1

7

8

9 Title: Differences in biotic interactions across range edges have only minor effects on plant

10 performance

11

12

13 Running Head: Will biotic interactions affect range shifts?

14

15 Daniel S.W. Katz[1]

16 Inés Ibáñez

17

18 School of Natural Resources and Environment, University of Michigan – Ann Arbor

19 440 Church St., Ann Arbor, MI 48109

20 Fax: 734-936-2195

21   Summary

22 **1.** It is widely expected that plant species will expand their ranges poleward in response to

23 climate change. In the process, individuals establishing beyond existing range margins will be

24 exposed to new biotic communities, including different assemblages of natural enemies. The

25 resulting differences in biotic interactions could lead to scenarios of enemy release or biotic

26 resistance and if the interactions are strong, they could influence plant performance and therefore

27 colonization success.

[1] Correspondence author. E-mail: dwkatz@umich.edu

28 **2.** In order to test whether natural enemies will affect range expansion dynamics, we transplanted

29 seven species along a 450 km latitudinal gradient that spanned the range edges of five of these

30 species. The experiment was conducted over five years with ~ 13,000 seedlings and included

31 pesticide treatments to reduce invertebrate herbivory. We measured foliar damage caused by

32 disease and invertebrate herbivores, seedling survival, light availability, soil moisture, soil

33 nutrient concentrations and several other variables in nine forests located in four regions along

34 the latitudinal gradient.

35 **3.** We found that several species (*Carya glabra, Liriodendron tulipifera, Quercus velutina* and

36 *Robinia pseudoacacia*) tended to have less foliar disease beyond their range but there were few

37 substantial differences in herbivory across range edges (with the exception of *Liriodendron*

38 *tulipifera*). After accounting for other variables, including environmental conditions and

39 vertebrate herbivory, we found that foliar disease decreased survival for four species (*Acer*

40 *rubrum, Quercus alba, Quercus rubra* and *Quercus velutina*) and foliar herbivory reduced

41 survival for three species (*Acer rubrum, Liriodendron tulipifera and Quercus rubra*).

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

43 reductions in survival at observed levels of damage after four years), which is verified by the

44 minor effects of the pesticide treatment on seedling survival.

45 **5.** *Synthesis.* Our results suggest that foliar herbivores and pathogens are unlikely to play a major

46 role in the range expansion dynamics of these temperate tree species.

47

48 **Key words:** biotic interactions, plant-insect interactions, plant-pathogen interactions, range

49 expansion, species distributions, survival, temperate forest

50

51 Survival of tree seedlings beyond current distributions is largely unrelated to differences in

52 herbivory and disease

53

54

55   INTRODUCTION

56   Climate change is expected to cause shifts in species distributions as plants and animals

57 track changing temperatures and precipitation (Parmesan & Yohe 2003; Hickling *et al.* 2006;

58 Crimmins *et al.* 2011). Predictions of poleward range expansion of plant species over the

59 coming decades and centuries are drawn from correlations between current species distributions

60 and climate (Iverson & Prasad 1998; Guisan & Zimmermann 2000; Pearson & Dawson 2003),

61 and paleo-reconstructions of shifts in vegetation composition during previous periods of climate

62 change (Davis 1983; Graumlich & Davis 1993; Petit *et al.* 2002; Williams *et al.* 2004). Some

63 studies have found empirical evidence for contemporary latitudinal shifts of tree species

64 distributions in North America (Woodall *et al.* 2009; Murphy, Vanderwal & Lovett-Doust 2010;

65 Boisvert-Marsh, Périé & de Blois 2014; Desprez *et al.* 2014), whereas others have not (Zhu,

66 Woodall & Clark 2012). The variability in how species distributions respond to climate change

67 highlights the potential importance of non-climatic drivers, such as biotic interactions.

68 Biotic interactions with natural enemies, competitors and mutualists have the potential to

69 influence range expansion dynamics of terrestrial plants by systematically affecting the

70 performance of plants establishing beyond their current range, where populations do not yet exist

71 (hereafter referred to as 'migrants') (Cairns & Moen 2004; Moorcroft, Pacala & Lewis 2006;

72 Morriën *et al.* 2010; Wisz *et al.* 2013; HilleRisLambers *et al.* 2013). The effects of natural

73 enemies on plant populations are often substantial (Katz 2016), as are their subsequent effects on

74 ecosystem function (Hicke *et al.* 2012). It is increasingly thought that predictions of changes in

75 species distributions in response to climate change should take herbivores and pathogens into

76 account (Van der Putten, Macel & Visser 2010; Zarnetske, Skelly & Urban 2012; Svenning *et al.*

77 2014). While several studies have investigated how soil communities differentially affect native

78 vs. migrant plants (van Grunsven *et al.* 2010; Stanton-Geddes & Anderson 2011; McCarthy-

79 Neumann & Ibáñez 2012), little is known about whether existing above-ground herbivore and

80 pathogen communities will affect latitudinal range expansion.

81 Populations on the expanding edge of a species distribution often escape from specialist

82 natural enemies, as is shown by an increasing number of case studies from various organisms

83 (Alexander *et al.* 2007; Menéndez *et al.* 2008; Phillips *et al.* 2010b; Patot *et al.* 2010; Tsai &

84 Manos 2010). This can happen because of low host densities on range edges and because

85 migrant populations on expanding range fronts originate from repeated founding events, each of

86 which offers a chance to leave specialists behind (Phillips, Brown & Shine 2010a). Moreover, in

87 a greenhouse experiment, successful range expanding plants were less affected by a naïve

88 herbivore (Engelkes *et al.* 2008) showing that migrants can also be released from generalist

89 herbivores. Even though enemy release is transient because of pest and pathogen accumulation

90   (Brändle *et al.* 2008; Mitchell *et al.* 2010; Diez *et al.* 2010), it could still help migrant plants

91   outperform native ones, increasing colonization success and overall rates of range expansion

92   (Moorcroft *et al.* 2006).

93   However, as range expanding species enter new areas, they will encounter indigenous

94   natural enemies; biotic resistance from the existing community could potentially prevent new

95   plant species from establishing there. There are many examples of native generalist herbivores

96   reducing the performance of plants of exotic (i.e., intercontinental) origin (Levine, Adler &

97   Yelenik 2004; Parker, Burkepile & Hay 2006). However, there are substantial differences

98   between intra-continental range expansion and inter-continental range expansion (as reviewed in

99   Morriën et al. 2010, Van der Putten et al. 2010). First, natural enemy community composition

100 may not change abruptly at the edge of a plant species range. Second, existing plant

101 communities may contain species that are closely related to the migrant; in this case, specialist

102 natural enemies may transfer quickly (Connor *et al.* 1980; Bertheau *et al.* 2010). Scenarios of

103 both enemy release and biotic resistance are possible and only in situ experimental field studies

104 can determine how the net effects of biotic interactions will vary across range edges (Morriën *et*

105 *al.* 2010; van der Putten 2011; Renwick & Rocca 2015).

106   Whether the net differences in biotic interactions are positive or negative, they are likely

107 to have the largest effect on early life stages, which tend to be more strongly affected by density

108 dependent forces (Green et al. 2014, Zhu et al. 2015 but see Piao et al. 2013). Many of the

109 strongest examples of habitat filtering driven by biotic interactions have been found at the

110 seedling stage (HilleRisLambers, Clark & Beckage 2002; Fine *et al.* 2006; Andersen, Turner &

111 Dalling 2014). This may be in part because small individuals have low energy reserves, are

112 especially vulnerable to biotic and abiotic forces and tend to have weaker chemical defenses

113 (Myers & Kitajima 2007; Barton & Koricheva 2010; Boege, Barton & Dirzo 2011; Massad

114 2013). If biotic forces have the potential to limit range expansion, the seedling stage would be

115 the first place to look for it.

116   Here, we test how biotic interactions vary across range edges and assess their effects on

117 plant performance. We use a seedling transplant experiment with seven temperate tree species

118 plants to answer the following questions: 1) Are migrant species exposed to different amounts of

119 herbivory and disease than in their native range? And, 2) How important are any differences in

120 herbivory and disease to plant survival? Answers to these questions will help determine whether

121   foliar herbivores and pathogens have the potential to substantially affect colonization success and

122   therefore range expansion dynamics.

123

124   METHODS

125   We initiated a seedling transplant experiment in 2010, and over the following four years

126   we planted seedlings in four regions across a 450 km latitudinal gradient (Fig. 1). Species

127   origins varied (Table 1): five were native or naturalized (self-sustaining populations were

128   present) at some regions and migrants at others (*Carya glabra* P. Mill., *Liriodendron tulipifera*

129   L*., Q. alba* L.*, Q. velutina* Lam. and *Robinia pseudoacacia* L.) and two species were native

130   across all regions (*Acer rubrum* L. and *Quercus rubra* L.). We selected species based on their

131   current and predicted distributions (Iverson *et al.* 2008) and on their light and soil moisture

132   requirements. At each region we established between one and four sites in different forest types,

133   and at each site we planted seedlings in two to 21 plots (Table 2; Fig. 1); this design was dictated

134   by logistical constraints (i.e., site establishment was restricted to University of Michigan

135   properties or areas we possessed permits to work in) and the unbalanced experimental set up

136   does not pose a challenge for the analyses used. Each plot was composed of between one and

137   three subplots, some of which were used for experimental treatments (see below). Sites and

138   plots were established in a variety of different forest types (Table 2; Fig. 1) and in a range of

139   environmental conditions (Supporting Information A: Plot Environmental Characteristics). A

140   total of 12,762 seedlings were planted between 2010 and 2013 (Table 1).

141

142   *Seedlings*

143   Seeds were germinated at the University of Michigan Matthaei Botanical Gardens (Ann

144   Arbor, MI) in potting soil (Metro-Mix 380; SunGro Horticulture, Agawam, Massachusetts,

145   USA), where they were watered daily. Seeds were collected from wild sources within Michigan

146   when available, but were otherwise obtained from outside of Michigan (Supporting Information

147   B: Seed Sources). To account for maternal effects (i.e., seed size), we measured the height of the

148   seedlings (defined as the distance from the soil to the tip of the apical meristem) one month after

149   emergence. Bare root seedlings were then transplanted into the study plots in May and June of

150   2010 – 2014, with a minimum distance of 25 cm between seedlings. Seedlings were watered

151   upon planting (125 ml/seedling) to decrease transplant shock and existing vegetation was left

152   intact. A total of 2196 seedlings were transplanted in the fall instead of in the spring in 2011,

153   2012 and 2013; this was done in order to both increase the range of seedling sizes and to increase

154   total sample size.

155

156   *Pesticide treatment*

157   We experimentally reduced herbivory in 48 sub-plots in 2012 and 2013 using a

158   pyrethroid pesticide (Talstar P, active ingredient bifenthrin; Fecko 1999). This pesticide has

159   been successfully used by other researchers (e.g., Suwa and Louda 2012, Spiers et al. 2006), and

160   does not contain nitrogen.   To ensure that it caused no direct effects on the plants, either through

161   phytotoxicity or phytostimulation, we conducted a greenhouse control experiment; survival and

162   relative growth rates were not impacted, although there is mixed evidence of mild phytotoxicity

163   for *Acer rubrum* (Supporting Information C: Greenhouse Control Experiment). We sprayed a

164   solution of bifenthrin (0.008% active ingredient) on the tops and bottoms of the leaves of

165   seedlings in treatment sub-plots three times a year during 2012 and 2013. We sprayed the same

166   amount of water on leaves in paired control sub-plots (Fig. 1, panel D). We also distributed a

167   molluscicide, metaldehyde, along one outside edge of pesticide sub-plots to reduce herbivory by

168   slugs and snails. The molluscicide was distributed on the side of the treatment plot furthest from

169   the paired control sub-plot; no metaldehyde was distributed within 5 m of a control sub-plot

170   seedling. Metaldehyde reduces slug abundance and herbivory at the microsite level, without

171   impacting plots as close as 5 m (Fergeson 2004). In 2010 and 2011 we built insect exclosures

172   around a subset of first year seedlings, but neither year's exclosure design consistently reduced

173   herbivory. Only mortality from years after the exclosures were removed is included in the

174   analysis.

175

176   *Seedling measurements*

177   Seedlings were censused three times a year, in early, mid and late summer. Seedling

178   height (defined as the distance from the soil to the highest bud) and diameter (1 cm above the

179   soil) were measured during the first and last census of each year. Leaf damage was quantified by

180   visually surveying up to 25 leaves per seedling using cover classes (<1%, 1-5%, 6-15%, 16-25%,

181   26-50%, 51-75%, >75%). For seedlings that had more than 25 leaves, the 25 leaves surveyed

182   were selected at random. The same person (D. Katz) conducted all surveys to ensure that visual

183   estimates were consistent. During each census foliar damage was categorized as being caused by

184   herbivory, disease, physical damage, or desiccation. Damage types counted as herbivory

185   included chewing (e.g., skeletonizing, window feeding, hole feeding), piercing-sucking (e.g.,

186   stippling; regularly shaped small round discolorations in leaves), leaf mining and galling.

187   Damage was counted as disease if symptoms included abnormal coloration, blackening of the

188   leaf, dark spots with necrosis, spots with discolorations surrounding them and the presence of

189   fungal fruiting bodies. Both infectious and non-infectious diseases (e.g., nutrient difficiencies)

190   are therefore included in the disease category (Sinclair & Lyon 2005). We also recorded whether

191   seedlings exhibited stem damage patterns typical of those caused by browsing by mammals at

192   each census; this was recorded as a binary variable. The role of vertebrate herbivores was

193   further investigated using deer exclosures and trail cameras that were deployed at study plots

194   during 2013 and 2014 (Supporting Information D: Vertebrate Herbivory). Although leaf litter

195   was disturbed during censuses, which could have reduced potentially fatal burial in leaf litter

196   (Patterson *et al.* 2011), this disturbance was consistent for all seedlings at all sites.

197

198   *Environmental Data*

199   Environmental variables measured included light availability, temperature, soil nutrients

200   and soil moisture. Hemispherical canopy photos were taken 1 m above seedlings, using a Sigma

201   SD14 camera (Sigma Corporation, Japan) with a sigma 4.5 mm circular fisheye lens (Sigma

202   Corporation, Japan) to measure light availability. At least two photos were taken per sub-plot

203   when canopy closure was greatest (i.e., in mid-summer). Photos were taken under uniform sky

204   conditions (i.e., dusk, dawn, or uniformly cloudy days). The global site factor (GSF), the

205   proportion of total possible sunlight reaching the forest floor, was calculated using Hemiview

206   (Delta-T Devices, Cambridge, UK). GSF was averaged across subplots and across years.

207   Temperature was measured hourly at each site with a HOBO Pro V2 U23 Temperature

208   Data Logger (Onset Computer Corporation, Pocasset, MA). Soil water (percent moisture by

209   volume) was measured hourly at each site with a HOBO Micro Station Data Logger (Onset

210   Computer Corporation, Pocasset, MA). Volumetric soil water content in the top 7.5 cm of soil

211   was measured with a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies,

212   Plainfield, IL, USA) in at least six points per sub-plot several times during the growing seasons

213   of 2011-2014. The relationship between soil moisture at the sub-plot level and at the site level

214 was quantified using linear regressions (mean $R^2 = 0.67$); these regressions were then used to

215 predict soil moisture between censuses. For the first census in each spring, soil moisture was

216 estimated from the beginning of the growing season, which we defined as starting after the last

217 day where the minimum temperature fell below -3° C. For other censuses, the soil moisture

218 values used in the analysis were the mean and standard deviation of soil moisture between that

219 and the previous census.

220   Soil nutrients were measured in 2013 using resin packs (Unibest International

221 Corporation, Walla Walla, WA, USA). Resin packs in the southernmost region (region A; see

222 Fig. 1) were deployed between 4/8/2013 – 10/30/2013 and resin packs were deployed from

223 4/23/2013 – 10/23/2013 in the other regions (regions B, C and D; see Fig. 1). Between two and

224 four resin packs were deployed per plot, depending on the number of subplots. Four resin packs

225 could not be retrieved because they were moved by burrowing animals or were otherwise

226 damaged, and no nutrient data are available for the two plots that were not yet established at the

227 time of resin pack deployment. Resin packs were retrieved and refrigerated until they were

228 shipped to Unibest for analysis. Analysis was conducted by Unibest; ions were extracted using

229 2mHCL and the ion exchange resin analysis was conducted using inductively coupled

230 plasmaspectroscopy analysis (Perkin Elmer 3300 DV; Ca, Mg, Mn, P) and FIA Lab Flow

231 Injection (FIA 2500; NO_3^-, NH_4^+).

232

233 *Statistical Analysis*

234 *Differences in foliar herbivory and disease.*– To compare foliar disease and herbivory across

235 species and sites, we used ANOVA and conducted post-hoc pairwise comparisons using max-t

236 tests through the multcomp package in R (Hothorn, Bretz & Westfall 2008). Max-t tests are

237 robust for comparisons of non-normal distributions, unbalanced sample sizes and heterogeneity

238 of variances (Herberich, Sikorski & Hothorn 2010). To compare whether herbivory varied

239 between seedlings in control and pesticide treatments, we used Wilcoxan Rank Sum Tests.

240

241 *Seedling survival*– To analyze how herbivory, foliar disease and region affected seedling

242 survival, we used a counting process in a Cox survival model (Andersen & Gill 1982) in which

243 we took into account both abiotic and biotic variables: light, soil moisture, soil nutrients,

244 seedling maternal effects, mammal browse and treatment effects (control and pesticide

245 application). This type of model has been used for seedling survival because it allows for the

246 inclusions of both fixed and random effects and for time dependent covariates (McCarthy-

247 Neumann & Ibáñez 2012). We only included seedlings that had survived to their second year in

248 this analysis, to minimize any artifacts from transplanting the seedlings and to reduce the effects

249 of seed resources on survival. The likelihood for the model is:

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

250 where N is whether seedling i was found dead at time t and λ is estimated as a function of the

251 intrinsic rate of mortality, or hazard h, and the extrinsic risk of mortality, or risk μ:

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

252 Parameter estimation was conducted using a Bayesian approach, which allowed us to incorporate

253 different sources of uncertainty and missing data (Gelman & Hill 2007). The hazard was

254 estimated at each time step, h_t, from a gamma distribution, $h_t \sim$ *Gamma* (1, 0.05). The hazard

255 reflects differences in mortality rates through the course of the experiment that are not accounted

256 for by the risk (e.g., survival rates that are age dependent).

257 The risk, μ_{it}, was estimated as a function of the covariates included in the analysis,

258 $\mu_{it} = X_{it}\beta$, where X_{it} is the matrix of covariates associated with each seedling i at time t. β is the

259 vector of fixed effect coefficients associated with each covariate. We explored several different

260 models, including different covariates and random effects (e.g., plot and year) and selected the

261 model with the lowest DIC (Deviance Information Criterion; Spiegelhalter et al. 2002) that

262 allowed us to answer our questions. In the final model, plot effects were drawn from a normal

263 distribution with a mean of μ_{native} or $\mu_{migrant}$ depending on whether the focal species was native in

264 that plot; plot effects ~ Normal(μ, σ^2), where σ ~ Uniform (0, 10). Thus, differences between

265 μ_{native} and $\mu_{migrant}$ represent a difference in survival within a species range compared to beyond a

266 species range. Random effects were included for site and the following covariates were also

267 included (data ranges are described in parentheses): observed proportion of leaf area affected by

268 herbivory over the previous year (continuous: 0 – 1), observed proportion of leaf area affected by

269 disease over the previous year (continuous: 0 – 1), whether or not the seedling was browsed by a

270 mammal since the previous census (binary: 0, 1), seedling height at planting (continuous, 3 – 390

271 mm), the number of leaves in the previous census (continuous, 0 – 60 leaves), the proportion of

272 available light that reached the seedling (continuous: 0 – 1), volumetric soil moisture since the

273 last census (continuous: 0 – 1), whether the seedling was planted in the spring or fall (binary: 0,

274   1) and a fixed effect was included for the indirect effects of the invertebrate herbivory pesticide

275   treatment (binary: 0,1). To improve comparisons between variables, we standardized seedling

276   height at time of transplant, the number of leaves, light and soil moisture. Light and soil

277   moisture were modeled as latent variables characterized by their measured mean and standard

278   deviation for each inter-census time period. Fixed effect coefficients were drawn from non-

279   informative prior distributions: β ~ Normal (0, 1000). The random effects for site was drawn

280   from a normal distribution: random effect ~ Normal (0, σ^2), where σ ~ Uniform (0, 10). We

281   predicted survival where seedlings were native or migrants, $\hat{S}_{native}$ or $\hat{S}_{migrant}$ at average

282   herbivory and disease levels for native and migrant seedlings. Survival of seedlings in the

283   pesticide treatment were estimated separately. The proportion of seedlings surviving, $\hat{S}$ was

284   predicted over time (up to five years), under the following conditions: average light, average soil

285   moisture, average transplant height, average number of leaves, no browsing and spring planting.

$$\hat{S}_{migratory\ status,\ treatment} \sim Power(e^{-\Sigma_t^{time} h_t}, e^{x\beta})$$

286   We then simulated survival for control seedlings throughout all regions across the range of

287   possible herbivory values but with no disease and then vice versa.

288   Survival of each species was modeled separately. Posterior densities of the parameters

289   were obtained by Gibbs sampling (Geman & Geman 1984) using JAGS 3.4 (Plummer 2003) via

290   the rjags package in R (Plummer 2014). Convergence occurred after 1,000 to 10,000 iterations

291   and chains were inspected visually. Each species was run for 40,000 iterations and posterior

292   parameter values were based on postconvergence results. Statistical model code is provided in

293   Supporting Information E: Model Code. Visualization was conducted using the ggplot2 package

294   in R (Wickham 2009). All analyses were conducted using R (R Core Team 2013).

295

296   RESULTS

297   *Differences in herbivory.*– We found extensive variation in herbivory across species and sites,

298   but there were few systematic differences in herbivory across range edges; four out of five

299   migrant species encountered some sites beyond their ranges where herbivory was higher and

300   others where herbivory was lower than in sites located within their ranges (Fig. 2). An exception

301   was *Liriodendron tulipifera;* the three sites within its range were the sites with the highest

302   herbivory levels, although herbivory was only consistently significantly higher at one site within

303   its range than at sites beyond its range (p < 0.05). In general, species showed wide amounts of

304   variation between sites, regardless of migratory status; this is especially apparent for the species

305   that were native at all regions (*Quercus rubra* and *Acer rubrum*). Likewise, migrant species did

306   not tend to have different amounts of herbivory than native species within sites. The pesticide

307   treatment successfully reduced observed herbivory at all sites for three species (Supporting

308   Information F: Efficacy of Pesticide), *Carya glabra, Q. velutina and Q. alba,* and significantly

309   reduced herbivory in some regions for the other species (*Q. rubra, A. rubrum, L. tulipifera* and

310   *Robinia pseudoacacia*; p < 0.05); in 22 out of 23 comparisons, herbivory was lower in the

311   pesticide plots.

312

313   *Differences in foliar disease.*–Foliar disease varied according to species and region, but four

314   species, *C. glabra, L. tulipifera, Q. velutina* and *Q. alba*, tended to have lower disease rates at

315   sites beyond their ranges, although these results were not always statistically significant (Fig. 2).

316   This resulted in migrant plants having somewhat lower foliar disease rates than native plants at

317   many sites. However, it should be noted that *Q. rubra*, which was native at all sites, also had

318   higher disease levels at two of the southern sites (p < 0.05). For *A. rubrum*, the other species that

319   was native in all areas, there were no consistent latitudinal patterns.

320

321   *Seedling survival.*– Herbivory tended to reduce survival for most species, but parameter

322   estimates for the effects of herbivory on survival were only statistically significant for three

323   species, *A. rubrum* (mean and 95% CI: 1.56, 0.53 – 2.55), *Q. rubra* (0.78, 0.23 – 1.31) *and Q.*

324   *velutina* (1.03, 0.10 – 1.92; Fig. 3). Foliar disease had a significantly negative effect on survival

325   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.*

326   *velutina* (1.73, 0.70 – 2.70; Fig. 3). A full list of parameter estimates for the survival model are

327   given in Table 3. Even for species for which leaf damage had significant negative effects on

328   survival, survival simulations showed it caused only small reductions in survival at average

329   amounts of herbivory (Fig. 4) and disease (Fig. 5). Seedling survival in pesticide treatments was

330   never significantly higher than in control treatments (Fig. 6), and overall differences were minor.

331   The modeled proportion of seedlings alive after five years was significantly higher beyond range

332   edges for *L. tulipifera* (mean ± SD for native: 0.003 ± 0.010 compared to migrant: 0.071 ±

333   0.055) and although not significant, some species had similar trends, including *Q. velutina*

334   (native: 0.177 ± 0.126 compared to migrant: 0.389 ± 0.136 and *C. glabra* (native: 0.163 ± 0.162

335   compared to migrant: 0.366 ± 0.146).

336

337   DISCUSSION

338   The potential importance of biotic interactions to plant range expansion has received increased

339   attention in recent years, but a lack of empirical evidence of how biotic interactions vary across

340   range edges has precluded understanding how this may affect plant species range expansion in

341   response to climate change. Our results reveal that systematic differences in invertebrate

342   herbivory across range edges are relatively uncommon, but do occur. In contrast, several plants

343   tended to have more foliar disease in regions where they are native than in regions where they

344   are migrant. Within many sites, migrant species also tended to have less disease than native

345   species. However, our analysis found only minor effects of foliar herbivory and disease on

346   seedling survival at common amounts of damage. This is supported by results from the pesticide

347   treatment, which was generally effective in reducing herbivory, but resulted in minor and

348   idiosyncratic responses in survival. Thus, our results suggest that foliar herbivores and disease

349   are unlikely to have strong effects on latitudinal range expansion dynamics of these temperate

350   trees.

351

352   *Foliar herbivory across range edges*.– There were few systematic differences in foliar herbivory

353   across range edges, which demonstrates that commonly occurring abundances of invertebrate

354   herbivores are unlikely to play a consistent role in intra-continental range expansion of these

355   species. Although it is possible that enemy release will occur for particular species (e.g., *L.

356   tulipifera*) or in particular forest types, foliar herbivory depended more upon conditions at the

357   site and plot level than upon whether a species was native or migrant. The magnitude of spatial

358   heterogeneity in herbivory between sites is similar to that found by other studies (Adams *et al.*

359   2008; Adams & Zhang 2009); if there are regional trends in herbivory, its signal is easily lost in

360   the high inter-site variability. One explanation for why there are not systematic differences is

361   that diet breadth is especially wide for leaf chewing invertebrates in temperate forests (Forister *et

362   al.* 2015).

363

364 *Foliar disease across range edges*.– Several migrant plants tended to have lower levels of foliar

365 disease symptoms outside of their ranges. These findings highlight the relatively higher

366 importance of enemy release from pathogens than from herbivores. The patterns we found are

367 also conservative because our measure of foliar disease includes non-infectious diseases (e.g.,

368 nutrient deficiencies), which are unlikely to be systematically lower beyond a species range.

369 Two of the species that tended to have reduced foliar disease outside of their ranges were *Q. alba*

370 and *Q. velutina*, even though the con-generic *Q. rubra* was common in all regions. This was

371 unexpected, because more closely related plants share more natural enemies, generally

372 facilitating transfer of natural enemies from indigenous relatives to newly arrived plants (Pearse

373 & Hipp 2009; Ness, Rollinson & Whitney 2011; Gilbert, Briggs & Magarey 2015; Parker *et al.*

374 2015), and pathogen host range is often somewhat constrained to host phylogeny (Gilbert &

375 Webb 2007). Thus, the species chosen in this study may lead to especially conservative

376 conclusions about the potential for enemy release from foliar pathogens.

377   The potential for escape from foliar pathogens at range edges is corroborated by other

378 studies on above-ground pathogens (e.g., Alexander et al. 2007), although substantially more

379 work has been conducted on differences in plant-soil interactions across range edges (e.g., van

380 Grunsven et al. 2010, Stanton-Geddes and Anderson 2011, Mccarthy-Neumann and Ibáñez

381 2012). For one of the focal species, *R. pseudoacacia*, negative soil feedbacks are more common

382 within than beyond its range (Callaway *et al.* 2011). Similar patterns are also implied by studies

383 that have found correlations between pathogen load and time since plant introduction (Diez *et al.*

384 2010; Flory & Clay 2013). There is also evidence of reduced negative soil feedback outside of

385 plant ranges from greenhouse experiments (Engelkes *et al.* 2008). These patterns may partially

386 result from migrant seedlings not being near adult con-specifics, which reduced negative plant-

387 soil feedback in the same system as this study (McCarthy-Neumann & Ibáñez 2012). Indeed,

388 even when species encounter the same types of pathogens outside of their range, those strains

389 may be less virulent (Reinhart *et al.* 2010). One potential explanation for why there was a

390 stronger signal of enemy release from pathogens than invertebrate herbivores is that invertebrate

391 herbivores in this system could be more on the generalist range of the spectrum (Forister *et al.*

392 2015) than the comparable pathogens (Barrett *et al.* 2009).

393

394   *Effects of leaf damage on survival.* – The modeled effects of foliar herbivory and foliar disease

395   on seedling survival tended to be small. Although even small responses can have important

396   effects at high levels of damage, herbivory and disease each tended to affect less than 10% of

397   leaf area on average. Thus, even though high levels of leaf damage were likely to kill individual

398   seedlings, the proportion of seedlings that were killed by foliar damage was low. Moreover, the

399   species that were most sensitive to foliar damage did not have large differences in damage across

400   range edges (e.g., *Q. velutina* responded strongly to disease, but it had similar amount of disease

401   in areas where it was native and migrant, whereas *L. tulipifera* had far less disease in areas where

402   it was a migrant, but that had only small and insignificant effects on survival). Our estimates for

403   the effects of foliar damage on survival are somewhat smaller than other researchers have

404   reported (e.g., Meiners et al. 2000, Yamazaki et al. 2009, Cleavitt et al. 2011, Coyle et al. 2014),

405   but are corroborated by similar levels of survival between the control and pesticide treatments,

406   although some caution is warranted, given that two species (*A. rubrum* and *Q. rubra*)

407   experienced negative indirect effects of the pesticide treatment on survival in the field. Although

408   seedlings that experienced vertebrate herbivory had low survival rates, vertebrate herbivory was

409   rare at our study sites. Thus, even though browse damage has the potential to shift competitive

410   hierarchies for temperate and boreal tree species in the transition zone (Fisichelli, Frelich &

411   Reich 2012), it seems unlikely to have much of an effect on colonization success by migrant

412   seedlings in these forests.

413

414   *Implications for range shifts in response to climate change.* – We found that seedlings from non-

415   native species can establish in areas beyond their current ranges, as have several other studies

416   (Kellman 2004; Ibáñez, Clark & Dietze 2009; Samis & Eckert 2009; McCarthy-Neumann &

417   Ibáñez 2012). Although we found cases where biotic interactions systematically varied beyond

418   range edges, commonly observed levels of foliar damage did not translate into substantial effects

419   on seedling survival. Similarly, even in cases where there were large differences in survival

420   across range edges, differences in foliar damage only accounted for very small amounts of these

421   differences. However, it is possible that other types of biotic interactions may be more

422   important; for example, below-ground herbivory was not explicitly measured in this study, but

423   can be an important source of damage to plants (Van der Putten et al. 2001, 2003) and often has

424   stronger effects on mortality than damage to leaves (Zvereva & Kozlov 2012; Dietze & Matthes

425 2014). It will also be important to test for effects on other plant performance metrics; lower

426 growth and reproductive rates beyond range edges can also play a role in determining species

427 distributions (Angert & Schemske 2005). Although much remains to be explored, our findings

428 show that even in cases where biotic interactions vary across range edges, they still may not have

429 important effects on colonization success or range expansion dynamics.

430

437

438   DATA ACCESSIBILITY

439   Seedling data (foliar damage, planting heights, vertebrate herbivory, etc.,) and

440 environmental data (soil moisture, light, temperature, soil nutrients etc.,) are available from the

441 Dryad Digital Repository (Katz & Ibáñez 2016).

442

443   REFERENCES

444 Adams, J.M., Rehill, B., Zhang, Y. & Gower, J. (2008) A test of the latitudinal defense

445   hypothesis: herbivory, tannins and total phenolics in four North American tree species.

446   *Ecological Research*, **24**, 697–704.

447 Adams, J.M. & Zhang, Y. (2009) Is there more insect folivory in warmer temperate climates? A

448   latitudinal comparison of insect folivory in eastern North America. *Journal of Ecology*, **97**,

449   933–940.

450 Alexander, H.M., Price, S., Houser, R., Finch, D. & Tourtellot, M. (2007) Is there reduction in

451   disease and pre-dispersal seed predation at the border of a host plant's range? Field and

452   herbarium studies of *Carex blanda*. *Journal of Ecology*, **95**, 446–457.

453 Andersen, P. & Gill, R. (1982) Cox's regression model for counting processes: a large sample

454   study. *The Annals of Statistics*, **10**, 1100–1120.

455 Andersen, K.M., Turner, B.L. & Dalling, J.W. (2014) Seedling performance trade-offs
456 influencing habitat filtering along a soil nutrient gradient in a tropical forest. *Ecology*, **95**,
457 3399–3413.

458 Angert, A.L. & Schemske, D.W. (2005) The evolution of species' distributions: reciprocal
459 transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution*, **59**,
460 1671–84.

461 Barrett, L.G., Kniskern, J.M., Bodenhausen, N., Zhang, W. & Bergelson, J. (2009) Continua of
462 specificity and virulence in plant host-pathogen interactions: causes and consequences. *The*
463 *New Phytologist*, **183**, 513–29.

464 Barton, K.E. & Koricheva, J. (2010) The ontogeny of plant defense and herbivory: characterizing
465 general patterns using meta-analysis. *The American Naturalist*, **175**, 481–93.

466 Bertheau, C., Brockerhoff, E.G., Roux-Morabito, G., Lieutier, F. & Jactel, H. (2010) Novel
467 insect-tree associations resulting from accidental and intentional biological "invasions": a
468 meta-analysis of effects on insect fitness. *Ecology Letters*, **13**, 506–15.

469 Boege, K., Barton, K.E. & Dirzo, R. (2011) Influence of tree ontogeny on plant-herbivore
470 interactions. *Size and Age Related Changes in Tree Structure and Function*, Tree
471 Physiology (eds F.C. Meinzer, B. Lachenbruch & T.E. Dawson), pp. 193–214. Springer
472 Netherlands, Dordrecht.

473 Boisvert-Marsh, L., Périé, C. & de Blois, S. (2014) Shifting with climate? Evidence for recent
474 changes in tree species distribution at high latitudes. *Ecosphere*, **5**, 1–33.

475 Brändle, M., Kühn, I., Klotz, S., Belle, C. & Brandl, R. (2008) Species richness of herbivores on
476 exotic host plants increases with time since introduction of the host. *Diversity and*
477 *Distributions*, **14**, 905–912.

478 Cairns, D.M. & Moen, J. (2004) Herbivory influences tree lines. *Journal of Ecology*, **92**, 1019–
479 1024.

480 Callaway, R.M., Bedmar, E.J., Reinhart, K.O., Silvan, C.G. & Klironomos, J. (2011) Effects of
481 soil biota from different ranges on *Robinia* invasion: acquiring mutualists and escaping
482 pathogens. *Ecology*, **92**, 1027–35.

483 Cleavitt, N.L., Fahey, T.J. & Battles, J.J. (2011) Regeneration ecology of sugar maple (*Acer*

484 *saccharum*): seedling survival in relation to nutrition, site factors, and damage by insects
485 and pathogens. *Canadian Journal of Forest Research*, **41**, 235–244.

486 Connor, E.F., Faeth, S.H., Simberloff, D. & Opler, P.A. (1980) Taxonomic isolation and the
487 accumulation of herbivorous insects: a comparison of introduced and native trees.
488 *Ecological Entomology*, **5**, 205–211.

489 Coyle, D., Mattson, W., Friend, A. & Raffa, K. (2014) Effects of an invasive herbivore at the
490 single plant scale do not extend to population-scale seedling dynamics. *Canadian Journal of*
491 *Forest Research*, **44**, 8–16.

492 Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011)
493 changes in climatic water balance drive downhill shifts in plant species' optimum
494 elevations. *Science*, **331**, 324–327.

495 Davis, M.B. (1983) Quaternary History of Deciduous Forests of Eastern North America and
496 Europe. *Annals of the Missouri Botanical Garden*, **70**, 550–563.

497 Desprez, J., Iannone III, B. V., Yang, P., Oswalt, C.M. & Fei, S. (2014) Northward migration
498 under a changing climate: a case study of blackgum (*Nyssa sylvatica*). *Climatic Change*,
499 **126**, 151–162.

500 Dietze, M.C. & Matthes, J.H. (2014) A general ecophysiological framework for modelling the
501 impact of pests and pathogens on forest ecosystems. *Ecology Letters*, **17**, 1418–1426.

502 Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J. & Duncan, R.P. (2010) Negative
503 soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, **13**, 803–
504 9.

505 Engelkes, T., Morriën, E., Verhoeven, K.J.F., Bezemer, T.M., Biere, A., Harvey, J.A., McIntyre,
506 L.M., Tamis, W.L.M. & van Der Putten, W.H. (2008) Successful range-expanding plants
507 experience less above-ground and below-ground enemy impact. *Nature*, **456**, 946–948.

508 Fecko, A. (1999) *Environmental Fate of Bifenthrin*. Sacramento, CA.

509 Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Schultz, J.C.
510 & Coley, P.D. (2006) The growth-defense trade-off and habitat specialization by plants in
511 Amazonian forests. *Ecology*, **87**, 150–162.

512 Fisichelli, N., Frelich, L.E. & Reich, P.B. (2012) Sapling growth responses to warmer
513   temperatures "cooled" by browse pressure. *Global Change Biology*, **18**, 3455–3463.

514 Flory, S. & Clay, K. (2013) Pathogen accumulation and long-term dynamics of plant invasions.
515   *Journal of Ecology*, **101**, 607–613.

516 Forister, M.L., Novotny, V., Panorska, A.K., Baje, L., Basset, Y. & Butterill, P.T. (2015) The
517   global distribution of diet breadth in insect herbivores. *Proceedings of the National*
518   *Academy of Sciences*, **112**, 442–447.

519 Gelman, A. & Hill, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical*
520   *Models*. Cambridge University Press, Cambridge, UK.

521 Geman, S. & Geman, D. (1984) Stochastic relaxation, Gibbs distributions, and the Bayesian
522   restoration of images. *IEEE Trans. Pattern Anal. Machine Intell*, **6**, 721–741.

523 Gilbert, G.S., Briggs, H.M. & Magarey, R. (2015) The Impact of Plant Enemies Shows a
524   Phylogenetic Signal. *Plos One*, **10**, e0123758.

525 Gilbert, G.S. & Webb, C.O. (2007) Phylogenetic signal in plant pathogen-host range.
526   *Proceedings of the National Academy of Sciences*, **104**, 4979–83.

527 Graumlich, L.J. & Davis, M.B. (1993) Holocene variation in spatial scales of vegetation patterns
528   in the Upper Great Lakes. *Ecology*, **74**, 826–839.

529 Green, P.T., Harms, K.E. & Connell, J.H. (2014) Nonrandom, diversifying processes are
530   disproportionately strong in the smallest size classes of a tropical forest. *Proceedings of the*
531   *National Academy of Sciences*, **111**.

532 van Grunsven, R.H.A., van der Putten, W.H., Martijn Bezemer, T., Berendse, F. & Veenendaal,
533   E.M. (2010) Plant-soil interactions in the expansion and native range of a poleward shifting
534   plant species. *Global Change Biology*, **16**, 380–385.

535 Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology.
536   *Ecological Modelling*, **135**, 147–186.

537 Herberich, E., Sikorski, J. & Hothorn, T. (2010) A robust procedure for comparing multiple
538   means under heteroscedasticity in unbalanced designs. *PLoS ONE*, **5**, 1–8.

539 Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Hogg, E.H.T., Kashian, D.M.,

540   Moore, D., Raffa, K.F., Sturrock, R.N. & Vogelmann, J. (2012) Effects of biotic

541   disturbances on forest carbon cycling in the United States and Canada. *Global Change*

542   *Biology*, **18**, 7–34.

543   Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide

544   range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

545   HilleRisLambers, J., Clark, J.S. & Beckage, B. (2002) Density-dependent mortality and the

546   latitudinal gradient in species diversity. *Nature*, **417**, 732–5.

547   HilleRisLambers, J., Harsch, M. a, Ettinger, A.K., Ford, K.R. & Theobald, E.J. (2013) How will

548   biotic interactions influence climate change-induced range shifts? *Annals of the New York*

549   *Academy of Sciences*, **1297**, 112–125.

550   Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric

551   models. *Biometrical Journal*, **50**, 346–363.

552   Ibáñez, I., Clark, J.S. & Dietze, M.C. (2009) Estimating colonization potential of migrant tree

553   species. *Global Change Biology*, **15**, 1173–1188.

554   Iverson, L.R. & Prasad, A.M. (1998) Predicting abundance of 80 tree species following climate

555   change in the Eastern United States. *Ecological Monographs*, **68**, 465–485.

556   Iverson, L.R., Prasad, A.M., Matthews, S.N. & Peters, M. (2008) Estimating potential habitat for

557   134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*,

558   **254**, 390–406.

559   Katz, D.S.W. (2016) The effects of invertebrate herbivores on plant population growth: A meta-

560   regression analysis. *Oecologia*, **182**, 43–53.

561   Katz, D.S.W. & Ibáñez, I. (2016) Data from: Foliar damage beyond species distributions is partly

562   explained by distance dependent interactions with natural enemies. *Dryad Data Repository,*

563   *doi:10.5061/dryad.1b433*.

564   Kellman, M. (2004) Sugar maple (*Acer saccharum* Marsh.) establishment in boreal forest: results

565   of a transplantation experiment. *Journal of Biogeography*, **31**, 1515–1522.

566   Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic

567   plant invasions. *Ecology Letters*, **7**, 975–989.

568 Massad, T.J. (2013) Ontogenetic differences of herbivory on woody and herbaceous plants: a
569   meta-analysis demonstrating unique effects of herbivory on the young and the old, the slow
570   and the fast. *Oecologia*, **172**, 1–10.

571 McCarthy-Neumann, S. & Ibáñez, I. (2012) Tree range expansion may be enhanced by escape
572   from negative plant-soil feedbacks. *Ecology*, **93**, 2637–2649.

573 Meiners, S., Handel, S. & Pickett, S. (2000) Tree seedling establishment under insect herbivory:
574   edge effects and inter-annual variation. *Plant Ecology*, **151**, 161–170.

575 Menéndez, R., González-Megías, A., Lewis, O.T., Shaw, M.R. & Thomas, C.D. (2008) Escape
576   from natural enemies during climate-driven range expansion: a case study. *Ecological
577   Entomology*, **33**, 413–421.

578 Mitchell, C.E., Blumenthal, D., Jarošík, V., Puckett, E.E. & Pyšek, P. (2010) Controls on
579   pathogen species richness in plants' introduced and native ranges: Roles of residence time,
580   range size and host traits. *Ecology Letters*, **13**, 1525–1535.

581 Moorcroft, P.R., Pacala, S.W. & Lewis, M. a. (2006) Potential role of natural enemies during
582   tree range expansions following climate change. *Journal of Theoretical Biology*, **241**, 601–
583   16.

584 Morriën, E., Engelkes, T., Macel, M., Meisner, A. & Van der Putten, W.H. (2010) Climate
585   change and invasion by intracontinental range-expanding exotic plants: the role of biotic
586   interactions. *Annals of Botany*, 843 –848.

587 Murphy, H.T., Vanderwal, J. & Lovett-Doust, J. (2010) Signatures of range expansion and
588   erosion in eastern North American trees. *Ecology Letters*, **13**, 1233–1244.

589 Myers, J.A. & Kitajima, K. (2007) Carbohydrate storage enhances seedling shade and stress
590   tolerance in a neotropical forest. *Journal of Ecology*, **95**, 383–395.

591 Ness, J.H., Rollinson, E.J. & Whitney, K.D. (2011) Phylogenetic distance can predict
592   susceptibility to attack by natural enemies. *Oikos*, **120**, 1327–1334.

593 Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic
594   herbivores on plant invasions. *Science*, **311**, 1459–61.

595 Parker, I.M., Saunders, M., Bontrager, M., Weitz, A.P., Hendricks, R., Magarey, R., Suiter, K. &

596 Gilbert, G.S. (2015) Phylogenetic structure and host abundance drive disease pressure in
597 communities. *Nature*, **520**, 542–544.

598 Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts
599 across natural systems. *Nature*, **421**, 37–42.

600 Patot, S., Martinez, J., Allemand, R., Gandon, S., Varaldi, J. & Fleury, F. (2010) Prevalence of a
601 virus inducing behavioural manipulation near species range border. *Molecular ecology*, **19**,
602 2995–3007.

603 Patterson, S.L., Zak, D.R., Burton, A.J., Talhelm, A.F. & Pregitzer, K.S. (2011) Simulated N
604 deposition negatively impacts sugar maple regeneration in a northern hardwood ecosystem.
605 *Journal of Applied Ecology*.

606 Pearse, I.S. & Hipp, A.L. (2009) Phylogenetic and trait similarity to a native species predict
607 herbivory on non-native oaks. *Proceedings of the National Academy of Sciences*, **106**,
608 18097–18102.

609 Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the
610 distribution of speces: are bioclimate envelope models useful? *Global Ecology and
611 Biogeography*, **12**, 361–371.

612 Petit, R.J., Brewer, S., Bordács, S., Burg, K., Cheddadi, R., Coart, E., Cottrell, J., Csaikl, U.M.,
613 Van Dam, B., Deans, J.D., Espinel, S., Fineschi, S., Finkeldey, R., Glaz, I., Goicoechea,
614 P.G., Jensen, J.S., König, A.O., Lowe, A.J., Madsen, S.F., Mátyás, G., Munro, R.C.,
615 Popescu, F., Slade, D., Tabbener, H., De Vries, S.G.M., Ziegenhagen, B., De Beaulieu, J.L.
616 & Kremer, A. (2002) Identification of refugia and post-glacial colonisation routes of
617 European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecology
618 and Management*, **156**, 49–74.

619 Phillips, B., Brown, G. & Shine, R. (2010a) Life-history evolution in range-shifting populations.
620 *Ecology*, **91**, 1617–1627.

621 Phillips, B., Kelehear, C., Pizzatto, L., Brown, G., Barton, D. & Shine, R. (2010b) Parasites and
622 pathogens lag behind their host during periods of host range advance. *Ecology*, **91**, 872–81.

623 Piao, T., Comita, L.S., Jin, G. & Kim, J.H. (2013) Density dependence across multiple life stages
624 in a temperate old-growth forest of northeast China. *Oecologia*, **172**, 207–217.

625   Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs
626   sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical*
627   *Computing*, pp. 1–10. Vienna, Austria.

628   Plummer, M. (2014) rjags: Bayesian graphical models using MCMC.

629   Van der Putten, W. (2003) Plant defense belowground and spatiotemporal processes in natural
630   vegetation. *Ecology*, **84**, 2269–2280.

631   van der Putten, W.H. (2011) Climate change, aboveground-belowground interactions, and
632   species' range shifts. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 365–83.

633   Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and
634   abundance responses to climate change: why it is essential to include biotic interactions
635   across trophic levels. *Philosophical Transactions of the Royal Society: Biology*, **365**, 2025–
636   34.

637   Van der Putten, W.H., Vet, L.E.M., Harvey, J. a. & Wäckers, F.L. (2001) Linking above- and
638   belowground multitrophic interactions of plants, herbivores, pathogens, and their
639   antagonists. *Trends in Ecology & Evolution*, **16**, 547–554.

640   R Core Team. (2013) R: A Language and Environment for Statistical Computing.

641   Reinhart, K.O., Tytgat, T., Van der Putten, W.H. & Clay, K. (2010) Virulence of soil-borne
642   pathogens and invasion by *Prunus serotina*. *The New Phytologist*, **186**, 484–95.

643   Renwick, K.M. & Rocca, M.E. (2015) Temporal context affects the observed rate of climate-
644   driven range shifts in tree species. *Global Ecology and Biogeography*, **24**, 44–51.

645   Samis, K.E. & Eckert, C.G. (2009) Ecological correlates of fitness across the northern
646   geographic range limit of a Pacific Coast dune plant. *Ecology*, **90**, 3051–61.

647   Sinclair, W. & Lyon, H. (2005) *Diseases of Trees and Shrubs.* Cornell University Press, Ithaca,
648   NY.

649   Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & van der Linde, A. (2002) Bayesian measures of
650   model complexity and fit. *Journal of the Royal Statistical Society*, **64**, 583–639.

651   Stanton-Geddes, J. & Anderson, C.G. (2011) Does a facultative mutualism limit species range
652   expansion? *Oecologia*, **167**, 149–155.

653   Svenning, J.C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers,

654   K.H., Dullinger, S., Edwards, T.C., Hickler, T., Higgins, S.I., Nabel, J.E.M.S., Pagel, J. &

655   Normand, S. (2014) The influence of interspecific interactions on species range expansion

656   rates. *Ecography*, 1198–1209.

657   Tsai, Y.-H.E. & Manos, P.S. (2010) Host density drives the postglacial migration of the tree

658   parasite, *Epifagus virginiana*. *Proceedings of the National Academy of Sciences*, **107**,

659   17035–17040.

660   Wickham, H. (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York, NY.

661   Williams, J.W., Shuman, B.N., Webb, T., Bartlein, P.J. & Leduc, P.L. (2004) Late-Quaternary

662   vegetation dynamics in North America:scaling from taxa to biomes. *Ecological*

663   *Monographs*, **74**, 309–334.

664   Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F.,

665   Forchhammer, M.C., Grytnes, J.A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I.,

666   Luoto, M., Maiorano, L., Nilsson, M.C., Normand, S., Öckinger, E., Schmidt, N.M.,

667   Termansen, M., Timmermann, A., Wardle, D. a., Aastrup, P. & Svenning, J.C. (2013) The

668   role of biotic interactions in shaping distributions and realised assemblages of species:

669   Implications for species distribution modelling. *Biological Reviews*, **88**, 15–30.

670   Woodall, C.W., Oswalt, C.M., Westfall, J.A., Perry, C.H., Nelson, M.D. & Finley, A.O. (2009)

671   An indicator of tree migration in forests of the eastern United States. *Forest Ecology and*

672   *Management*, **257**, 1434–1444.

673   Yamazaki, M., Iwamoto, S. & Seiwa, K. (2009) Distance- and density-dependent seedling

674   mortality caused by several diseases in eight tree species co-occurring in a temperate forest.

675   *Plant Ecology*, **201**, 181–196.

676   Zarnetske, P., Skelly, D. & Urban, M. (2012) Biotic multipliers of climate change. *Science*, **336**,

677   1516–1518.

678   Zhu, Y., Comita, L.S., Hubbell, S.P. & Ma, K. (2015) Conspecific and phylogenetic density-

679   dependent survival differs across life stages in a tropical forest. *Journal of Ecology*, **103**,

680   957–966.

681   Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in

682   response to climate change. *Global Change Biology*, **18**, 1042–1052.

683 Zvereva, E.L. & Kozlov, M. V. (2012) Sources of variation in plant responses to belowground
684   insect herbivory: A meta-analysis. *Oecologia*, **169**, 441–452.

685

686 **Table 1.**

687 Plant species used in transplant experiments and their residency status at each study region.

688 Species residency status (native, naturalized, or migrant) was determined using Little's range

689 maps, FIA data (via the Climate Change Tree Atlas; Prasad et al. 2007- ongoing), and county

690 data from the USDA Plants database and the Michigan Flora Online. In some cases these data

691 sources provide conflicting information, which is indicated with an asterisk. The number of

692 seedlings of each species planted in each region is also included

693

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
Total planted			6602	1741	3508	1367

694

695 **Table 2.**

696 Description of sites used in the transplant experiment. Environmental variables at the plot and

697 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

698 **Table 3.**

699 Survival model parameters (mean ± standard deviation) indicate effects on mortality (i.e., higher values indicate higher probability of

700 death). Parameter estimates that were significantly different from zero (95% CI does not include zero) are in bold, except for the fixed

701 effects for migratory status, which are in bold if μ_{native} is significantly different from $\mu_{migrant}$.

Parameter	*Acer rubrum*	*Quercus rubra*	*Quercus alba*	*Quercus velutina*	*Carya glabra*	*Liriodendron tulipifera*	*Robinia pseudoacacia*
browse	1.02 ± 0.60	**0.81 ± 0.27**	**1.62 ± 0.49**	-1.19 ± 1.30	**2.09 ± 0.46**	0.17 ± 0.65	0.36 ± 0.54
disease	**2.27 ± 0.52**	**1.11 ± 0.26**	**1.59 ± 0.47**	**1.74 ± 0.51**	0.23 ± 0.41	0.45 ± 0.56	1.58 ± 2.13
herbivory	**1.56 ± 0.52**	**0.78 ± 0.28**	0.34 ± 1.00	**1.03 ± 0.46**	0.65 ± 0.48	0.78 ± 0.43	0.42 ± 0.71
light	0.95 ± 0.88	-0.67 ± 0.53	-0.67 ± 0.91	-1.57 ± 0.84	-0.36 ± 0.84	0.30 ± 0.75	0.19 ± 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
$\mu_{migrant}$	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 ± 0.16**	**0.21 ± 0.09**	-0.16 ± 0.20	-0.09 ± 0.25	0.08 ± 0.09	-0.06 ± 0.11	0.09 ± 0.16
planting height	0.03 ± 0.16	-0.04 ± 0.09	-0.27 ± 0.19	0.00 ± 0.17	-0.05 ± 0.10	-0.18 ± 0.12	0.06 ± 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 ± 1.47
time of planting	0.61 ± 0.91	0.59 ± 0.89	0.81 ± 0.89	-0.48 ± 0.90	0.57 ± 0.83	-0.48 ± 0.87	-0.99 ± 0.93

702

703

Fig. 1.

705 Regions A – D (panel a) contained one to four sites (panel b), which were located in distinct

706 forest types (e.g., sites C1 - C4). Each site had between two and 21 plots (white boxes in panel

707 c). Each plot had between one and three subplots (grey boxes in panel d) to which pesticide or

708 control treatments were applied.
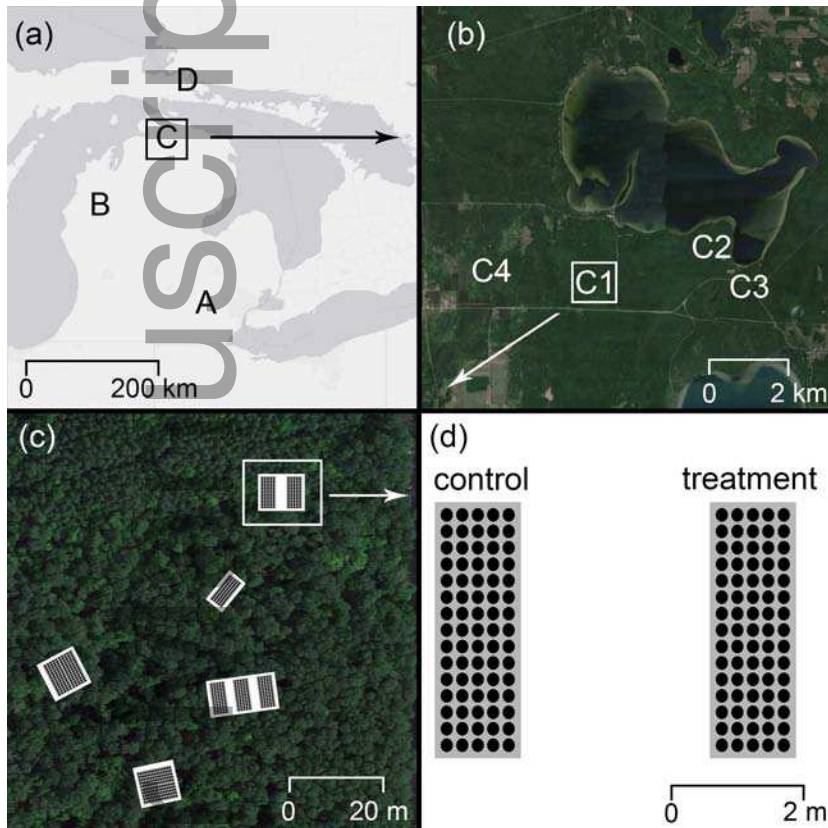

709
710
711
712
713
714
715
716
717 **Fig. 2.**

718 Boxplots of the proportion of leaf area affected by foliar herbivory (column 1) and disease

719 (column 2) in midsummer for each species across the latitudinal gradient, which extended from

720   the southern region (A) to the northernmost region (D). The box consists of the first, second, and

721   third quartiles, the whiskers extend to the 10th and 90th percentiles, the mean is shown with a

722   circle, the sample size is shown below the boxplot for each site, and different letters above the

723   whiskers represent significant differences in foliar herbivory between sites. Boxplot tone

724   represents migratory status (dark gray = native, light gray = migrant). Data from seedlings in

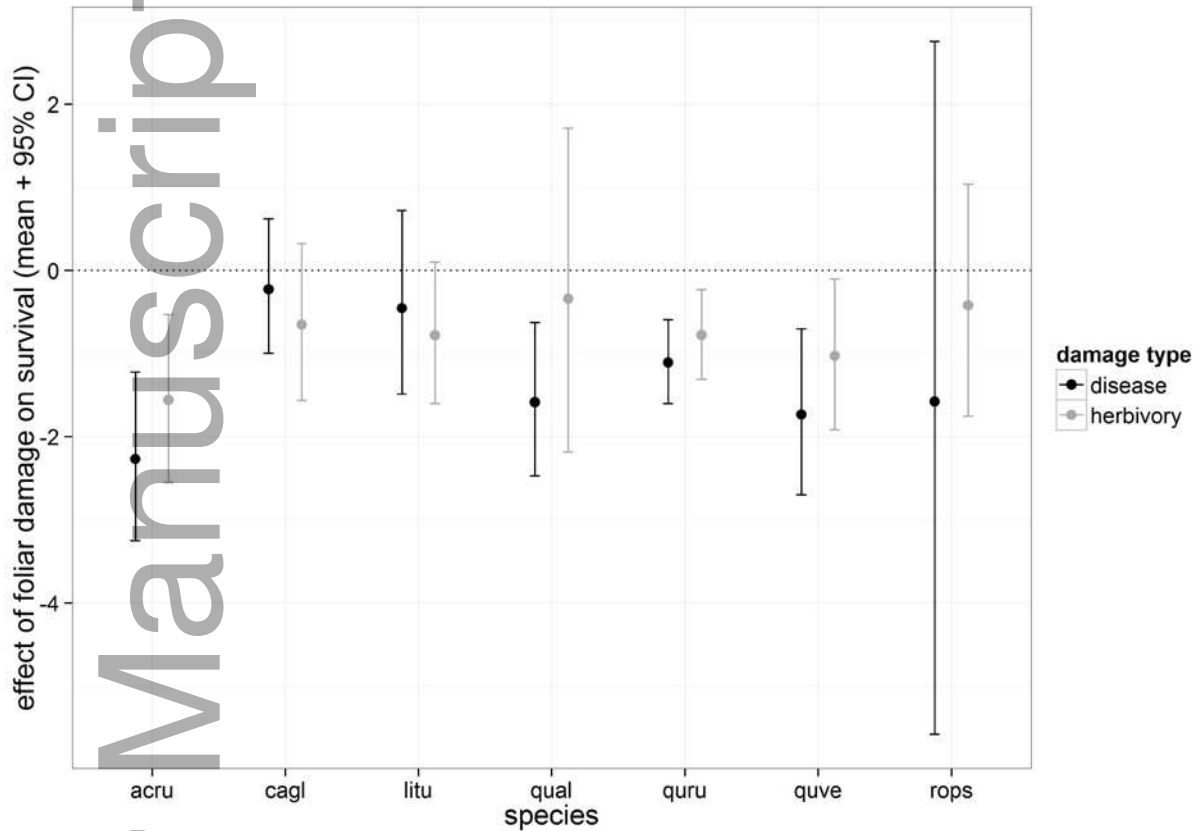725   experimental treatments are not shown.

726
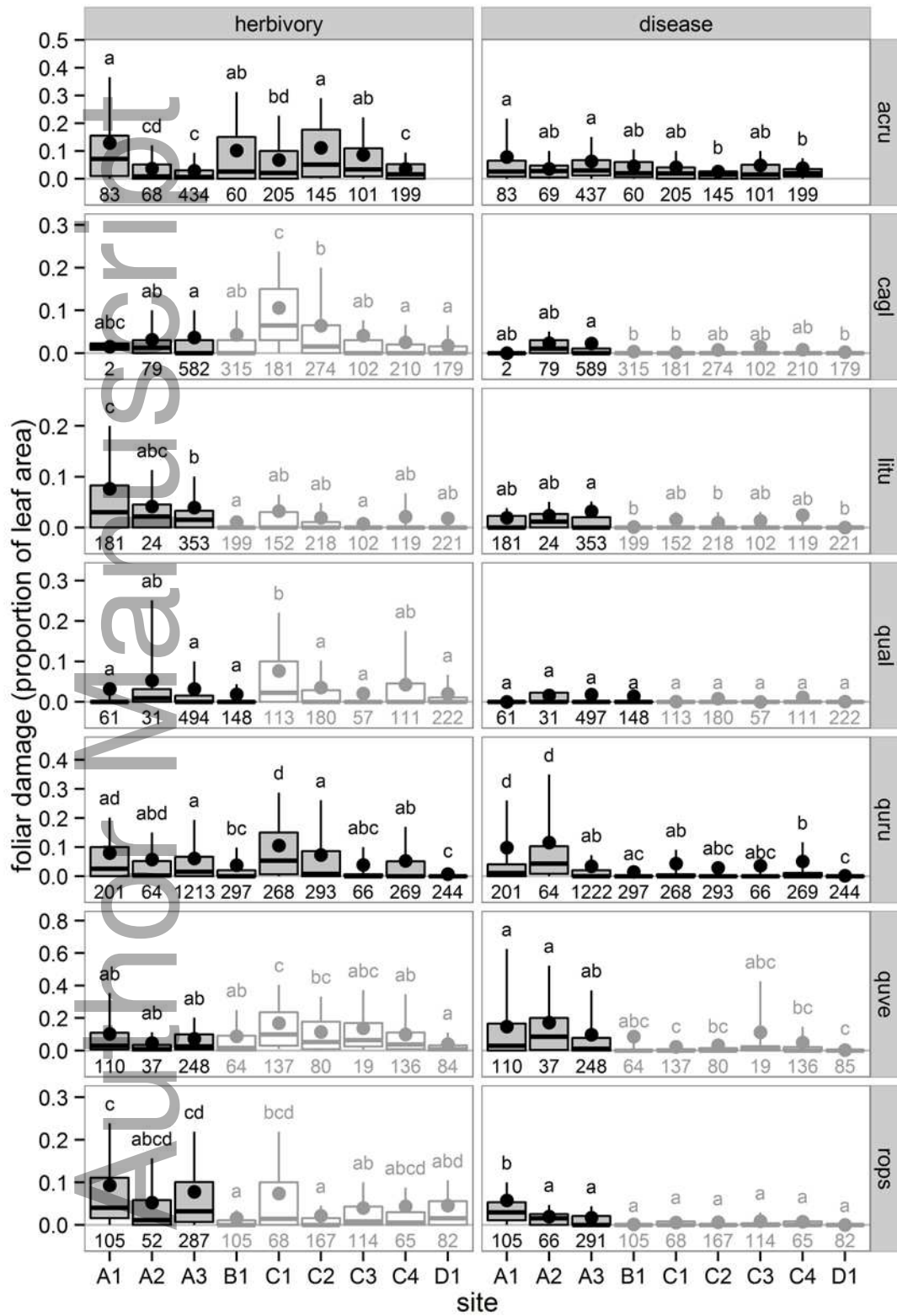
Fig. 3.

728   Effects of foliar herbivory and foliar disease on seedling survival (estimates from the mortality

729   model are multiplied by -1). Parameter estimates below 0 indicate a negative effect on survival;

730   95% credible intervals that cross zero are not statistically significant.


731

732

733

734

735

736

737

738   **Fig. 4.**

739   Simulated seedling survival at invertebrate herbivory levels ranging from 0% (light) to 100%

740   (dark). Simulations assumed average environmental conditions, planting height, number of

741   leaves, and spring planting with no foliar disease or vertebrate herbivory. The dotted line shows

742   simulated survival at the average level of observed herbivory across all regions. Simulations

743   begin one year after planting.
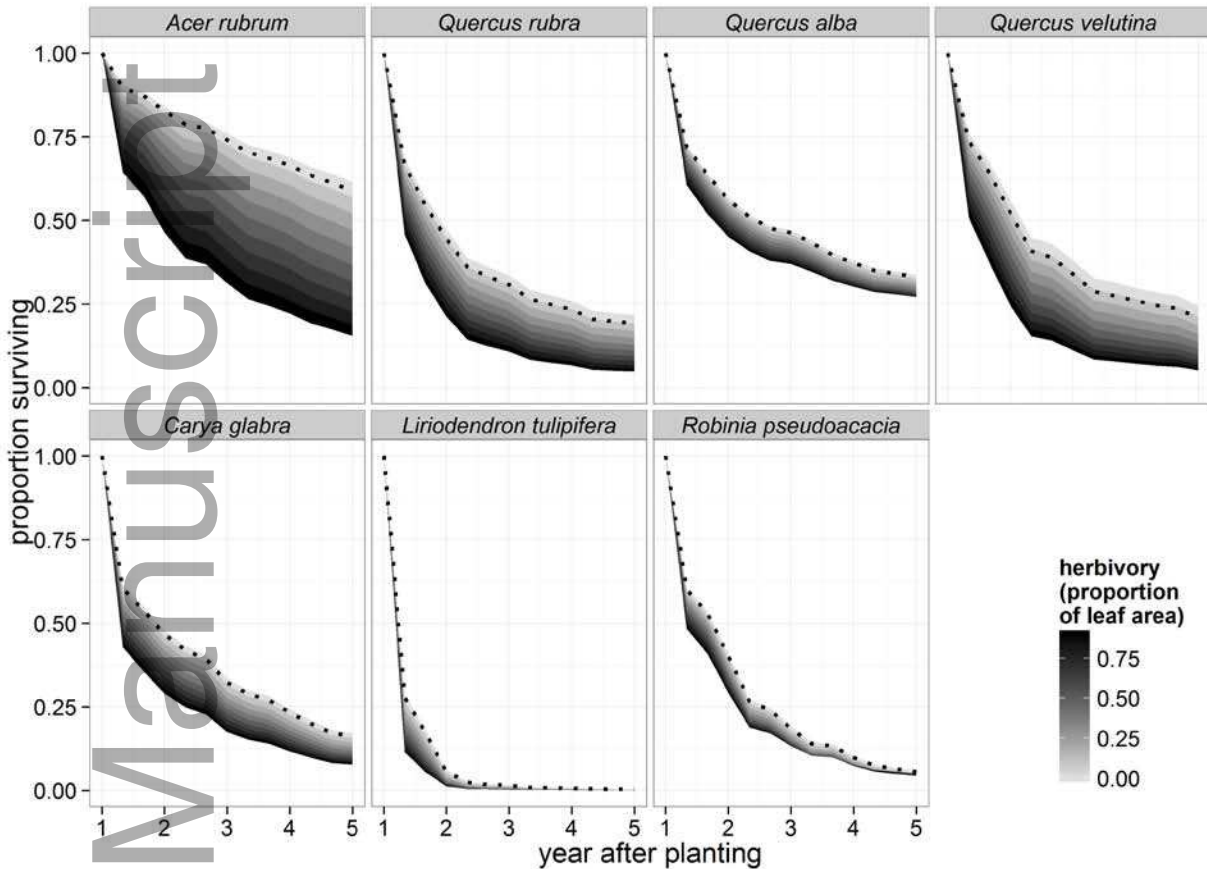
744
745
746
747

748   **Fig. 5.**

749   Simulated seedling survival at disease levels ranging from 0% (light) to 100% (dark).

750   Simulations assumed average environmental conditions, planting height, number of leaves, and

751   spring planting and no herbivory. The dotted line shows simulated survival at the average level

752   of observed foliar damage due to disease across all regions. Simulations begin one year after
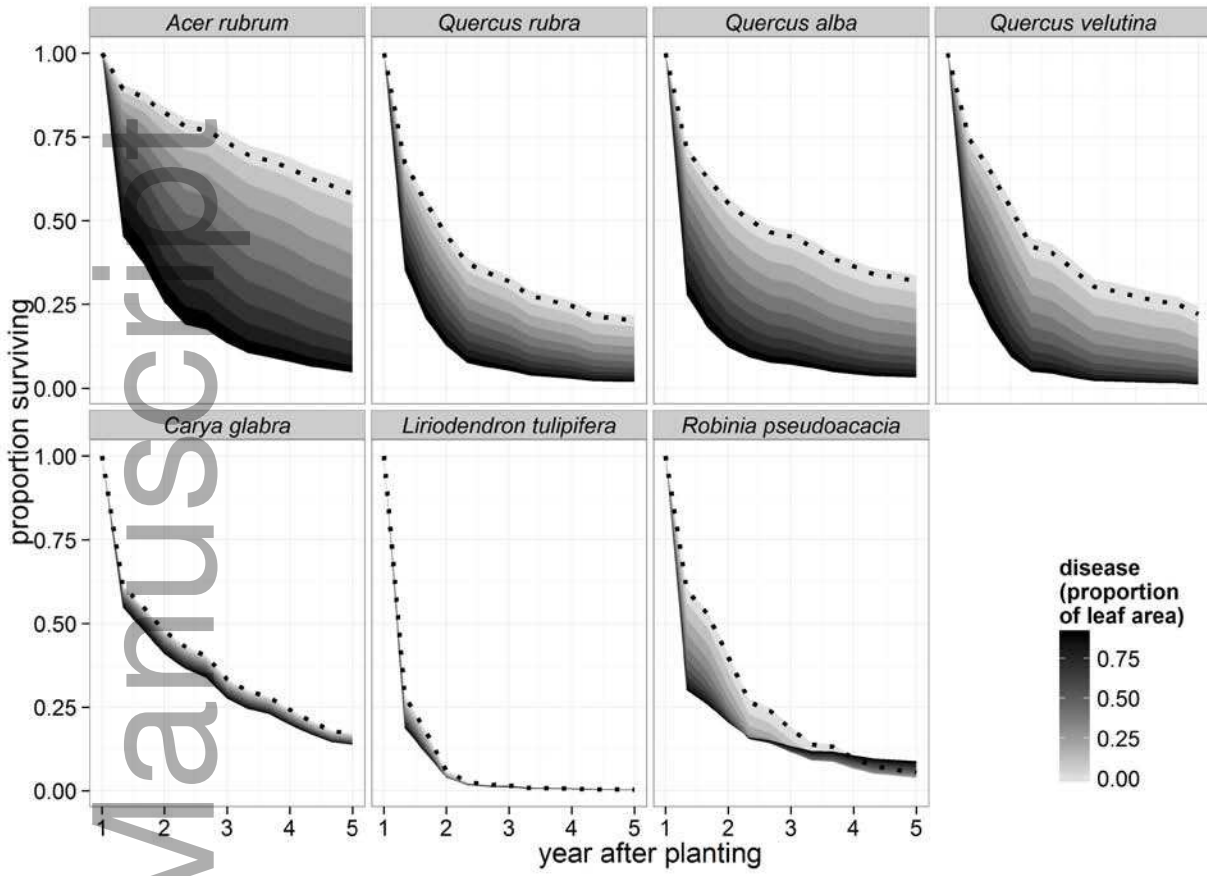
753   planting.

754

755

Fig. 6.

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.