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Distance dependent damage across scales

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Foliar damage beyond species distributions is partly explained by distance dependent interactions with natural enemies

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ABSTRACT

Plant distributions are expected to shift in response to climate change, and range expansion dynamics will be shaped by the performance of individuals at the colonizing front. 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 disease and invertebrate herbivory over five years. Foliar disease and herbivory 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*. Beyond range edges there was even less foliar disease for *C. glabra*, *Q. alba* and *R. pseudoacacia* (*A. rubrum* was not planted outside its range). *Liriodendron tulipifera* did not experience reduced disease within or beyond its range. In contrast, *Quercus velutina* displayed significant but idiosyncratic patterns in disease at varying distances from conspecifics. 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 dependent biotic interactions will change across range edges in other systems.

Key Words: range expansion, biotic interactions, species distributions, distance dependence, Janzen-Connell Hypothesis, Enemy Release Hypothesis, herbivory, foliar disease, seedlings, transplant experiment, recruitment, temperate forests

INTRODUCTION

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Some plant species distributions in North America are beginning to shift in response to changes in temperature and precipitation (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 (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, Birnbaum and Leishman 2013). However, few studies have tested how foliar herbivory or disease vary across latitudinal range edges (but see Lakeman-Fraser and Ewers 2013).

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 low host breath). 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 and weaker interactions with specialist enemies (Alexander et al. 2007, Menéndez et al. 2008, Phillips et al. 2010a, Patot et al. 2010). 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) and herbivore host preferences can be influenced by plant abundance (Kuussaari et al. 2000). While in some circumstances generalist natural enemies may be unequipped to deal with novel plant defenses (Verhoeven et al. 2009), there is also evidence that generalist natural enemies often prefer exotic hosts (Parker and Hay 2005, Schultheis et al. 2015). The consequences of differing amounts of damage from generalist enemies in new areas can be substantial (e.g., Halbritter et al. 2012). While studies are often framed in the context of specialist vs. generalist enemies, host breadth is a continuous variable (Gilbert and Webb 2007, Barrett et al. 2009, Forister et al. 2015) and the natural enemies that may affect range expansion dynamics are at varying spots along that spectrum.

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The sum difference in interactions between plants and their natural enemies is very well studied in the context of inter-continental range expansion, and a rich literature surrounds the Enemy Release Hypothesis (ERH; Keane and Crawley 2002), including many cases that support it and many that do not (Mitchell and Power 2003, 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). A separate body of literature documents how biotic interactions vary within species ranges as a function of distance to or density of conspecific adults, often through tests of the Janzen-Connell Hypothesis (JCH; Janzen 1970, Connell 1971). These studies 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, Yamazaki et al. 2009, Johnson et al. 2012), but others have found mixed results (HilleRisLambers et al. 2002, McCarthy-Neumann and Ibáñez 2013, Piao et al. 2013). 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.

The same framework of distance dependence underlies the differences in biotic interactions with natural enemies predicted by the JCH at small spatial scales and by the ERH at large spatial scales. The concepts from both apply to the intermediate spatial scales relevant to range expansion and given the shared framework of distance dependence, there may also be empirical similarities across spatial scales. Here, we hypothesize that the importance of distance dependent biotic interactions within a species range may provide insight into how biotic interactions vary beyond range edges. Specifically, we predict that species that experience reduced damage when planted within their range but far from conspecific adults will experience even lower amounts of damage when planted beyond their current range edge (Fig. 1, species A). Similarly, we predict that species that do not experience distance dependent reductions in damage within their range will not have lower amounts of damage beyond their range (Fig. 1, species B).

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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. Even though differences in interactions with natural enemies are generally transient even for exotic species (Hawkes 2007, Diez et al. 2010, Flory and Clay 2013, Schultheis et al. 2015), they still has the potential to alter range expansion dynamics (Moorcroft et al. 2006) and understanding them could improve 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 limits of five of these species (Table 1; Fig. 2). 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 (Fig. 2; Appendix S1). Plots were located across a range of environmental conditions (e.g., light, soil moisture, and nutrients; Appendix S2) and many were situated near adults of the focal species. Each plot consisted of one to three subplots. A total of 12,762 seedlings were planted between 2010 and 2013 (Table 1). 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 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., they varied in their drought tolerance, shade tolerance, and growth rates).

Seedlings. –Wild seeds were generally collected within Michigan, but if unavailable, they were obtained from outside of Michigan (Appendix S3). 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

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the distance from the soil to the tip of the apical meristem, 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. Seedling survival varied by species and site; patterns in survival are documented elsewhere (Katz and Ibáñez *manuscript in review*).

Leaf damage.–Biotic interactions were measured by visually assessing leaf damage on seedlings in midsummer (June 19 – July 27) from 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%) and the average amount of leaf damage for each plant was used in the analysis. 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 disease and herbivory were assessed. 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 such as nutrient deficiencies (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). 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. Vertebrate herbivory was recorded separately and is not reported here.

Mapping.–We mapped all living trees ≥10 cm DBH (diameter at breast height, 1.37 m) 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 measured using a compass and we also recorded tree DBH 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

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per Fig. 2). 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 (e.g., Masaki and Nakashizuka 2002, 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 in the other regions resin packs were deployed from 4/23/2013 - 10/23/2013. 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

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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^+). All collected data are available in a data repository (Katz and Ibáñez 2016).

Statistical analysis.–We used several statistical models to analyze foliar damage, disease and invertebrate herbivory, as a function of distance to or density of conspecific and congeneric adults. Foliar herbivory and disease followed a zero-inflated log normal distribution. 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. For each process we used a different likelihood (seedling *i* at time *j*):

$$Observed\ Incidence_{ij} \sim Bernoulli(incidence_{ij})$$

$$Observed\ Severity_{ij} \sim Log\ Normal(severity_{ij}, \sigma^2)$$

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 (note that this category is somewhat limited because it is based on a relatively low number of site to site comparisons), and adult conspecific not present in the region (as per Fig. 2). 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 $\mathbf{X}_{ij}$ (Appendix S4), where $\mathbf{X}_{ij}$ 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., soil nutrients, plot, year) and selected the model with the lowest DIC (Deviance Information Criterion;

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Spiegelhalter et al. 2002) that allowed us to answer our questions. The final models included several environmental variables (α), the proportion of available light that reached the seedling, average volumetric soil moisture since the last census; and several seedling specific variables (δ) the age of the seedling in days, the number of leaves, and the height of the seedling when planted. Random effects were also included for each seedling and year (γ). 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.

The models for distance included a fixed effect intercept that varied according to the proximity of the nearest conspecific (β; 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*:

$$\text{logit}(\text{incidence}_{ij}) = \beta_{\text{distance category (i)}} + \alpha_1 * Light_{\text{i}} + \alpha_2 * Soil\ Moisture_{\text{ij}} + \delta_1 * Height_{\text{i}} + \delta_2 * No.Leaves_{\text{ij}} + \delta_3 * Age_{\text{ij}} + \gamma_{\text{seedling (i)}} + \gamma_{\text{year (j)}}$$

The density models included the amount of basal area (BA) 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 (κ), and additional random effects (γ) for region, thus the incidence model is:

$$\text{logit}(\text{incidence}_{\text{ij}}) = \kappa_1 * \text{BA conspecific}_{\text{i}} + \kappa_2 * \text{BA congeneric}_{\text{i}} + \kappa_3 * \textit{Relative BA conspecific}_{\text{i}} + \kappa_4 * \textit{Relative BA congeneric}_{\text{i}} + \alpha_1 * \textit{Light}_{\text{i}} + \alpha_2 * \textit{Soil Moisture}_{\text{ij}} + \delta_1 * \textit{Height}_{\text{i}} + \delta_2 * \textit{No. Leaves}_{\text{ij}} + \delta_3 * \textit{Age}_{\text{ij}} + \gamma_{\text{seedling (i)}} + \gamma_{\text{year (j)}} + \gamma_{\text{region (i)}}$$

Models of leaf damage severity for distance and density did not use the logit link but included the same covariates.

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: β_*, α_*, δ_*, κ_*: Normal (0, 1000). The random effects for seedling, year, and region were drawn from a normal distribution: $\gamma_* \sim$ Normal (0, σ^2), where $\sigma_* \sim$ Uniform (0, 10), as was the variance of the log normal distribution.

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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 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. Model code is available in Supplement 1. Visualization was conducted using the ggplot2 package (Wickham 2009) in R. All analyses were conducted using R (R Core Team 2013).

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RESULTS

The R^2 of the statistical models ranged from 0.11 to 0.92; specific values for each species model are reported in Appendix S5. The parameter estimates for each statistical model are reported in Appendix S6; in this section we focus on the results of the distance and density related parameters (β and κ).

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, top row). For some species this relationship occurred for damage incidence (*A. rubrum*, *C. glabra,* and *Q. alba*) whereas for others it was 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). In contrast, *Liriodendron tulipifera* did not show signs of differing amounts of disease either within its range or beyond its range edge. However, *Quercus velutina* had less foliar disease when planted farther than 10 m from conspecific adults in sites where conspecifics occurred, but experienced less foliar disease when planted in areas beyond its range, although less than most other migrant species (Fig. 3).

Foliar herbivory: The effects of distance from conspecific adults on seedling herbivory varied by species and there were fewer statistically significant relationships than for disease (Fig.

3, bottom row). Some species had greater herbivory close to adult conspecifics within sites (*A. rubrum* and *Q. velutina*) whereas another had higher herbivory farther from adults (*Q. rubra*). 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 reduced herbivory when planted in sites where conspecific adults occurred but the seedling was farther than 10 m from the nearest conspecific adult.

Density dependent biotic relationships

Foliar disease: Higher conspecific basal area (within 10 m) was associated with higher disease for three species (*A. rubrum, C. glabra,* and *Q. alba*; Fig. 4). One species had significantly lower disease severity at higher conspecific basal area (*R. pseudoacacia*). Only *Q. rubra* had significantly higher disease at higher congeneric local basal area, although *Q. velutina* showed a similar but non-significant pattern. Conspecific relative basal area at a site was correlated with higher disease severity for *Q. rubra* (Fig. 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. 4). Both *A. rubrum* and *Q. rubra* had significantly 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. 5).

DISCUSSION

Potential differences in biotic interactions beyond range edges hampers our ability to predict how plant species distributions will shift in response to climate change. 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 lower disease incidence or severity when planted farther from conspecific adults within their ranges tended to have even lower disease incidence or severity when planted beyond their range edges. The resulting decreases in disease beyond range edges have the potential to affect migrant plant population growth and range expansion dynamics,

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although they did not in this experiment (Katz and Ibáñez, *manuscript in review*). Most species that that did not experience lower damage incidence or severity when planted farther from conspecific adults within ranges did not experience different damage incidence or severity beyond their range; this encompasses almost all examples of herbivory in our study. The idea 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 experiencing relatively less damage from natural enemies beyond their range is supported at a broad scale in invasion biology (Blumenthal et al. 2009, Prior et al. 2015). Overall, our findings show that distance dependent biotic interactions at small spatial scales, the strength of which varies considerably by species, have some capacity to predict differences in biotic interactions across range edges. This in turn suggests that species in other functional groups or in other ecosystems that experience stronger distance dependent interactions with natural enemies will have more potential for reduced damage beyond range edges.

Interspecific differences in the strength of distance dependence. – Tests of the JCH and ERH provide many instances where plants that are isolated from conspecifics on spatial scales of meters and thousands of kilometers are associated with fewer natural enemies and receive less damage, but there almost as many counter examples (Liu and Stiling 2006, Johnson et al. 2012, Comita et al. 2014, Heger and Jeschke 2014, Schultheis et al. 2015). A similar spectrum is evident in our results; the presence and strength of distance dependence varies between species and damage type. While much effort has been put in to determining the overall effect size of distance dependence, less is known about the causes of interspecific variation. The answer to this question is tied to natural enemy communities, and while we did not identify foliar pathogens in this study, we did conduct three years of insect censuses on these seedlings (Katz, *unpublished data*), which may provide a way to test competing explanations for herbivory. Here, we explore some of the potential mechanisms that could lead to variation in distance dependence for disease; future studies could test these by identifying natural enemies and linking them to their symptoms.

First, some insight may be gained from a close examination of our study species. For example, *L. tulipifera* seedlings did not have different amounts of damage when planted closer to or near more conspecific adults. This may be because *L. tulipifera* is uncommon even in our southernmost study region, and could therefore be exposed to fewer relevant natural enemies

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even at the one site in which it occurred. This would explain why another study found signs of density dependence for this species (Johnson et al. 2014) but we did not. For other species, we may simply have planted seedlings near conspecific adults with especially active specialist pathogens; for example, *C. glabra* seedlings were more likely to have diseased leaves when they were planted near more conspecific adults, or when planted close to conspecific adults. Indeed, on some *C. glabra* seedlings planted within their range, we observed symptoms consistent with those created by hickory downy leaf spot (*Microstroma juglandis;* Katz, *personal observation*). On a more general level, the number of pathogens native plant species have within their own range, as well as their effects, have been linked to growth vs. defense tradeoffs, physiology, size of individuals, the size of their distribution, and the number of habitats the plant occupies (Blumenthal et al. 2009, Mitchell et al. 2010, Cronin et al. 2010). Thus, future studies may be able to use these ecological and biogeographic traits to explain variation in distance dependent interactions with natural enemies, as they have in invasion biology (e.g., Van Kleunen et al. 2010); a better understanding of distance dependence for these species could in turn lead to a better understanding of how biotic interactions with natural enemies will affect range expansion.

Differences between disease and herbivory. – Isolated seedlings were far more likely to escape from disease than from herbivory. One plausible explanation is that the most important herbivores in this system have high host breadth, which could lead to consistent amounts of damage at varying distances from conspecific adults. This is supported by studies that show the importance of generalist herbivores to plant fitness (e.g., Halbritter et al. 2012) as well as by the fact that some of the more important feeding guilds in temperate forests tend to have relatively broad host breadth (Forister et al. 2015). In this system, some of the most abundant insect families (e.g., *Cicadellidae* and *Aphididae*) were found on most seedling species at most sites (Katz, *unpublished data*) and invertebrate community composition on native *Q. rubra* seedlings was fairly similar across sites (Appendix S7). While generalist natural enemies can selectively target alien plants (Parker and Hay 2005), that is less likely to cause changes in herbivory during intra-continental range expansion; plant communities do not shift cohesively in response to climate change (Williams and Jackson 2007), and many of the plants and natural enemies along this latitudinal gradient are likely to have some shared evolutionary history.

Two observations that suggest an alternate explanation were that *C. glabra* and *Q. rubra* actually had higher herbivory farther from conspecifics and when there were fewer conspecifics

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within 10 m or at the site. This could potentially be explained by species accumulating mutualists near conspecific adults. Specifically, isolated seedlings might be 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, endophytes and mycorrhizae can directly reduce plant palatability or enhance seedling performance and therefore defensive capabilities, although their effects vary according to herbivore feeding guild and specialization (Hartley and Gange 2009, Koricheva et al. 2009). In one case, higher abundances of mycorrhizae around conspecific adults is credited with counter-acting the negative distance dependent effects of soil pathogens in a sub-tropical forest (Liang et al. 2015). Although we lack the relevant information to assert this was the case in our study system, in a multi-trophic interaction like herbivory, this dynamic could lead to idiosyncratic results, like the ones we report, 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. If host plants' mutualists and natural enemies have similar host breadth, then a plant beyond its range could be exposed to fewer of each, effectively canceling out the signals of distance dependence.

Phylogenetic conservation of natural enemies.– 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). 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. Spatial correlations between related species occurrence or density could also underlie some of the patterns we found, such as the apparent contradiction that *Q. velutina* had higher rates of disease when conspecifics were present at the site compared to when conspecifics were present within 10 m, yet it tended to have higher rates of disease when basal area within 10 m was higher. Depending on spatial correlations, the abundant *Q. rubra*, which is closely related to and often hybridizes with *Q.*

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velutina, may be overwriting the signals of distance dependence. This possibility is supported by the general phylogenetic conservation of pathogens and herbivore host breadth (Gilbert and Webb 2007, Pearse and Hipp 2009, Barrett et al. 2009, Forister et al. 2015) and by the phylogenetic clustering of plant defenses (Ricklefs 2008). Accounting for phylogenetic distance has been important in understanding disease in other systems (Parker et al. 2015) and may be of use here too.

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Supporting Information

Appendix S1: Description of sites used in the transplant experiment

Appendix S2: Plot environmental characteristics

Appendix S3: Seed sources

Appendix S4: Covariates included in statistical models

Appendix S5: Model fit

Appendix S6: Covariate parameter estimates

Appendix S7: Insect community composition for *Quercus rubra*

Supplement 1: Model code

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Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.1b433

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Table 1.Plant species used in transplant experiments and their residency status at each study region. Species residency status (native, naturalized [defined as species that were introduced to a region but have self-sustaining populations], and migrant [defined as species that are predicted to be able to colonize an area in future climates]) 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	Native	Native	Native
			487	75	282	0
Carya glabra	cagl	Pignut hickory	Native	Migrant	Migrant	Migrant
			930	344	344	110
Liriodendron tulipifera	litu	Tulip tree	Native/naturalized*	Migrant	Migrant	Migrant
			836	255	656	255
Quercus rubra	quru	Red oak	Native	Native	Native	Native
			1937	345	989	315
Quercus alba	qual	White oak	Native	Native	Migrant/rare*	Migrant
			829	140	344	187
Quercus velutina	quve	Black oak	Native	Migrant/rare*	Migrant	Migrant
			777	417	417	230
Robinia pseudoacacia	rops	Black locust	Native/naturalized*	Migrant; planted	Migrant; planted	Migrant
			806		476	270

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		165		
Total planted	6602	1741	3508	1367

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Figure 1. We hypothesize that distance dependent biotic interactions with natural enemies within species ranges will predict differences in biotic interactions across range edges. In this conceptual figure, species A experiences distance dependent reductions in damage within its range and is hypothesized to have even lower amounts of damage beyond its range whereas species B does not experience distance dependent reductions in damage within its range and is therefore not hypothesized to have differences in interactions with natural enemies beyond its range.

Figure 2. The study area in North America (a); the study regions (b) which encompass the approximate range edges of several focal species (line between regions A and B). Each region (A - D) contained one to four sites (c), each located in distinct forest types (e.g., sites C1 - C4). Each site had between two and 21 plots (gray boxes) and a datalogger (star) (d). Each plot had between one and three subplots (white boxes), in which seedlings were planted (black dots) (e). Trees within 10 m of seedlings were mapped and identified to species (colored circles).

Figure 3. Effects of distance from adult conspecifics on foliar damage. Parameter estimates 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). The 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 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 had insufficient neighboring congeneric adults to calculate their effects on foliar damage.

Figure 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.*

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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.

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Figure 1

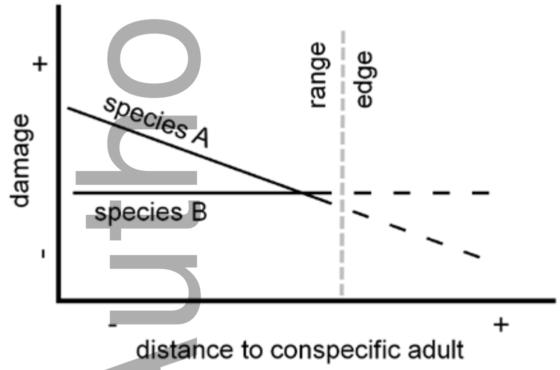

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Figure 2

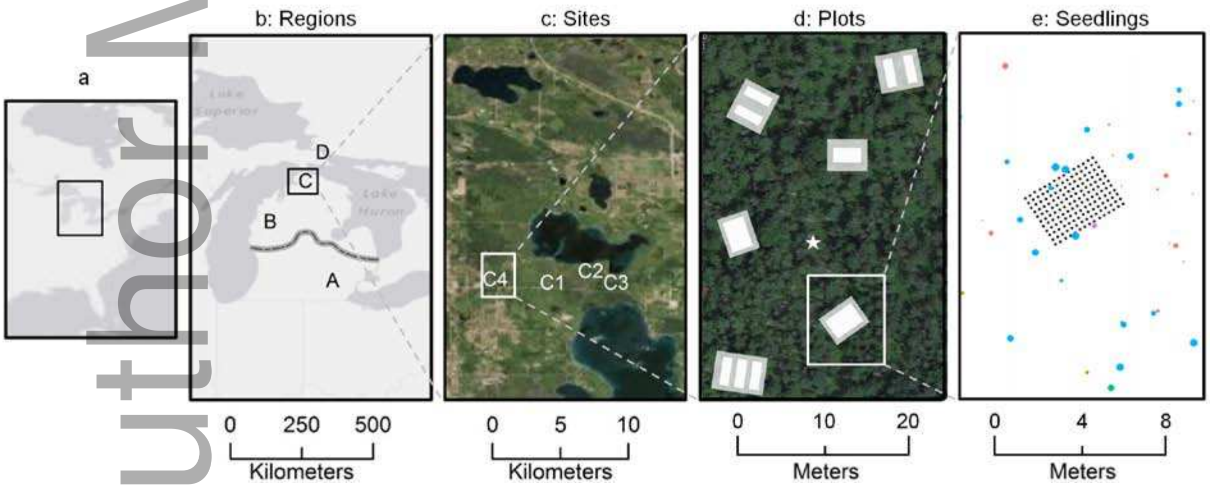

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Figure 3

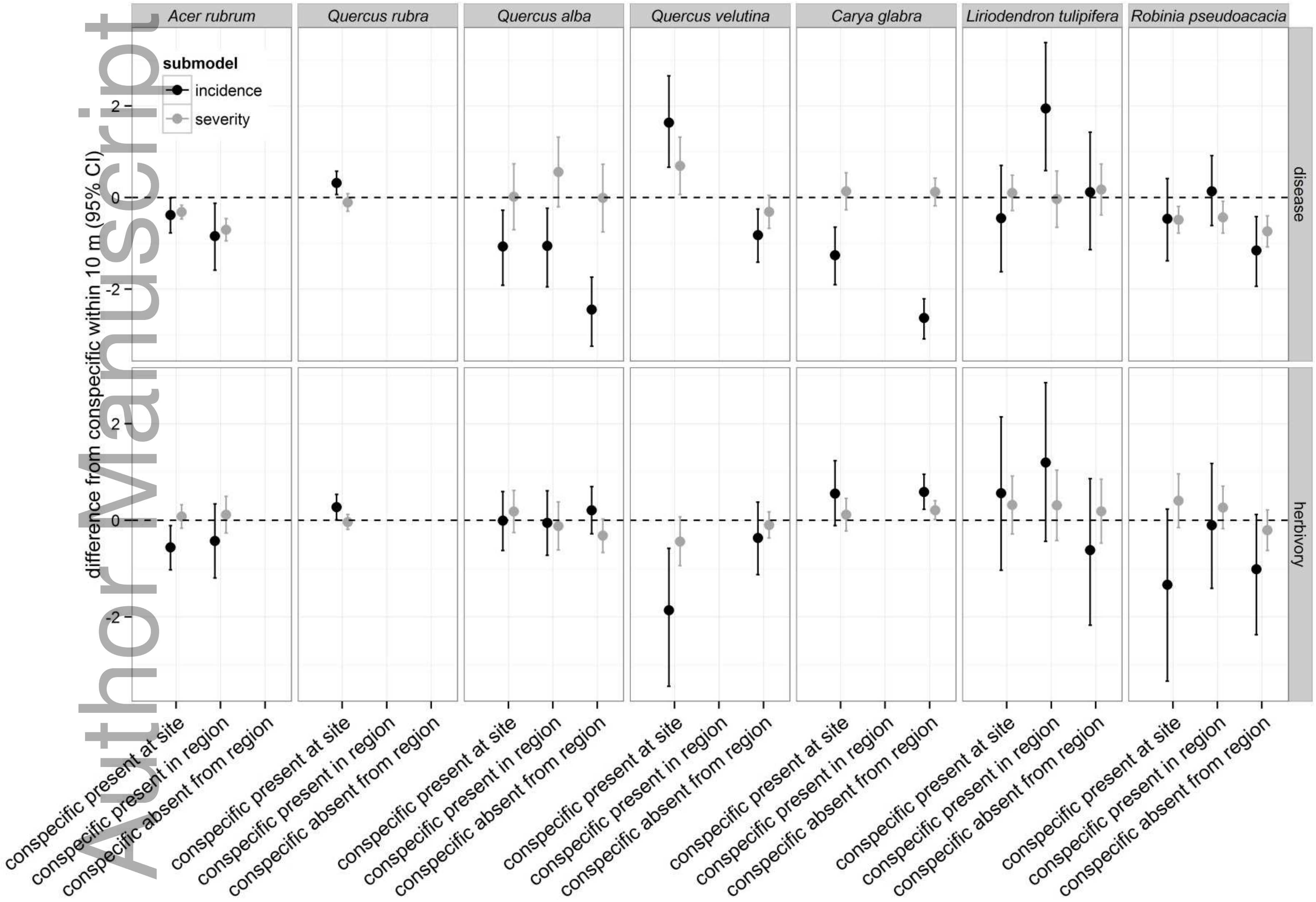

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Figure 4

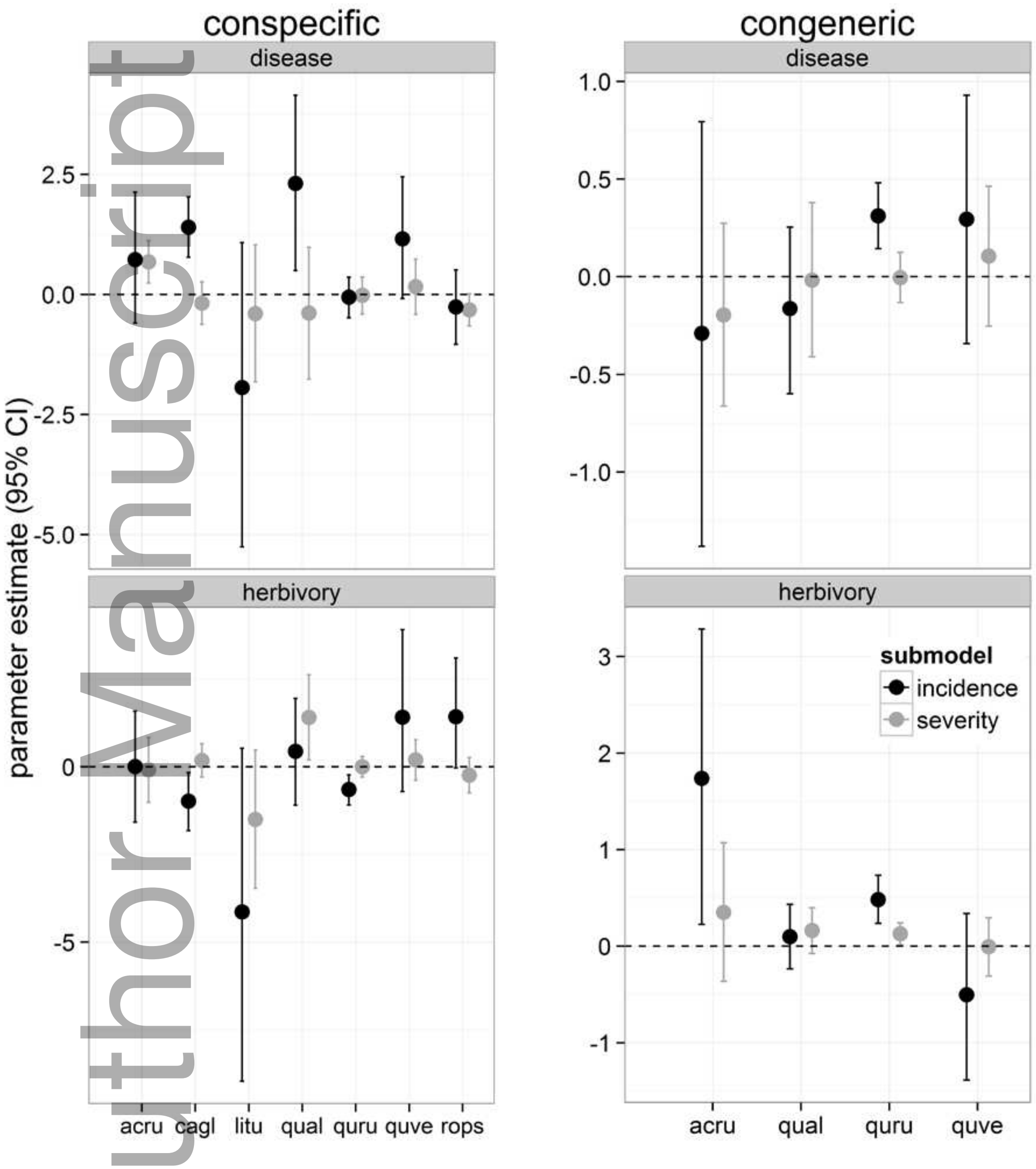

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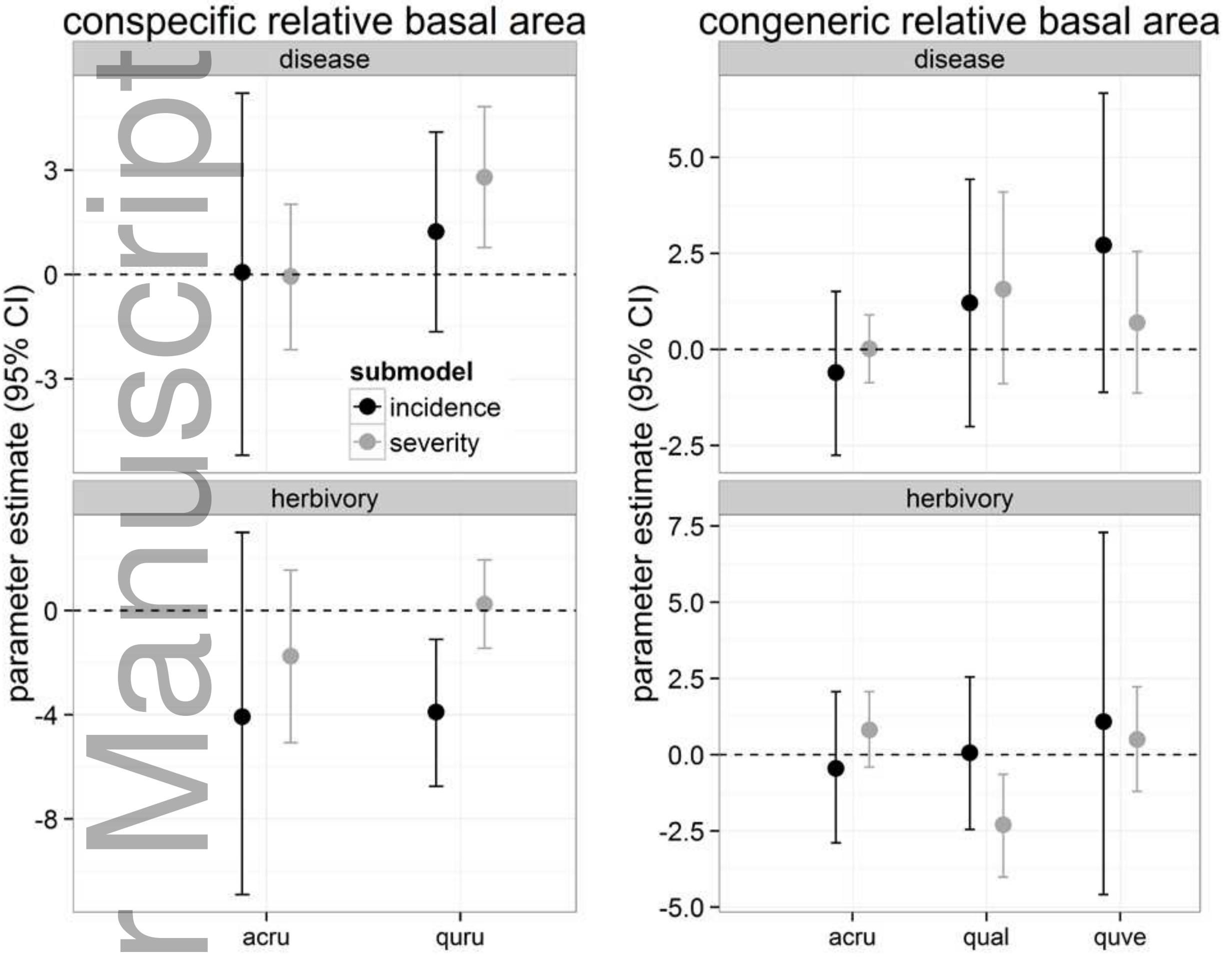
Figure 5



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