

Differences in biotic interactions across range edges have only minor effects on plant performance

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Summary

1. 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.

2. In order to test whether natural enemies will affect range expansion dynamics, we transplanted seven species along a 450-km latitudinal gradient that spanned the range edges of five of these species. The experiment was conducted over 5 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.

3. 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 four species (*Acer rubrum*, *Quercus alba*, *Quercus rubra* and *Quercus velutina*) and foliar herbivory reduced survival for three species (*Acer rubrum*, *Liriodendron tulipifera* and *Quercus rubra*).

4. However, the effects of these biotic interactions on survival were very small (0–5% 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.

5. *Synthesis.* 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.

Key-words: biotic interactions, plant–insect interactions, plant–pathogen interactions, range expansion, species distributions, survival, temperate forest

Introduction

Climate change is expected to cause shifts in species distributions as plants and animals track changing temperatures and precipitation (Parmesan & Yohe 2003; Hickling *et al.* 2006; Crimmins *et al.* 2011). Predictions of poleward range expansion of plant species over the coming decades and centuries are drawn from correlations between current species distributions and climate (Iverson & Prasad 1998; Guisan & Zimmermann 2000; Pearson & Dawson 2003), and palaeoreconstructions of shifts in vegetation composition during previous periods of climate change (Davis 1983; Graumlich &

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, Vanderwal & Lovett-Doust 2010; Boisvert-Marsh, Périé & de Blois 2014; Desprez *et al.* 2014), whereas others have not (Zhu, Woodall & Clark 2012). 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 current range, where populations do not yet exist (hereafter referred to as ‘migrants’) (Cairns & Moen 2004; Moorcroft, Pacala & Lewis

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2006; Morriën *et al.* 2010; HilleRisLambers *et al.* 2013; Wisz *et al.* 2013). The effects of natural enemies on plant populations are often substantial (Katz 2016), as are their subsequent effects on ecosystem function (Hicke *et al.* 2012). 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, Macel & Visser 2010; Zarnetske, Skelly & Urban 2012; Svenning *et al.* 2014). While several studies have investigated how soil communities differentially affect native versus migrant plants (van Grunsven *et al.* 2010; Stanton-Geddes & Anderson 2011; McCarthy-Neumann & 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; Patot *et al.* 2010; Phillips *et al.* 2010b; Tsai & 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, Brown & Shine 2010a). Moreover, in a glasshouse experiment, successful range-expanding plants were less affected by a naïve herbivore (Engelkes *et al.* 2008), showing that migrants can also be released from generalist herbivores. Even though enemy release is transient because of pest and pathogen accumulation (Brändle *et al.* 2008; Diez *et al.* 2010; Mitchell *et al.* 2010), it could still help migrant plants outperform native ones, increasing colonization success and overall rates of range expansion (Moorcroft, Pacala & Lewis 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, Adler & Yelenik 2004; Parker, Burkepile & Hay 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, Macel & Visser 2010). First, natural enemy community composition may not change abruptly at the edge of a plant species range. Secondly, 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 & 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, Harms & Connell 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, Clark & Beckage 2002; Fine *et al.* 2006; Andersen, Turner & Dalling 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 defences (Myers & Kitajima 2007; Barton & Koricheva 2010; Boege, Barton & Dirzo 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 seven temperate tree species to answer the following questions: (i) Are migrant species exposed to different amounts of herbivory and disease than in their native range?, and (ii) 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.

Materials and methods

We initiated a seedling transplant experiment in 2010, and over the following 4 years, we planted seedlings in four regions across a 450-km latitudinal gradient (Fig. 1). Species origins varied (Table 1): five were native or naturalized (self-sustaining populations were present) at some regions and migrants at others (*Carya glabra* P. Mill., *Liriodendron tulipifera* L., *Q. alba* L., *Q. velutina* Lam. and *Robinia pseudoacacia* L.) and two species were native across all regions (*Acer rubrum* L. and *Quercus rubra* L.). We selected species based on their current and predicted distributions (Iverson *et al.* 2008) and on their

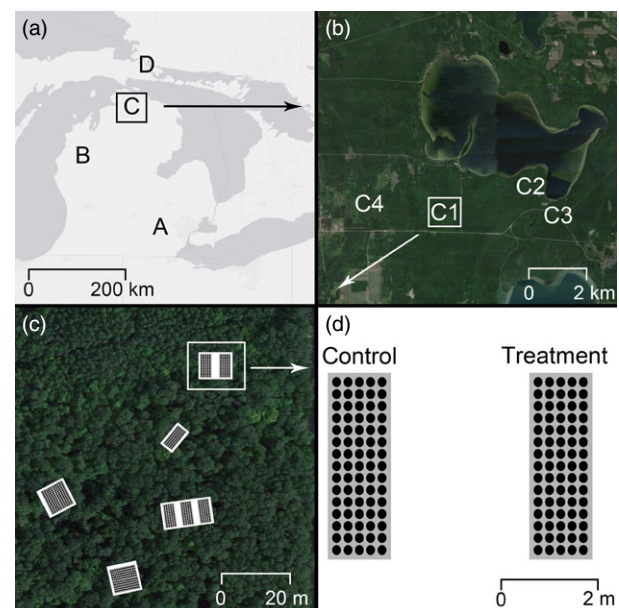


Fig. 1. Regions A–D (panel a) contained one to four sites (panel b), which were located in distinct forest types (e.g. sites C1–C4). Each site had between 2 and 21 plots (white boxes in panel c). Each plot had between one and three subplots (grey boxes in panel d) to which pesticide or control treatments were applied. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Plant species used in transplant experiments and their residency status at each study region. Species residency status (native, naturalized or migrant) 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
<i>Acer rubrum</i>	acru	Red maple	Native 487	Native 75	Native 282	Native 0
<i>Quercus rubra</i>	quru	Red oak	Native 1937	Native 345	Native 989	Native 315
<i>Quercus alba</i>	qual	White oak	Native 829	Native 140	Migrant/rare* 344	Migrant 187
<i>Quercus velutina</i>	quve	Black oak	Native 777	Migrant/rare* 417	Migrant 417	Migrant 230
<i>Carya glabra</i>	cagl	Pignut hickory	Native 930	Migrant 344	Migrant 344	Migrant 110
<i>Robinia pseudoacacia</i>	rops	Black locust	Native/naturalized * 806	Migrant; planted horticulturally 165	Migrant; planted horticulturally 476	Migrant 270
<i>Liriodendron tulipifera</i>	litu	Tulip tree	Native/naturalized * 836	Migrant 255	Migrant 656	Migrant 255
Total planted			6602	1741	3508	1367

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 2–21 plots (Table 2; Fig. 1); this design was dictated by logistical constraints (i.e. site establishment was restricted to University of Michigan properties or areas we possessed permits to work in) and the unbalanced experimental set-up does not pose a challenge for the analyses used. 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 2; Fig. 1) and in a range of environmental conditions (Appendix S1, Supporting Information). A total of 13 218 seedlings were planted between 2010 and 2013 (Table 1).

SEEDLINGS

Seeds were germinated at the University of Michigan Matthaei Botanical Gardens (Ann Arbor, MI, USA) in potting soil (Metro-Mix 380; SunGro Horticulture, Agawam, MA, USA), where they were watered daily. Seeds were collected from wild sources within Michigan when available, but were otherwise obtained from outside of Michigan (Appendix S2). To account for maternal effects (i.e. seed size), we measured the height of the seedlings (defined as the distance from the soil to the tip of the apical meristem) 1 month after emergence. Bare root seedlings were then transplanted into the study plots in May and June of 2010–2014, with a minimum distance of 25 cm between seedlings. Seedlings were watered upon planting (125 mL per seedling) to decrease transplant shock and existing vegetation was left

intact. A total of 2196 seedlings were transplanted in the fall instead of in the spring in 2011, 2012 and 2013; this was done in order to increase both the range of seedling sizes and total sample size.

PESTICIDE TREATMENT

We experimentally reduced herbivory in 48 subplots 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 & Louda 2012, Spiers *et al.* 2006), and does not contain nitrogen. To ensure that it caused no direct effects on the plants, through either phytotoxicity or phytostimulation, we conducted a glasshouse control experiment; survival and relative growth rates were not impacted, although there is mixed evidence of mild phytotoxicity for *Acer rubrum* (Appendix S3). We sprayed a solution of bifenthrin (0.008% active ingredient) on the tops and bottoms of the leaves of seedlings in treatment subplots three times a year during 2012 and 2013. We sprayed the same amount of water on leaves in paired control subplots (Fig. 1, panel D). We also distributed a molluscicide, metaldehyde, along one outside edge of pesticide subplots to reduce herbivory by slugs and snails. The molluscicide was distributed on the side of the treatment plot furthest from the paired control subplot; no metaldehyde was distributed within 5 m of a control subplot seedling. Metaldehyde reduces slug abundance and herbivory at the microsite level, without impacting plots as close as 5 m (Ferguson 2004). In 2010 and 2011, we built insect enclosures around a subset of first year seedlings, but neither year's enclosure design

Table 2. Description of sites used in the transplant experiment. Environmental variables at the plot and subplot levels are given in Appendix S4

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

consistently reduced herbivory. Only mortality from years after the exclosures were removed is 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. The same person (D. Katz) conducted all surveys to ensure that visual estimates were consistent. 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. Both infectious and non-infectious diseases (e.g. nutrient deficiencies) are therefore included in the disease category (Sinclair & 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 (Appendix S4). Although leaf litter was disturbed during censuses, which could have reduced potentially fatal burial in leaf litter (Patterson *et al.* 2012), this disturbance was consistent for all seedlings at all sites.

ENVIRONMENTAL DATA

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

Temperature was measured hourly at each site with a HOBO Pro V2 U23 Temperature Data Logger (Onset Computer Corporation, Pocasset, MA, USA). Soil water (per cent moisture by volume) was measured hourly at each site with a HOBO Micro Station Data Logger (Onset Computer Corporation). Volumetric soil water content in the top 7.5 cm of soil was measured with a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, Plainfield, IL, USA) in at least six points per subplot several times during the growing seasons of 2011–2014. The relationship between soil moisture at the subplot level and at the site level was quantified using linear regressions (mean $R^2 = 0.67$); these regressions were then used to predict soil moisture between censuses. 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 and the previous census.

Soil nutrients were measured in 2013 using resin packs (Unibest International Corporation, Walla Walla, WA, USA). Resin packs in the southernmost region (region A; see Fig. 1) were deployed between 8 April 2013 and 30 October 2013 and resin packs were deployed from 23 April 2013 to 23 October 2013 in the other regions (regions B, C and D; see Fig. 1). Between two and four resin packs were deployed per plot, depending on the number of subplots. 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 resin 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 2 M HCl and the ion exchange resin analysis was conducted using inductively coupled plasma spectroscopy analysis (PerkinElmer 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, Bretz & Westfall 2008). *Max-t* tests are robust for comparisons of non-normal distributions, unbalanced sample sizes and heterogeneity of variances (Herberich, Sikorski & Hothorn 2010). To compare whether herbivory varied between seedlings in control and pesticide treatments, we used Wilcoxon rank sum tests.

Seedling survival

To analyse how herbivory, foliar disease and region affected seedling survival, we used a counting process in a Cox survival model (Anderesen & 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 & Ibáñez 2012). We only included seedlings that had survived to their second year in this analysis, to minimize any artefacts from transplanting the seedlings and to reduce the effects of seed resources on survival. The likelihood for the model is:

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

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 & Hill 2007). The hazard was estimated at each time step, h_t , from a gamma distribution, $h_t \sim \text{Gamma}(1, 0.05)$. 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. In the final model, plot effects were drawn from a normal distribution with a mean of μ_{native} or μ_{migrant} depending on whether the focal species was native in that plot; plot effects $\sim \text{Normal}(\mu, \sigma^2)$, where $\sigma \sim \text{Uniform}(0, 10)$. Thus, differences between μ_{native} and μ_{migrant} represent a difference in survival within a species range compared with beyond a species range. Random effects were included for site, and the following covariates were also included (data ranges 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: 0–60 leaves), the proportion of available light that reached the seedling (continuous: 0–1), volumetric soil moisture since the last census (continuous: 0–1), whether the seedling was planted in the spring or fall (binary: 0, 1) and a fixed effect was included for the indirect effects of the invertebrate herbivory pesticide treatment (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 modelled 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: $\beta \sim \text{Normal}(0, 1000)$. The random effects for site were drawn from a normal distribution: random effect $\sim \text{Normal}(0, \sigma^2)$, where $\sigma \sim \text{Uniform}(0, 10)$. We predicted survival where seedlings were native or migrants, \hat{S}_{native} or \hat{S}_{migrant} at average herbivory and disease levels for native and migrant seedlings. Survival of seedlings in the pesticide treatment was estimated separately. The proportion of seedlings surviving, \hat{S} , was predicted over time (up to 5 years), under the following conditions: average light, average soil moisture, average transplant height, average number of leaves, no browsing and spring planting.

$$\hat{S}_{\text{migratory status, treatment}} \sim \text{Power}\left(e^{-\sum_{it} h_{it}}, e^{x\beta}\right)$$

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 modelled separately. Posterior densities of the parameters were obtained by Gibbs sampling (Geman & Geman 1984) using JAGS 3.4 (Plummer 2003) via the RJAGS package in R (Plummer 2014). Convergence occurred after 1000 to 10 000 iterations and chains were inspected visually. Each species was run for 40 000 iterations and posterior parameter values were based on post-convergence results. Statistical model code is provided in Appendix S5. Visualization was conducted using the GGLOT2 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 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. 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 ($P < 0.05$). 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. The pesticide treatment successfully reduced observed herbivory at all sites for three species (Appendix S6), *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*; $P < 0.05$); 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. 2). This resulted in migrant plants having somewhat lower foliar disease rates than native plants at many sites. 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 ($P < 0.05$). 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* (mean and 95% CI: 1.56, 0.53–2.55), *Q. rubra* (0.78, 0.23–1.31) and *Q. velutina* (1.03, 0.10–1.92; Fig. 3). Foliar disease had a significantly negative effect on survival for *A. rubrum* (2.27, 1.22–3.25), *Q. alba* (1.59, 0.62–2.47), *Q. rubra* (1.10, 0.59–1.60) and *Q. velutina* (1.73, 0.70–2.70; Fig. 3). A full list of parameter estimates for the survival model is given in Table 3. 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) and disease (Fig. 5). Seedling survival in pesticide treatments was never significantly higher than in control treatments (Fig. 6), and overall differences were minor. The modelled proportion of seedlings alive after five years was significantly higher beyond range edges for *L. tulipifera* (mean \pm SD for native: 0.003 ± 0.010 compared with migrant: 0.071 ± 0.055) and although not significant, some species had similar trends, including *Q. velutina*

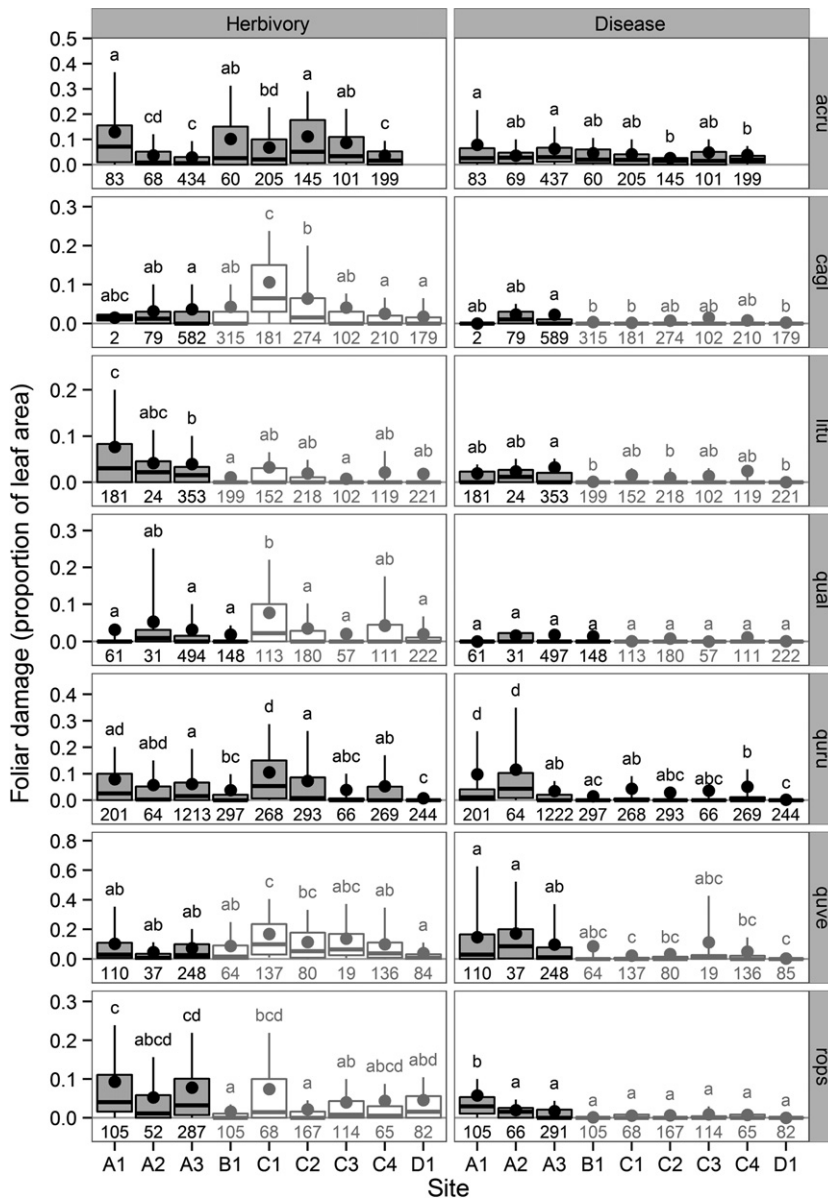


Fig. 2. Boxplots of the proportion of leaf area affected by foliar herbivory (column 1) and disease (column 2) in midsummer for each species across the latitudinal gradient, which extended from the southern region (A) to the northernmost region (D). The box consists of the first, second and third quartiles, 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 (dark grey = native, light grey = migrant). Data from seedlings in experimental treatments are not shown.

(native: 0.177 ± 0.126 compared with migrant: 0.389 ± 0.136 and *C. glabra* (native: 0.163 ± 0.162 compared with migrant: 0.366 ± 0.146).

Discussion

The potential importance of biotic interactions to plant range expansion has received increased attention in recent years, but a lack of empirical evidence of how biotic interactions vary across range edges has precluded understanding how this may affect plant species range expansion in response to 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 suggest 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 commonly occurring abundances of 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

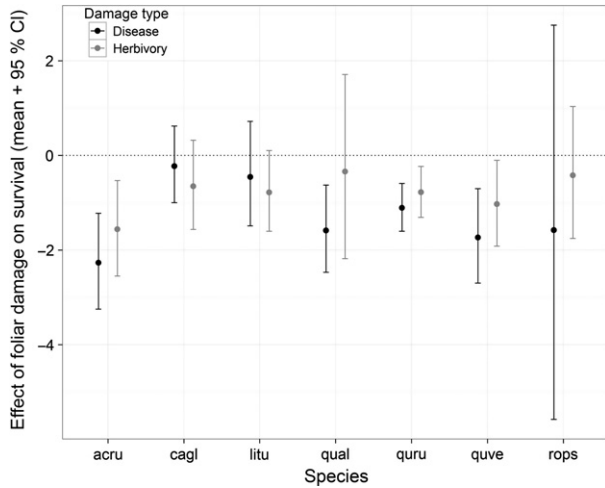


Fig. 3. Effects of foliar herbivory and foliar disease on seedling survival (estimates from the mortality model are multiplied by -1). Parameter estimates below 0 indicate a negative effect on survival; 95% credible intervals that cross zero are not statistically significant.

forest types, foliar herbivory depended more upon conditions at the site and plot levels than upon whether a species was native or migrant. The magnitude of spatial heterogeneity in herbivory between sites is similar to that found by other studies (Adams *et al.* 2008; Adams & 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).

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 (e.g. nutrient deficiencies), 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 congeneric *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 & Hipp 2009; Ness, Rollinson & Whitney 2011; Gilbert, Briggs & Magarey 2015; Parker *et al.* 2015), and pathogen host range is often somewhat constrained to host phylogeny (Gilbert & 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 & Anderson 2011; McCarthy-Neumann & 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 & Clay 2013). There is also evidence of reduced negative soil feedback outside of plant ranges from glasshouse experiments (Engelkes *et al.* 2008). These patterns may partially result from migrant seedlings not being near adult conspecifics, which reduced negative plant–soil feedback in the same system as this study (McCarthy-Neumann & 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 was 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).

Table 3. Survival model parameters (mean \pm standard deviation) indicate effects on mortality (i.e. higher values indicate higher probability of death). Parameter estimates that were significantly different from zero (95% CI does not include zero) are in bold, except for the fixed effects for migratory status, which are in bold if μ_{native} is significantly different from μ_{migrant}

Parameter	<i>Acer rubrum</i>	<i>Quercus rubra</i>	<i>Quercus alba</i>	<i>Quercus velutina</i>	<i>Carya glabra</i>	<i>Liriodendron tulipifera</i>	<i>Robinia pseudoacacia</i>
Browse	1.02 \pm 0.60	0.81 \pm 0.27	1.62 \pm 0.49	-1.19 ± 1.30	2.09 \pm 0.46	0.17 \pm 0.65	0.36 \pm 0.54
Disease	2.27 \pm 0.52	1.11 \pm 0.26	1.59 \pm 0.47	1.74 \pm 0.51	0.23 \pm 0.41	0.45 \pm 0.56	1.58 \pm 2.13
Herbivory	1.56 \pm 0.52	0.78 \pm 0.28	0.34 \pm 1.00	1.03 \pm 0.46	0.65 \pm 0.48	0.78 \pm 0.43	0.42 \pm 0.71
Light	0.95 \pm 0.88	-0.67 ± 0.53	-0.67 ± 0.91	-1.57 ± 0.84	-0.36 ± 0.84	0.30 \pm 0.75	0.19 \pm 0.76
μ_{native}	-4.06 ± 0.52	-2.85 ± 0.38	-3.18 ± 0.55	-2.91 ± 0.55	-2.62 ± 0.72	-1.27 ± 0.44	-2.13 ± 0.47
μ_{migrant}	NA	NA	-3.16 ± 0.54	-3.57 ± 0.49	-3.34 ± 0.51	-2.27 ± 0.41	-2.32 ± 0.44
Number of leaves	-1.67 ± 0.25	-1.64 ± 0.14	-1.07 ± 0.27	-1.62 ± 0.22	-0.42 ± 0.12	-0.73 ± 0.11	-1.52 ± 0.19
Pesticide	0.44 \pm 0.16	0.21 \pm 0.09	-0.16 ± 0.20	-0.09 ± 0.25	0.08 \pm 0.09	-0.06 ± 0.11	0.09 \pm 0.16
Planting height	0.03 \pm 0.16	-0.04 ± 0.09	-0.27 ± 0.19	0.00 \pm 0.17	-0.05 ± 0.10	-0.18 ± 0.12	0.06 \pm 0.15
Soil moisture	-0.63 ± 1.61	-3.57 ± 0.94	-3.29 ± 2.21	-0.15 ± 1.56	-2.63 ± 1.8	-2.85 ± 0.98	0.98 \pm 1.47
Time of planting	0.61 \pm 0.91	0.59 \pm 0.89	0.81 \pm 0.89	-0.48 ± 0.90	0.57 \pm 0.83	-0.48 ± 0.87	-0.99 ± 0.93

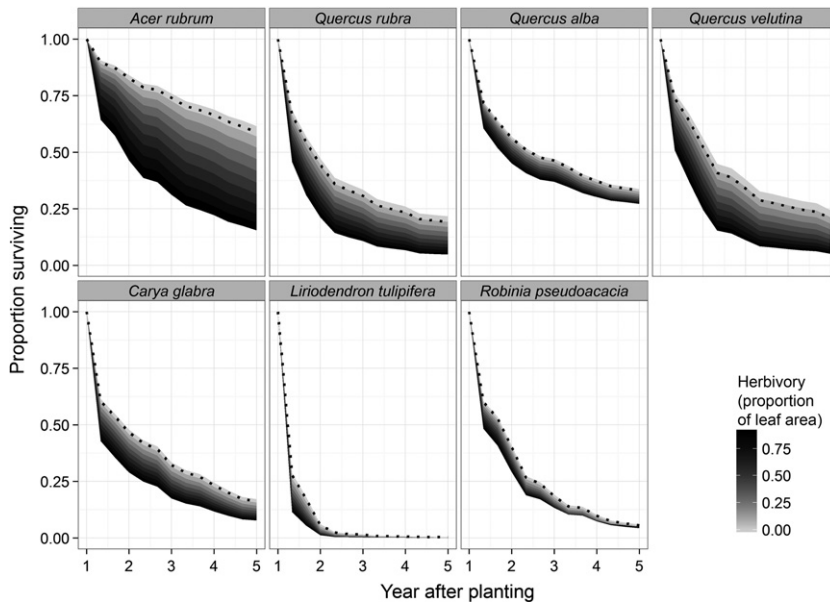


Fig. 4. Simulated seedling survival at invertebrate herbivory levels ranging from 0% (light) to 100% (dark). Simulations assumed average environmental conditions, planting height, number of leaves, and spring planting with no foliar disease or vertebrate herbivory. The dotted line shows simulated survival at the average level of observed herbivory across all regions. Simulations begin 1 year after planting.

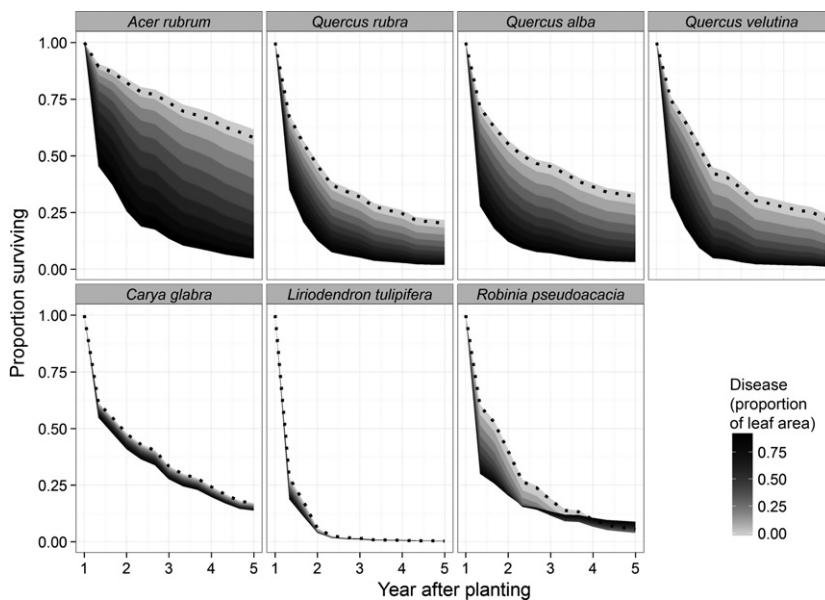


Fig. 5. Simulated seedling survival at disease levels ranging from 0% (light) to 100% (dark). Simulations assumed average environmental conditions, planting height, number of leaves, and spring planting and no herbivory. The dotted line shows simulated survival at the average level of observed foliar damage due to disease across all regions. Simulations begin 1 year after planting.

EFFECTS OF LEAF DAMAGE ON SURVIVAL

The modelled 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 <10% of leaf area on average. Thus, even though high levels of leaf damage were likely to kill individual seedlings, the proportion of seedlings that were killed by foliar damage was low. Moreover, the species that were most sensitive to foliar damage did not have large differences in damage across range edges (e.g. *Q. velutina* responded strongly to disease, but it had similar amount of disease in areas where it was native and migrant, whereas *L. tulipifera* had far less disease in areas where it was a migrant, but that had only small and insignificant effects on survival). Our estimates for the effects of

foliar damage on survival are somewhat smaller than other researchers have reported (e.g. Meiners, Handel & Pickett 2000; Yamazaki, Iwamoto & Seiwa 2009; Cleavitt, Fahey & Battles 2011; Coyle *et al.* 2014), but are corroborated by similar levels of survival between the control and pesticide treatments, although some caution is warranted, given that two species (*A. rubrum* and *Q. rubra*) experienced negative indirect effects of the pesticide treatment on survival in the field. 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, Frelich & Reich 2012), it seems unlikely to have much of an effect on colonization success by migrant seedlings in these forests.

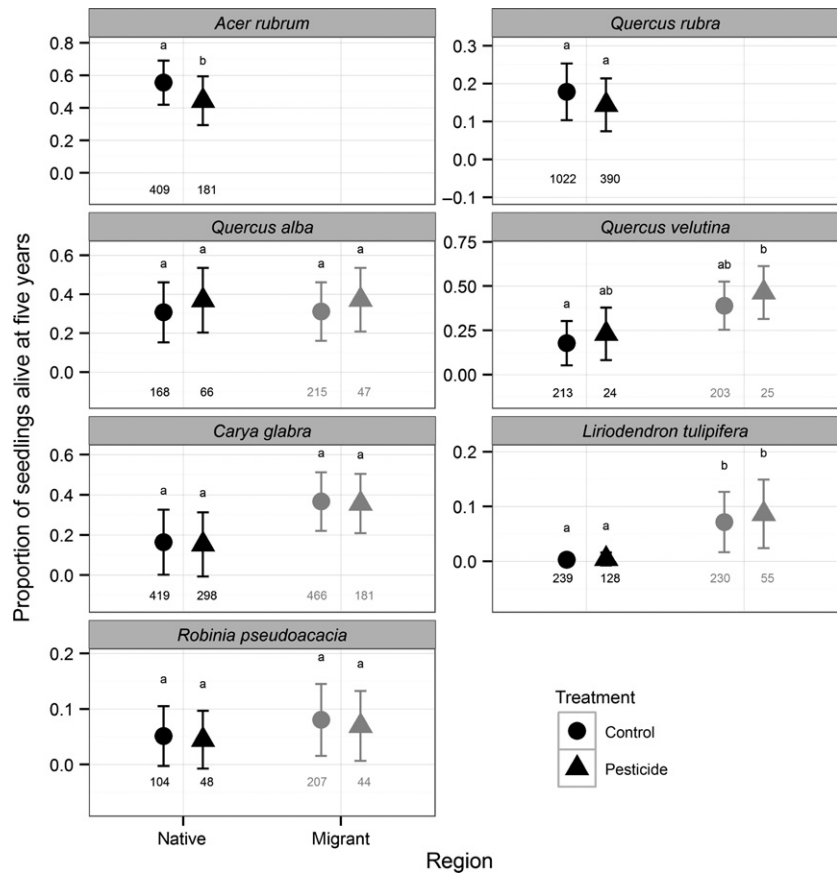


Fig. 6. Modelled survival after 5 years for seedlings in control and pesticide treatments (± 1 SD). Survival estimates include the variability associated with the intercept for each treatment in each region and the average effects of herbivory and disease in each region. Survival is estimated at the 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.

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, Clark & Dietze 2009; Samis & Eckert 2009; McCarthy-Neumann & Ibáñez 2012). Although we found cases where biotic interactions systematically varied beyond range edges, commonly observed levels of foliar damage did not translate into substantial effects on seedling survival. Similarly, even in cases where there were large differences in survival across range edges, differences in foliar damage only accounted for very small amounts of these differences. 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; Van der Putten 2003) and often has stronger effects on mortality than damage to leaves (Zvereva & Kozlov 2012; Dietze & Matthes 2014). 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 & 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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Data accessibility

Seedling data (foliar damage, planting heights, vertebrate herbivory, etc.) and environmental data (soil moisture, light, temperature, soil nutrients, etc.) are available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.1b433> (Katz & Ibáñez 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Plot environmental characteristics.

Appendix S2. Seed sources.

Appendix S3. Greenhouse control experiment.

Appendix S4. Vertebrate herbivory.

Appendix S5. Model code.

Appendix S6. Efficacy of pesticide.