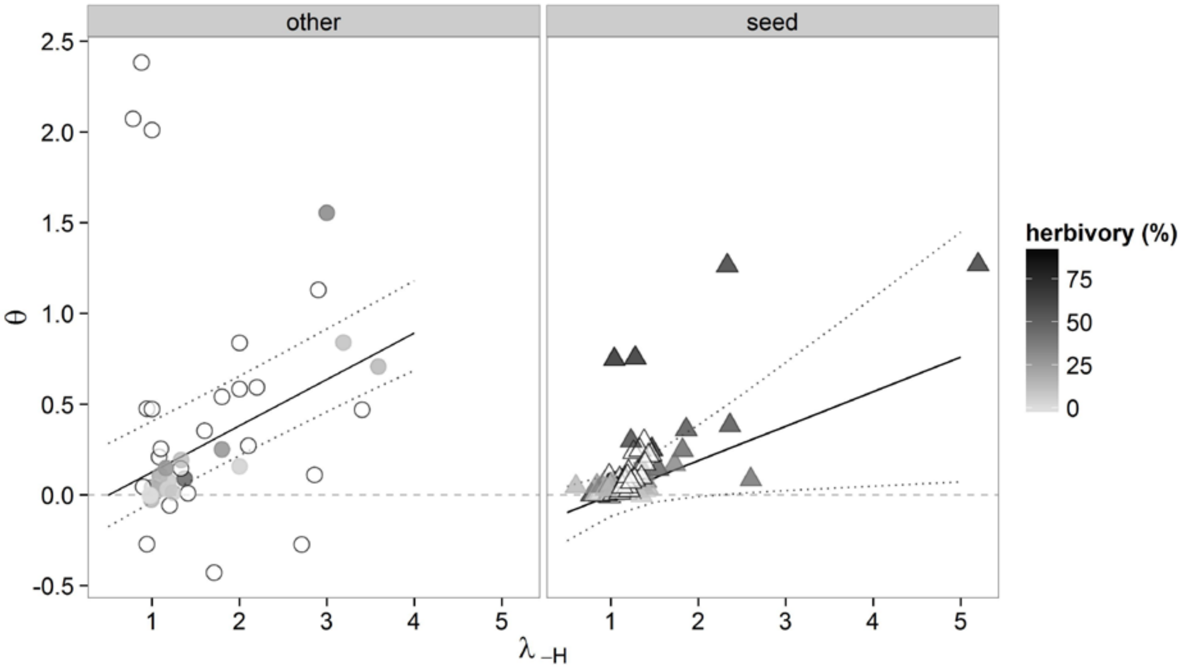
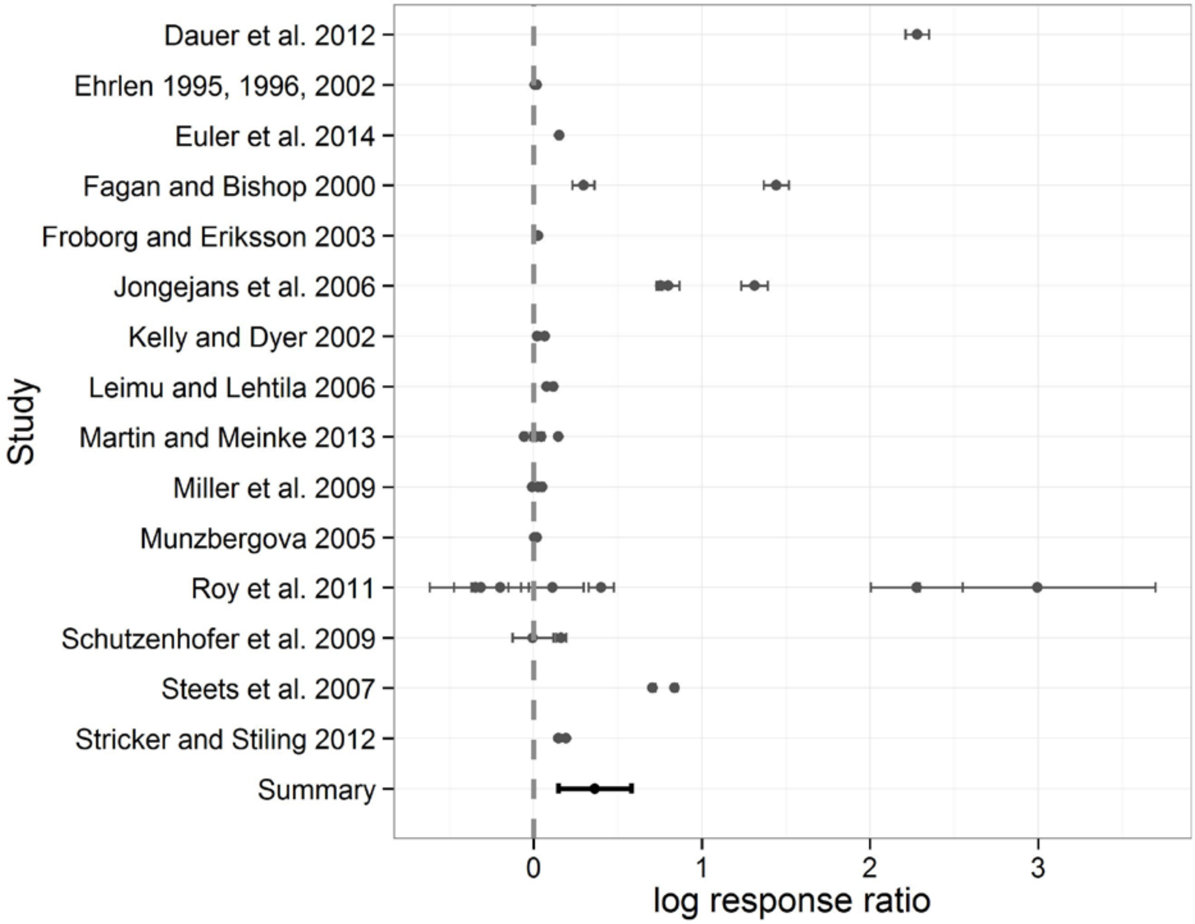


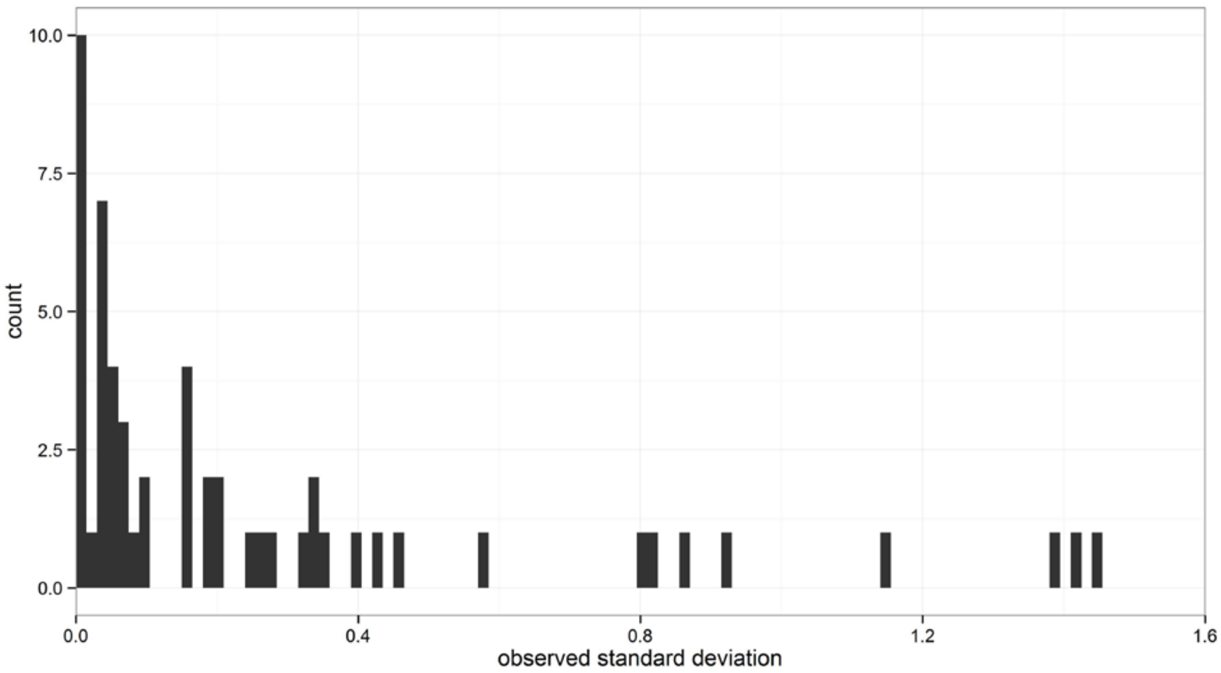
Figure 2.4. Traditional random effects meta-analysis.

Traditional random effects meta-analysis including study random effects. A forest plot of the effects of herbivores on plant population growth is shown below (mean effect size and 95 % CI are shown for each observation for which variance was provided or could be calculated). This analysis used inverse variance weighting.



Supporting Information 2.A. Reported standard deviations for λ

Figure SI. 2.5. Histogram of reported standard deviations for λ.

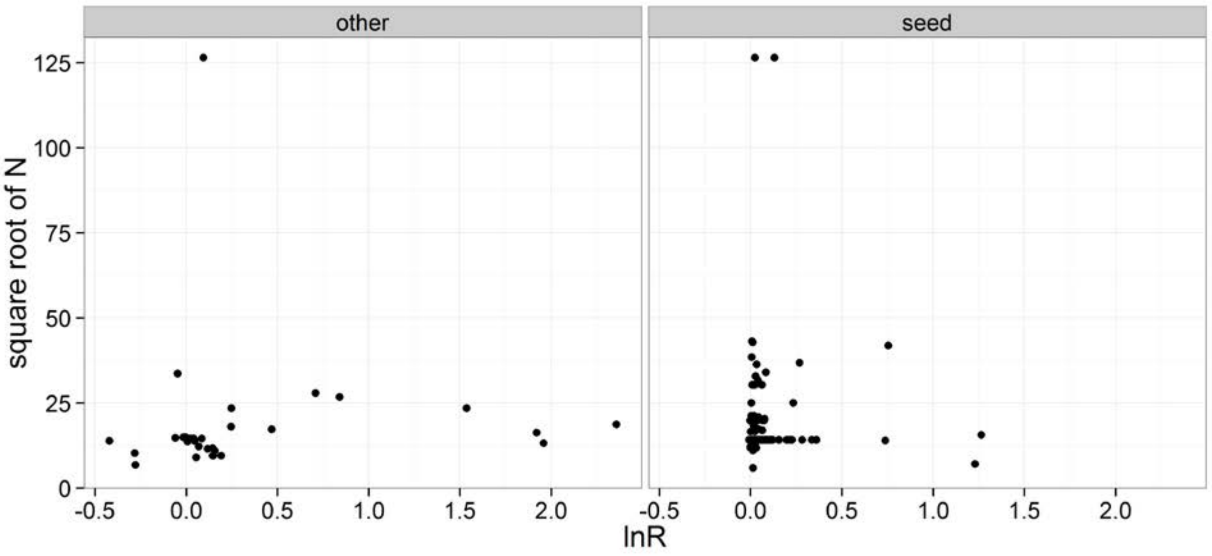


Supporting Information 2.B. Publication bias.

I used two methods to assess whether publication bias occurred and its potential impact. First, I created funnel plots for studies of other herbivores and seed predators (Fig. SI 2.6, below). Data are for studies for which variance was either reported or could be calculated using inter-annual variability. The absence of a relationship between sample size and effect size is most likely explained by the inherent differences between study systems and the high levels of spatial and temporal heterogeneity. I also calculated that Orwin's fail-safe number was 40, meaning that an additional 40 publications averaging null results would be required to reduce the significance of the random effects meta-analysis to below 0.05.

Figure SI.2.6. Funnel plots for studies of other herbivores and seed predators.

The square root of the sample size is given on the y axis, and is calculated based on the number of juvenile or adult plants reported in the study (the number of seeds used is not included).



Supporting Information 2.C. Selected publications

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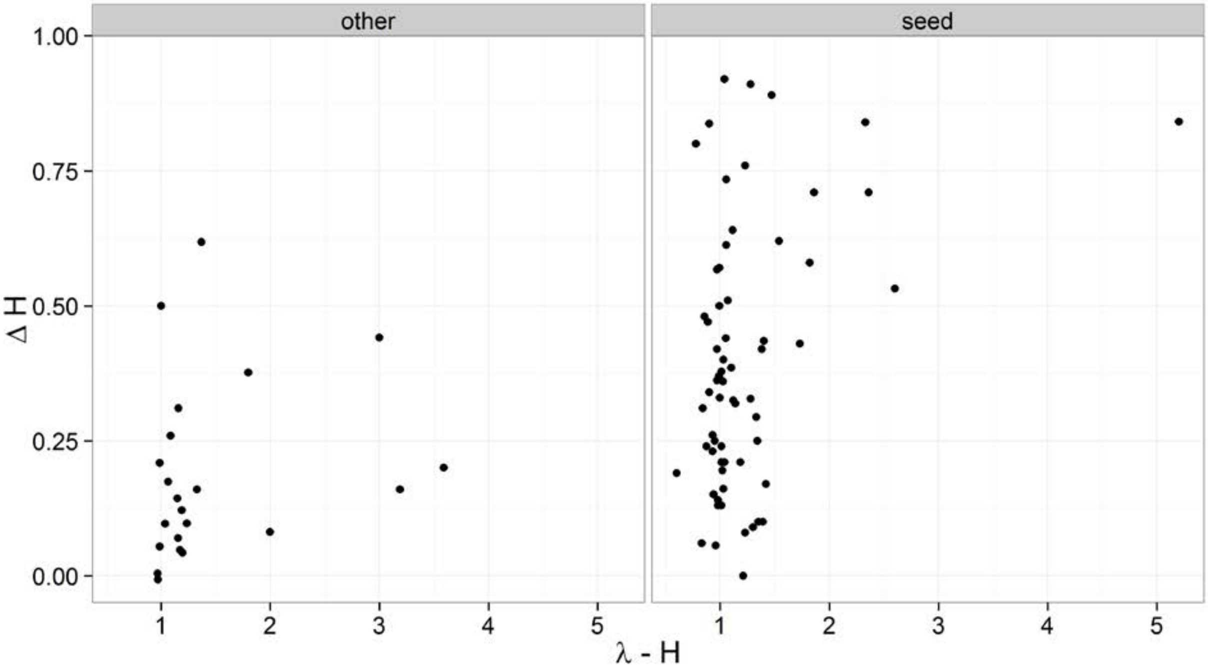
Supporting Information 2.D. Seed predation and $\lambda_{\text{-H}}$.

Figure SI 2.7. Seed predation and $\lambda_{\text{-H}}$.

Correlations between herbivory and $\lambda_{\text{-H}}$ are shown for **a)** other herbivory and **b)** seed predation. The y-axis on the first panel is the percent of herbivory recorded, whereas in the second panel it is the observed percent of seeds lost to seed predation in a particular observation. For seed predation studies there was a significant correlation between measured herbivory and $\lambda_{\text{-H}}$ (Spearman's $r = 0.27$, $p < 0.05$); observations with high population growth rates ($\lambda_{\text{-H}} > 1.5$) had very high seed predation rates.



Supporting Information 2.E. Parameter estimates for models

Table SI 2.1. Parameter estimates for models

Parameter estimates (mean and 95% CI) for the models for observations on other types of herbivory and for observations on seed predation.

parameter	Other types of herbivory	Seed predation
β_1 : slope for herbivory	0.01 (-0.01 – 0.03)	-1.24 (-2.51 – 0.22)
β_2 : quadratic term for herbivory	–	1.64 (-0.04 – 3.07)
κ : coefficient for $\lambda_{\sim H}$	0.26 (0.21 – 0.31)	0.20 (0.03 – 0.39)
α_1 : mean of study effects	-0.14 (-0.32 – 0.15)	-0.03 (-0.33 – 0.39)
σ_{study} : standard deviation of study effects	0.18 (0.02 – 0.61)	0.08 (0.00 – 0.27)

CHAPTER III:

DISTANCE DEPENDENT ESCAPE FROM NATURAL ENEMIES WITHIN PLANT SPECIES DISTRIBUTIONS EXPLAINS DIFFERENCES IN BIOTIC INTERACTIONS ACROSS RANGE EDGES

ABSTRACT

Plant distributions are expected to shift poleward in response to global warming, and it will be the performance of individuals at the colonizing front that will shape range expansion dynamics. These plants will encounter new biotic communities beyond their range edges, and the net outcome of these encounters could profoundly affect colonization success. However, little is known about how biotic interactions vary across range edges and this has hindered efforts to predict changes in species distributions in response to climate change. In contrast, a rich literature documents how biotic interactions within species ranges vary according to distance to and density of conspecific individuals. Here, we test whether this framework can be extended to explain how biotic interactions differ beyond range edges, where conspecific adults are basically absent. To do so, we planted seven species of trees along a 450 km latitudinal gradient that crossed the current distributional range of five of these species and monitored foliar invertebrate herbivory and disease over five years. Foliar herbivory and disease were analyzed as a function of distance to and density of conspecific and congeneric trees at several spatial scales. We found that within species ranges foliar disease was lower for seedlings that were farther from conspecific adults for *Acer rubrum, Carya glabra, Quercus alba,* and *Robinia pseudoacacia.* Enemy release was even stronger beyond range edges for *C. glabra*, *Q. alba* and *R.*

pseudoacacia (*A. rubrum* was not planted outside its range). The species that did not show signs of enemy release within their ranges, *Liriodendron tulipifera* and *Quercus velutina*, showed no signs of enemy release or relatively weak signs of enemy release beyond their ranges. Patterns of distance dependent herbivory across spatial scales was generally weak and in some cases negative (i.e., seedlings further from conspecific adults had more herbivory). Overall, we conclude that differences in biotic interactions across range edges can be thought of as a spatial extension to the concept of distance dependent biotic interactions. This framework also provides the basis for general predictions of how distance/density dependent biotic interactions will change across range edges in other systems.

INTRODUCTION

Some plant species distributions in North America are beginning to shift in response to changes in temperature and precipitation (Woodall et al. 2009, Murphy et al. 2010, Boisvert-Marsh et al. 2014, Desprez et al. 2014; but see Zhu et al. 2012). However, much remains unknown about how contemporary range expansion will occur, in part because plants beyond range edges will interact with different suites of organisms in these new areas. If biotic interactions systematically differ across range edges, they could potentially affect colonization success and range expansion dynamics. An increasing number of researchers have called attention to this issue (Morriën et al. 2010, van der Putten 2011, Renwick and Rocca 2015), and several investigations have quantified net changes in plant-soil feedback across range edges (van Grunsven et al. 2010, Stanton-Geddes and Anderson 2011, Mccarthy-Neumann and Ibáñez 2012). However, to our knowledge, no studies have tested how foliar herbivory or disease vary across latitudinal range edges.

Expanding range edges are characterized by low population densities that are often incapable of supporting associated specialist organisms (i.e., herbivores, pathogens, and mutualists with high host specificity). Likewise, populations on range edges are often the product of repeated founding events, each of which increases the probability that specialists will be left behind (Phillips et al. 2010b). There is both theoretical and empirical evidence that organisms of various taxa that establish beyond their range (hereafter referred to as 'migrants') or near their range edge have fewer specialist enemies and when they do the interactions are weaker (Alexander et al. 2007, Menéndez et al. 2008, Phillips et al. 2010a, Patot et al. 2010, Tsai and Manos 2010). Enemy release from herbivores and pathogens is very well studied in the context of inter-continental range expansion, i.e., invasion biology (Liu and Stiling 2006, Heger and Jeschke 2014). Although less explored, interactions with mutualists, such as mycorrhizae or other soil biota, seem to be weaker beyond a species' range (e.g., Stanton-Geddes and Anderson 2011, Callaway et al. 2011). Generalist natural enemy preferences can also result in weaker relationships between natural enemies and plants beyond their range edges; for example, pathogens adapt to local plant genotypes (Sicard et al. 2007, Reinhart et al. 2010) and herbivore host preferences can be influenced by plant abundance (Kuussaari et al. 2000). In the context of range expansion, biotic interactions across range edges will be determined by the loss of natural enemies and mutualists from the plants' original range, and by the biotic community already present.

Although little is known about differences in interactions with natural enemies across distributional range edges, many studies have quantified how biotic interactions vary within species ranges as a function of distance to or density of conspecific adults (Comita et al. 2014). Consequently, the importance of distance and density dependent biotic interactions within a species range may provide insight into how biotic interactions will vary beyond range edges; both migrant plants and plants that are within their range but far from conspecific adults are likely to have fewer interactions with associated specialist species.

Tests of the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) reveal a wide range of distance/density dependent relationships for trees in temperate forests (Comita et al. 2014). Some studies have found that seedlings close to conspecific adults or in areas with more conspecific adults experienced lower survival or higher natural enemy attack rates (Packer and Clay 2000, Masaki and Nakashizuka 2002, Gómez-Aparicio et al. 2008, Pigot and Leather 2008, Yamazaki et al. 2009, Johnson et al. 2012), but others have found mixed results (HilleRisLambers et al. 2002, Reinhart et al. 2012a, 2012b, McCarthy-Neumann and Ibáñez 2013, Piao et al. 2013, Johnson et al. 2014). Although some of these findings can be attributed to confounding correlations between conspecific occurrence, seed dispersal, and environmental conditions, these examples still highlight inter-specific variation in distance and density dependent biotic interactions at smaller spatial scales.

We argue that the same mechanisms that determine net changes in biotic interactions across small spatial scales could also lead to differences in biotic interactions at larger spatial scales. In this study, we characterize interactions between plants and foliar pathogens and invertebrate herbivores across a gradient of distances between seedlings and con-specific adults, ranging from meters to hundreds of kilometers (i.e., beyond species range edges). We use a seedling transplant experiment with seven tree species to answer the following questions: 1) What is the direction and magnitude of distance dependent biotic interactions within these species ranges? And, 2) can within-range distance dependent relationships help predict differences in biotic interactions beyond species ranges? Answers to these questions will illustrate whether the theoretical framework of distance dependence can be used to understand how biotic interactions might vary across range edges and aid with future predictions of plant range shifts.

METHODS

We planted seedlings of seven tree species in four regions along a 450-km latitudinal gradient in Michigan, USA, that included the geographic range limit of five of these species (Table 3.1; Fig. 3.1). At each region we established between one and four sites in different temperate forest types, and at each site we planted seedlings in two to 21 plots (Table 3.2; Fig. 3.1). Plots were located across a range of environmental conditions (e.g., light, soil moisture, and nutrients; Supporting Information 3.A: plot characteristics) and many were situated near adults of the focal species. Each plot consisted one to three subplots. A total of 12,762 seedlings were planted between 2010 and 2013 (Table 3.1 and 3.2). Species origins varied: two species were native across all regions (*Acer rubrum* L. and *Quercus rubra* L.) and five were native or naturalized at some regions and potential migrants at others (*Carya glabra* P. Mill., *Liriodendron tulipifera* L., *Q. alba* L., *Q. velutina* Lam., and *Robinia pseudoacacia* L.; Table 3.1). Species were selected based on their current and predicted distributional shifts (Iverson et al. 2008) and because they represented a range of ecological traits (e.g., shade tolerance).

Seedlings

Wild seeds were collected within Michigan, but if unavailable they were obtained from outside of Michigan (Supporting Information 3.B: Seed Sources). Seeds were germinated at the University of Michigan Matthaei Botanical Gardens (Ann Arbor, MI) in potting soil (Metro-Mix

380; SunGro Horticulture, Agawam, Massachusetts, USA), where they were watered daily. At approximately one month after emergence, we measured the height of the seedlings, defined as the distance from the soil to the tip of the apical mertistem, which we used as a proxy for maternal effects (i.e., seed size). Bare root seedlings were then transplanted into the study plots with a minimum spacing of 25 cm between seedlings. Existing vegetation was left intact. To decrease transplant shock, seedlings were watered upon planting (125 ml/seedling). A subset of seedlings (2196) were transplanted in the fall instead of in the spring. This was done in 2011, 2012, and 2013 in order to both increase the range of seedling sizes and to increase total sample size.

Leaf damage

Biotic interactions were measured by visually assessing leaf damage on seedlings in the summers (June 19th – July 27) of 2010 – 2014. Leaf damage was quantified by visually surveying the leaves on each seedling using damage cover classes (<1%, 1-5%, 6-15%, 16-25%, 26-50%, 51-75%, >75%). All leaves were measured on seedlings that had less than 26 leaves; for other seedlings, 25 leaves were selected at random and surveyed. To ensure consistent visual estimates, the same person conducted all surveys (D. Katz). During each census signs of herbivory and disease were assessed. Damage signs attributed to herbivory included chewing (e.g., skeletonizing, window feeding, hole feeding), piercing-sucking (e.g., stippling; regularly shaped small round discolorations in leaves), leaf mining, and galling. Damage was counted as disease if symptoms included abnormal coloration, blackening of the leaf, dark spots with necrosis, spots with discolorations surrounding them, and the presence of fungal fruiting bodies. The disease category therefore includes both infectious and non-infectious diseases (Sinclair and

Lyon 2005). Although it can be difficult to distinguish pathogen identity visually, visual surveys of disease can still provide important information about causes of death (Yamazaki et al. 2009). Vertebrate herbivory was recorded separately and is not reported here.

Mapping

We mapped all living trees ≥10 cm DBH (diameter at breast height) that were within 10 m of a focal seedling. We determined the distance from a central point to each tree to the nearest 10 cm with an Impulse 200 laser range finder (Laser Technology, Englewood, CO, USA). The heading of each tree was obtained using a compass and we also recorded tree diameter at breast height (DBH; 1.37 m) and species identity. Transplanted seedling locations were measured by recording the distance and heading from the same central point to plot corner locations, and then seedling locations within plots were calculated according to the standardized planting design (as per Fig. 3.1). Basal area (m^2) was calculated for all trees within 10 m of each focal seedling ($314m^2$); other studies have found the strongest effects of neighborhood at 5 – 10 m (Masaki and Nakashizuka 2002, Gómez-Aparicio et al. 2008, Piao et al. 2013). Presence at the site of a particular species was determined by whether any individuals of that species were recorded during stem mapping; this method agreed with personal observations during fieldwork.

Environmental Data

The environmental variables we measured were light availability, soil water, and soil nutrients. Light was measured each year using hemispherical canopy photos after the full canopy had developed. Photos were taken 1 m above seedlings, using a Sigma SD14 camera (Sigma Corporation, Japan) with a Sigma 4.5 mm circular fisheye lens (Sigma Corporation, Japan). The proportion of total possible sunlight reaching the forest floor, the global site factor, was calculated using Hemiview (Delta-T Devices, Cambridge, UK). At least two photos were taken per sub-plot each year in midsummer, when canopy coverage was complete. Photos were taken under uniform sky conditions (i.e., dusk, dawn, or uniformly cloudy days). Light was averaged across subplots and across years; the mean of these measurements and their standard deviation were used in the analysis.

Soil water (percent moisture by volume) was measured hourly at each site with a HOBO Micro Station Data Logger (Onset Computer Corporation, Pocasset, MA). Volumetric soil water content in the top 7.5 cm of soil was measured in at least six points per sub-plot several times each growing season with a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, Plainfield, IL, USA). The relationship between soil moisture at the sub-plot level (taken a few times each summer) and at the site level (recorded hourly at one point within each site) was quantified using linear regressions, and these regressions were used to predict soil moisture at each sub-plot between censuses; the mean R^2 value was 0.67.

Soil nutrients were measured once using resin packs (Unibest International Corporation, Walla Walla, WA, USA). Resin packs in the southernmost region (A) were deployed between 4/8/2013 – 10/30/2013 and resin packs were deployed from 4/23/2013 - 10/23/2013 in the other regions. Depending on the number of subplots, between two and four resin packs were deployed per plot. Four resin packs could not be retrieved because they were moved by burrowing animals or were otherwise damaged, and no nutrient data are available for the two plots that were not yet established at the time of nutrient pack deployment. Resin packs were retrieved and refrigerated until they were shipped to Unibest for analysis. Analysis was conducted by Unibest; ions were extracted using 2mHCL and the ion exchange resin analysis was conducted using inductively coupled plasmaspectroscopy analysis (Perkin Elmer 3300 DV; Ca, Mg, Mn, P) and FIA Lab Flow Injection (FIA 2500; NO_3^-, NH_4^+).

Statistical analysis

We used several statistical models to analyze foliar damage, disease and invertebrate herbivory, as a function of distance to and density of conspecific and congeneric adults. Foliar herbivory and disease followed a zero-inflated log normal distribution and it is likely that different processes govern whether a plant was attacked (referred to as incidence), versus how much damage attacked plants experienced (referred to as severity). Thus data were analyzed in two distinct submodels: a logistic regression for foliar damage incidence and a log-normal function to account for foliar damage severity. The different distance categories were: adult conspecific present within 10 m of a seedling, adult conspecific present at the site but not within 10 m, adult conspecific present in the region but not at the site, and adult conspecific not present in the region (as per Fig. 3.1). The effects of conspecific density were analyzed as a function of conspecific basal area within 10 m of the focal seedling and, for *A. rubrum* and *Q. rubra,* we added a second terms to account for conspecific relative basal area at the site (these are the only two species for which we could add this term). We also estimated the effects of congeneric basal area within 10 m and at the site level (congeneric relative basal area) on leaf damage. In summary, we ran eight different models for each species (two leaf damage types: disease or herbivory; two processes: incidence or severity; and two dynamics: distance or density).

Parameter estimation was conducted using a Bayesian approach, which allowed us to incorporate different sources of uncertainty and missing data (Gelman and Hill 2007). Leaf damage incidence and severity were estimated as a function of several covariates X_{ij} (Table 3), where X_{ij} is the matrix of covariates associated with each seedling *i* at time *j*. We explored several different models, including different covariates and random effects (e.g., individuals, year) and selected the model with the lowest DIC (Deviance Information Criterion; Spiegelhalter et al. 2002) that allowed us to answer our questions. The final models included the proportion of available light that reached the seedling, average volumetric soil moisture since the last census, the age of the seedling in days, the number of leaves, and the height of the seedling when planted (Table 3). Random effects were also included for each seedling and year. The models for distance included a fixed effect intercept that varied according to the proximity of the nearest conspecific (within 10 m, more than 10 m away but within the site, absent in the site but present in region, or absent in region), thus the incidence model for seedling *i* in census *j*:

$$\mathrm{logit}(\mathrm{incidence}_{ij}) = \beta_{\mathrm{distance\ category\ (i)}} + \alpha_1 * \mathrm{Li_i} + \alpha_2 * \mathrm{M_{ij}} + \delta_1 * \mathrm{H_i} + \delta_2 * \mathrm{Le_{ij}} + \delta_3 * \mathrm{A_{ij}} + \gamma_{\mathrm{seedling\ (i)}} + \gamma_{\mathrm{year\ (j)}}$$

The density models included the amount of basal area within 10 m of the focal seedling for both conspecific and congeneric trees, the relative basal area at the site for conspecific and congeneric trees for common species, and random effects for region, thus the incidence model is:

$$\mathrm{logit}(\mathrm{incidence}_{ij}) = \kappa_1 * \mathrm{BS_i} + \kappa_2 * \mathrm{BG_i} + \kappa_3 * \mathrm{SS_i} + \kappa_4 * \mathrm{SG_i} + \alpha_1 * \mathrm{Li_i} + \alpha_2 * \mathrm{M_{ij}} + \delta_1 * \mathrm{H_i} + \delta_2 * \mathrm{Le_{ij}} + \delta_3 * \mathrm{A_{ij}} + \gamma_{\mathrm{seedling\ (i)}} + \gamma_{\mathrm{year\ (j)}} + \gamma_{\mathrm{region\ (j)}}$$

Models of leaf damage severity for distance and density included the same covariates but are not shown.

To improve comparisons between variables, we standardized seedling height at time of transplant, the number of leaves, light, and soil moisture. Light and soil moisture were modeled as normally distributed latent variables characterized by their measured mean and standard deviation. Fixed effect coefficients were drawn from non-informative prior distributions: Normal (0, 1000). The random effects for seedling, year, and region were drawn from a normal distribution: random effect ~ Normal (0, σ^2), where σ ~ Uniform (0, 10), as was the variance of the log normal distribution.

To assess the effects of increasing distance from conspecifics we estimated the difference from the $\beta_{conspecific\ within\ 10\ m}$ parameter to the other three distance parameters; differences that do not include zero in their 95% CIs were considered statistically significant. Fixed effects coefficients associated with the rest of the continuous variables were considered statistically significant if their 95% CIs did not include zero. Posterior densities of the parameters were obtained by Gibbs sampling (Geman and Geman 1984) using JAGS 3.4 (Plummer 2003) via the rjags package in R (Plummer 2014). Convergence occurred after 1,000 to 10,000 iterations and chains were inspected visually. Each species was run for 40,000 iterations and posterior parameter values were based on postconvergence results. Visualization was conducted using the ggplot2 package in R (Wickham 2009). All analyses were conducted using R (R Core Team 2013).

RESULTS

Model fit and effects of environmental and seedling variables.

The R^2 of the statistical models ranged from 0.11 to 0.92; specific values for each model are reported in Supporting Information 3.C: Model fit. The parameter estimates for each statistical model are reported in Supporting Information 3.D: Covariate Parameter Estimates, in this section we focus on the results of the distance and density related parameter (parameters β and κ). The inclusion of soil nutrients did not generally lead to lower DIC values for most species, and so were not included in the final models.

Distance dependent biotic relationships across scales

Foliar disease: For several species, seedlings had higher disease when they were planted within 10 m of a conspecific adults compared to when they were planted further from conspecific adults (Fig. 3.2). For some species this trend occurred for damage incidence (*A. rubrum, C. glabra,* and *Q. alba*) whereas for others it is apparent in damage severity (*A. rubrum* and *Robinia pseudoacacia*). Seedlings of these species had even less disease when they were planted hundreds of kilometers from conspecifics (i.e., conspecifics were absent from the region). *Liriodendron tulipifera* did not show signs of enemy release either within its range or beyond its range edge. *Quercus velutina* had more foliar disease when it was at sites where conspecifics occurred but did experience a small amount of enemy release when planted in areas beyond its range, although less than most other migrant species (Fig. 3.2).

Foliar herbivory: The effects of distance from conspecific adults on seedling herbivory varied by species and did not show consistent overall trends (Fig. 3.3). Some species had higher herbivory close to adult conspecifics within sites (*A. rubrum* and *Q. velutina*) whereas others had higher herbivory farther from adults (*Q. rubra* and *R. pseudoacacia*). In three cases, a lack of strong intra-range differences in herbivory continued beyond range edges (*L. tulipifera, Q. alba,* and *R. pseudoacacia*) and in another case distance dependent increases in herbivory continued beyond range edges (*C. glabra*). However, for *Q. velutina*, there was enemy release within but not beyond range edges.

Density dependent biotic relationships

Foliar disease: Higher conspecific basal area (within 10 m) was associated with higher disease for four species (*A. rubrum, C. glabra, Q. alba*, and *Q. velutina*; Fig. 3.4). One species had significantly lower disease severity at higher conspecific basal area (*R. pseudoacacia*). Only *Q. rubra* had higher disease at higher congeneric local basal area. Conspecific relative basal area at a site was correlated with higher disease incidence for *Q. rubra* (Fig. 3.5). Both *Q. alba* and *Q. velutina* tended to have more disease at higher congeneric basal area, but this was not statistically significant.

Foliar herbivory: Higher conspecific basal area (within 10 m) was associated with higher foliar herbivory for *Q. alba* and *R. pseudoacacia* and lower foliar herbivory for *C. glabra* and *Q. rubra* (Fig. 3.4). Both *A. rubrum* and *Q. rubra* had higher herbivory where there was higher congeneric basal area. Higher conspecific relative basal area at each site reduced herbivory for *Q. rubra* and higher congeneric relative basal area significantly reduced herbivory for *Q. alba* (Fig. 3.5).

DISCUSSION

In this study, we assessed differences in biotic interactions across the range edges of several tree species that are common in eastern North American forests, and determined whether intra-range distance and density dependent biotic interactions explained biotic interactions beyond range edges. We found that the species that experienced enemy release from disease when planted farther from conspecific adults within their ranges tended to have even greater enemy release when planted beyond their range edges. This finding suggests that similar mechanisms of enemy release apply across spatial scales and shows that distance dependent biotic interactions at small spatial scales inform and roughly predict differences in biotic interactions across range edges. Our results also show that in this study system distance to conspecifics has a larger effect on disease than on herbivory, which may reflect higher host specificity of pathogens than herbivores. The resulting decreases in disease beyond range edges have the potential to affect the demography (e.g., growth and survival) of migrant plant populations and through them range expansion dynamics.

Differences in biotic interactions across varying distances to and densities of conspecific adults.

Tests of the Janzen-Connell hypothesis and of the enemy release hypothesis show that plants that are isolated from conspecifics on spatial scales of meters and thousands of kilometers tend to be associated with fewer natural enemies and receive less damage (Liu and Stiling 2006, Comita et al. 2014); our results demonstrate these patterns also occur on the intermediate spatial scales relevant to tree range expansion. On small spatial scales, enemy release occurs when seedlings are farther away from conspecific adults, which increase local abundance of natural enemies, including both specialists and generalists with feeding preferences for that plant (Comita et al. 2014). At inter-continental spatial scales, exotic plants have fewer specialist natural enemies (Liu and Stiling 2006) and in some circumstances generalist natural enemies may be unequipped to deal with novel plant defenses (Verhoeven et al. 2009) or may not have adapted to that plant type (Reinhart et al. 2010). In both cases, isolation from conspecific adults reduces the probability that a seedling will be encountered either by a specialist or a generalist natural enemy that has a feeding preference for it. The same mechanisms should apply across range edges and help to explain our finding that seedlings planted further from conspecific adults both within and beyond their distributional ranges had less disease.

Despite commonalities in enemy release mechanisms, the effects of distance and density of conspecific adults on foliar damage vary according to study species. Our finding that *Q. rubra* is relatively insensitive to distance dependence and that *A. rubrum* is more sensitive fits well with the results reported by other researchers (e.g., McCarthy-Neumann and Kobe 2010). Although others have found *L. tulipifera* to be sensitive to conspecific adults (Johnson et al. 2014), we did not. This may be because *L. tulipifera* is uncommon even in our southernmost study region, and could therefore have experienced enemy release at all the sites included in this study. Regardless of cause, the concept that species that are most affected by distance and density dependent interactions with natural enemies within their range are those with the greatest potential for enemy release beyond their range is both intuitive and supported at a broad scale in invasion biology (Prior et al. 2015). It is also supported by our results for *C. glabra*, *Q. alba*, and *R. pseudoacacia*

Comparing trends in disease and herbivory damage

Isolated seedlings were far more likely to escape from disease than from herbivory, and *C. glabra* and *Q. rubra* actually had higher herbivory farther from conspecifics and when there were fewer conspecifics within 10 m or at the site. One explanation for why more isolated seedlings did not escape from herbivory is that herbivores in temperate forests tend to be less specialized than pathogens (compare the results of Barrett et al. 2009 and Forister et al. 2015). Another potential explanation is that isolated seedlings are less likely to attract or interact with mutualists that can reduce herbivory by providing indirect defenses (e.g., via attracting predators and parasitoids by releasing volatile organic compounds; Heil 2008, Farkas and Singer 2013). Likewise, in some cases mycorrhizae and endophytes can enhance seedling performance and therefore defensive capabilities or directly reduce plant palatability, although their effects vary according to herbivore feeding guild and specialization (Hartley and Gange 2009, Koricheva et al. 2009). Although the accumulation of mutualists around host plants is understudied, in one case study, higher abundances of mycorrhizae around conspecific adults is credited with counter-acting the negative effects of soil pathogens in a sub-tropical forest (Liang et al. 2015). Thus, it is likely that seedlings far from conspecific adults escape from antagonists but at the same time lose mutualists (Callaway et al. 2011). In a multi-trophic biotic interaction like herbivory, this dynamic could lead to idiosyncratic results where some species experience less foliar damage farther from conspecifics (e.g., *A. rubrum*) whereas others experience less foliar damage closer to conspecifics (e.g., *C. glabra*), depending on the relative accumulation of mutualists and natural enemies around conspecific adults.

The effects of congeneric adult trees

Several species were planted near adult congeneric trees and for *A. rubrum, Q. alba,* and *Q. rubra* congeneric trees affected foliar damage rates, although usually less than conspecific adults (Fig. 3.4). One point of interest is that *Q. alba* had less herbivory when there was more congeneric relative basal area at a site, whereas *Q. rubra* had higher foliar disease and herbivory when there were more congeneric adults within 10 m. Regardless of whether these findings are caused by shared environmental niches that we did not capture with our environmental measurements or overlapping mutualists and natural enemies, our results suggest that biotic interactions could facilitate the establishment of *Q. alba* during range expansion in forests where *Q. rubra* is dominant. In general though, the presence of more closely related species tends to increase herbivory rates (Pearse and Hipp 2009, Pearse et al. 2013); this, and phylogenetic clustering of plant defenses (Ricklefs 2008), may partially account for why *Q. velutina* did not experience stronger enemy release from herbivory beyond range edges.

Applications to other systems

There are reasons to suspect that differences in biotic interactions across range edges will vary for other growth forms or in other systems. First, growth forms besides trees tend to have stronger negative plant soil feedbacks (Kulmatiski et al. 2008). This could be in part because of the buildup of mutualistic organisms, such as arbuscular mycorhizzal fungi around adult conspecifics, which has been documented in a sub-tropical forest (Liang et al. 2015). Next, although observed patterns of negative density/distance dependent survival are not stronger in tropical than in temperate forests (HilleRisLambers et al. 2002, Comita et al. 2014), invertebrate insects in temperate forests tend to be less specialized than those in tropical forests (Dyer et al. 2007, Forister et al. 2015). This suggests that species in other functional groups or in other ecosystems may experience higher negative density/distance dependent biotic interactions and therefore potential for enemy release beyond range edges.

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Table 3.1. Study species

Plant species used in transplant experiments and their residency status at each study region. Species residency status (native, migrant, or invasive) was determined using Little's range maps, FIA data (via the Climate Change Tree Atlas; Prasad et al. 2007-ongoing), and county data from the USDA Plants database and the Michigan Flora Online. In some cases these data sources provide conflicting information, which is indicated with an asterisk. The number of seedlings of each species planted in each region is also included

Species	Species code	Common name	Region A most southern	Region B southern	Region C northern	Region D most northern
Acer rubrum	acru	Red maple	Native 487	Native 75	Native 282	Native 0
Carya glabra	cagl	Pignut hickory	Native 930	Migrant 344	Migrant 344	Migrant 110
Liriodendron tulipifera	litu	Tulip tree	Native/naturalized* 836	Migrant 255	Migrant 656	Migrant 255
Quercus rubra	quru	Red oak	Native 1937	Native 345	Native 989	Native 315
Quercus alba	qual	White oak	Native 829	Native 140	Migrant/rare* 344	Migrant 187
Quercus velutina	quve	Black oak	Native 777	Migrant/rare* 417	Migrant 417	Migrant 230
Robinia pseudoacacia	rops	Black locust	Native/naturalized* 806	Migrant; planted 165	Migrant; planted 476	Migrant 270
Total planted			6602	1741	3508	1367

Table 3. 2. Study sites

Description of sites used in the transplant experiment. Environmental variables at the plot and sub-plot level are given in Supporting Information 3.A: Plot Environmental Characteristics. Longitude and Latitude are in decimal degrees.

Site	Longitude	Latitude	Average number of frost free days	Soil texture	Major vegetation	Average growing season length-days	No. of plots
A1	-83.673	42.324	175	loam	maple	205	9
A2	-84.023	42.457	167	sandy loam	oak-maple	203	21
A3	-84.012	42.459	169	sandy loam	oak-hickory	199	2
B1	-85.751	44.218	157	sand	oak-maple	187	8
C1	-84.714	45.553	164	loamy sand	aspen-maple	205	5
C2	-84.682	45.568	180	sand	maple-beech	212	7
C3	-84.673	45.559	180	sand	maple	212	3
C4	-84.748	45.556	118	sand	pine-aspen-oak	146	6
D1	-84.141	46.350	161	loamy sand	oak-maple	179	6

Table 3.3. Covariates included in statistical models

Statistical models were run separately for each species for each damage type, and for distance vs. density of conspecific adults. Incidence submodels used logistic regression to determine the probability of damage whereas severity submodels used log-normal distributions to estimate the amount of damage. Basal area (m^2) is abbreviated to BA.

Covariate name, abbreviation, unit, and pre-standardization range	Model(s) that covariate is included in
light (Li, % full sun): continuous (0 – 1)	distance and density
soil moisture (M, % volume): continuous (0 – 1)	distance and density
planting height (H, mm): continuous (3 – 390)	distance and density
number of leaves (Le): continuous (0 – 60)	distance and density
seedling age (A, days): continuous (30 – 1583)	distance and density
seedling: individual random effects $\gamma_{seedling}$	distance and density
year: year random effects γ_{year}	distance and density
distance category (β): categorical (conspecific within 10 m, present at site, present in region, or absent in region)	distance
conspecific BA at plot (BS, $m^2/314m^2$): continuous (0 – 2.19)	density
congeneric BA at plot (BG, $m^2/314m^2$): continuous (0 – 3.62)	density
conspecific relative BA at site (SS, m^2 conspecific BA/m^2 total BA): continuous (0 – 0.74)	density
congeneric relative BA at site (SG, $m^2/314m^2$): continuous (0 – 0.79)	density
region (R): region random effects	density

Figure 3.1. Experimental design layout

The distribution of study regions in North America (**Panel A**) encompasses the approximate range edges of several focal species (**Panel B**: line between regions A and B). Each region (A - D) contained one to four sites **(Panel C)**, each located in distinct forest types (sites C1 - C4 for region C). Each site had between two and 21 **plots** (gray boxes; **Panel D**) and a datalogger (star). Each plot (**Panel E)** had between one and three subplots (white boxes), in which **seedlings** were planted (black dots). All trees within 10 m of a planted seedling were mapped (colored circles; species identity is represented by color).

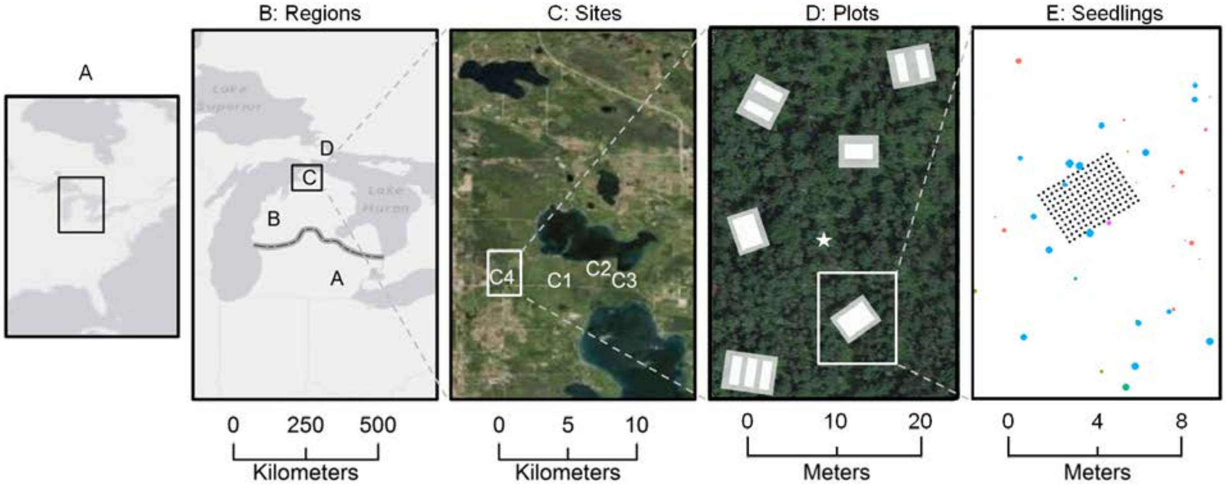


Figure 3.2. Effects of distance from adult conspecifics on foliar disease across scales

Plots represent the difference in model intercepts between seedlings that were within 10 m of a conspecific adult and seedlings that were at other distances from conspecific adult trees (present within the site, present within the region, and absent in the region). 95% credible intervals that are below the zero line show that seedlings in that distance category had significantly less foliar disease than seedlings within 10 m of a conspecific (zero line).

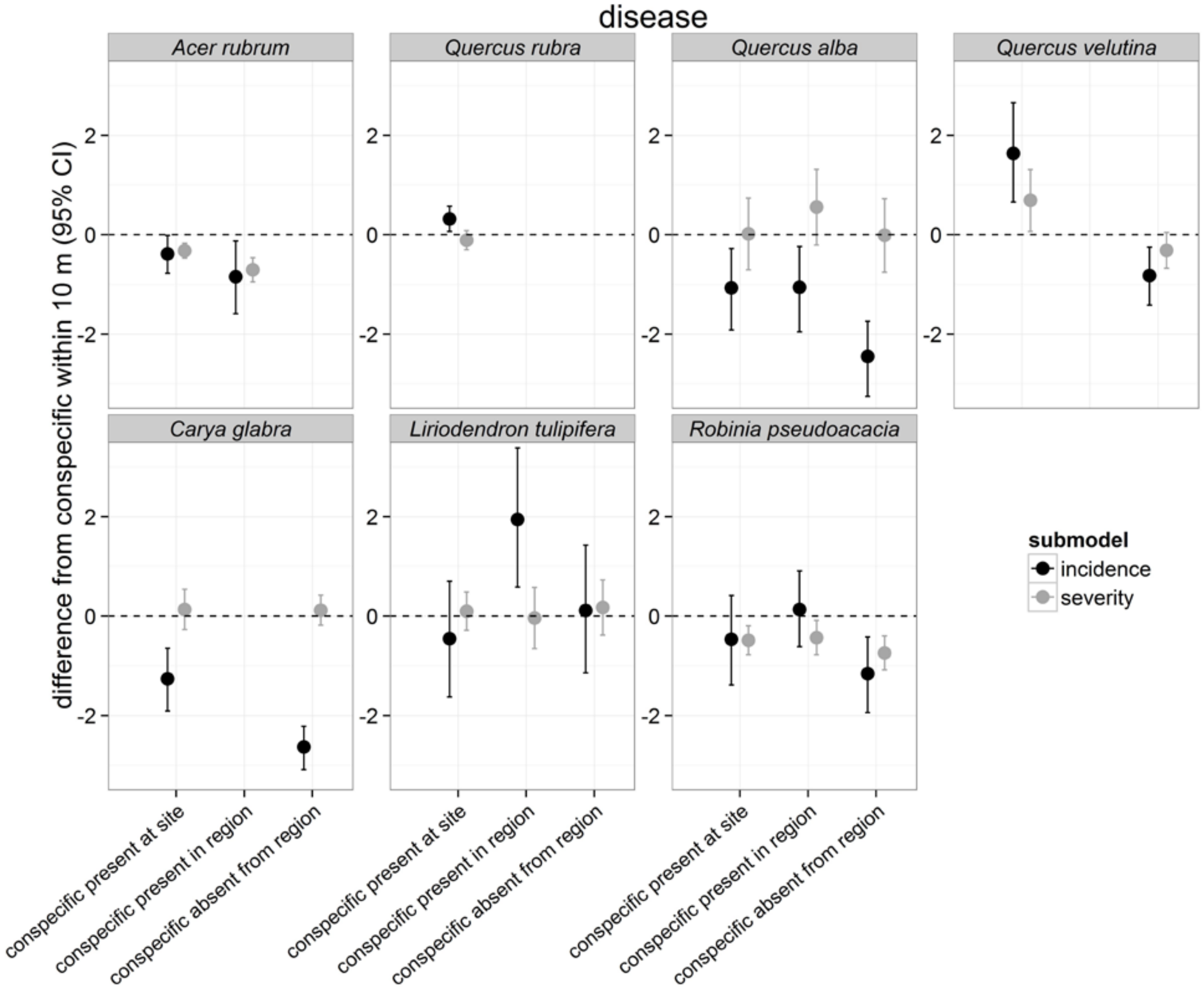


Figure 3.3. Effects of distance from adult conspecifics on foliar herbivory across scales

Plots represent the difference in model intercepts between seedlings that were within 10 m of a conspecific adult and seedlings that were at other distances from conspecific adult trees (present within the site, present within the region, and absent in the region). 95% credible intervals that are below the zero line show that seedlings in that distance category had significantly less foliar herbivory than seedlings within 10 m of a conspecific (zero line).

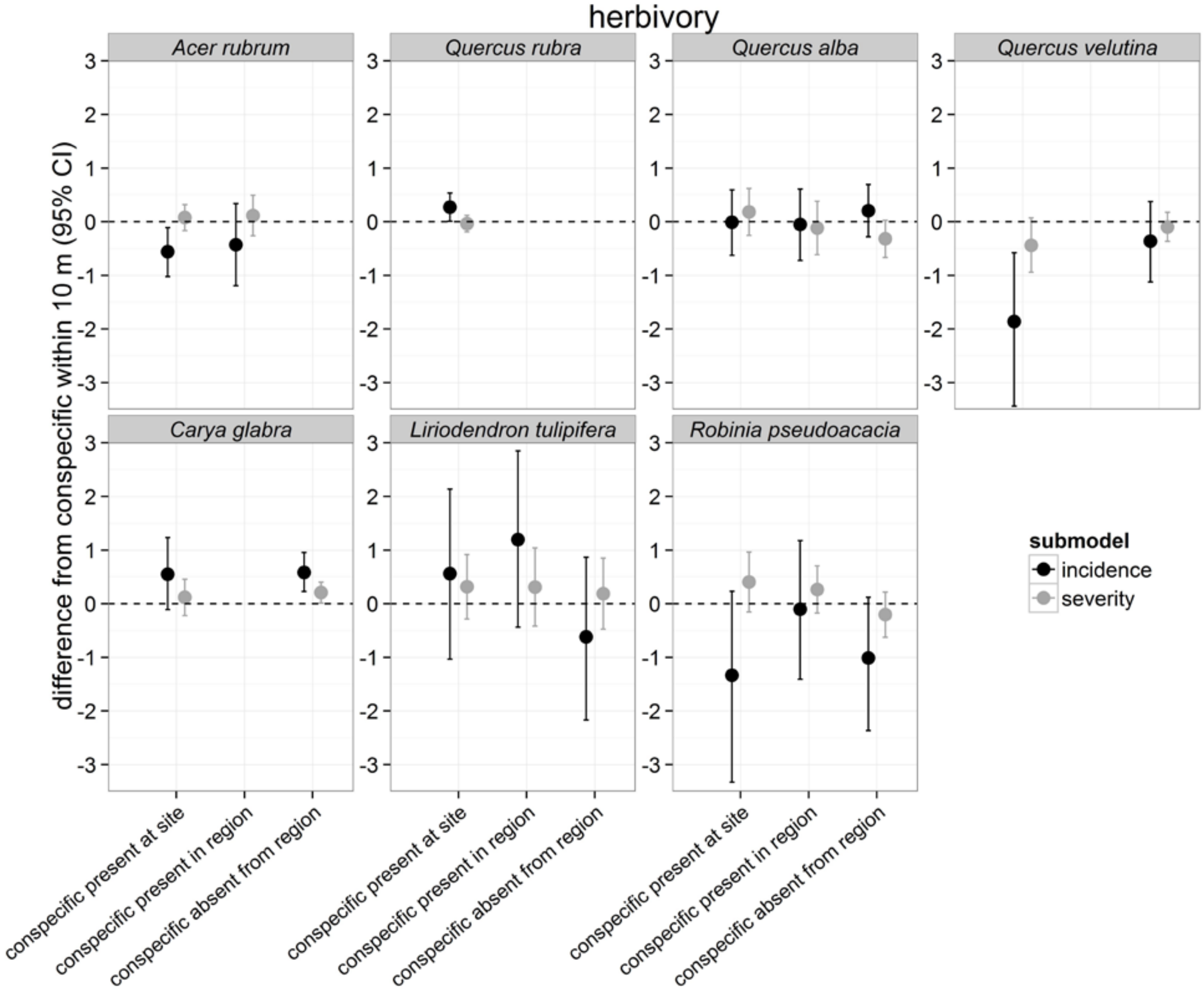


Figure 3.4. The effects of conspecific and congeneric local density (basal area within 10 m) on foliar damage.

Parameter estimates above 0 indicate a positive effect of basal area on the amount of leaf damage; 95% credible intervals that cross zero are not statistically significant. Three species did not have enough neighboring congeneric adults to calculate their effects on foliar damage.

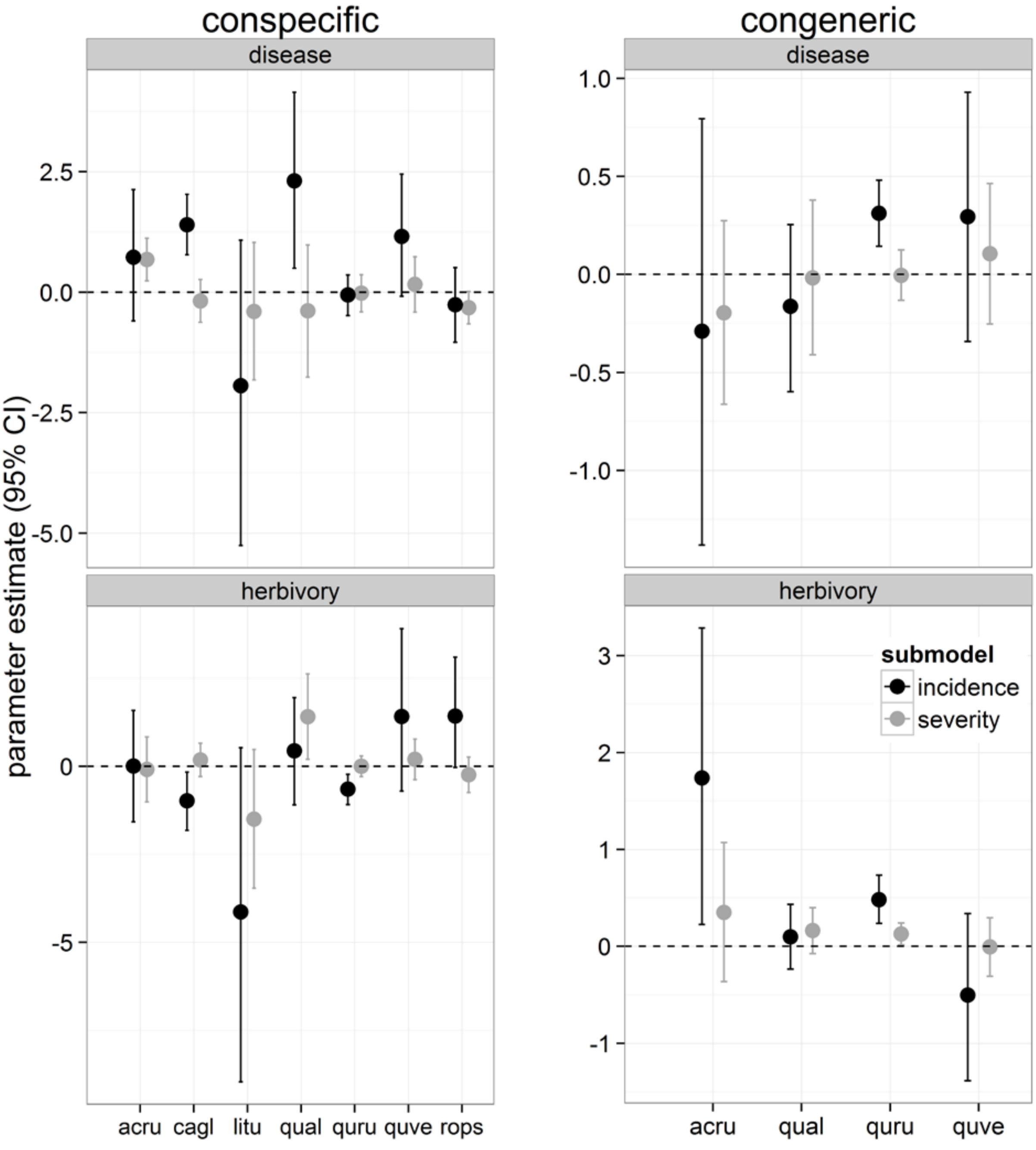
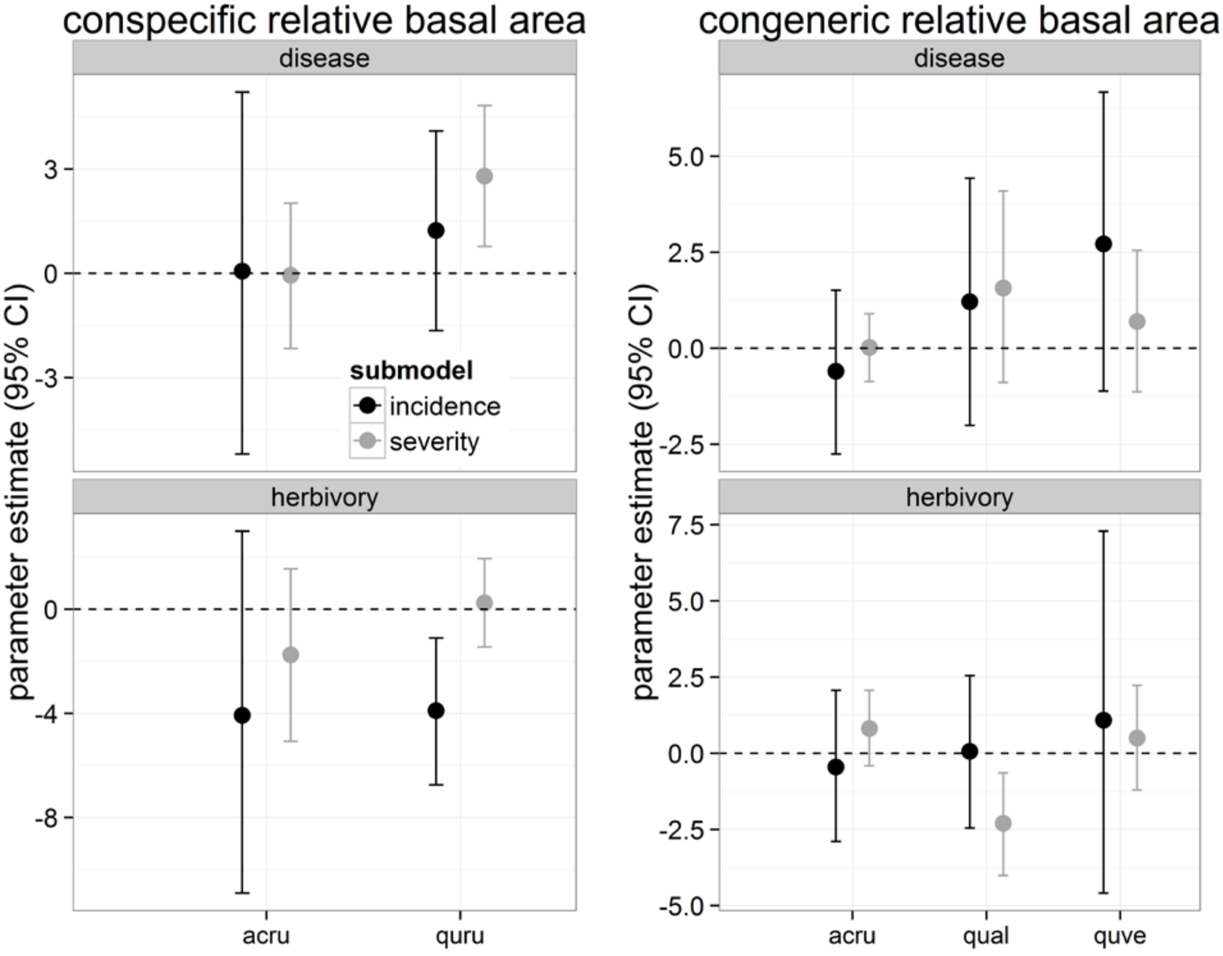


Figure 3.5. Parameter estimates for the effects of conspecific and congeneric relative basal area at the site level on foliar disease and herbivory.

Only *A. rubrum* and *Q. rubra* occurred at enough sites (8 and 9, respectively) to assess this relationship for conspecific adults. Similarly, the effects of congeneric relative basal area were only assessed for *A. rubrum*, *Q. alba*, and *Q. velutina*. Parameter estimates above 0 indicate a positive effect on the amount of leaf damage; 95% credible intervals that cross zero are not statistically significant.



Supporting Information 3.A. Plot environmental characteristics

Table SI 3.4. Plot environmental characteristics

Light is measured as GSF, the proportion of light that is available at one meter above ground, relative to full sun (0 is no light, 1 is full light); values presented here are averaged across both years and subplots. Soil moisture is the average volumetric soil moisture at each plot during the growing season, averaged across years; the standard deviation is across years. Although light and soil moisture are given at the plot level in this table, measurements at the subplot and subplot section were used in the survival analysis. Soil nutrient values were determined using resin capsules and the average value for resin capsules at each plot are presented.

Site	Plot	light (± SD)	Soil moisture (± SD)	NO_3	NH_4	P	Ca	Mg	Mn
A1	105	0.06 ± 0.02	0.23 ± 0.10	6.80	6.80	4.53	0.37	207.60	50.07
A1	109	0.08 ± 0.03	0.23 ± 0.11	19.84	19.84	12.43	1.50	268.69	69.31
A1	110	0.10 ± 0.03	0.23 ± 0.10	20.31	20.31	2.86	0.41	203.18	47.02
A1	112	0.11 ± 0.02	0.21 ± 0.07	31.10	31.10	6.15	0.46	200.33	44.74
A1	113	0.07 ± 0.02	0.21 ± 0.07	42.23	42.23	5.85	1.18	271.32	48.65
A1	130	0.06 ± 0.02	0.19 ± 0.05	75.47	75.47	6.70	0.48	185.07	36.84
A1	131	0.07 ± 0.02	0.20 ± 0.05	39.90	39.90	6.22	0.31	140.22	35.33
A1	132	0.09 ± 0.02	0.15 ± 0.06	15.87	15.87	4.60	0.16	58.53	14.55
A1	133	0.09 ± 0.02	0.25 ± 0.08	NA	NA	NA	NA	NA	NA
A2	103	0.75 ± 0.14	0.09 ± 0.02	8.03	8.03	7.73	0.44	36.25	8.39
A2	104	0.16 ± 0.06	0.10 ± 0.02	9.29	9.29	8.03	0.21	34.00	11.33
A3	101	0.10 ± 0.07	0.13 ± 0.02	8.48	8.48	5.59	0.72	63.40	15.70
A3	102	0.34 ± 0.15	0.10 ± 0.01	7.15	7.15	6.91	0.22	26.49	8.83
A3	106	0.14 ± 0.05	0.11 ± 0.01	7.47	7.47	6.44	0.22	23.84	5.40
A3	107	0.16 ± 0.05	0.10 ± 0.01	5.42	5.42	4.58	1.10	13.80	8.13
A3	108	0.54 ± 0.09	0.10 ± 0.00	11.06	11.06	8.86	1.40	42.22	14.73
A3	114	0.12 ± 0.03	0.11 ± 0.01	3.12	3.12	2.92	0.26	22.82	5.44
A3	115	0.15 ± 0.05	0.09 ± 0.01	8.28	8.28	7.83	1.02	24.62	11.77
A3	116	0.13 ± 0.06	0.08 ± 0.01	8.59	8.59	5.80	1.15	43.62	15.95
A3	117	0.10 ± 0.05	0.09 ± 0.01	5.94	5.94	4.92	0.93	43.59	13.88
A3	118	0.16 ± 0.06	0.08 ± 0.01	9.26	9.26	6.89	0.49	40.43	10.60
A3	119	0.06 ± 0.02	0.10 ± 0.01	5.09	5.09	2.56	0.43	69.78	12.09
A3	120	0.10 ± 0.03	0.08 ± 0.01	5.08	5.08	4.38	1.60	44.60	9.37
A3	121	0.10 ± 0.03	0.12 ± 0.01	9.72	9.72	7.94	1.22	64.43	16.89
A3	122	0.11 ± 0.03	0.11 ± 0.01	5.70	5.70	5.58	0.11	15.51	4.72
A3	123	0.07 ± 0.02	0.11 ± 0.01	4.38	4.38	3.54	1.12	37.23	10.02
A3	124	0.08 ± 0.02	0.12 ± 0.01	8.66	8.66	8.05	0.80	18.39	5.76
A3	125	0.13 ± 0.05	0.11 ± 0.02	3.75	3.75	3.04	0.24	27.55	6.42
A3	126	0.15 ± 0.05	0.11 ± 0.01	2.64	2.64	2.41	0.37	31.55	6.94
A3	127	0.10 ± 0.05	0.12 ± 0.01	1.80	1.80	1.76	0.14	17.58	4.28
A3	128	0.50 ± 0.06	0.09 ± 0.00	5.16	5.16	4.72	0.91	39.59	17.87
A3	129	0.13 ± 0.02	0.09 ± 0.01	3.58	3.58	2.78	0.33	21.87	5.64

B1	301	0.08 ± 0.03	0.11 ± 0.04	6.19	6.19	3.85	2.60	19.63	5.44
B1	302	0.06 ± 0.01	0.13 ± 0.04	9.96	9.96	8.57	0.57	35.62	6.18
B1	303	0.09 ± 0.03	0.10 ± 0.03	17.90	17.90	4.11	2.55	37.89	8.72
B1	304	0.10 ± 0.03	0.13 ± 0.04	17.29	17.29	7.68	1.26	70.19	11.16
B1	305	0.10 ± 0.05	0.11 ± 0.04	10.77	10.77	9.69	1.32	32.28	6.60
B1	306	0.07 ± 0.01	0.12 ± 0.05	10.62	10.62	6.20	1.32	78.44	9.56
B1	307	0.19 ± 0.05	0.07 ± 0.02	8.85	8.85	8.71	0.44	17.82	5.20
B1	308	0.12 ± 0.05	0.09 ± 0.04	26.02	26.02	14.30	4.12	75.50	11.36
C1	207	0.12 ± 0.03	0.20 ± 0.01	5.88	5.88	4.68	2.01	53.06	10.93
C1	208	0.14 ± 0.04	0.18 ± 0.01	4.84	4.84	4.65	1.17	27.70	5.72
C1	210	0.14 ± 0.04	0.11 ± 0.01	6.22	6.22	5.37	2.19	17.61	3.51
C1	219	0.12 ± 0.04	0.12 ± 0.01	5.88	5.88	5.25	0.79	22.45	5.44
C1	221	0.08 ± 0.02	0.10 ± 0.01	3.56	3.56	3.06	2.02	33.92	6.29
C2	201	0.10 ± 0.04	0.13 ± 0.05	15.15	15.15	10.47	2.20	83.82	16.11
C2	202	0.08 ± 0.04	0.12 ± 0.04	4.44	4.44	2.89	1.83	72.07	10.02
C2	211	0.10 ± 0.04	0.15 ± 0.04	11.94	11.94	6.88	1.83	69.56	14.95
C2	213	0.07 ± 0.03	0.12 ± 0.03	8.39	8.39	5.34	0.60	83.69	16.11
C2	214	0.08 ± 0.02	0.10 ± 0.03	4.59	4.59	3.82	0.77	64.23	7.03
C2	218	0.12 ± 0.03	0.11 ± 0.03	6.00	6.00	5.50	1.56	53.09	8.42
C2	220	0.07 ± 0.04	0.13 ± 0.03	16.41	16.41	8.34	7.70	90.89	19.55
C3	212	0.14 ± 0.06	0.10 ± 0.03	5.77	5.77	5.27	0.24	32.93	8.57
C3	216	0.11 ± 0.06	0.09 ± 0.02	7.23	7.23	6.49	0.62	49.76	12.78
C3	217	0.17 ± 0.03	0.09 ± 0.03	6.26	6.26	5.06	0.44	44.20	11.60
C4	203	0.21 ± 0.08	0.09 ± 0.01	6.41	6.41	3.83	3.20	28.32	8.17
C4	204	0.54 ± 0.09	0.08 ± 0.01	5.12	5.12	3.42	0.82	34.55	10.06
C4	209	0.58 ± 0.05	0.06 ± 0.01	5.10	5.10	4.51	0.68	24.90	7.24
C4	215	0.46 ± 0.06	0.06 ± 0.01	5.00	5.00	3.97	1.78	14.24	5.72
C4	222	0.44 ± 0.08	0.07 ± 0.01	3.01	3.01	2.49	0.99	16.55	6.07
C4	223	0.34 ± 0.08	0.07 ± 0.01	5.67	5.67	4.22	1.48	11.96	4.77
D1	401	0.10 ± 0.03	0.18 ± 0.05	9.23	9.23	9.23	1.69	122.23	30.99
D1	402	0.15 ± 0.05	0.13 ± 0.03	4.50	4.50	4.39	0.72	24.88	5.29
D1	403	0.26 ± 0.04	0.14 ± 0.04	8.23	8.23	5.93	3.40	43.92	6.33
D1	404	0.16 ± 0.04	0.13 ± 0.04	4.96	4.96	4.60	1.19	13.32	3.33
D1	405	0.61 ± 0.04	0.11 ± 0.02	6.75	6.75	6.66	0.39	14.33	2.49
D1	406	0.10 ± 0.03	0.10 ± 0.01	NA	NA	NA	NA	NA	NA

Supporting Information 3.B. Seed Sources

Table SI 3.5. Seed sources

Seed sources for transplanted seedlings by Michigan county or, if local seeds were unavailable that year, by state of origin. Seeds that originated outside of Michigan were purchased from Sheffield's Seed Co (Locke, NY, USA).

species	seed sources
Acer rubrum	Calhoun, Cheyboygan, Manistee, Newaygo, KY, PA
Carya glabra	Ingham, Livingston, Oakland, Washtenaw, IA
Liriodendron tulipifera	Washtenaw, Wayne, KY
Quercus alba	Ingham, Oakland
Quercus rubra	Berrien, Ingham, Livingston, Roscommon, Wayne, Washtenaw, Van Buren
Quercus velutina	Allegan, Waterloo, Wayne, IL
Robinia pseudoacacia	Ingham, Washtenaw

Supporting Information 3.C. Model fit

Table SI 3.6. Model fit.

R^2 values for the statistical models of the leaf damage severity submodel for each species. Model descriptions are included in Table 3.3.

damage type		distance		density	
disease	Acru	0.14	Acru	0.13	
	Cagl	0.28	Cagl	0.23	
	Litu	0.35	Litu	0.35	
	Qual	0.92	Qual	0.89	
	Quru	0.40	Quru	0.32	
	Quve	0.42	Quve	0.36	
	Rops	0.30	Rops	0.23	
herbivory	Acru	0.32	Acru	0.26	
	Cagl	0.42	Cagl	0.30	
	Litu	0.34	Litu	0.38	
	Qual	0.24	Qual	0.21	
	Quru	0.11	Quru	0.11	
	Quve	0.24	Quve	0.23	
	Rops	0.12	Rops	0.19	

Supporting Information 3.D. Covariate parameter estimates

Table SI 3.7. Covariate parameter estimates

Parameter estimates for statistical models (mean and 95% CI). Statistical models were run separately for each species for each damage type, and for distance vs. density. Incidence submodels used logistic regression to determine the probability of damage whereas severity submodels used log-normal distributions to estimate the amount of damage. 95% CIs that do not include zero are statistically significant. Note that even if 95% CI along β parameters overlap, the 95% CI around their differences did not always overlap with zero, which is due to covariance between parameter values.

***Acer rubrum:* distance**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	0.52 (-1.10 – 2.20)	1.16 (0.64 – 1.67)	-2.56 (-4.29 – -0.94)	-0.44 (-1.31 – 0.45)
α_2 : soil moisture	-1.74 (-5.37 – 1.79)	-0.28 (-1.56 – 1.00)	1.08 (-3.21 – 5.52)	3.28 (0.87 – 5.56)
δ_1 : planting height	0.21 (-0.16 – 0.59)	0.20 (0.07 – 0.34)	0.38 (-0.08 – 0.86)	0.25 (0.02 – 0.47)
δ_2 : number of leaves	3.02 (2.31 – 3.80)	-0.32 (-0.46 – -0.19)	2.74 (2.00 – 3.56)	-0.44 (-0.65 – -0.23)
δ_3 : seedling age	-0.31 (-0.85 – 0.22)	-0.05 (-0.27 – 0.17)	0.40 (-0.25 – 1.04)	0.07 (-0.22 – 0.37)
β : conspecific within 10 m	1.97 (0.45 – 3.51)	-2.91 (-4.14 – 3.54)	2.10 (0.57 – 3.69)	-3.47 (-4.12 – -2.76)
β : conspecific at site	1.58 (0.10 – 3.06)	-3.23 (-4.46 – 3.22)	1.54 (0.03 – 3.05)	-3.39 (-4.00 – -2.71)
β : conspecific in region	1.12 (-0.47 – 2.76)	-3.62 (-4.84 – 2.84)	1.67 (0.09 – 3.29)	-3.35 (-4.01 – -2.63)
β : absent at region	-	-	-	-

***Acer rubrum:* density**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	-0.47 (-1.95 – 1.02)	0.61 (0.08 – 1.14)	-2.06 (-3.51 – -0.71)	-0.23 (-1.13 – 0.65)
α_2 : soil moisture	-2.64 (-6.50 – 1.19)	0.56 (-0.91 – 2.07)	2.44 (-2.34 – 7.30)	3.05 (0.38 – 5.71)
δ_1 : planting height	0.25 (-0.09 – 0.59)	0.20 (0.07 – 0.33)	0.38 (-0.02 – 0.79)	0.22 (0.01 – 0.42)
δ_2 : number of leaves	2.70 (2.07 – 3.37)	-0.38 (-0.51 – -0.26)	2.61 (1.95 – 3.34)	-0.35 (-0.56 – -0.15)
δ_3 : seedling age	0.13 (-0.42 – 0.68)	0.02 (-0.20 – 0.24)	-0.21 (-0.76 – 0.39)	-0.01 (-0.30 – 0.29)
κ_1 : Conspecific BA 10 m	0.73 (-0.60 – 2.13)	0.68 (0.24 – 1.12)	0.00 (-1.58 – 1.58)	-0.09 (-1.01 – 0.83)
κ_2 : Congeneric BA	-0.29 (-1.38 – 0.79)	-0.20 (-0.66 – 0.27)	1.74 (0.23 – 3.28)	0.35 (-0.36 – 1.07)
κ_3 : Conspecific relative BA at site	0.07 (-5.19 – 5.21)	0.02 (-0.87 – 0.90)	-4.08 (-10.90 – 3.00)	0.81 (-0.41 – 2.06)
κ_4 : Congeneric relative BA at site	-0.60 (-2.75 – 1.51)	-0.05 (-2.16 – 2.01)	-0.45 (-2.89 – 2.07)	-1.75 (-5.08 – 1.55)

***Carya glabra:* distance**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	0.73 (-0.70 – 2.18)	-0.21 (-1.16 – 0.71)	-1.76 (-3.05 – -0.52)	-0.74 (-1.43 – -0.05)
α_2 : soil moisture	0.49 (-4.51 – 5.31)	-3.76 (-7.73 – 0.24)	10.13 (5.72 – 14.87)	3.46 (1.44 – 5.55)
δ_1 : planting height	-0.12 (-0.71 – 0.44)	-0.20 (-0.65 – 0.37)	0.28 (-0.28 – 0.82)	-0.04 (-0.30 – 0.20)
δ_2 : number of leaves	0.40 (0.10 – 0.71)	-0.42 (-0.63 – -0.21)	0.79 (0.44 – 1.14)	-0.44 (-0.59 – -0.29)
δ_3 : seedling age	1.38 (0.66 – 2.16)	-0.10 (-0.65 – 0.36)	1.11 (0.46 – 1.81)	0.01 (-0.28 – 0.33)
β : conspecific within 10 m	-0.32 (-2.47 – 2.09)	-2.90 (-3.65 – -2.19)	-0.60 (-2.15 – 0.86)	-3.38 (-3.87 – -2.91)
β : conspecific at site	-1.58 (-3.82 – 0.89)	-2.77 (-3.60 – -1.97)	-0.05 (-1.68 – 1.47)	-3.26 (-3.80 – -2.75)
β : conspecific in region	-	-	-	-
β : absent at region	-2.96 (-5.10 – -0.56)	-2.78 (-3.53 – -2.07)	-0.02 (-1.57 – 1.42)	-3.18 (-3.64 – -2.72)

***Carya glabra:* density**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	0.15 (-1.18 – 1.45)	0.04 (-0.81 – 0.85)	-0.50 (-1.76 – 0.78)	-0.23 (-0.91 – 0.45)
α_2 : soil moisture	-3.51 (-8.65 – 1.36)	-2.57 (-6.27 – 1.05)	19.81 (14.07 – 26.60)	5.30 (3.23 – 7.47)
δ_1 : planting height	0.28 (-0.21 – 0.78)	-0.13 (-0.57 – 0.41)	-0.08 (-0.61 – 0.44)	-0.19 (-0.43 – 0.05)
δ_2 : number of leaves	0.34 (0.06 – 0.63)	-0.42 (-0.60 – -0.23)	0.83 (0.50 – 1.19)	-0.40 (-0.55 – -0.26)
δ_3 : seedling age	0.83 (0.22 – 1.45)	-0.20 (-0.67 – 0.19)	0.98 (0.36 – 1.61)	0.08 (-0.20 – 0.37)
κ_1 : Conspecific BA 10 m	1.40 (0.77 – 2.03)	-0.18 (-0.63 – 0.26)	-0.99 (-1.82 – -0.17)	0.17 (-0.29 – 0.65)
κ_2 : Congeneric BA	-	-	-	-
κ_3 : Conspecific relative BA at site	-	-	-	-
κ_4 : Congeneric relative BA at site	-	-	-	-

***Liriodendron tulipifera:* distance**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	-0.30 (-2.20 – 1.55)	1.88 (1.08 – 2.66)	-0.05 (-1.62 – 1.53)	0.92 (0.02 – 1.82)
α_2 : soil moisture	6.60 (0.19 – 13.13)	0.35 (-2.52 – 3.21)	9.77 (4.25 – 16.21)	4.14 (1.07 – 7.16)
δ_1 : planting height	0.42 (-0.20 – 1.04)	-0.21 (-0.47 – 0.06)	0.73 (0.09 – 1.45)	0.00 (-0.29 – 0.29)
δ_2 : number of leaves	1.07 (0.66 – 1.51)	-0.44 (-0.63 – -0.26)	0.63 (0.21 – 1.07)	-0.86 (-1.09 – -0.64)
δ_3 : seedling age	0.11 (-0.64 – 0.88)	-0.56 (-1.03 – -0.09)	0.02 (-0.68 – 0.73)	-0.04 (-0.38 – 0.26)
β : conspecific within 10 m	-3.86 (-8.19 – 0.60)	-3.70 (-5.01 – -2.60)	-1.41 (-3.82 – 1.23)	-4.28 (-5.27 – -3.28)
β : conspecific at site	-4.32 (-8.63 – 0.16)	-3.60 (-4.87 – -2.53)	-0.85 (-2.95 – 1.53)	-3.96 (-4.85 – -3.05)
β : conspecific in region	-1.92 (-5.91 – 2.24)	-3.74 (-4.71 – -2.97)	-0.22 (-1.66 – 1.54)	-3.97 (-4.45 – -3.49)
β : absent at region	-3.75 (-7.79 – 0.41)	-3.52 (-4.53 – -2.71)	-2.03 (-3.65 – -0.19)	-4.09 (-4.64 – -3.54)

***Liriodendron tulipifera:* density**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	-0.45 (-2.35 – 1.43)	1.90 (1.15 – 2.66)	0.20 (-1.45 – 1.92)	1.17 (0.16 – 2.15)
α_2 : soil moisture	-1.53 (-5.72 – 2.62)	1.28 (-0.20 – 2.71)	9.90 (5.38 – 15.42)	4.90 (3.04 – 6.77)
δ_1 : planting height	0.37 (-0.15 – 0.89)	-0.20 (-0.45 – 0.05)	0.48 (-0.14 – 1.17)	-0.02 (-0.32 – 0.30)
δ_2 : number of leaves	1.09 (0.70 – 1.50)	-0.45 (-0.62 – -0.28)	0.63 (0.23 – 1.05)	-0.83 (-1.05 – -0.61)
δ_3 : seedling age	0.21 (-0.45 – 0.89)	-0.65 (-1.15 – -0.17)	0.11 (-0.58 – 0.80)	-0.07 (-0.43 – 0.25)
κ_1 : Conspecific BA 10 m	-1.94 (-5.26 – 1.08)	-0.40 (-1.82 – 1.03)	-4.14 (-8.97 – 0.53)	-1.51 (-3.46 – 0.48)
κ_2 : Congeneric BA	-	-	-	-
κ_3 : Conspecific relative BA at site	-	-	-	-
κ_4 : Congeneric relative BA at site	-	-	-	-

***Quercus alba:* distance**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	1.28 (-0.68 – 3.28)	-1.74 (-3.71 – 0.11)	-0.38 (-1.75 – 1.00)	-0.51 (-1.40 – 0.39)
α_2 : soil moisture	1.08 (-4.80 – 6.87)	-9.71 (-16.85 – -2.30)	4.24 (-0.58 – 9.48)	1.41 (-1.19 – 4.00)
δ_1 : planting height	0.08 (-0.55 – 0.74)	0.04 (-0.68 – 0.71)	0.69 (0.26 – 1.16)	0.14 (-0.11 – 0.39)
δ_2 : number of leaves	0.30 (-0.11 – 0.72)	-0.60 (-0.97 – -0.22)	0.76 (0.18 – 1.39)	-0.35 (-0.57 – -0.13)
δ_3 : seedling age	0.22 (-0.49 – 0.91)	-0.29 (-1.11 – 0.54)	1.41 (0.86 – 1.98)	0.51 (0.22 – 0.81)
β : conspecific within 10 m	-1.10 (-5.47 – 2.97)	-1.59 (-3.39 – -0.02)	-0.06 (-1.66 – 1.63)	-3.14 (-3.97 – -2.39)
β : conspecific at site	-2.17 (-6.59 – 1.97)	-1.57 (-3.42 – 0.08)	-0.07 (-1.76 – 1.70)	-2.96 (-3.84 – -2.18)
β : conspecific in region	-2.16 (-6.55 – 1.91)	-1.03 (-2.81 – 0.61)	-0.11 (-1.71 – 1.58)	-3.26 (-4.11 – -2.48)
β : absent at region	-3.55 (-7.98 – 0.52)	-1.60 (-3.47 – 0.08)	0.15 (-1.49 – 1.88)	-3.46 (-4.29 – -2.74)

***Quercus alba:* density**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	-1.17 (-3.50 – 1.08)	-0.68 (-2.75 – 1.39)	0.00 (-1.59 – 1.59)	0.40 (-0.66 – 1.44)
α_2 : soil moisture	1.81 (-4.78 – 8.29)	-3.38 (-9.57 – 2.78)	5.31 (-1.26 – 12.33)	0.69 (-2.66 – 4.03)
δ_1 : planting height	0.32 (-0.25 – 0.91)	-0.21 (-0.76 – 0.39)	0.66 (0.21 – 1.15)	0.16 (-0.09 – 0.41)
δ_2 : number of leaves	0.33 (-0.04 – 0.70)	-0.52 (-0.82 – -0.24)	0.74 (0.17 – 1.38)	-0.30 (-0.52 – -0.09)
δ_3 : seedling age	0.00 (-0.67 – 0.65)	-0.58 (-1.29 – 0.12)	1.41 (0.82 – 2.02)	0.52 (0.19 – 0.84)
κ_1 : Conspecific BA 10 m	2.31 (0.50 – 4.15)	-0.39 (-1.77 – 0.98)	0.44 (-1.10 – 1.95)	1.40 (0.19 – 2.62)
κ_2 : Congeneric BA	-0.16 (-0.60 – 0.25)	-0.02 (-0.41 – 0.38)	0.10 (-0.23 – 0.43)	0.16 (-0.07 – 0.40)
κ_3 : Conspecific relative BA at site	-	-	-	-
κ_4 : Congeneric relative BA at site	1.21 (-2.01 – 4.42)	1.57 (-0.89 – 4.09)	0.06 (-2.45 – 2.54)	-2.30 (-4.01 – -0.64)

Quercus rubra: **distance**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	1.00 (0.18 – 1.84)	0.77 (0.21 – 1.34)	-1.85 (-2.74 – -0.98)	-0.58 (-1.14 – -0.03)
α_2 : soil moisture	4.07 (1.82 – 6.38)	-1.47 (-2.90 – -0.06)	2.60 (0.23 – 5.00)	1.39 (0.04 – 2.70)
δ_1 : planting height	-0.06 (-0.39 – 0.28)	0.23 (0.00 – 0.46)	0.27 (-0.02 – 0.56)	0.09 (-0.12 – 0.30)
δ_2 : number of leaves	0.38 (0.15 – 0.61)	-0.64 (-0.80 – -0.48)	1.84 (1.33 – 2.37)	-0.18 (-0.31 – -0.05)
δ_3 : seedling age	0.48 (0.16 – 0.81)	-0.49 (-0.78 – -0.19)	3.14 (2.66 – 3.64)	0.38 (0.21 – 0.56)
β : conspecific within 10 m	-1.10 (-3.08 – 1.18)	-3.28 (-4.11 – -2.55)	1.14 (-0.29 – 2.35)	-2.99 (-3.67 – -2.39)
β : conspecific at site	-0.78 (-2.74 – 1.49)	-3.39 (-4.21 – -2.66)	1.41 (-0.02 – 2.62)	-3.03 (-3.71 – -2.43)
β : conspecific in region	-	-	-	-
β : absent at region	-	-	-	-

Quercus rubra: **density**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	2.80 (1.81 – 3.81)	0.71 (0.05 – 1.37)	-0.29 (-1.29 – 0.71)	-0.15 (-0.75 – 0.44)
α_2 : soil moisture	3.17 (-0.72 – 7.31)	0.49 (-2.01 – 3.07)	2.10 (-1.64 – 6.01)	3.13 (0.83 – 5.44)
δ_1 : planting height	0.04 (-0.24 – 0.33)	0.05 (-0.16 – 0.26)	0.23 (-0.06 – 0.51)	0.04 (-0.17 – 0.24)
δ_2 : number of leaves	0.30 (0.09 – 0.52)	-0.62 (-0.77 – -0.47)	1.79 (1.31 – 2.29)	-0.12 (-0.25 – 0.01)
δ_3 : seedling age	0.76 (0.43 – 1.10)	-0.53 (-0.83 – -0.23)	2.76 (2.27 – 3.27)	0.13 (-0.06 – 0.32)
κ_1 : Conspecific BA 10 m	-0.06 (-0.49 – 0.36)	-0.02 (-0.41 – 0.36)	-0.66 (-1.09 – -0.23)	0.00 (-0.30 – 0.29)
κ_2 : Congeneric BA	0.31 (0.14 – 0.48)	-0.01 (-0.13 – 0.12)	0.48 (0.24 – 0.73)	0.13 (0.01 – 0.24)
κ_3 : Conspecific relative BA at site	1.23 (-1.64 – 4.09)	0.64 (-0.46 – 1.79)	-3.90 (-6.74 – -1.11)	0.52 (-0.52 – 1.58)
κ_4 : Congeneric relative BA at site	-2.42 (-4.22 – -0.63)	2.79 (0.77 – 4.82)	-2.73 (-4.43 – -0.95)	0.24 (-1.45 – 1.94)

Quercus velutina: **distance**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	0.67 (-1.04 – 2.44)	-0.45 (-1.67 – 0.76)	0.45 (-1.66 – 2.74)	-0.59 (-1.40 – 0.21)
α_2 : soil moisture	-7.26 (-12.69 – -2.02)	-4.56 (-8.21 – -0.88)	13.30 (6.32 – 22.31)	3.16 (0.49 – 5.72)
δ_1 : planting height	-0.66 (-1.20 – -0.15)	-0.23 (-0.49 – 0.02)	0.09 (-0.55 – 0.75)	-0.19 (-0.42 – 0.05)
δ_2 : number of leaves	0.26 (-0.19 – 0.69)	-1.00 (-1.31 – -0.69)	2.18 (1.31 – 3.27)	-0.24 (-0.46 – -0.02)
δ_3 : seedling age	-0.32 (-0.95 – 0.30)	-0.81 (-1.50 – -0.06)	1.82 (1.02 – 2.83)	0.64 (0.37 – 0.90)
β : conspecific within 10 m	0.59 (-2.19 – 3.15)	-2.55 (-3.47 – -1.67)	0.65 (-2.32 – 3.24)	-2.90 (-4.14 – -1.72)
β : conspecific at site	2.22 (-0.84 – 5.08)	-1.86 (-3.19 – -0.56)	-1.22 (-4.93 – 1.82)	-3.34 (-4.74 – -1.99)
β : conspecific in region	-0.23 (-3.03 – 2.35)	-2.86 (-3.89 – -1.89)	0.28 (-2.79 – 2.93)	-3.00 (-4.25 – -1.82)
β : absent at region	0.67 (-1.04 – 2.44)	-0.45 (-1.67 – 0.76)	0.45 (-1.66 – 2.74)	-0.59 (-1.40 – 0.21)

Quercus velutina: **density**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	4.25 (2.35 – 6.28)	1.20 (0.22 – 2.17)	-1.98 (-4.55 – 0.46)	-1.20 (-2.02 – -0.37)
α_2 : soil moisture	1.60 (-2.21 – 5.42)	-0.19 (-2.20 – 1.83)	2.10 (-2.67 – 7.17)	1.45 (-0.44 – 3.33)
δ_1 : planting height	-0.24 (-0.72 – 0.24)	0.04 (-0.18 – 0.27)	0.04 (-0.65 – 0.75)	-0.14 (-0.36 – 0.08)
δ_2 : number of leaves	0.34 (-0.08 – 0.75)	-1.05 (-1.32 – -0.77)	2.00 (1.14 – 2.98)	-0.22 (-0.43 – -0.01)
δ_3 : seedling age	-0.12 (-0.82 – 0.57)	-1.06 (-1.66 – -0.30)	1.72 (0.75 – 2.80)	0.42 (0.10 – 0.73)
κ_1 : Conspecific BA 10 m	1.15 (-0.09 – 2.45)	0.16 (-0.42 – 0.73)	1.41 (-0.71 – 3.91)	0.19 (-0.38 – 0.77)
κ_2 : Congeneric BA	0.29 (-0.34 – 0.93)	0.11 (-0.25 – 0.46)	-0.50 (-1.39 – 0.34)	-0.01 (-0.31 – 0.29)
κ_3 : Conspecific relative BA at site	-	-	-	-
κ_4 : Congeneric relative BA at site	2.71 (-1.12 – 6.67)	0.69 (-1.14 – 2.55)	1.08 (-4.58 – 7.28)	0.50 (-1.21 – 2.22)

***Robinia pseudoacacia:* distance**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	0.32 (-0.99 – 1.67)	0.39 (-0.09 – 0.87)	-2.20 (-4.73 – -0.12)	-1.09 (-2.01 – -0.16)
α_2 : soil moisture	6.64 (2.68 – 11.01)	1.17 (-0.59 – 3.01)	10.53 (3.15 – 21.07)	1.36 (-1.13 – 3.85)
δ_1 : planting height	-0.37 (-0.85 – 0.09)	0.27 (0.06 – 0.48)	-0.44 (-1.16 – 0.19)	-0.02 (-0.26 – 0.22)
δ_2 : number of leaves	0.71 (0.26 – 1.20)	-1.05 (-1.32 – -0.78)	3.23 (1.98 – 4.96)	-0.51 (-0.75 – -0.28)
δ_3 : seedling age	-0.41 (-1.05 – 0.16)	-0.35 (-0.66 – -0.04)	0.12 (-0.64 – 0.85)	-0.01 (-0.29 – 0.27)
β : conspecific within 10 m	-1.70 (-4.15 – 0.97)	-3.63 (-4.31 – -2.95)	1.14 (-0.84 – 3.68)	-3.28 (-3.98 – -2.62)
β : conspecific at site	-2.17 (-4.69 – 0.51)	-4.12 (-4.78 – -3.45)	-0.20 (-2.60 – 2.30)	-2.87 (-3.65 – -2.14)
β : conspecific in region	-1.57 (-3.92 – 0.99)	-4.06 (-4.57 – -3.54)	1.03 (-0.78 – 3.39)	-3.02 (-3.58 – -2.50)
β : absent at region	-2.86 (-5.27 – -0.29)	-4.37 (-4.91 – -3.82)	0.12 (-1.67 – 2.42)	-3.48 (-4.08 – -2.96)

***Robinia pseudoacacia:* density**

	disease		herbivory	
	incidence	severity	incidence	severity
α_1 : light	-0.03 (-1.27 – 1.23)	0.32 (-0.18 – 0.83)	-2.92 (-5.42 – -0.84)	-1.19 (-2.10 – -0.28)
α_2 : soil moisture	4.79 (1.28 – 8.39)	1.72 (0.46 – 3.01)	0.59 (-6.05 – 7.72)	1.25 (-1.08 – 3.60)
δ_1 : planting height	-0.22 (-0.66 – 0.22)	0.18 (-0.03 – 0.39)	-0.47 (-1.12 – 0.13)	-0.09 (-0.32 – 0.14)
δ_2 : number of leaves	0.89 (0.43 – 1.39)	-1.03 (-1.29 – -0.77)	3.31 (2.13 – 4.81)	-0.52 (-0.75 – -0.30)
δ_3 : seedling age	-0.67 (-1.30 – -0.10)	-0.33 (-0.64 – -0.02)	0.26 (-0.47 – 0.98)	0.08 (-0.20 – 0.35)
κ_1 : Conspecific BA 10 m	-0.26 (-1.04 – 0.51)	-0.32 (-0.66 – 0.01)	1.42 (-0.04 – 3.10)	-0.24 (-0.75 – 0.26)
κ_2 : Congeneric BA	-	-	-	-
κ_3 : Conspecific relative BA at site	-	-	-	-
κ_4 : Congeneric relative BA at site	-	-	-	-

Chapter IV:

DIFFERENCES IN BIOTIC INTERACTIONS ACROSS RANGE EDGES HAVE ONLY MINOR EFFECTS ON PLANT PERFORMANCE

ABSTRACT

It is widely expected that plant species will expand their ranges poleward in response to climate change. In the process, individuals establishing beyond existing range margins will be exposed to new biotic communities, including different assemblages of natural enemies. The resulting differences in biotic interactions could lead to scenarios of enemy release or biotic resistance, and if the interactions are strong, they could influence plant performance and therefore colonization success. In order to test whether natural enemies will affect range expansion dynamics, we transplanted ten species along a 450 km latitudinal gradient that spanned the range edges of five of these species. The experiment was conducted over five years with > 13,000 seedlings and included pesticide treatments to reduce invertebrate herbivory. We measured foliar damage caused by disease and invertebrate herbivores, seedling survival, light availability, soil moisture, soil nutrient concentrations, and several other variables in nine forests located in four regions along the latitudinal gradient. We found that several species (*Carya glabra, Liriodendron tulipifera, Quercus velutina*, and *Robinia pseudoacacia*) tended to have less foliar disease beyond their range but there were few substantial differences in herbivory across range edges (with the exception of *Liriodendron tulipifera*). After accounting for other variables,

including environmental conditions and vertebrate herbivory, we found that foliar disease decreased survival for five species (*Acer rubrum, Berberis thunbergii, Quercus alba, Quercus rubra,* and *Quercus velutina*) and foliar herbivory reduced survival for three species (*Acer rubrum, Liriodendron tulipifera,* and *Quercus rubra*). However, the effects of these biotic interactions on survival were very small (0 – 7 percent reductions in survival at observed levels of damage after four years), which is verified by the minor effects of the pesticide treatment on seedling survival. As such, our results suggest that foliar herbivores and pathogens are unlikely to play a major role in the range expansion dynamics of these temperate tree species.

INTRODUCTION

Climate change is expected to result in shifts in species distributions as plants and animals track changing temperatures and precipitation (Parmesan and Yohe 2003, Hickling et al. 2006, Crimmins et al. 2011). Predictions of how plant ranges will expand over the coming decades and centuries draw from correlations between current species distributions and climate (Iverson and Prasad 1998, Guisan and Zimmermann 2000, Pearson and Dawson 2003), and paleo-reconstructions of shifts in vegetation composition during previous periods of climate change (Davis 1983, Graumlich and Davis 1993, Petit et al. 2002, Williams et al. 2004). Some studies have found empirical evidence for contemporary latitudinal shifts of tree species distributions in North America (Woodall et al. 2009, Murphy et al. 2010, Boisvert-Marsh et al. 2014, Desprez et al. 2014), whereas others have not (Zhu et al. 2012). One finding that all of these studies share is that species responses are idiosyncratic. The variability in how species distributions respond to climate change highlights the potential importance of non-climatic drivers, such as biotic interactions.

Biotic interactions with natural enemies, competitors, and mutualists have the potential to influence range expansion dynamics of terrestrial plants by systematically affecting the performance of plants establishing beyond their range (hereafter referred to as ‘migrants’) (Cairns and Moen 2004, Moorcroft et al. 2006, Morriën et al. 2010, Wisz et al. 2013, HilleRisLambers et al. 2013). It is increasingly thought that predictions of changes in species distributions in response to climate change should take herbivores and pathogens into account (Van der Putten et al. 2010b, Zarnetske et al. 2012, Svenning et al. 2014). While several studies have investigated how soil communities differentially affect native vs. migrant plants (van Grunsven et al. 2010, Stanton-Geddes and Anderson 2011, Mccarthy-Neumann and Ibáñez

2012), little is known about whether existing above-ground herbivore and pathogen communities will affect latitudinal range expansion.

Populations on the expanding edge of a species distribution often escape from specialist natural enemies, as is shown by an increasing number of case studies from various organisms (Alexander et al. 2007, Menéndez et al. 2008, Phillips et al. 2010b, Patot et al. 2010, Tsai and Manos 2010). This can happen because of low host densities on range edges and because migrant populations on expanding range fronts originate from repeated founding events, each of which offers a chance to leave specialists behind (Phillips et al. 2010a). Moreover, in a greenhouse experiment, successful range expanding plants were less affected by a naïve herbivore (Engelkes et al. 2008). Even if enemy release is transient (Brändle et al. 2008, Mitchell et al. 2010, Diez et al. 2010), it could still help migrant plants outperform native ones, increasing colonization success and overall rates of range expansion (Moorcroft et al. 2006).

However, as range expanding species enter new areas, they will encounter indigenous natural enemies; biotic resistance from the existing community could potentially prevent new plant species from establishing there. There are many examples of native generalist herbivores reducing the performance of plants of exotic (i.e., intercontinental) origin (Levine et al. 2004, Parker et al. 2006). However, there are substantial differences between intra-continental range expansion and inter-continental range expansion (as reviewed in Morriën et al. 2010, Van der Putten et al. 2010). First, natural enemy community composition may not change abruptly at the edge of a plant species range. Second, existing plant communities may contain species that are closely related to the migrant; in this case, specialist natural enemies may transfer quickly (Connor et al. 1980, Bertheau et al. 2010). Scenarios of both enemy release and biotic resistance are possible and only in situ experimental field studies can determine how the net effects of biotic interactions will vary across range edges (Morriën et al. 2010, van der Putten 2011, Renwick and Rocca 2015).

Whether the net differences in biotic interactions are positive or negative, they are likely to have the largest effect on early life stages, which tend to be more strongly affected by density dependent forces (Green et al. 2014, Zhu et al. 2015 but see Piao et al. 2013). Many of the strongest examples of habitat filtering driven by biotic interactions have been found at the seedling stage (HilleRisLambers et al. 2002, Fine et al. 2006, Andersen et al. 2014). This may be in part because small individuals have low energy reserves, are especially vulnerable to biotic and abiotic forces, and tend to have weaker chemical defenses (Myers and Kitajima 2007, Barton and Koricheva 2010, Boege et al. 2011, Massad 2013). If biotic forces have the potential to limit range expansion, the seedling stage would be the first place to look for it.

Here, we test how biotic interactions vary across range edges and assess their effects on plant performance. We use a seedling transplant experiment with ten species of woody plants to answer the following questions: 1) Are migrant species exposed to different amounts of herbivory and disease than in their native range? 2) Do migrant plants have different amounts of herbivory and disease than native plants within particular sites? 3) How important are any differences in herbivory and disease to plant survival? Answers to these questions will help determine whether foliar herbivores and pathogens have the potential to substantially affect colonization success and therefore range expansion dynamics.

METHODS

We initiated a seedling transplant experiment in 2010, and over the following four years we planted seedlings in four regions across a 450 km latitudinal gradient (Fig. 4.1). Species origins varied: two species were native across all regions, five were native or naturalized at some regions and potential migrants at others, and three were exotic invasive species that are common in the southern region and expected to become more important in the Northern region (Table 4.1). We selected species based on their current and predicted distributions (Iverson et al. 2008) and on their light and soil moisture requirements. At each region we established between one and four sites in different forest types, and at each site we planted seedlings in two to 21 plots (Table 4.2; Fig. 4.1). Each plot was composed of between one and three subplots, some of which were used for experimental treatments (see below). Sites and plots were established in a variety of different forest types (Table 4.2; Fig. 4.1) and in a range of environmental conditions (Supporting Information 4.A: Plot Environmental Characteristics). A total of 13,427 seedlings were planted between 2010 and 2013 (Table 4.1).

Seedlings

Wild seeds were collected within Michigan, but if unavailable they were obtained from outside of Michigan (Supporting Information 4.B: Seed Sources). Seeds were germinated at the University of Michigan Matthaei Botanical Gardens (Ann Arbor, MI) in potting soil (Metro-Mix 380; SunGro Horticulture, Agawam, Massachusetts, USA), where they were watered daily. At approximately one month after emergence we measured the height of the seedlings, defined as the distance from the soil to the tip of the apical mertistem, which we used as a proxy for maternal effects (i.e., seed size). Bare root seedlings were then transplanted into the study plots with a minimum distance of 25 cm between seedlings. Existing vegetation was left intact. To decrease transplant shock, seedlings were watered upon planting (125 ml/seedling). A subset of seedlings (2196) were transplanted in the fall instead of in the spring. This was done in 2011, 2012, and 2013 in order to both increase the range of seedling sizes and to increase total sample size.

Pesticide treatment

We experimentally reduced herbivory in 48 sub-plots in 2012 and 2013 using a pyrethroid pesticide (Talstar P, active ingredient bifenthrin; Fecko 1999). This pesticide has been successfully used by other researchers (e.g., Suwa and Louda 2012, Spiers et al. 2006), and does not contain nitrogen. To ensure that it caused no direct effects on the plants, either through phytotoxicity or phytostimulation, we conducted a greenhouse control experiment; survival and relative growth rates were not impacted, although there is mixed evidence of mild phytotoxicity for *Acer rubrum* (Supporting Information 4.C: Greenhouse Control Experiment). We sprayed a solution of bifenthrin (0.008% active ingredient) on the tops and bottoms of the leaves of seedlings in treatment sub-plots three times a year during 2012 and 2013. We sprayed the same amount of water on leaves in paired control sub-plots. We also distributed a molluscicide, metaldehyde, along one outside edge of pesticide sub-plots to reduce herbivory by slugs and snails. The molluscicide was distributed on the side of the treatment plot furthest from the paired control sub-plot; no metaldehyde was distributed within 5 m of a control sub-plot seedling. Metaldehyde reduces slug abundance and herbivory at the microsite level, without impacting plots as close as 5 m (Fergeson 2004). In 2010 and 2011 we built insect exclosures around a subset of first year seedlings, but neither year’s exclosure design consistently reduced herbivory. Only mortality from after the exclosures were removed are included in the analysis.

Seedling measurements

Seedlings were censused three times a year, in early, mid, and late summer. Seedling height (defined as the distance from the soil to the highest bud) and diameter (1 cm above the soil) were measured during the first and last census of each year. Leaf damage was quantified by visually surveying up to 25 leaves per seedling using cover classes (<1%, 1-5%, 6-15%, 16-25%, 26-50%, 51-75%, >75%). For seedlings that had more than 25 leaves, the 25 leaves surveyed were selected at random. To ensure consistent visual estimates, the same person conducted all surveys (D. Katz). During each census foliar damage was categorized as being caused by herbivory, disease, physical damage, or desiccation. Damage types counted as herbivory included chewing (e.g., skeletonizing, window feeding, hole feeding), piercing-sucking (e.g., stippling; regularly shaped small round discolorations in leaves), leaf mining, and galling. Damage was counted as disease if symptoms included abnormal coloration, blackening of the leaf, dark spots with necrosis, spots with discolorations surrounding them, and the presence of fungal fruiting bodies. The disease category therefore includes both infectious and non-infectious diseases (Sinclair and Lyon 2005). We also recorded whether seedlings exhibited stem damage patterns typical of those caused by browsing by mammals at each census; this was recorded as a binary variable. The role of vertebrate herbivores was further investigated using deer exclosures and trail cameras that were deployed at study plots during 2013 and 2014 (Supporting Information 4.D: Vertebrate Herbivory). Although leaf litter was disturbed during censuses, which could have reduced potentially fatal burial in leaf litter (Patterson et al. 2011), this disturbance was consistent for all seedlings at all sites.

Environmental Data

Environmental variables included light conditions, temperature, soil nutrients, and soil moisture. Light was measured using hemispherical canopy photos. Photos were taken 1 m above seedlings, using a Sigma SD14 camera (Sigma Corporation, Japan) with a sigma 4.5 mm circular fisheye lens (Sigma Corporation, Japan). The proportion of total possible sunlight reaching the forest floor, the global site factor (GSF), was calculated using Hemiview (Delta-T Devices, Cambridge, UK). At least two photos were taken per sub-plot in mid-summer, when canopy closure was greatest. Photos were taken under uniform sky conditions (i.e., dusk, dawn, or uniformly cloudy days). GSF was averaged across subplots and across years.

Soil moisture was measured hourly at each site with a HOBO Micro Station Data Logger (Onset Computer Corporation, Pocasset, MA). Volumetric soil water content in the top 7.5 cm of soil was measured in at least six points per sub-plot several times during the growing season with a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, Plainfield, IL, USA). The relationship between soil moisture at the sub-plot level and at the site level was quantified using linear regressions, and these regressions were used to predict soil moisture between censuses; the mean R^2 value was 0.67. For the first census in each spring, soil moisture was estimated from the beginning of the growing season, which we defined as starting after the last day where the minimum temperature fell below -3° C. For other censuses, the soil moisture values used in the analysis were the mean and standard deviation of soil moisture between that census and the previous censuses.

Soil nutrients were measured once using resin packs (Unibest International Corporation, Walla Walla, WA, USA). Resin packs in the southernmost region (A) were deployed between 4/8/2013 – 10/30/2013 and resin packs were deployed from 4/23/2013 - 10/23/2013 in the other regions. Depending on the number of subplots, between two and four resin packs were deployed per plot. Four resin packs could not be retrieved because they were moved by burrowing animals or were otherwise damaged, and no nutrient data are available for the two plots that were not yet established at the time of nutrient pack deployment. Resin packs were retrieved and refrigerated until they were shipped to Unibest for analysis. Analysis was conducted by Unibest; ions were extracted using 2mHCL and the ion exchange resin analysis was conducted using inductively coupled plasmaspectroscopy analysis (Perkin Elmer 3300 DV; Ca, Mg, Mn, P) and FIA Lab Flow Injection (FIA 2500; NO_3^-, NH_4^+).

Statistical Analysis

Differences in foliar herbivory and disease.– To compare foliar disease and herbivory across species and sites, we used ANOVA and conducted post-hoc pairwise comparisons using max-t tests through the multcomp package in R (Hothorn et al. 2008). Max-t tests are robust for comparisons of non-normal distributions, unbalanced sample sizes, and heterogeneity of variances (Herberich et al. 2010). To compare whether herbivory varied between seedlings in control and pesticide treatments, we used Wilcoxan Rank Sum Tests.

Seedling survival– To analyze how herbivory, foliar disease, and region affected seedling survival, we used a counting process in a Cox survival model (Andersen and Gill 1982) in which we took into account both abiotic and biotic variables (light, soil moisture, soil nutrients, seedling maternal effects, mammal browse, and treatment effects [control and pesticide application]). This type of model has been used for seedling survival because it allows for the inclusions of both fixed and random effects and for time dependent covariates (Mccarthy-Neumann and Ibáñez 2012). We only included seedlings that had survived to their second year in this analysis, to minimize any artifacts from transplanting the seedlings and to reduce the effects of seed resources on survival. The likelihood for the model is:

$$N_{it} \sim Poisson(\lambda_{it})$$

where N is whether seedling *i* was found dead at time *t* and λ is estimated as a function of the intrinsic rate of mortality, or hazard h, and the extrinsic risk of mortality, or risk μ:

$$\lambda_{it} = h_t e^{\mu_{it}}$$

Parameter estimation was conducted using a Bayesian approach, which allowed us to incorporate different sources of uncertainty and missing data (Gelman and Hill 2007). The hazard was estimated at each time step, h_t, from a gamma distribution, $h_t \sim Gamma\ (1, 0.05)$. The hazard reflects differences in mortality rates through the course of the experiment that are not accounted for by the risk (e.g., survival rates that are age dependent).

The risk, μ_{it}, was estimated as a function of the covariates included in the analysis, $\mu_{it} = X_{it}\beta$, where X_{it} is the matrix of covariates associated with each seedling *i* at time *t*. β is the vector of fixed effect coefficients associated with each covariate. We explored several different models, including different covariates and random effects (e.g., plot and year) and selected the model with the lowest DIC (Deviance Information Criterion; Spiegelhalter et al. 2002) that allowed us to answer our questions. The final model included a fixed effect for the combination of region and invertebrate herbivory pesticide treatment, random effects for site and plot, and the following covariates (data are described in parentheses): observed proportion of leaf area affected by herbivory over the previous year (continuous: 0 – 1), observed proportion of leaf area affected by disease over the previous year (continuous: 0 – 1), whether or not the seedling was browsed by a mammal since the previous census (binary: 0, 1), seedling height at planting (continuous, 3 – 390 mm), the number of leaves in the previous census (continuous, 0 – 575 leaves), the proportion of available light that reached the seedling (continuous: 0 – 1), volumetric soil moisture since the last census (continuous: 0 – 1), and whether the seedling was planted in the spring or fall (binary: 0, 1). To improve comparisons between variables, we standardized seedling height at time of transplant, the number of leaves, light, and soil moisture. Light and soil moisture were modeled as latent variables characterized by their measured mean and standard deviation for each inter-census time period. Fixed effect coefficients were drawn from non-informative prior distributions: β ~ Normal (0, 1000). The random effects for sites and plots were drawn from a normal distribution: random effect ~ Normal (0, σ^2), where σ ~ Uniform (0, 10). We predicted survival in each region, $\hat{S}_{region}$, at average herbivory and disease levels in that region for each treatment. The proportion of seedlings surviving, $\hat{S}$ was estimated over time (up to five years), under the following conditions: average light, average soil moisture, average transplant height, average number of leaves, no browsing, and spring planting.

$$\hat{S}_{region} \sim Power(e^{-\sum_t^{time} h_t}, e^{xB_{region}})$$

We then simulated survival for control seedlings throughout all regions across the range of possible herbivory values but with no disease and then vice versa.

Survival of each species was modeled separately. Posterior densities of the parameters were obtained by Gibbs sampling (Geman and Geman 1984) using JAGS 3.4 (Plummer 2003) via the rjags package in R (Plummer 2014). Convergence occurred after 1,000 to 10,000 iterations and chains were inspected visually. Each species was run for 40,000 iterations and posterior parameter values were based on postconvergence results. Visualization was conducted using the ggplot2 package in R (Wickham 2009). All analyses were conducted using R (R Core Team 2013).

RESULTS

Differences in herbivory.– We found extensive variation in herbivory across species and sites, but there were few systematic differences in herbivory across range edges; four out of five potential migrant species encountered some sites beyond their ranges where herbivory was higher and others where herbivory was lower than in sites located within their ranges (Fig. 4.2). An exception was *Liriodendron tulipifera;* the three sites within its range were the sites with the highest herbivory levels, although herbivory was only consistently significantly higher at one site within its range than at sites beyond its range. An invasive species, *Elaeagnus umbellata*, experienced less herbivory in the Southern region where it is common and higher herbivory in a Northern region, where it is relatively rare. In general, species showed wide amounts of variation between sites, regardless of migratory status; this is especially apparent for the species that were native at all regions (*Quercus rubra* and *Acer rubrum*). Likewise, migrant species did not tend to have different amounts of herbivory than native species within sites (Supporting Information 4.E: Foliar damage). The pesticide treatment successfully reduced observed herbivory at all sites for three species (Supporting Information 4.F: Efficacy of Pesticide), *Carya glabra*, *Q. velutina,* and *Q. alba,* and significantly reduced herbivory in some regions for the other species (*Q. rubra, A. rubrum, L. tulipifera* and *Robinia pseudoacacia*); in 22 out of 23 comparisons, herbivory was lower in the pesticide plots.

Differences in foliar disease.–Foliar disease varied according to species and region, but four species, *C. glabra, L. tulipifera, Q. velutina,* and *Q. alba*, tended to have lower disease rates at sites beyond their ranges, although these results were not always statistically significant (Fig. 4.3). This resulted in migrant and exotic plants having somewhat lower foliar disease rates than native plants at many sites (Supporting Information 4.E: Foliar damage). However, it should be noted that *Q. rubra*, which was native at all sites, also had higher disease levels at two of the southern sites. For *A. rubrum,* the other species that was native in all areas, there were no consistent latitudinal patterns.

Seedling survival.– Herbivory tended to reduce survival for most species, but parameter estimates for the effects of herbivory on survival were only statistically significant for three species, *A. rubrum*, *Q. rubra,* and *Q. velutina* (Fig. 4.4). In contrast, foliar disease was significantly negative for five out of ten species (Fig. 4.4). However, even for species for which leaf damage had significant negative effects on survival, survival simulations showed it caused only small reductions in survival at average amounts of herbivory (Fig. 4.5) and disease (Fig. 4.6). A full list of parameter estimates for the survival model are given in Table 4.3. Seedling survival in pesticide treatments was rarely significantly higher than in control treatments (Supporting Information 4.G: Modeled survival by treatment and region), and overall differences were minor. Seedling survival was often higher beyond range edges (Supporting Information 4.G), suggesting that contemporary temperatures and growing season length at the sites beyond range edges are not prohibitive for seedlings of these species.

DISCUSSION

The potential importance of biotic interactions to plant range expansion has received increased attention in recent years, but to our knowledge, no previous study has quantified invertebrate herbivory or foliar disease symptoms both within a species native range and in more poleward areas that it is expected to colonize because climate change. Our results reveal that systematic differences in invertebrate herbivory across range edges are relatively uncommon, but do occur. In contrast, several plants tended to have more foliar disease in regions where they are native than in regions where they are migrant. Within many sites, migrant species also tended to have less disease than native species. However, our analysis found only minor effects of foliar herbivory and disease on seedling survival at common amounts of damage. This is supported by results from the pesticide treatment, which was generally effective in reducing herbivory, but resulted in minor and idiosyncratic responses in survival. Thus, our results show that foliar herbivores and disease are unlikely to have strong effects on latitudinal range expansion dynamics of these temperate trees.

Foliar herbivory across range edges.– There were few systematic differences in foliar herbivory across range edges, which demonstrates that invertebrate herbivores are unlikely to play a consistent role in intra-continental range expansion of these species. Although it is possible that enemy release will occur for particular species (e.g., *L. tulipifera*) or in particular forest types, foliar herbivory depended more upon conditions at the site and plot level than upon whether a species was native or a potential migrant. The magnitude of spatial heterogeneity in herbivory between sites is similar to that found by other studies (Adams et al. 2008, Adams and Zhang 2009); if there are regional trends in herbivory, its signal is easily lost in the high inter-site variability. One explanation for why there are not systematic differences is that diet breadth is especially wide for leaf chewing invertebrates in temperate forests (Forister et al. 2015). Enemy release from specialist natural enemies could also be made up for by increases in the amount of herbivory caused by generalists; for example, the invasive species *B. thunbergii* had somewhat lower herbivory rates in the Southern region where it is common compared to in a Northern region, where it was also more likely to experience herbivory by mollusks (Katz, unpublished data).

Foliar disease across range edges.– Several migrant plants tended to have lower levels of foliar disease symptoms outside of their ranges. These findings highlight the relatively higher importance of enemy release from pathogens than from herbivores. The patterns we found are also conservative because our measure of foliar disease includes non-infectious diseases, which are unlikely to be systematically lower beyond a species range. Two of the species that tended to have reduced foliar disease outside of their ranges were *Q. alba* and *Q. velutina*, even though the con-generic *Q. rubra* was common in all regions. This was unexpected, because more closely related plants share more natural enemies, generally facilitating transfer of natural enemies from indigenous relatives to newly arrived plants (Pearse and Hipp 2009, Ness et al. 2011, Gilbert et al. 2015, Parker et al. 2015), and pathogen host range is often somewhat constrained to host phylogeny (Gilbert and Webb 2007). Thus, the species chosen in this study may lead to especially conservative conclusions about the potential for enemy release from foliar pathogens.

The potential for escape from foliar pathogens at range edges is corroborated by other studies on above-ground pathogens (e.g., Alexander et al. 2007), although substantially more work has been conducted on differences in plant-soil interactions across range edges (e.g., van Grunsven et al. 2010, Stanton-Geddes and Anderson 2011, Mccarthy-Neumann and Ibáñez 2012). For one of the focal species, *R. pseudoacacia*, negative soil feedbacks are more common within than beyond its range (Callaway et al. 2011). Similar patterns are also implied by studies that have found correlations between pathogen load and time since plant introduction (Diez et al. 2010, Flory and Clay 2013). There is also evidence of reduced negative soil feedback outside of plant ranges from greenhouse experiments (Engelkes et al. 2008). These patterns may partially result from migrant seedlings not being near adult con-specifics, which reduced negative plant-soil feedback in the same system as this study (Mccarthy-Neumann and Ibáñez 2012). Indeed, even when species encounter the same types of pathogens outside of their range, those strains may be less virulent (Reinhart et al. 2010). One potential explanation for why there seemed to be a stronger signal of enemy release from pathogens than invertebrate herbivores is that invertebrate herbivores in this system could be more on the generalist range of the spectrum (Forister et al. 2015) than the comparable pathogens (Barrett et al. 2009).

Effects of leaf damage on survival. – The modeled effects of foliar herbivory and foliar disease on seedling survival tended to be small. Although even small responses can have important effects at high levels of damage, herbivory and disease each tended to affect less than 10% of leaf area on average. Thus, even though high levels of leaf damage were likely to kill individual seedlings, the effect on a population level was minimal. The effects of foliar damage on survival we report are somewhat smaller than other researchers have reported (e.g., Meiners et al. 2000, Yamazaki et al. 2009, Cleavitt et al. 2011, Coyle et al. 2014), but are corroborated by similar levels of survival between the control and pesticide treatments. Although seedlings that experienced vertebrate herbivory had low survival rates, vertebrate herbivory was rare at our study sites. Thus, even though browse damage has the potential to shift competitive hierarchies for temperate and boreal tree species in the transition zone (Fisichelli et al. 2012), it seems unlikely to have much of an effect on colonization success by migrant seedlings in these forests.

Implications for range shifts in response to climate change. – We found that seedlings from non-native species can establish in areas beyond their current ranges, as have several other studies (Kellman 2004, Ibáñez et al. 2009, Samis and Eckert 2009, Mccarthy-Neumann and Ibáñez 2012). Although we found cases where biotic interactions systematically varied beyond range edges, commonly observed levels of foliar damage did not translate in to substantial effects on seedling survival. However, it is possible that other types of biotic interactions may be more important; for example, below-ground herbivory was not explicitly measured in this study, but can be an important source of damage to plants (Van der Putten et al. 2001, 2003). It will also be important to test for effects on other plant performance metrics; lower growth and reproductive rates beyond range edges can also play a role in determining species distributions (Angert and Schemske 2005). Although much remains to be explored, our findings show that even in cases where biotic interactions vary across range edges, they still may not have important effects on colonization success or range expansion dynamics.

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Table 4.1. Study species

Plant species used in transplant experiments and their residency status at each study region. Species residency status (native, migrant, or invasive) was determined using Little's range maps, FIA data (via the Climate Change Tree Atlas; Prasad et al. 2007- ongoing), and county data from the USDA Plants database and the Michigan Flora Online. In some cases these data sources provide conflicting information, which is indicated with an asterisk. The number of seedlings of each species planted in each region is also included

Species	Species code	Common name	Region A	Region B	Region C	Region D
Acer rubrum	acru	Red maple	Native 487	Native 75	Native 282	Native 0
Quercus rubra	quru	Red oak	Native 1937	Native 345	Native 989	Native 315
Quercus alba	qual	White oak	Native 829	Native 140	Migrant/rare* 344	Migrant 187
Quercus velutina	quve	Black oak	Native 777	Migrant/rare* 417	Migrant 417	Migrant 230
Carya glabra	cagl	Pignut hickory	Native 930	Migrant 344	Migrant 344	Migrant 110
Robinia pseudoacacia	rops	Black locust	Native/ naturalized * 806	Migrant; planted horticulturally 165	Migrant; planted horticulturally 476	Migrant 270
Liriodendron tulipifera	litu	Tulip tree	Native/ naturalized * 836	Migrant 255	Migrant 656	Migrant 255
Berberis thunbergii	beth	Japanese barberry	Invasive/ common 81	Invasive/rare 0	Invasive/rare 121	Invasive/rare 0
Celastrus orbiculatus	ceor	Oriental bittersweet	Invasive/ common 73	Invasive/rare 0	Invasive/rare 114	Invasive/rare 0
Elaeagnus umbellata	elum	Autumn olive	Invasive/ common 112	Invasive/rare 0	Invasive/rare 164	Invasive/rare 0
Total planted			6868	1741	3907	1367

Table 4.2. Study sites
Description of sites used in the transplant experiment. Environmental variables at the plot and sub-plot level are given in Supporting Information 4.A: Plot Environmental Characteristics.

Site	**Longitude (decimal degrees)**	**Latitude (decimal degrees)**	**Average number of frost free days**	**Soil texture**	**Major vegetation**	**Average growing season length (days)**	**Number of plots**
A1	-83.673	42.324	175	loam	maple	205	9
A2	-84.023	42.457	167	sandy loam	oak-maple	203	21
A3	-84.012	42.459	169	sandy loam	oak-hickory	199	2
B1	-85.751	44.218	157	sand	oak-maple	187	8
C1	-84.714	45.553	164	loamy sand	aspen-maple	205	5
C2	-84.682	45.568	180	sand	maple-beech	212	7
C3	-84.673	45.559	180	sand	maple	212	3
C4	-84.748	45.556	118	sand	pine-aspen-oak	146	6
D1	-84.141	46.350	161	loamy sand	oak-maple	179	6

Table 4.3. Survival model parameter estimates

Survival model parameters (mean and standard deviation).indicate effects on mortality (i.e., higher values indicate higher probability of death). Parameters for which there were no data to inform estimates (e.g., browse for *Berberis thunbergii*) are labeled as NA. Likewise, the invasive species were only planted in the spring so the effect of time of planting was not estimated. Parameter estimates that were significantly different from zero (95% CI does not include zero) are in bold.

Species	browse	disease	herbivory	light	number of leaves	planting height	soil moisture	time of planting	site random effect (σ)	plot random effect (σ)
Acer rubrum	0.95 ± 0.59	**2.24 ± 0.53**	**1.53 ± 0.51**	-0.02 ± 0.72	**-1.19 ± 0.2**	0.07 ± 0.14	-0.05 ± 1.22	0.37 ± 0.88	0.51 ± 0.42	0.66 ± 0.14
Quercus rubra	**0.89 ± 0.27**	**1.05 ± 0.25**	**0.69 ± 0.26**	-0.36 ± 0.48	**-1.22 ± 0.1**	0 ± 0.06	**-2.87 ± 0.81**	0.55 ± 0.8	0.37 ± 0.26	0.46 ± 0.07
Quercus alba	**1.54 ± 0.5**	**1.48 ± 0.46**	-0.24 ± 0.93	-0.22 ± 0.93	-0.36 ± 0.2	-0.23 ± 0.17	**-3.54 ± 1.85**	0.93 ± 0.92	0.41 ± 0.4	0.58 ± 0.15
Quercus velutina	-1.12 ± 1.31	**1.72 ± 0.49**	0.55 ± 0.46	-1.03 ± 0.84	**-1 ± 0.18**	-0.09 ± 0.15	1.58 ± 1.37	-0.51 ± 0.94	0.39 ± 0.36	0.54 ± 0.2
Carya glabra	**1.98 ± 0.45**	0.15 ± 0.38	0.68 ± 0.4	-0.94 ± 0.71	**-0.23 ± 0.11**	-0.11 ± 0.07	-2.21 ± 1.34	0.75 ± 0.98	0.81 ± 0.69	0.75 ± 0.14
Liriodendron tulipifera	0.22 ± 0.65	0.18 ± 0.56	**0.88 ± 0.43**	0.37 ± 0.61	**-0.68 ± 0.11**	-0.12 ± 0.08	**-3.79 ± 0.88**	-0.48 ± 0.96	0.28 ± 0.28	0.67 ± 0.12
Robinia pseudoacacia	0.37 ± 0.55	1.76 ± 2.07	0.44 ± 0.71	-0.41 ± 0.73	**-1.21 ± 0.16**	0.12 ± 0.15	0.89 ± 1.18	-0.79 ± 0.97	0.23 ± 0.19	0.24 ± 0.13
Berberis thunbergii	NA	**6.13 ± 2.55**	1.25 ± 1.67	0.7 ± 1.34	**-1.84 ± 0.54**	-0.41 ± 0.45	0.06 ± 3.69	NA	0.7 ± 0.77	0.94 ± 0.5
Elaeagnus umbellata	2.07 ± 1.38	-4.57 ± 5.46	-0.06 ± 2.19	0.73 ± 0.72	**-2.44 ± 0.43**	-0.45 ± 0.24	-1.55 ± 2.15	NA	0.46 ± 0.69	0.23 ± 0.19
Celastrus orbiculatus	1.22 ± 0.7	1.56 ± 1.85	2.49 ± 1.71	2.2 ± 1.12	**-1.34 ± 0.39**	**-0.7 ± 0.33**	-0.78 ± 3.5	NA	1.16 ± 1.08	1.2 ± 0.61

Figure 4.1. Study design
The distribution of study **regions** in North America (left panel) encompasses the approximate range edges of several focal species (line between regions A and B). Each region (A - D) contained one to four **sites**, each located in distinct forest types (sites C1 - C4 for region C). Each site had between two and 21 **plots** (gray boxes) and a datalogger (star). Each plot had between one and three subplots (white boxes), in which **seedlings** were planted (black circles).

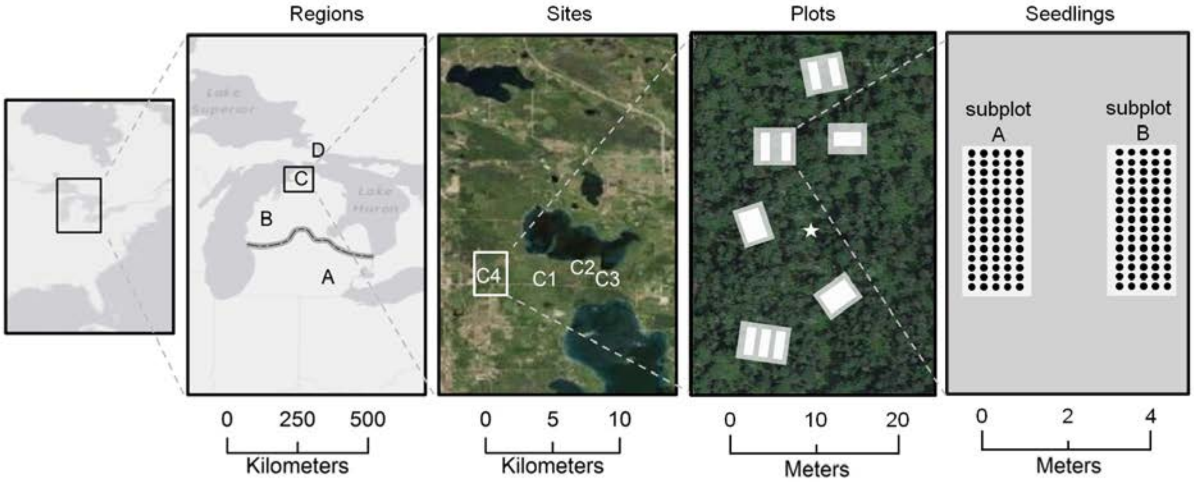


Figure 4.2. Boxplots of foliar herbivory

Boxplots of the proportion of leaf area affected by foliar herbivory in midsummer for each species across the latitudinal gradient, which extended from the southern region (A) to the northernmost region (D). The box consists of the first, second, and third quartiles, the whiskers extend to the 10th and 90th percentiles, the mean is shown with a circle, the sample size is shown below the boxplot for each site, and different letters above the whiskers represent significant differences in foliar herbivory between sites. Boxplot tone represents migratory status (medium gray = native, light gray = migrant, and dark gray = invasive). Data from seedlings in experimental treatments are not shown.

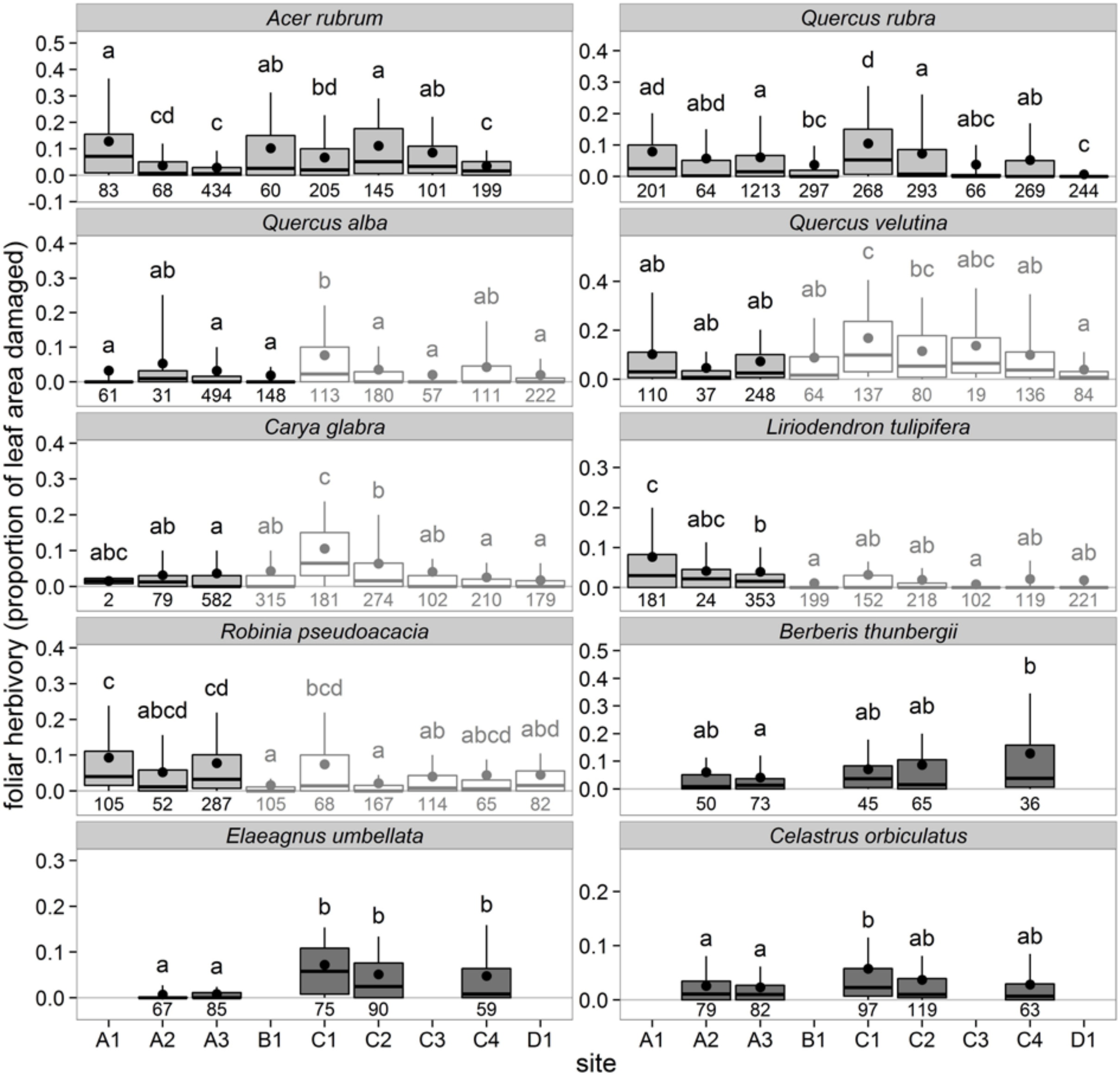


Figure 4.3. Boxplots of foliar disease

Boxplots of the proportion of leaf area affected by foliar disease in midsummer for each species across the latitudinal gradient, which extended from the southern region (A) to the northernmost region (D). The box consists of the first, second, and third quartiles, the whiskers extend to the 10^{th} and 90^{th} percentiles, the mean is shown with a circle, the sample size is shown below the boxplot for each site, and different letters above the whiskers represent significant differences in foliar disease between sites. Boxplot tone represents migratory status (medium gray = native, light gray = migrant, and dark gray = invasive).

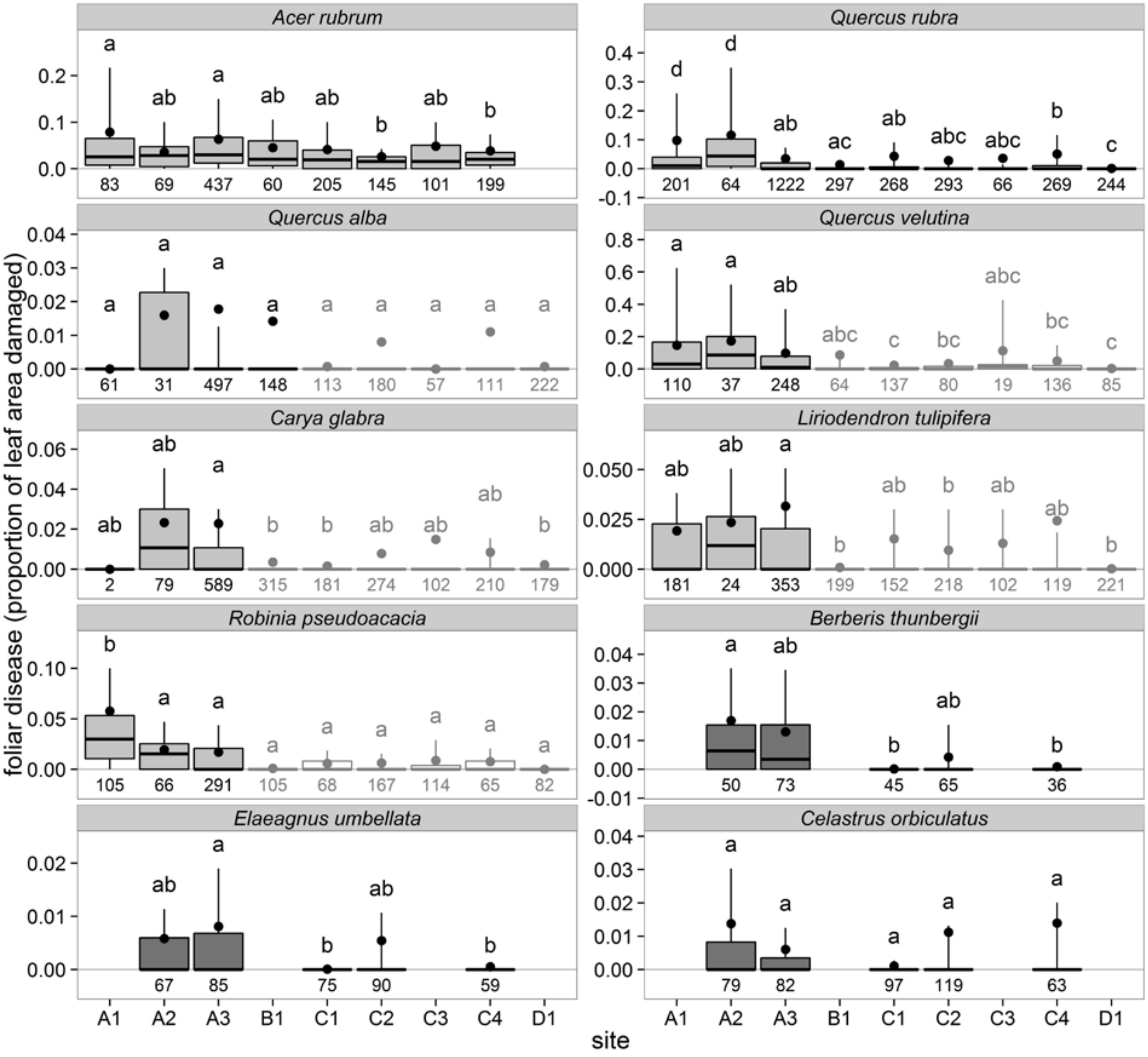


Figure 4.4. Parameter estimates for the effects of disease and herbivory

Effects of foliar herbivory and foliar disease on seedling survival (estimates from the mortality model are multiplied by -1). Parameter estimates below 0 indicate a negative effect on survival; 95% credible intervals that cross zero are not statistically significant. The invasive species (beth, ceor, and elum) had higher variability because of lower sample sizes.

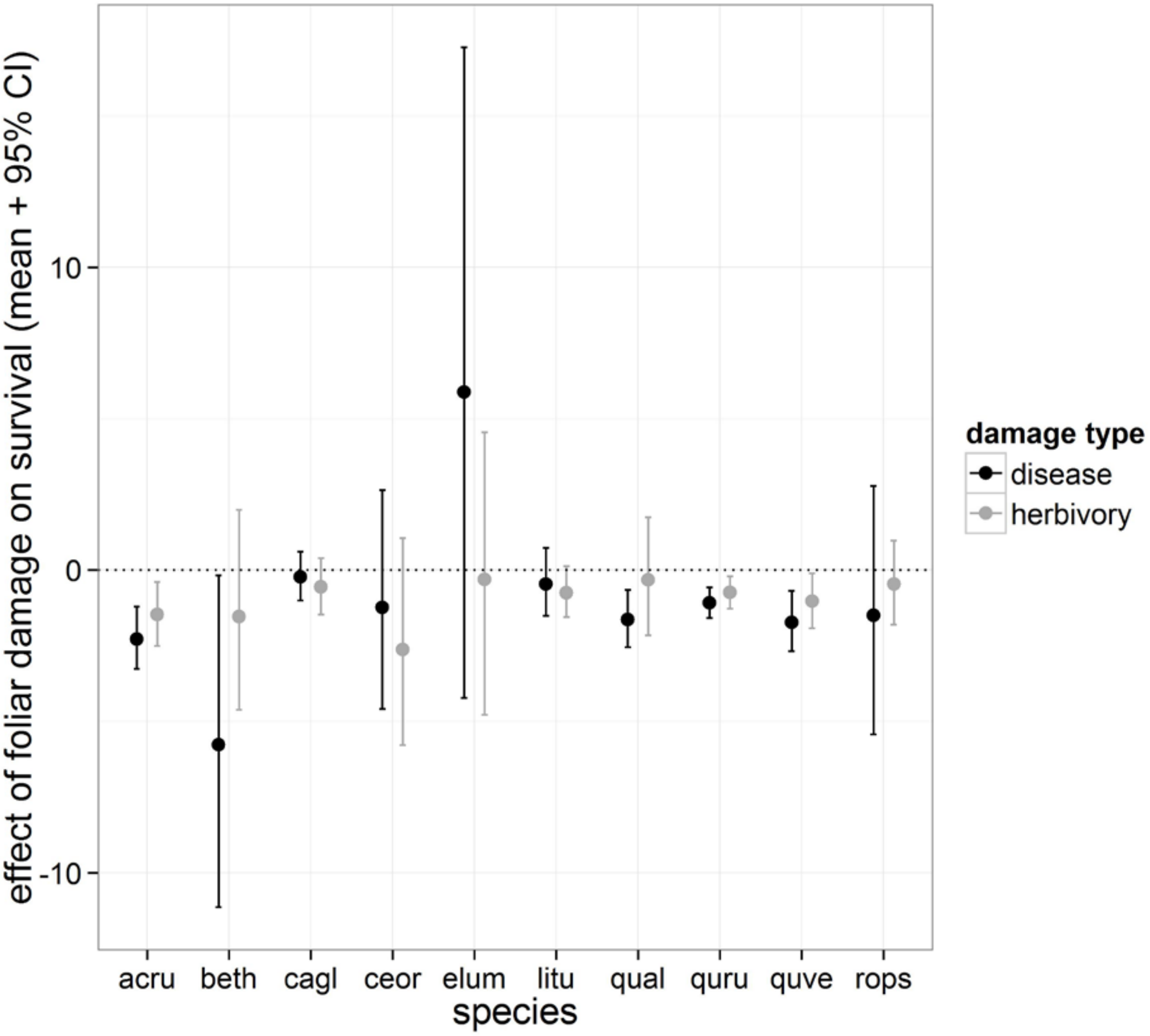


Figure 4.5. Simulated seedling survival as a function of herbivory

Simulated seedling survival at invertebrate herbivory levels ranging from 0% (light) to 100% (dark). Simulations assumed average environmental conditions, planting height, number of leaves, and spring planting with no foliar disease or vertebrate herbivory. The dotted line shows simulated survival at the average level of observed herbivory across all regions. Simulations begin one year after planting. The simulations for *Quercus alba* and *Elaeagnus umbellate* are not shown because there was no evidence for a negative effect of disease on survival.

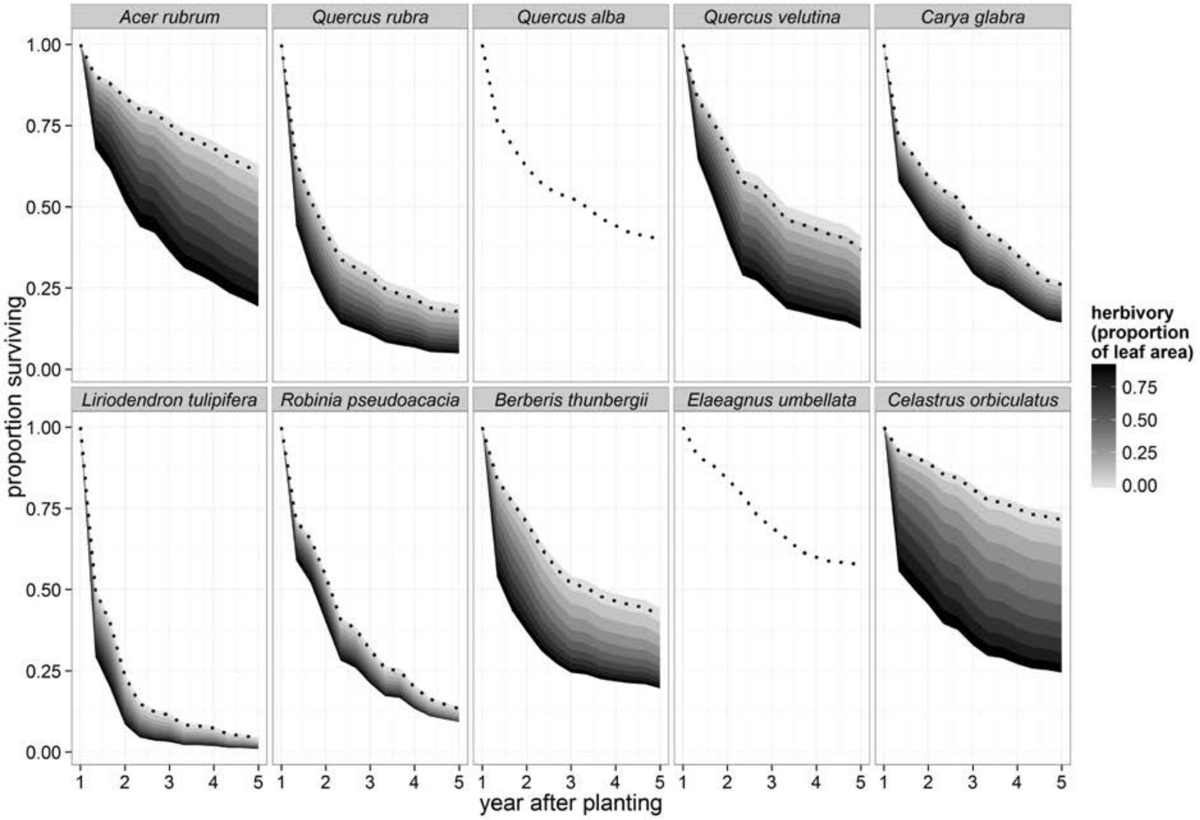
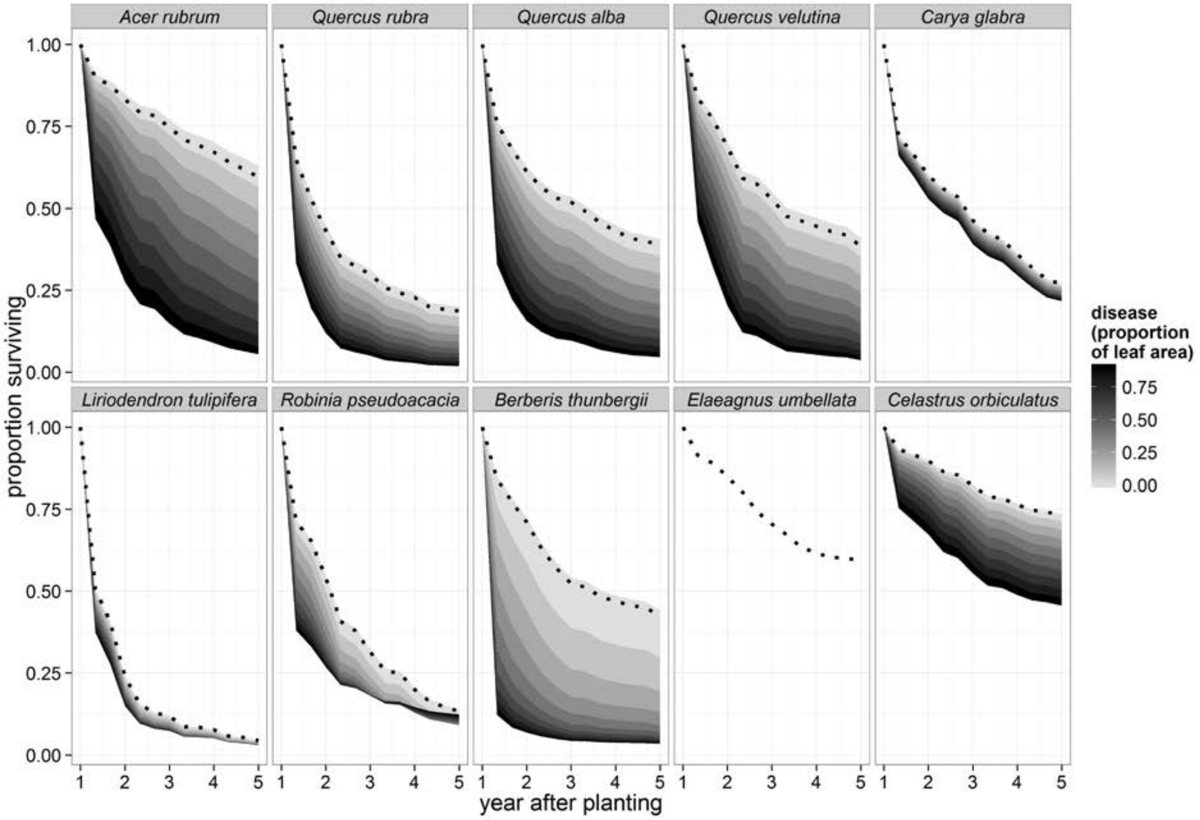


Figure 4.6. Simulated survival as a function of disease

Simulated seedling survival at disease levels ranging from 0% (light) to 100% (dark). Simulations assumed average environmental conditions, planting height, number of leaves, and spring planting and no herbivory. The dotted line shows simulated survival at the average level of observed foliar damage due to disease across all regions. Simulations begin one year after planting. The simulations for *Elaeagnus umbellate* are not shown because there was no evidence for a negative effect of disease on survival.



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Supporting Information 4.A. Plot environmental characteristics.

Table SI 4.4. Plot environmental characteristics.

Light is measured as GSF, the proportion of light that is available at one meter above ground, relative to full sun (0 is no light, 1 is full light); values presented here are averaged across both years and subplots. Soil moisture is the average volumetric soil moisture at each plot during the growing season, averaged across years; the standard deviation is across years. Although light and soil moisture are given at the plot level in this table, measurements at the subplot and subplot section were used in the survival analysis. Soil nutrient values were determined using resin capsules and the average value for resin capsules at each plot are presented.

Site	Plot	Light (± SD)	Soil moisture (± SD)	NO_3	NH_4	P	Ca	Mg	Mn
A1	105	0.06 ± 0.02	0.23 ± 0.10	6.80	6.80	4.53	0.37	207.60	50.07
A1	109	0.08 ± 0.03	0.23 ± 0.11	19.84	19.84	12.43	1.50	268.69	69.31
A1	110	0.10 ± 0.03	0.23 ± 0.10	20.31	20.31	2.86	0.41	203.18	47.02
A1	112	0.11 ± 0.02	0.21 ± 0.07	31.10	31.10	6.15	0.46	200.33	44.74
A1	113	0.07 ± 0.02	0.21 ± 0.07	42.23	42.23	5.85	1.18	271.32	48.65
A1	130	0.06 ± 0.02	0.19 ± 0.05	75.47	75.47	6.70	0.48	185.07	36.84
A1	131	0.07 ± 0.02	0.20 ± 0.05	39.90	39.90	6.22	0.31	140.22	35.33
A1	132	0.09 ± 0.02	0.15 ± 0.06	15.87	15.87	4.60	0.16	58.53	14.55
A1	133	0.09 ± 0.02	0.25 ± 0.08	NA	NA	NA	NA	NA	NA
A2	103	0.75 ± 0.14	0.09 ± 0.02	8.03	8.03	7.73	0.44	36.25	8.39
A2	104	0.16 ± 0.06	0.10 ± 0.02	9.29	9.29	8.03	0.21	34.00	11.33
A3	101	0.10 ± 0.07	0.13 ± 0.02	8.48	8.48	5.59	0.72	63.40	15.70
A3	102	0.34 ± 0.15	0.10 ± 0.01	7.15	7.15	6.91	0.22	26.49	8.83
A3	106	0.14 ± 0.05	0.11 ± 0.01	7.47	7.47	6.44	0.22	23.84	5.40
A3	107	0.16 ± 0.05	0.10 ± 0.01	5.42	5.42	4.58	1.10	13.80	8.13
A3	108	0.54 ± 0.09	0.10 ± 0.00	11.06	11.06	8.86	1.40	42.22	14.73
A3	114	0.12 ± 0.03	0.11 ± 0.01	3.12	3.12	2.92	0.26	22.82	5.44
A3	115	0.15 ± 0.05	0.09 ± 0.01	8.28	8.28	7.83	1.02	24.62	11.77
A3	116	0.13 ± 0.06	0.08 ± 0.01	8.59	8.59	5.80	1.15	43.62	15.95
A3	117	0.10 ± 0.05	0.09 ± 0.01	5.94	5.94	4.92	0.93	43.59	13.88
A3	118	0.16 ± 0.06	0.08 ± 0.01	9.26	9.26	6.89	0.49	40.43	10.60
A3	119	0.06 ± 0.02	0.10 ± 0.01	5.09	5.09	2.56	0.43	69.78	12.09
A3	120	0.10 ± 0.03	0.08 ± 0.01	5.08	5.08	4.38	1.60	44.60	9.37
A3	121	0.10 ± 0.03	0.12 ± 0.01	9.72	9.72	7.94	1.22	64.43	16.89
A3	122	0.11 ± 0.03	0.11 ± 0.01	5.70	5.70	5.58	0.11	15.51	4.72
A3	123	0.07 ± 0.02	0.11 ± 0.01	4.38	4.38	3.54	1.12	37.23	10.02
A3	124	0.08 ± 0.02	0.12 ± 0.01	8.66	8.66	8.05	0.80	18.39	5.76
A3	125	0.13 ± 0.05	0.11 ± 0.02	3.75	3.75	3.04	0.24	27.55	6.42
A3	126	0.15 ± 0.05	0.11 ± 0.01	2.64	2.64	2.41	0.37	31.55	6.94
A3	127	0.10 ± 0.05	0.12 ± 0.01	1.80	1.80	1.76	0.14	17.58	4.28
A3	128	0.50 ± 0.06	0.09 ± 0.00	5.16	5.16	4.72	0.91	39.59	17.87
A3	129	0.13 ± 0.02	0.09 ± 0.01	3.58	3.58	2.78	0.33	21.87	5.64
B1	301	0.08 ± 0.03	0.11 ± 0.04	6.19	6.19	3.85	2.60	19.63	5.44

B1	302	0.06 ± 0.01	0.13 ± 0.04	9.96	9.96	8.57	0.57	35.62	6.18
B1	303	0.09 ± 0.03	0.10 ± 0.03	17.90	17.90	4.11	2.55	37.89	8.72
B1	304	0.10 ± 0.03	0.13 ± 0.04	17.29	17.29	7.68	1.26	70.19	11.16
B1	305	0.10 ± 0.05	0.11 ± 0.04	10.77	10.77	9.69	1.32	32.28	6.60
B1	306	0.07 ± 0.01	0.12 ± 0.05	10.62	10.62	6.20	1.32	78.44	9.56
B1	307	0.19 ± 0.05	0.07 ± 0.02	8.85	8.85	8.71	0.44	17.82	5.20
B1	308	0.12 ± 0.05	0.09 ± 0.04	26.02	26.02	14.30	4.12	75.50	11.36
C1	207	0.12 ± 0.03	0.20 ± 0.01	5.88	5.88	4.68	2.01	53.06	10.93
C1	208	0.14 ± 0.04	0.18 ± 0.01	4.84	4.84	4.65	1.17	27.70	5.72
C1	210	0.14 ± 0.04	0.11 ± 0.01	6.22	6.22	5.37	2.19	17.61	3.51
C1	219	0.12 ± 0.04	0.12 ± 0.01	5.88	5.88	5.25	0.79	22.45	5.44
C1	221	0.08 ± 0.02	0.10 ± 0.01	3.56	3.56	3.06	2.02	33.92	6.29
C2	201	0.10 ± 0.04	0.13 ± 0.05	15.15	15.15	10.47	2.20	83.82	16.11
C2	202	0.08 ± 0.04	0.12 ± 0.04	4.44	4.44	2.89	1.83	72.07	10.02
C2	211	0.10 ± 0.04	0.15 ± 0.04	11.94	11.94	6.88	1.83	69.56	14.95
C2	213	0.07 ± 0.03	0.12 ± 0.03	8.39	8.39	5.34	0.60	83.69	16.11
C2	214	0.08 ± 0.02	0.10 ± 0.03	4.59	4.59	3.82	0.77	64.23	7.03
C2	218	0.12 ± 0.03	0.11 ± 0.03	6.00	6.00	5.50	1.56	53.09	8.42
C2	220	0.07 ± 0.04	0.13 ± 0.03	16.41	16.41	8.34	7.70	90.89	19.55
C3	212	0.14 ± 0.06	0.10 ± 0.03	5.77	5.77	5.27	0.24	32.93	8.57
C3	216	0.11 ± 0.06	0.09 ± 0.02	7.23	7.23	6.49	0.62	49.76	12.78
C3	217	0.17 ± 0.03	0.09 ± 0.03	6.26	6.26	5.06	0.44	44.20	11.60
C4	203	0.21 ± 0.08	0.09 ± 0.01	6.41	6.41	3.83	3.20	28.32	8.17
C4	204	0.54 ± 0.09	0.08 ± 0.01	5.12	5.12	3.42	0.82	34.55	10.06
C4	209	0.58 ± 0.05	0.06 ± 0.01	5.10	5.10	4.51	0.68	24.90	7.24
C4	215	0.46 ± 0.06	0.06 ± 0.01	5.00	5.00	3.97	1.78	14.24	5.72
C4	222	0.44 ± 0.08	0.07 ± 0.01	3.01	3.01	2.49	0.99	16.55	6.07
C4	223	0.34 ± 0.08	0.07 ± 0.01	5.67	5.67	4.22	1.48	11.96	4.77
D1	401	0.10 ± 0.03	0.18 ± 0.05	9.23	9.23	9.23	1.69	122.23	30.99
D1	402	0.15 ± 0.05	0.13 ± 0.03	4.50	4.50	4.39	0.72	24.88	5.29
D1	403	0.26 ± 0.04	0.14 ± 0.04	8.23	8.23	5.93	3.40	43.92	6.33
D1	404	0.16 ± 0.04	0.13 ± 0.04	4.96	4.96	4.60	1.19	13.32	3.33
D1	405	0.61 ± 0.04	0.11 ± 0.02	6.75	6.75	6.66	0.39	14.33	2.49
D1	406	0.10 ± 0.03	0.10 ± 0.01	NA	NA	NA	NA	NA	NA

Supporting Information 4.B. Seed sources.

Table SI 4.5. Seed sources.

Seed sources for transplanted seedlings by Michigan county or, if local seeds were unavailable that year, by state of origin. Seeds that originated outside of Michigan were purchased from Sheffield's Seed Co (Locke, NY, USA).

Species	Seed sources
Acer rubrum	Calhoun, Cheyboygan, Manistee, Newaygo, KY, PA
Berberis thunbergii	Barry, Jackson, Washtenaw
Celastrus orbiculatus	Oakland, Jackson, Wayne
Elaeagnus umbellata	Ingham, Jackson
Carya glabra	Ingham, Livingston, Oakland, Washtenaw, IA
Liriodendron tulipifera	Washtenaw, Wayne, KY
Quercus alba	Ingham, Oakland
Quercus rubra	Berrien, Ingham, Livingston, Roscommon, Wayne, Washtenaw, Van Buren
Quercus velutina	Allegan, Waterloo, Wayne, IL
Robinia pseudoacacia	Ingham, Washtenaw

Supporting Information 4.C. Greenhouse control experiment

We conducted a greenhouse control experiment in order to test for any direct effects of the pesticide Talstar P (bifenthrin) on seedling growth and survival. A subset of seedlings (20 per species) were transplanted in to pots at Matthaei Botanical Garden (University of Michigan, Ann Arbor, MI). These seedlings were planted in soils that were composed of a combination of peat, vermiculite, and perlite. Nutrient concentrations in these soils were comparable to those at established plots (NO_3: 0.52, NH_4: 12.73, Ca 9.88, P 1.81; compare to Supporting Information 4.A: Plot Environmental Characteristics). Seedlings for this experiment were transplanted at the same time as other seedlings were transplanted to the field and were grown for four months. Seedling height, diameter, and wet weight were measured before transplanting. Each seedling was enclosed in mesh netting to prevent herbivory on the seedlings (invertebrate herbivores are uncommon but not entirely absent from the greenhouse used). Seedlings were watered bi-weekly. Pesticide was applied at the same rate and frequency to half of the seedlings; water was applied in the same manner to the other seedlings. At the end of the greenhouse control experiment, seedlings were measured, harvested, and dried in a drying oven at 80° C for 72 hours. Individual seedling components (leaves, stems, roots) were weighed separately. A similar experiment was also conducted in 2012, although seedlings were watered daily and grown in higher light conditions and in potting soil (NO3: 0.45, NH4: 16.84, Ca 7.02, P 1.44); the results of both are reported below, although the environmental conditions in 2013 are more representative of field conditions. Differences between treatments for each species within each year were calculated using t tests.

There were no significant differences between seedling survival in treatments (SI 4.C.Fig. 7), and only small differences in seedling biomass (S.I. 4.C.Fig. 8), height (S.I. 4.C.Fig. 9) and diameter (S.I. 4.C.Fig. 10). There were two significant differences in between treatments: *Quercus alba* had higher mass in the pesticide treatment in 2013 ($p = 0.01$), and *Acer rubrum* had higher growth in diameter in control plots in 2013 ($p = 0.04$). However, neither difference was significant in 2012 or significant for other response variables.

Figure SI 4.7. Greenhouse control experiment: survival

Seedling survival in control and pesticide treatments in 2012 and 2013. *Quercus velutina* was not planted in 2012 and *Carya glabra* was not planted in 2013 due to a lack of availability.

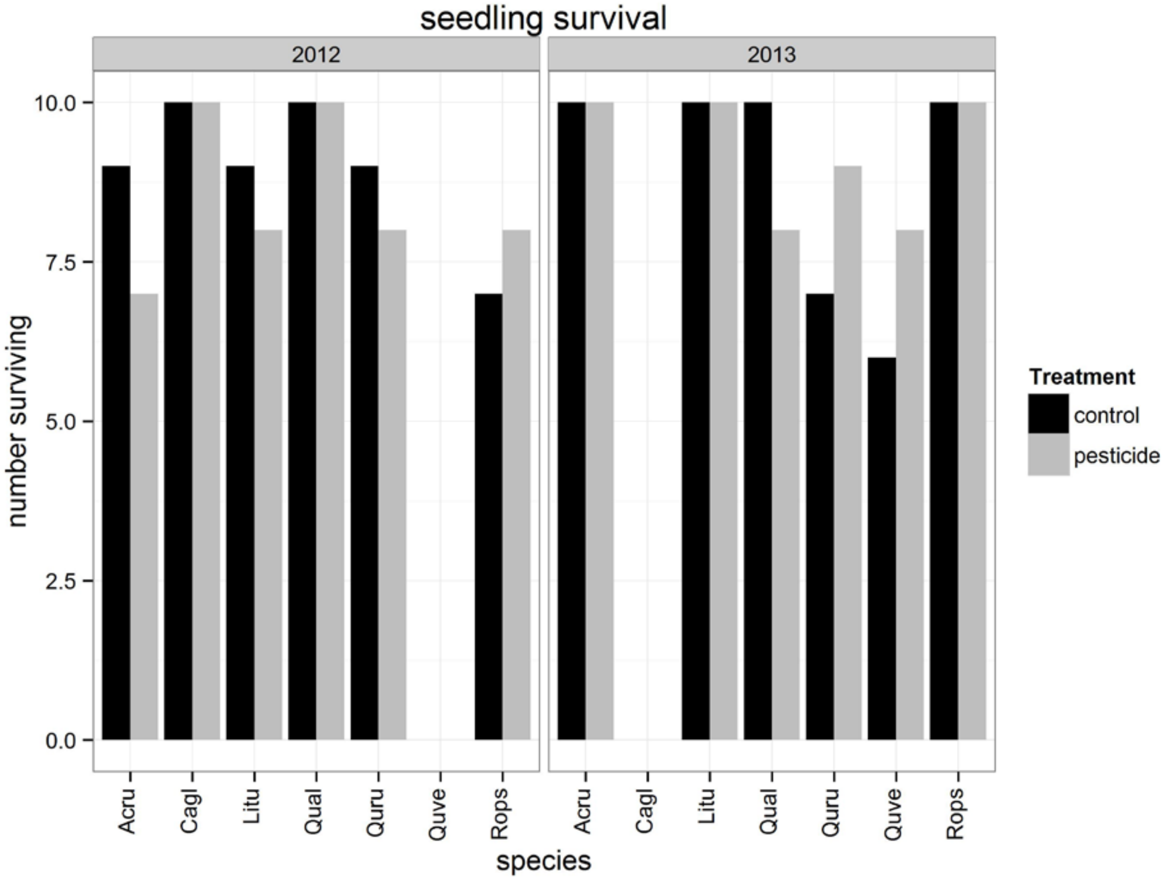


Figure SI 4.8. Greenhouse control experiment: dry biomass

Seedling dry biomass in control and pesticide treatments. Higher growth in 2012 reflects higher soil moisture and light availability (as described above). A significant difference between treatments is denoted with an asterisk.

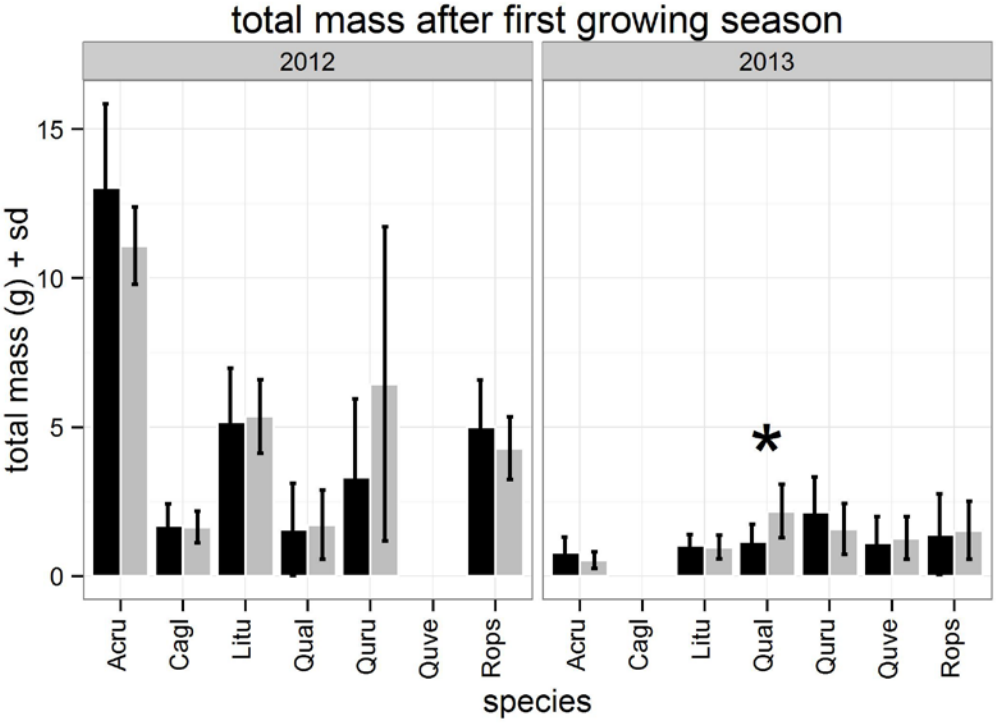


Figure SI 4.9. Greenhouse control experiment: height

Difference in seedling height between transplanting and harvesting in control and pesticide treatments. Higher growth in 2012 reflects higher soil moisture and light availability.

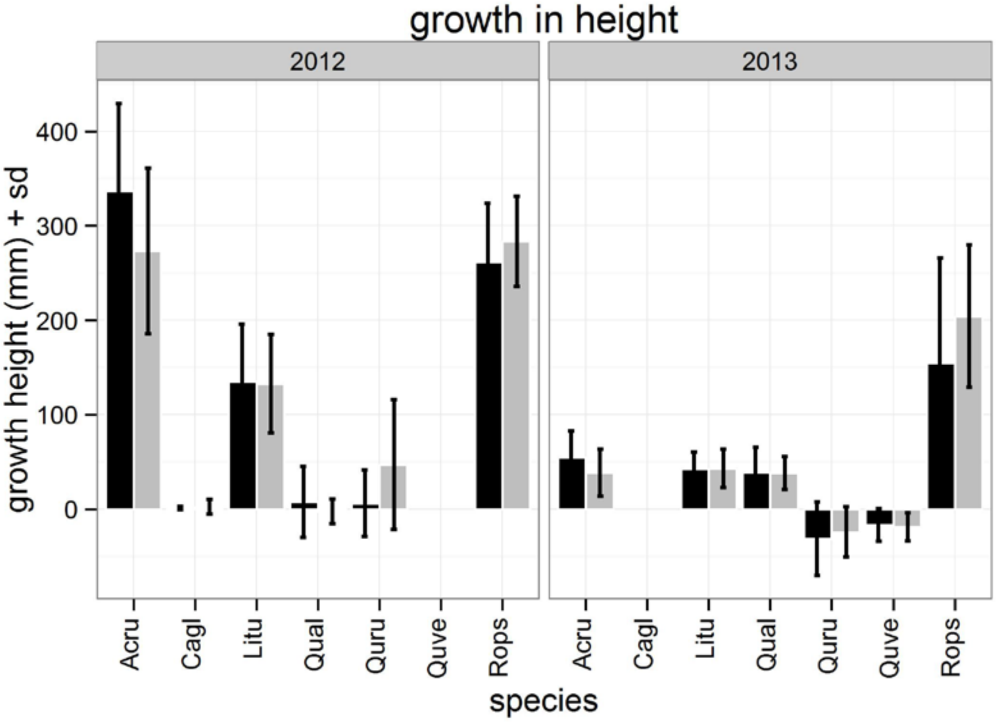
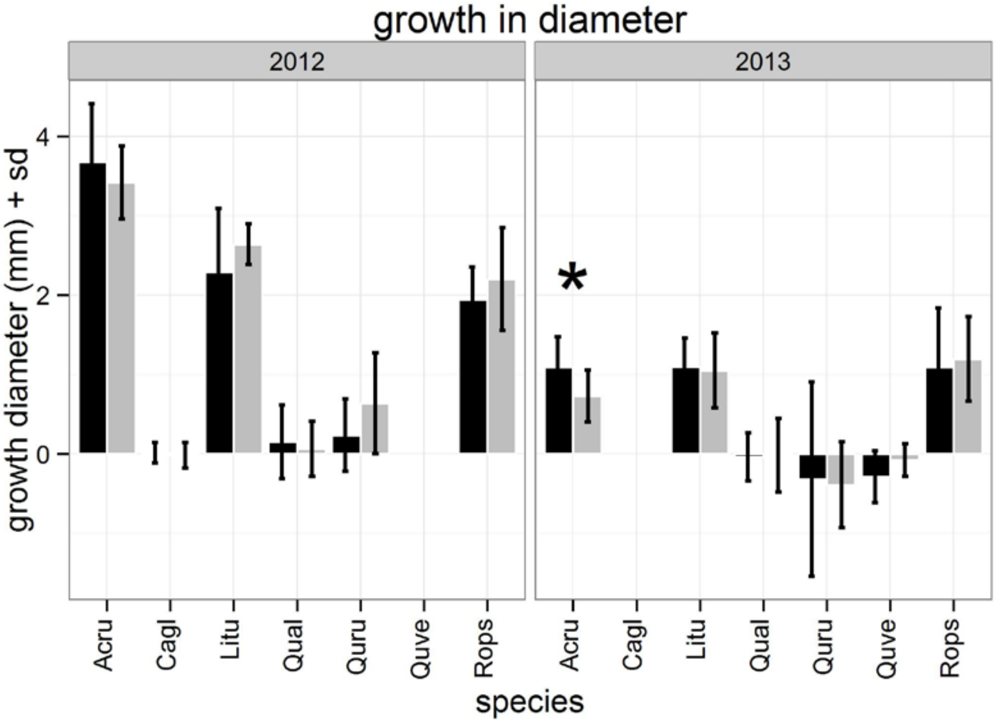


Figure SI 4.10. Greenhouse control experiment: diameter

Difference in seedling diameter between transplanting and harvesting in control and pesticide treatments. Higher growth in 2012 reflects higher soil moisture and light availability. A significant difference between treatments is denoted with an asterisk.



Supporting Information 4.D. Vertebrate herbivory

We monitored vertebrate herbivores and herbivory using three techniques: recording browse on individual seedlings, determining vertebrate community composition and activity using trail cameras, and constructing deer exclosures. Browsing was recorded at each census for seedlings that exhibited damage patterns characteristic of those caused by white-tailed deer (*Odocoileus virginianus*). This type of damage can be identified visually by missing stems where one edge of the seedling's bark is ragged and remains attached. The highest browse rates recorded in a site approached 6% of seedlings browsed per year; average rates were far lower (SI 4.D.Fig. 1).

Deer exclosures were constructed at five sites using 2 m high wire fencing. Similarly designed deer exclosures from a related experiment were built at two other sites. Although deer are able to jump higher than 2 m, no browse or other signs of deer activity were detected within a deer exclosure. Because of the high variability in plant performance between plots, and low overall browse rates, no differences were observed between seedling survival in deer exclosures and adjacent plots. The visual estimates of deer browsing on individual seedlings provided higher resolution measurements of the effects of deer browse, so deer exclosures were not used in the analysis.

Trail cameras (M880 Game Camera, Moultrie, Alabaster, AL, USA) were also installed at each site to characterize vertebrate community composition. Motion activated trail cameras were placed at ~ 1 m above ground and were deployed in at least two plots per site in 2013 and 2014. Unfortunately, camera theft and malfunction reduced coverage at several sites. Community composition varied according to site, but the most common animals photographed were white tailed deer (SI 4.D Figure 2). These data were not used in the analysis.

Figure SI 4.11. Vertebrate herbivory: observed browse

Proportion of seedlings browsed per site per year by deer. No species were browsed at all sites that they were planted in.

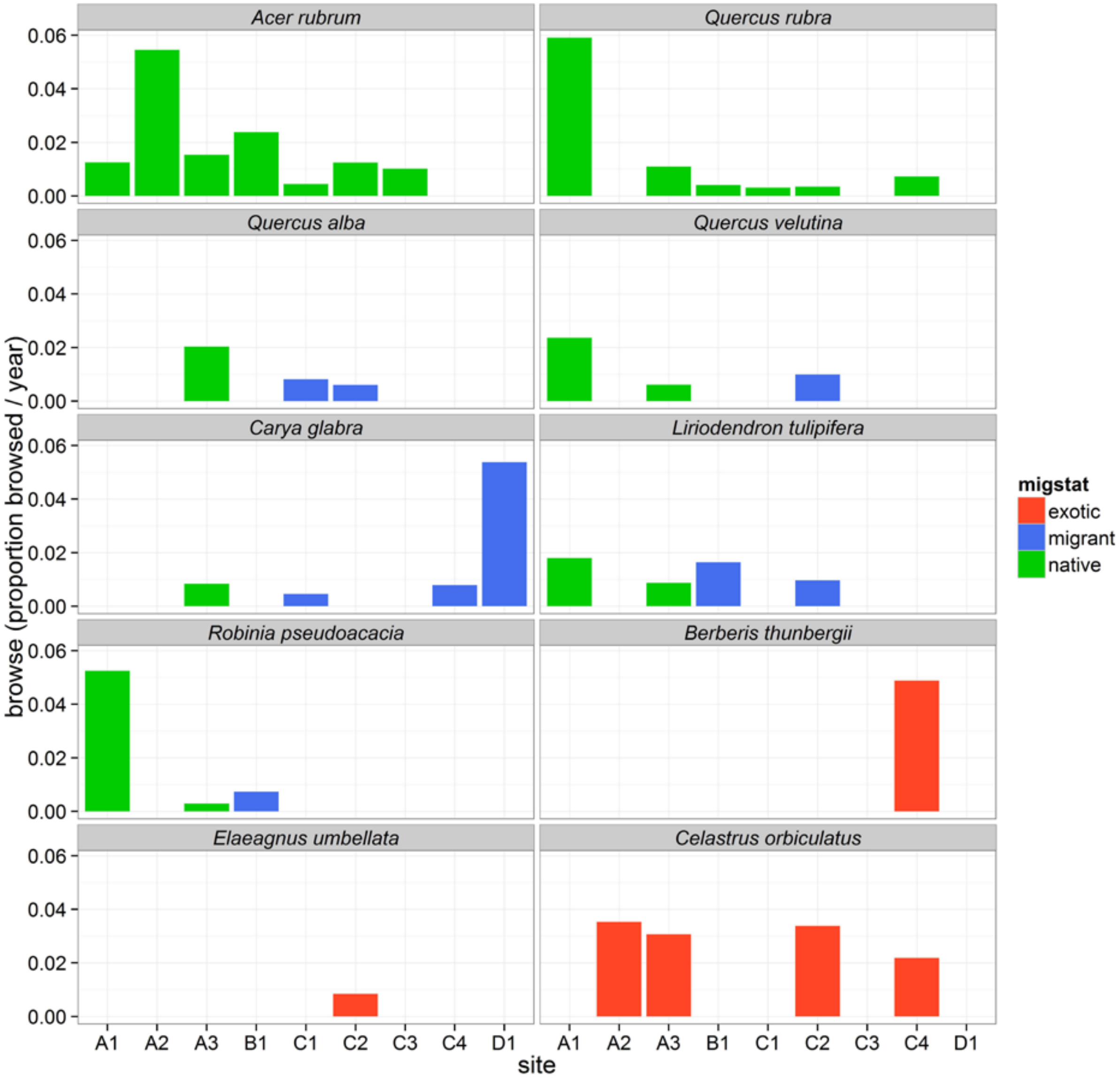
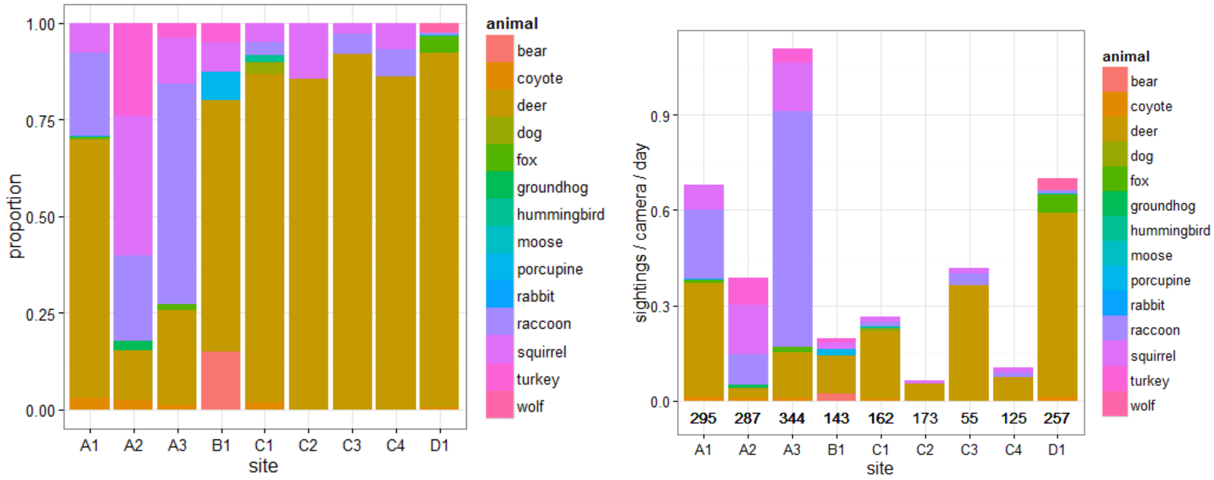


Figure SI 4.12. Vertebrate herbivory: vertebrate community composition

Vertebrate community composition according to site. Relative composition is shown in panel A and the number of sightings per camera per day are shown in panel B. The total number of camera days are given below the bars in panel B.



Supporting Information 4.E. Foliar damage for each species at each site

In this section, we compared foliar damage between species within each site. This was done for herbivory (Fig. SI 4.13.) and for disease (Fig. SI 4.14.).

Figure SI 4.13. Boxplot of leaf area affected by foliar herbivory at each site

The box consists of the first, second, and third quartiles, the whiskers extend to the 10^{th} and 90^{th} percentiles, the mean is shown with a triangle, the sample size is shown for each site, and different letters above the whiskers represent significant differences in foliar herbivory between sites. Colors represent migratory status (green = native, blue = migrant, and red = invasive). Herbivory was measured in spring, mid-summer, and late summer; this graph uses average across seasons for each seedling in each year of the experiment. Data from seedlings in experimental treatments are not shown.

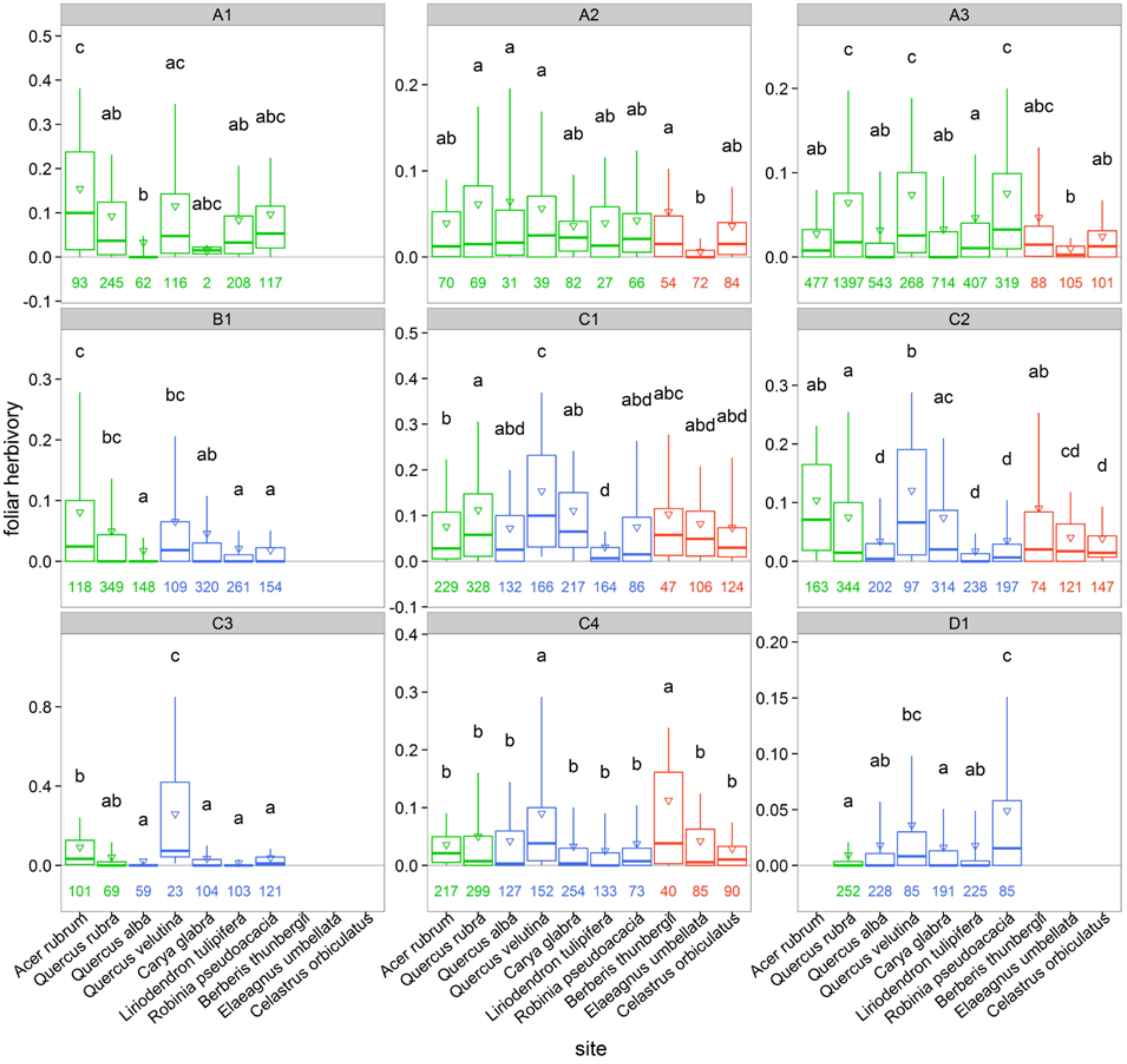
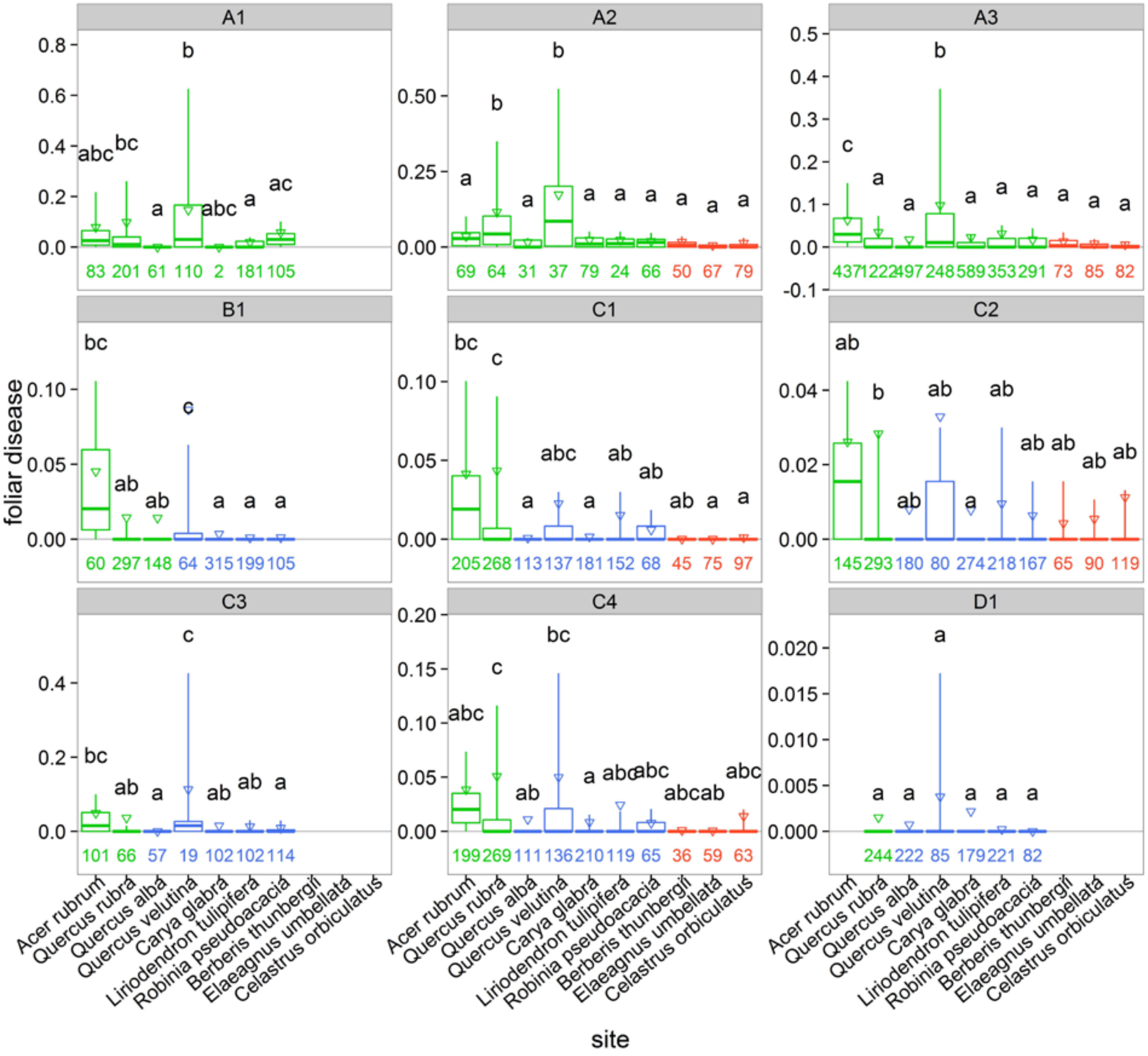


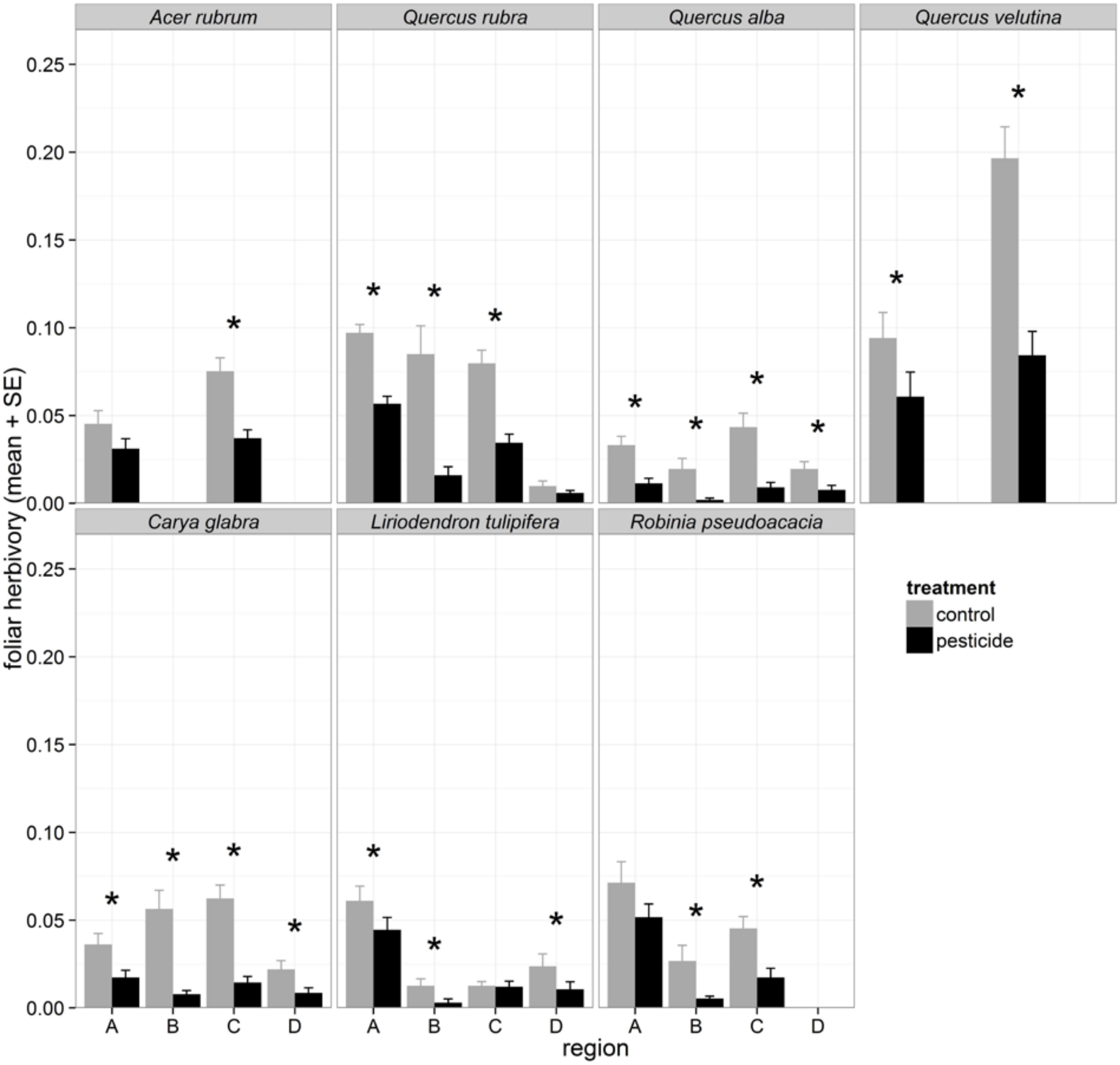
Figure SI 4.14. Boxplot of leaf area affected by foliar disease at each site. The box consists of the first, second, and third quartiles, the whiskers extend to the 10th and 90th percentiles, the mean is shown with a triangle, the sample size is shown for each site, and different letters above the whiskers represent significant differences in foliar disease between sites. Colors represent migratory status (green = native, blue = migrant, and red = invasive). Foliar disease measurements are from mid-summer; this graph uses each seedling in each year of the experiment.



Supporting Information 4.F. Efficacy of pesticide

Figure SI 4.15. Efficacy of pesticide.

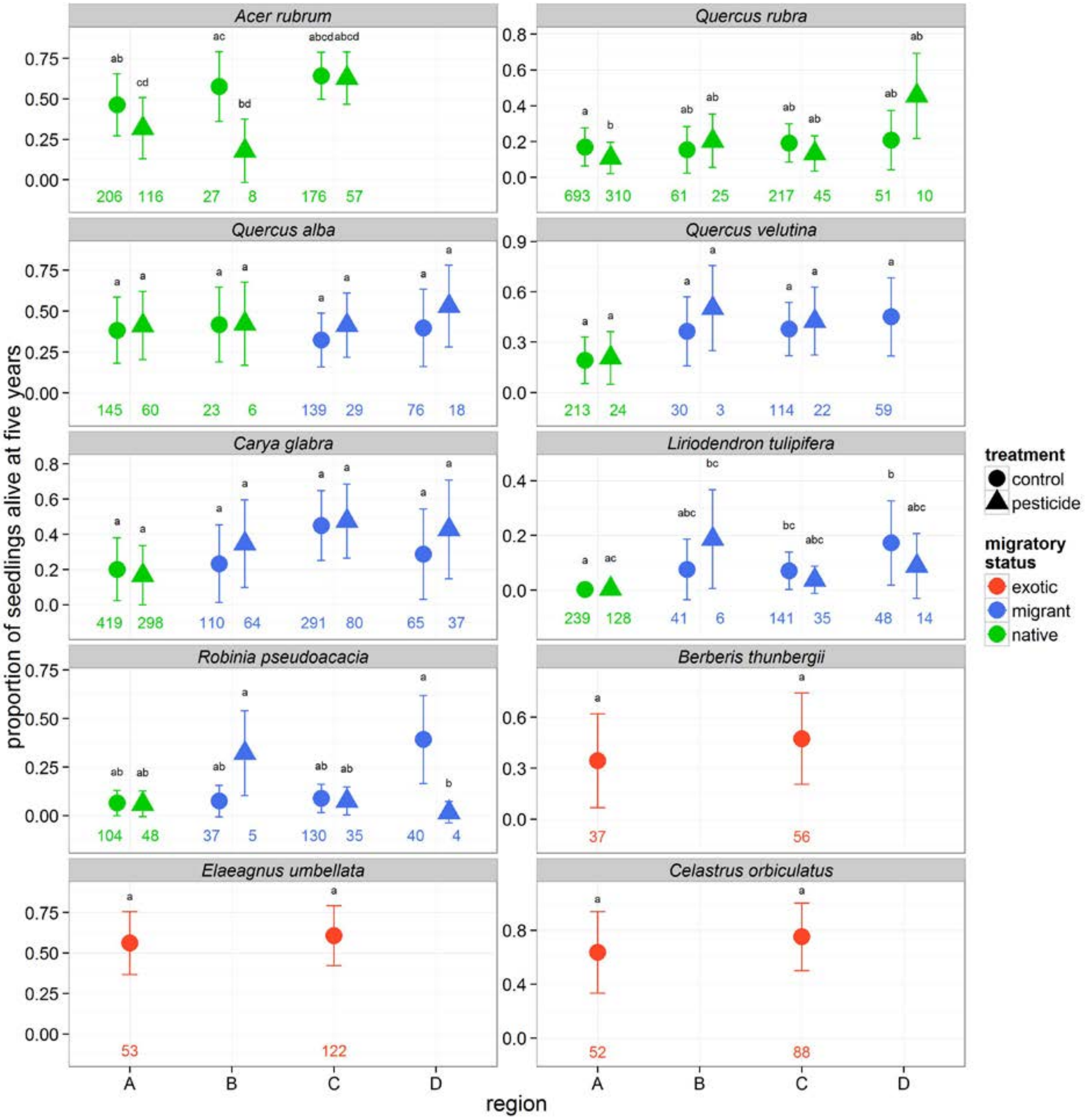
Mean proportion of leaf area affected by herbivory in pesticide and paired control treatments during 2012 and 2013. Significant differences within a region are shown by asterisks. Regions with fewer than 20 measurements of foliar herbivory or 20 unique seedlings in either treatment are not shown. Treatments were not applied to the invasive species.



Supporting Information 4.G. Modeled survival

Figure SI 4.16. Modeled survival by treatment and region.

Modeled survival after five years for seedlings in control and pesticide treatments (± 1 SD). Survival estimates include the variability associated with the intercept for each treatment in each region and the average effects of herbivory and disease in each region. Survival is estimated at the average conditions for the following covariates: initial seedling height, light availability, and soil moisture. Different letters above different bars denote statistically significant differences and sample sizes are listed below bars.



Chapter V:

CONCLUSIONS

In my dissertation, I used field experiments and a meta-analysis to investigate the potential for biotic interactions with natural enemies to affect range expansion dynamics. In Chapter II, I conducted a meta-regression analysis and found that invertebrate herbivores often reduce and stabilize plant population growth rates, although the amount of measured herbivory was not a good proxy for population levels effects. This emphasizes the potential for herbivores to play important roles in range expansion. In Chapter III, I conducted a field experiment to test whether herbivory or disease varied across range edges. I found that there were not large changes in herbivory across range edges, but there was generally less disease beyond a species range edge. Moreover, species that escaped the most from disease beyond their range edges were the same species that were less diseased when grown at farther distances from conspecific adults within their range. This finding shows that differences in biotic interactions across range edges can be understood within the framework of distance dependence. Finally, in Chapter IV, I tested how foliar damage affected seedling survival, and found that commonly occurring levels of foliar herbivory and disease had only minor effects on seedling survival. This suggests that the biotic interactions I studied (foliar herbivory and foliar disease on seedlings) are unlikely to influence the range expansion dynamics of the study species.

The results of my dissertation provide empirical data on differences in biotic interactions across range edges, a well acknowledged gap in our understanding of range expansion. My findings also give some insight into the circumstances in which biotic interactions with natural enemies are most likely to affect range expansion dynamics: when there are strong distance dependent biotic interactions that substantially affect plant performance.

The core contribution of my dissertation is to range expansion dynamics but several findings are of potential interest to other subfields within plant ecology. First, is the pattern that differences in biotic interactions beyond range edges paralleled distance dependent interactions within species ranges. Although recent work in invasion biology shows that plant groups that experience more damage in their original range have more potential for enemy release (Prior et al. 2015), I show a similar pattern in the context of tree range expansion. This suggests a potentially useful way to predict inter-continental differences in biotic interactions: measure distance dependent biotic interactions within species ranges to understand interactions with communities beyond ranges. The similarities between range expansion dynamics and invasion biology (Van der Putten et al. 2010) may allow for a useful flow of ideas between sub-fields.

My transplant experiments may also provide insight in to the processes driving recruitment dynamics within species ranges. In Chapter III, I found that seedlings of two species, *Quercus rubra* and *Carya glabra* had lower herbivory closer to adult conspecifics. This finding contradicts the general paradigm in forest ecology that natural enemy abundances are higher near adult conspecific trees, which results in negative distance/density dependent patterns. Although this is often the case, it is not always so (Johnson et al. 2012, Comita et al. 2014), and, indeed, in many forests it is the species that least display these effects that are the most abundant (Mangan et al. 2010, Johnson et al. 2012). In many studies, hints of positive distance dependent biotic interactions have been ascribed to chance, confounding environmental factors, or the effects of adult conspecifics on environmental variables (e.g., Yamazaki et al. 2009). However, I took environmental variables into account, and in some cases these patterns occur across widely varying distances from conspecific adults. An alternate explanation is that mutualists also build up around conspecific adults. Although the importance of mutualists has been generally underemphasized in ecology (Bruno et al. 2003), they can have important effects counter-acting the effects of density dependent natural enemies (Liang et al. 2015). My results could bolster the idea that distance dependent biotic interactions with natural enemies are determined by the net balance of negative and positive interactions; this implies that positive distance dependent interactions could be another major driver of species abundances and local spatial distributions in temperate forests, an idea that has been severely neglected. This concept is also important to range expansion because interactions with both antagonists and beneficial organisms are likely to weaken for individuals beyond range edges, potentially explaining in part why seedlings planted beyond their range edges did not often experience enemy release from herbivory.

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