1   Short-term responses to warming vary between native *vs.* exotic species and with latitude in an

2   early successional plant community

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22 **Abstract**

23 Climate change is expected to favor exotic plant species over native species because exotics tend

24 to have wider climatic tolerances and greater phenological plasticity, and also because climate

25 change may intensify enemy release. Here, we examine direct effects of warming (+1.8°C above

26 ambient) on plant abundance and phenology, as well as indirect effects of warming propagated

27 through herbivores, in two heavily invaded plant communities in Michigan, USA separated by

28 approximately three degrees latitude. At the northern site, warming increased exotic plant

29 abundance by 19% but decreased native plant abundance by 31%, indicating that exotic species

30 may be favored in a warmer world. Warming also resulted in earlier spring green-up

31 (1.65 ± 0.77 days), earlier flowering (2.18 ± 0.92 days), and greater damage by herbivores (2-fold

32 increase), affecting exotic and native species equally. Contrary to expectations, native and exotic

33 plants experienced similar amounts of herbivory. Warming did not have strong ecological effects

34 at the southern site, only resulting in a delay of flowering time by 2.42 ± 0.83 days for both native

35 and exotic species. Consistent with the enemy release hypothesis, exotic plants experienced less

36 herbivory than native plants at the southern site. Herbivory was lower under warming for both

37 exotic and native species at the southern site. Thus, climate warming may favor exotic over

38 native plant species, but the response is likely to depend on additional environmental and

39 individual species' traits.

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41 **Keywords:** climate-change, global warming, invasive species, open-top chamber, plant

42 community ecology

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Introduction

Understanding the mechanisms for the success of exotic plants in their introduced range is a longstanding ecological question (Tilman 1985; Davies 2011; Simberloff 2013). The rapid spread and eventual dominance of exotic plants may result from their ability to take advantage of vacant spatial or temporal niche space (Elton 1958), especially following disturbance (Herbold and Moyle 1986). A second proposed mechanism is enemy release, in which exotic plants experience reduced herbivore, disease, and pest pressure compared to their native counterparts (Williamson 1996; Keane and Crawley 2002). However, anthropogenic climate change is likely to interact with each of these mechanisms through extended growing season length and rapidly warming temperatures (Wolkovich and Cleland 2011). These changes are also expected to shift plant-herbivore relationships (Dijkstra et al. 2012). Understanding the mechanisms that influence exotic plants' success under warmer temperatures in their introduced range is critical for understanding and forecasting plant community dynamics.

Warmer temperatures driven by climate change are known to influence the abundance of exotic species (Dukes 2010). For example, warmer temperatures could reduce cold constraints that currently limit exotic survival and open potential opportunities for range expansion (Dukes and Mooney 1999). Further, native species that are stressed by a rapidly changing climate may have reduced competitive abilities and therefore, allow opportunities for exotic establishment or growth in the introduced range (Alpert et al. 2000; Chambers et al. 2016; Ma et al. 2017). Warmer temperatures also lead to extended growing seasons and may create open niche space for exotic species that are able to establish earlier in the season or extend their life cycle past those of native species (Wolkovich and Cleland 2011), and has been seen in both terrestrial and aquatic systems (Stachowicz et al. 2002; Fridley 2012). Thus, exotic species may also be favored

68　in their introduced range due to high phenological plasticity (Richards et al. 2006). Accordingly,

69　these species may have an advantage in a rapidly changing environment (Willis et al. 2008;

70　Matesanz et al. 2010). However, some evidence exists that climate change may lead to neutral

71　and potentially negative responses for exotic and invasive species, suggesting their success may

72　depend on abiotic and biotic interactions (Williams et al. 2007; Bradley et al. 2010).

73　　　The success of exotic species under climate change is also likely to depend on their

74　interactions with herbivores. Exotic plants benefit from enemy release when herbivores prefer

75　native species and therefore indirectly enable exotic species to thrive under relatively less

76　consumptive pressure (Bremm et al. 2016). Climate change may moderate the magnitude and

77　direction of herbivore impacts on exotic plant success by warmer temperatures directly

78　increasing insect metabolic rate (Bale et al. 2002; Fey and Herren 2014). The warming induced

79　reduction of plant food quality may also require herbivores to consume greater quantities to meet

80　nutritional demands (Hillebrand et al. 2009; Sardans et al. 2012). If native species experience

81　increased herbivory due to warming, but this increase is lower in magnitude for exotic species

82　(i.e. enemy release), then exotic species would experience greater success under warmer climate

83　conditions. Alternatively, herbivores may limit the growth of competitive plant species and

84　therefore promote community stability (Van der Putten et al. 2010; Blois et al. 2013; Post 2013;

85　Borer et al. 2014). Thus, forecasting community consequences of exotic plant success may

86　depend on the influence of herbivores in a warmer world.

87　　　Given these direct and indirect responses to climate change, exotic species may be

88　favored in their introduced ranges (Dukes and Mooney 1999; Hellmann et al. 2008). However,

89　these predictions are largely based on theory and observational studies rather than manipulative

90　experiments (Wolkovich and Cleland 2011; Sandel and Dangremond 2012; Wolkovich et al.

91 2013). Further, experiments that test the differential effects of warming on exotic and native

92 species often use simplified biotic communities, which may reduce the ability to make

93 predictions under the full complexity of realistic communities (Lu et al. 2015; Munier et al.

94 2010). Also, *in situ* field-based warming experiments in plant communities have been almost

95 entirely limited to high-latitude and high-elevation ecosystems with low-stature plant

96 communities, and we lack sufficient understanding in mid-latitude and lower-elevation

97 ecosystems (Arft et al. 1999). Finally, in order to best examine the effects of warming on exotic

98 success we must examine ecosystems where introductions of exotics are most prevalent

99 (Simberloff and Von Holle 1999; Turbelin et al. 2017).

100   We addressed these research gaps with an *in situ* field experiment that manipulated warming

101 in highly invaded early successional, mid-latitude plant communities. We examined the effects

102 of warming exotic vs. native species for one annual cycle to test the following hypotheses:

103   *1) Warming will increase exotic species cover more than co-occurring native species cover.*

104   *2) Warming will advance exotic species phenology more than co-occurring native species*

105   *phenology.*

106   *3) Warming will indirectly favor exotic species through increased leaf herbivory compared*

107   *to co-occurring native species.*

108

109 **Methods**

110 *Site Description*

111   We examined two invaded, early successional plant communities in Michigan, USA

112 separated by 354 km and approximately three degrees latitude (Appendix A) from May 2015

113 through October 2016. The northern site is a forest clearing at The University of Michigan's

114   Biological Station (UMBS) located at 45.56° N, -84.71° W and 239 meters above sea level

115   (Appendix A). The 1.53 km^2 clearing was clear-cut in 1994 and is dominated by *Danthonia*

116   *spicata*, *Centaurea stoebe,* and *Poa pratensis* (Table 1). The site was maintained through

117   mowing to prevent forest succession until the beginning of the experiment. The mean annual

118   temperature in Emmet County where the site is located is 5.4 °C with the mean monthly

119   temperature for the hottest month (July) reaching 17.0 °C (1981-2010 normals, Menne et al.

120   2012a; Menne et al. 2012b). Mean annual rainfall and snowfall in Emmet County are 76.7 cm

121   and 244 cm, respectively (1981-2010 normals, Menne et al. 2012a; Menne et al. 2012b). The

122   southern site is an early successional grassland (previously agriculture field) at Kellogg

123   Biological Station's Long Term Ecological Research Site (KBS-LTER) located at 42.40° N, -

124   85.40° W and 289 meters above sea level (Appendix A). The site is dominated by *Solidago*

125   *canadensis*, *Poa pratensis*, and *Hieracium pratense* (Table 1) and was maintained through

126   mowing to prevent succession prior to the beginning of the experiment. The mean annual

127   temperature in Kalamazoo County where the site is located is 10.1 °C with the mean monthly

128   temperature for the hottest month (July) reaching 22.9 °C (1981-2010 normals, Menne et al.

129   2012a; Menne et al. 2012b). Mean annual rainfall and snowfall at this site are 100.4 cm and 127

130   cm, respectively (1981-2010 climate normal, Menne et al. 2012a; Menne et al. 2012b).

131   *Experimental Design*

132   At each site, we established 24 1m^2 plots within a 25 meter by 36 meter area surrounded

133   by a 3 meter tall fence to prevent deer browsing. Plots were separated by at least 4 m of buffer

134   area to prevent edge impacts from chambers (e.g. shading) in neighboring plots and to serve as

135   walkways for sampling. As part of a larger, long-term experiment, the plots were treated with a

136   randomized, fully factorial design that included insect reduction and small mammal exclosure in

137   addition to the warming treatment (Appendix B).

138   We warmed the plots year-round using a passive, open-top chamber design commonly

139   used in tundra ecosystems (Molau and Mølgaard 1996), modified to warm taller stature (≤1.5 m)

140   plant communities and to allow for migration of flying and ground dwelling organisms in and

141   out of the chambers (Welshofer et al. 2018). We used clear, UV-transmitting, 1/8" Lexan

142   Polycarbonate sheets to elevate temperatures using sunlight (ePlastics, San Diego, CA; Appendix

143   A). We installed the chambers during spring 2015 at both sites. The chambers warmed plots

144   during the daytime, on average, by (+1.84±0.79 ºC (SE) and +1.73±0.19 ºC (SE)) in the forest

145   clearing and old agriculture field, respectively, with no evidence for differences in relative

146   humidity. Warming varied with irradiance and therefore exhibited the hottest temperatures (up to

147   approximately 45 °C) during the daytime in the growing season. At the southern site, the

148   chambers led to drier soil by 3.66±0.57 % (SE), but this trend was not observed at the northern

149   site where moisture drained quickly from the sandy soil composition (Welshofer et al.

150   2018). Further, the chambers reduced winter soil temperature, presumably due to reduced

151   snowpack insulation, and resulted in greater variability in soil freeze/thaw cycles (Welshofer et

152   al. 2018). Here we report ecological data collected during the second growing season (2016),

153   after nearly a full year of the warming treatment.

154   *Data collection*

155   Because this study was part of a longer-term experiment, we used non-destructive

156   sampling methods. We visually estimated percent cover for each species in each 1m^2 plot taken

157   at the beginning of the experiment (Spring 2015) and at the end of the second growing season

158   (August 2016). KW performed all estimates to prevent bias between plots or sampling occasions.

159   The origin of each species was classified as either 'native' or 'exotic' according to the PLANTS

160   Database (USDA, NRCS 2006).

161   We monitored the phenology in each plot every 3-4 days from March through October

162   2016. We recorded 'green-up' for each species in each plot by visually estimating the percent of

163   active plant cover in each $1m^2$ plot during the time period (March-May). We recorded a species

164   as 'flowering' as the period between flower bud break and flower senescence. 'Seed set' was

165   determined when an individual exhibited withering of the stigma along with swelling of the

166   ovaries. For both flowering and seed set, we recorded the date when at least one individual for

167   each species in each plot exhibited the phenological stage.

168   We visually estimated the percent of leaf tissue missing (presumably due to herbivory) at

169   the end of the second growing season to capture cumulative damage throughout the season

170   (Schultheis et al. 2015). We haphazardly selected four leaves vertically dispersed along the stem

171   on three individuals of each species within each plot (n=12 leaves per species per plot). When

172   three individuals of that species were not present within a plot, we sampled the maximum

173   number of individuals present. We sampled all species except for *Achillea millefolium*, because

174   visual estimates of tissue damage on its feather-like leaves were difficult to assess. For

175   graminoid species, many ends of the blade were removed making it difficult to determine the

176   amount of tissue eaten. To standardize our results between treatments, we used the average

177   length of undamaged blades for each species as a reference for each leaf herbivory estimate. We

178   only recorded the percent of missing plant tissue, as browning of the tissue could have been a

179   response to abiotic stress or fungal infections (Green et al. 1990). To prevent bias, KW

180   completed all estimates with visual aids depicting species-specific examples of exact herbivory

181   percentages that were calculated using ImageJ software (Schneider et al. 2012). To further

182   determine the probability of leaf attack, we later calculated a binomial response as to whether the

183   leaf experienced any herbivory (1), or no herbivory (0).

184   *Statistical Analysis*

185   We took several steps to prepare the data for analysis. We natural log transformed each

186   percent cover value to conform to the assumptions of general linear regression. As an index of

187   spring green-up phenology, we computed the date at which each species reached 50% of its

188   maximum cover value per plot. For time of flowering and seed set, we computed the minimum

189   date that each species was observed in each phenological stage in each plot. For the leaf

190   herbivory models, we did not consider plots with the reduced insect treatment (n=12 per site).

191   We fit mixed-effect ANOVA models to evaluate the separate and interactive effects of

192   warming and origin (native vs. exotic) on plant percent cover, spring green-up phenology,

193   flowering phenology, seed set phenology, and leaf herbivory. For each response variable at each

194   site, we used a 2-step process to compare complex and reduced models using likelihood ratio

195   tests ($\alpha=0.05$) to select the most parsimonious model. To account for the additional treatments

196   applied as part of the long-term experiment, even though they are not a focus of this study, we

197   first compared the full models including terms for insect reduction and small mammal exclusion

198   treatments to models without those terms. Next, we compared the model including an interaction

199   between warming and origin to a model without the interaction to test for interactive effects of

200   warming and plant species origin on each response variable. A significant interaction term would

201   indicate that the change in the response variable caused by warming depends on plant species

202   origin. Plant species identity was included as a random intercept in each model to account for

203   additional species-specific variation within all response variables. For leaf herbivory models, the

204   data did not conform to a normal distribution and could not be transformed as such; therefore, we

205 used a generalized linear regression model with Poisson error to determine the amount of the leaf

206 eaten and a binomial error to determine the probability of herbivore attack. For both herbivory

207 models the identity of individual plants was also included as a random intercept because multiple

208 observations were made on each individual. 95% confidence intervals were calculated for each

209 parameter estimate using bootstrap methods (number of simulations=999). We calculated the

210 denominator degrees of freedom using the Satterthwaite approximation method (Bolker et al.

211 2009). We used Likelihood Ratio Tests (α=0.05) to evaluate whether initial differences in species

212 cover between warmed and ambient plots existed prior to the start of the experiment, and

213 completed all analyses using R version 3.1.2 (R Development Core Team 2008) and the R

214 package lme4 (Pinheiro and Bates 2000). There were no initial differences between warmed and

215 ambient plots in average percent cover across species at either site in 2015 at the beginning of

216 the experiment (Northern Site: (χ^2=0.84, df=1, p=0.36); Southern Site: (χ^2=0.35, df=1, p=0.55)).

217

218 **Results**

219   At the northern site, the response of plant cover to warming depended on origin (Table 2,

220 Figure 1A). Warming increased exotic plant cover by 19% and decreased native plant cover by

221 31% relative to the average cover in ambient plots ((($\bar{x}_{warmed}$- $\bar{x}_{ambient}$)/ $\bar{x}_{ambient}$)*100). The

222 greatest increases in cover were found in *Rumex acetosella*, *Poa pratensis*, and *Hypericum*

223 *perforatum* (all exotic). However, we did not find evidence that warming influenced plant cover

224 for either native or exotic species in the southern old agriculture field (Table 2, Figure 1B). We

225 also did not find evidence for an interactive effect between warming and origin on average

226 species cover at this site (Appendix C). However, we observed the greatest increases in cover

227   due to warming of *Trifolium* sp. (exotic) and *Euthamia graminofolia* (native), with the greatest

228   decrease in *Poa pratensis* (exotic). Responses of individual species are reported in Appendix D.

229   At the northern forest clearing, plant species greened-up an average of 1.61±0.57 (SE)

230   days earlier in warmed plots than ambient plots (Table 2, Figure 2A). Native and exotic plants

231   shifted green-up phenology by the same amount of time, on average (i.e. the interaction of

232   warming and origin was not present in the most parsimonious model, Appendix C). Plants

233   flowered 2.18±0.92 days earlier in the warmed plots than plants in the ambient plots at the

234   northern site (Table 2, Figure 2C), and the magnitude of this shift was also indistinguishable

235   between native and exotic species (Appendix C). We found that plots at the northern site without

236   the insecticide treatment flowered 2.13±0.86 days later than plots with the insecticide treatment

237   (Table 2). The timing of seed set did not vary according to warming treatment or origin at the

238   northern site (Table 2, Figure 2E). At the southern old agriculture field, warming did not affect

239   spring green-up phenology for native or exotic plants (Table 2, Figure 2B), but exotic plants

240   greened-up an average of 10.35±4.34 days earlier than native plants, regardless of warming.

241   Warming delayed plant flowering by 2.42±0.83 days for both native and exotic species (Table 2,

242   Figure 2D). At this site, exotic plants flowered 37.14±16.57 days earlier than native plants,

243   regardless of warming (Figure 2D). The timing of seed set also did not vary according to

244   warming treatment or origin at the southern site (Table 2, Figure 2F). The interaction between

245   warming and origin was not present in the most parsimonious model for any of the phenology

246   responses at the northern or southern study site (Appendix C).

247   Warming increased the amount of leaf herbivory approximately two-fold at the northern

248   site (Table 3, Figure 3). Native and exotic species experienced similar amounts of herbivory

249   (Table 3, Figure 3), but the way herbivory varied according to warming treatment was

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250 statistically indistinguishable for native vs. exotic species (Appendix C). Warming decreased the

251 amount of leaf herbivory in the southern old agriculture field by approximately half, and native

252 species experienced about 6-fold greater herbivory than exotic species (Table 3). Similarly, at the

253 southern site, the probability of an herbivore attacking a leaf decreased in warmed plots

254 compared to ambient plots and native species experienced a higher probability of attack than

255 exotic species (Table 3). However, the probability of herbivore attack at the northern site did not

256 differ between warmed and ambient treatments, nor by species origin (Table 3). The most

257 parsimonious models for both the amount of leaf eaten and the probability of herbivore attack at

258 both sites did not contain a term for the interaction of warming and herbivory (Appendix C).

259 **Discussion**

260 　　　We found evidence that warming favored exotic species over native species at the

261 northern forest clearing site, where the effects of warming were largely consistent with our

262 predictions. However, the same level of warming did not have strong ecological effects at the

263 southern old agricultural field site. We also found evidence for enemy release at the southern old

264 agriculture field site where native plant species were more likely to experience leaf herbivory

265 and a greater amount of tissue damage than exotic species. However, these trends were not

266 observed at the northern forest clearing site.

267 　　　The moderate ecological effects observed at the northern forest clearing site were

268 consistent with our expectations. Warmed plots had greater plant cover compared to ambient

269 plots, consistent with experimental studies that found warming increases plant productivity

270 (Rustad et al. 2001) or increases the abundance of more productive species (Fridley et al. 2016).

271 Also consistent with predictions, the change in cover was positive for exotic species but negative

272   for native species. The observed shifts in earlier green-up and flowering time at the northern site

273   are consistent with the literature, as plants respond to warmer temperature cues earlier in the

274   season (Dunnell and Travers 2011; Calinger et al. 2013). Warmed plants also experienced

275   greater amounts of herbivory than those in ambient conditions. This could be due to lower food

276   quality (as a result of increased C:N ratios) and therefore increased herbivore demand

277   (Hillebrand et al. 2009; Sardans et al. 2012). Additionally, warmer temperatures may have

278   increased the metabolism of insects within the warmed plots, in turn increasing the amount of

279   leaf tissue required by herbivores (Gillooly 2001). Exotic species greened-up an entire week

280   earlier than native species, indicating their broad climatic tolerance early in the growing season,

281   but the reproductive phenology of native and exotic species responded similarly to warming.

282   Responses at the southern old agriculture field site were not consistent with our original

283   predictions. We observed delayed flowering phenology and a slight but statistically insignificant

284   decrease in plant cover in the warmed plots. We suggest that physiological stress may have

285   prevented both native and exotic plants from benefiting from warming at the southern site with

286   the extreme temperatures (+44 days where temperatures reached 35°C) exacerbated by lower soil

287   moisture conditions ($-3.66 \pm 0.57\%$) in the warmed plots (Welshofer et al. 2017). Although there

288   is considerable variability among plant species in the conditions that cause physiological stress

289   (Wahid et al. 2007), combined heat and drought conditions have shown to delay flowering

290   phenology (Savin and Nicolas 1996; Kazan and Lyons 2016) and decrease aboveground plant

291   biomass (Vile et al. 2011). Additionally, lower soil moisture in the warmed plots could have

292   resulted from increased transpiration at higher temperatures and contributed to plant stress

293   (Pandey et al. 2015). Hence, such extreme conditions could explain these observed plant

294   responses to warming at the southern site.

13

295   Overall, we found limited evidence that exotic plant species will respond to climate

296   change differently than native species, with the exception that warming caused a significantly

297   greater increase in exotic cover relative to native cover at the northern site. The lack of

298   differential effects of warming between native or exotic species may be due to similar ruderal

299   traits shared by species of both origins. Because these systems are both heavily disturbed (clear-

300   cut and agriculture), weedy species dominate the plant assemblage at both sites. Weedy species

301   that readily establish in disturbed environments are likely to have broad climatic tolerances and

302   be relatively insensitive to moderate warming, regardless of their continent of origin

303   (Theoharides and Dukes 2007). For example, plant species that have an affinity for warmer soils

304   and that produce wind-dispersed seeds tended to be the best colonizers of newly available habitat

305   patches as temperatures increased in an alpine system (Matteodo et al. 2013). Notably, warming

306   did not produce changes in the most abundant species at each site, including exotic species of

307   national concern *Centaurea stoebe* (USDA, NRCS 2006). Thus, it is likely that species traits, in

308   addition to species origin, are likely to play an important role in predicting species success in a

309   warmer climate.

310   This experiment suggests climate warming can benefit exotic plant species more than

311   native species, but our results suggest the magnitude and direction of responses are also likely to

312   depend on the environmental temperature as well as species' traits within the community. While

313   short-term experiments such as this increase our understanding of annual ecological variation,

314   they also suggest potential mechanisms that lead to long-term ecological dynamics (Chesson and

315   Huntly 1989; Magnuson 1990; Shriver 2016). We suggest that future research examining the

316   influence of warming on the physiological tolerances of native and exotic species as well as

317 plant-herbivore interactions will provide insight to whether these short-term direct and indirect

318 responses to warming translate into greater success of exotic plant species over time.

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330 **References**

331 Alpert, P., Bone, E., and Holzapfel, C. (2000). Invasiveness, invasibility and the role of

332   environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology,*

333   *Evolution and Systematics*, *3*(1), 52–66.

334 Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer,

335   M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jónsdóttir, I. S., Laine,

336   K., Lévesque, E., Marion, G. M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V.,

337   Robinson, C. H., Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, P. L.,

338   Walker, L. J., Webber, P. J., Welker, J. M. and Wookey, P. A. (1999), Responses of

339   tundra plants to experimental warming: Metal-analysis of the International Tundra

340   Experiment. *Ecological Monographs*, 69: 491–511.

341 Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K.,

342   Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley,

343   S., Jones, T. H., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D. and

344   Whittaker, J. B. (2002), Herbivory in global climate change research: direct effects of

345   rising temperature on insect herbivores. *Global Change Biology*, 8: 1–16.

346 Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., and Finnegan, S. (2013). Climate Change and

347   the Past, Present, and Future of Biotic Interactions. *Science*, *341*(6145), 499–504.

348 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. and

349   White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology

350   and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135.

351 Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler,

352   P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown,

353   C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M.

354   J., Daleo, P., Damschen, E. I., Davies, K. F., Decrappeo, N. M., Du, G., Firn, J., Hautier,

355   Y., Heckman, R. W., Hector, A., Hillerislambers, J., Iribarne, O., Klein, J. A., Knops, J.

356   M. H., La Pierre, K. J., Leakey, A. D. B., Li, W., MacDougall, A. S., McCulley, R. L.,

357   Melbourne, B. A., Mitchell, C. E., Moore, J. L., Mortensen, B., O'Halloran, L. R.,

358   Orrock, J. L., Pascual, J., Prober, S. M., Pyke, D. A., Risch, A. C., Schuetz, M., Smith,

359   M. D., Stevens, C. J., Sullivan, L. L., Williams, R. J., Wragg, P. D., Wright, J. P. and

360   Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light

361   limitation. *Nature*, *508*(7497), 517–520.

362 Bradley, B.A., Blumenthal, D.M., Wilcove, D.S. and Ziska, L.H. (2010). Predicting plant

363 invasions in an era of global change. *Trends in Ecology and Evolution*, 25 (5): 310-318.

364 Bremm, C., Carvalho, P. C. F., Fonseca, L., Amaral, G. A., Mezzalira, J. C., Perez, N. B.,

365 Nabinger, C. and Laca, E. A. (2016). Diet Switching by Mammalian Herbivores in

366 Response to Exotic Grass Invasion. *PLOS ONE*, *11*(2), e0150167.

367 Calinger, K. M., Queenborough, S., and Curtis, P. S. (2013). Herbarium specimens reveal the

368 footprint of climate change on flowering trends across north-central North America.

369 *Ecology Letters*, *16*(8), 1037–1044.

370 Chambers, J. C., Germino, M. J., Belnap, J., Brown, C. S., Schupp, E. W. and Clair, S. B. S.

371 (2016). Plant Community Resistance to Invasion by Bromus Species: The Roles of

372 Community Attributes, Bromus Interactions with Plant Communities, and Bromus Traits.

373 In M. J. Germino, J. C. Chambers, and C. S. Brown (Eds.), *Exotic Brome-Grasses in Arid*

374 *and Semiarid Ecosystems of the Western US* (pp. 275–304). Cham: Springer International

375 Publishing.

376 Chesson, P. and Huntly, N. (1989). Short-term instabilities and long-term community dynamics.

377 *Trends in Ecology & Evolution*, *4*(10), 293–298.

378 Davies, K. W. (2011). Plant community diversity and native plant abundance decline with

379 increasing abundance of an exotic annual grass. *Oecologia*, *167*(2), 481–491.

380 Dell, A. I., Pawar, S., and Savage, V. M. (2011). Systematic variation in the temperature

381 dependence of physiological and ecological traits. *Proceedings of the National Academy*

382 *of Sciences*, *108*(26), 10591–10596.

383 Dijkstra, F. A., Pendall, E., Morgan, J. A., Blumenthal, D. M., Carrillo, Y., LeCain, D. R.,

384 Follett, R. F. and Williams, D. G. (2012). Climate change alters stoichiometry of

385 phosphorus and nitrogen in a semiarid grassland. *New Phytologist*, *196*(3), 807–815.

386 Dukes, J. S. (2010). Responses of Invasive Species to a Changing Climate and Atmosphere. In

387   D. M. Richardson (Ed.), *Fifty Years of Invasion Ecology* (pp. 345–357). Oxford, UK:

388   Wiley-Blackwell.

389 Dukes, J. S. and Mooney, H. A. (1999). Does global change increase the success of biological

390   invaders? *Trends in Ecology & Evolution*, *14*(4), 135–139.

391 Dunnell, K. L. and Travers, S. E. (2011). Shifts in the flowering phenology of the northern Great

392   Plains: Patterns over 100 years. *American Journal of Botany*, *98*(6), 935–945.

393 Elton, C. S. (1958). *The ecology of invasions by animals and plants* (University of Chicago Press

394   ed). Chicago: University of Chicago Press.

395 Fey, S. B. and Herren, C. M. (2014). Temperature-mediated biotic interactions influence enemy

396   release of nonnative species in warming environments. *Ecology*, *95*(8), 2246–2256.

397 Fridley, J. D. (2012). Extended leaf phenology and the autumn niche in deciduous forest

398   invasions. *Nature*, *485*(7398), 359–362.

399 Fridley, J. D., Lynn, J. S., Grime, J. P. and Askew, A. P. (2016). Longer growing seasons shift

400   grassland vegetation towards more-productive species. *Nature Climate Change*, *6*(9),

401   865–868.

402 Gillooly, J. F. (2001). Effects of Size and Temperature on Metabolic Rate. *Science*, *293*(5538),

403   2248–2251.

404 Green, J. L., Capizzi, J. and Maloy, O. (1990). *A Systematic Approach to Diagnosing Plant

405   Damage* (Ornamentals Northwest Archive No. Vol. 13 Issue 6) (p. ii-24). Oregon State

406   University Extension.

407 Hellmann, J. J., Byers, J. E., Bierwagen, B. G. and Dukes, J. S. (2008). Five Potential

408   Consequences of Climate Change for Invasive Species. *Conservation Biology*, *22*(3),

409   534–543.

410   Herbold, B. and Moyle, P. B. (1986). Introduced Species and Vacant Niches. *The American*

411   *Naturalist*, *128*(5), 751–760.

412   Hillebrand, H., Borer, E. T., Bracken, M. E. S., Cardinale, B. J., Cebrian, J., Cleland, E. E.,

413   Elser, J. J., Gruner, D. S., Stanley Harpole, W., Ngai, J. T., Sandin, S., Seabloom, E. W.,

414   Shurin, J. B., Smith, J. E. and Smith, M. D. (2009). Herbivore metabolism and

415   stoichiometry each constrain herbivory at different organizational scales across

416   ecosystems. *Ecology Letters*, *12*(6), 516–527.

417   Kazan, K. and Lyons, R. (2016). The link between flowering time and stress tolerance. *Journal*

418   *of Experimental Botany*, 67(1), 47-60.

419   Keane, R. and Crawley, M. (2002). Exotic plant invasions and the enemy release hypothesis.

420   *Trends in Ecology & Evolution*, *17*(4), 164–170.

421   Lu, X., Siemann, E., Wei, H., Shao, X. and Ding, J. (2015). Effects of warming and nitrogen on

422   above- and below-ground herbivory of an exotic invasive plant and its native congener.

423   *Biological Invasions*, *17*(10), 2881–2892.

424   Ma, Z., Liu, H., Mi, Z., Zhang, Z., Wang, Y., Xu, W., Jiang, L. and He, J.-S. (2017). Climate

425   warming reduces the temporal stability of plant community biomass production. *Nature*

426   *Communications*, *8*, 15378.

427   Magnuson, J. J. (1990). Long-Term Ecological Research and the Invisible Present. *BioScience*,

428   *40*(7), 495–501.

429   Matesanz, S., Gianoli, E. and Valladares, F. (2010). Global change and the evolution of

430   phenotypic plasticity in plants: Global change and plasticity. *Annals of the New York*

431   *Academy of Sciences*, *1206*(1), 35–55.

432   Matteodo, M., Wipf, S., Stöckli, V., Rixen, C. and Vittoz, P. (2013). Elevation gradient of

433   successful plant traits for colonizing alpine summits under climate change.

434   *Environmental Research Letters*, *8*(2), 024043.

435   Menne, M. J., Durre, I., Korzeniewski, B., McNeill, S., Thomas, K., Yin, X., Anthony, S., Ray,

436   R., Vose, R. S., Gleason, B. E. and Houston, T. G. (2012a). Global Historical

437   Climatology Network - Daily (GHCN-Daily), Version 3. NOAA National Climatic Data

438   Center.

439   Menne, M. J., Durre, I., Vose, R. S., Gleason, B. E. and Houston, T. G. (2012b). An Overview of

440   the Global Historical Climatology Network-Daily Database. *Journal of Atmospheric and*

441   *Oceanic Technology*, *29*(7), 897–910.

442   Molau, U. and Mølgaard, P. (1996). *ITEX Manual* (2nd ed.). Copenhagen: Danish Polar Center.

443   Munier, A., Hermanutz, L., Jacobs, J. D. and Lewis, K. (2010). The interacting effects of

444   temperature, ground disturbance, and herbivory on seedling establishment: implications

445   for treeline advance with climate warming. *Plant Ecology*, *210*(1), 19–30.

446   Pandey, P., Ramegowda, V., and Senthil-Kumar, M. (2015). Shared and unique responses of

447   plants to multiple individual stresses and stress combinations: physiological and

448   molecular mechanisms. *Frontiers in Plant Science*, 6:723.

449   Post, E. S. (2013). *Ecology of climate change: the importance of biotic interactions*. Princeton:

450   Princeton University Press.

451   R Development Core Team. (2008). R: A language and environment for statistical computing.

452   Vienna: R Foundation for Statistical Computing. Retrieved from http://www.R-

453   project.org

454 Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J. and Pigliucci, M. (2006). Jack of all

455   trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology*

456   *Letters*, *9*(8), 981–993.

457 Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J. and

458   Gurevitch, J. (2001). A meta-analysis of the response of soil respiration, net nitrogen

459   mineralization, and aboveground plant growth to experimental ecosystem warming.

460   *Oecologia*, *126*(4), 543–562.

461 Sandel, B. and Dangremond, E. M. (2012). Climate change and the invasion of California by

462   grasses. *Global Change Biology*, *18*(1), 277–289.

463 Sardans, J., Rivas-Ubach, A., and Peñuelas, J. (2012). The C:N:P stoichiometry of organisms and

464   ecosystems in a changing world: A review and perspectives. *Perspectives in Plant*

465   *Ecology, Evolution and Systematics*, *14*(1), 33–47.

466 Savin, R. and Nicolas, M.E. (1996). Effects of Short Periods of Drought and High Temperature

467   on Grain Growth and Starch Accumulation of Two Malting Barley Cultivars. *Australian*

468   *Journal of Plant Physiology*. 23(2), 201-210.

469 Schneider, C. A., Rasband, W. S., and Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of

470   image analysis. *Nature Methods*, *9*(7), 671–675.

471 Schultheis, E. H., Berardi, A. E., and Lau, J. A. (2015). No release for the wicked: enemy release

472   is dynamic and not associated with invasiveness. *Ecology*, *96*(9), 2446–2457.

473 Shriver, R. K. (2016). Quantifying how short-term environmental variation leads to long-term

474   demographic responses to climate change. *Journal of Ecology*, *104*(1), 65–78.

475 Simberloff, D. (2013). *Invasive species: what everyone needs to know*. Oxford: Oxford

476   University Press.

477   Simberloff, D. and Von Holle, B. (1999). Positive Interactions of Nonindigenous Species:

478   Invasional Meltdown? *Biological Invasions*, *1*(1), 21–32.

479   Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B. and Osman, R. W. (2002). Nonlinear partial

480   differential equations and applications: Linking climate change and biological invasions:

481   Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National*

482   *Academy of Sciences*, *99*(24), 15497–15500.

483   Theoharides, K. A. and Dukes, J. S. (2007). Plant invasion across space and time: factors

484   affecting nonindigenous species success during four stages of invasion. *New Phytologist*,

485   *176*(2), 256–273.

486   Tilman, D. (1985). The Resource-Ratio Hypothesis of Plant Succession. *The American*

487   *Naturalist*, *125*(6), 827–852.

488   Turbelin, A. J., Malamud, B. D. and Francis, R. A. (2017). Mapping the global state of invasive

489   alien species: patterns of invasion and policy responses: Mapping the global state of

490   invasive alien species. *Global Ecology and Biogeography*, *26*(1), 78–92.

491   USDA, NRCS. (2006). The PLANTS Database, 6 March 2006 (http://plants.usda.gov). National

492   Plant Data Center, Baton Rouge, LA 70874-4490 USA.

493   Van der Putten, W. H., Macel, M. and Visser, M. E. (2010). Predicting species distribution

494   and abundance responses to climate change: why it is essential to include biotic

495   interactions across trophic levels. *Philosophical Transactions of the Royal Society B:*

496   *Biological Sciences*, 365(1549), 2025-2034.

497   Vile, D., Pervent, M., Belluau, M., Vasseur, F., Bresson, J., Muller, B., Granier, C., and

498   Simonneau, T. (2012). Arabidopsis growth under prolonged high temperature and water

499   deficit: independent or interactive effects?. *Plant, Cell, and Environment*, 35, 702-718.

500   Wahid, A., Gelani, S., Ashraf, M., and Foolad, M.R. (2007). Heat tolerance in plants: an

501   overview. *Environmental and Experimental Botany*, 61: 199-223.

502   Welshofer, K. B., Zarnetske, P. L., Lany, N. K. and Thompson, L. A. E. (2018). Open-

503   top chambers for temperature manipulation in taller-stature plant communities. *Methods*

504   *Ecology and Evolution*, 9: 254-259.

505   Williams, A. L., Wills, K. E., Janes, J. K., Vander Schoor, J. K., Newton, P. C. D. and

506   Hovenden, M. J. (2007), Warming and free-air CO2 enrichment alter demographics in

507   four co-occurring grassland species. *New Phytologist*, 176: 365–374.

508   Williamson, M. H. (1996). *Biological invasions* (1st ed). London ; New York: Chapman & Hall.

509   Willis, C., Ruhfel, B., Primack, R., Abraham, J. and Davis, C. (2008). Phylogenetic patterns of

510   species loss in Thoreau's woods are driven by climate change. *Proceedings of the*

511   *National Academy of Sciences*, *105*(44), 17029–17033.

512   Wolkovich, E. M., Davies, T. J., Schaefer, H., Cleland, E. E., Cook, B. I., Travers, S. E. and

513   Davis, C. C. (2013). Temperature-dependent shifts in phenology contribute to the success

514   of exotic species with climate change. *American Journal of Botany*, *100*(7), 1407–1421.

515   Wolkovich, E. M. and Cleland, E. E. (2011). The phenology of plant invasions: a community

516   ecology perspective. *Frontiers in Ecology and the Environment*, *9*(5), 287–294.

Table 1. Species list for each site, and site-level relative abundance**.** All origin values retrieved from USDA Plant Database at the county level. Species relative abundance based on composition estimates collected in August 2016. Relative abundance calculated for each site as the (sum of each species' cover/sum of all species)*100.

Northern Forest Clearing			Southern Old Agriculture Field		
Species	**Origin**	**Relative Abundance (%)**	**Species**	**Origin**	**Relative Abundance (%)**
Danthonia spicata	Native	38.34	*Solidago canadensis*	Native	34.27
Centaurea stoebe	Exotic	29.65	*Poa pratensis*	Exotic	33.74
Poa pratensis	Exotic	11.44	*Hieracium pratense*	Exotic	10.17
Carex pensylvanica	Native	6.21	*Phleum pratense*	Exotic	4.73
Pteridium aquilinum	Native	4.83	*Achillea millefolium*	Native	4.56
Rumex acetosella	Exotic	2.84	*Trifolium pratense*	Exotic	3.28
Hypericum perforatum	Exotic	1.11	*Centaurea stoebe*	Exotic	2.82
Hieracium pilosella	Exotic	<1	*Euthamia graminifolia*	Native	1.66
Poa compressa	Exotic	<1	*Rubus allegheniensis*	Native	1.05
Quercus rubra	Native	<1	*Potentilla recta*	Exotic	<1
Fragaria vesca	Native	<1	*Dactylis glomerata*	Exotic	<1
Vaccinium angustifolium	Native	<1	*Daucus carota*	Exotic	<1
Solidago gigantea	Native	<1	*Trifolium repens*	Exotic	<1
Pilosella aurantiaca	Exotic	<1	*Alliaria petiolata*	Exotic	<1
Asclepias sp.	Native	<1	*Celastrus orbiculatus*	Exotic	<1
Betula sp.	Native	<1	*Arrhenatherum elatius*	Exotic	<1
Antennaria sp.	Native	<1	*Hypericum perforatum*	Exotic	<1
Solidago nemoralis	Native	<1	*Elymus repens*	Exotic	<1
Tragopogon dubius	Exotic	<1	*Asclepias* sp.	Native	<1
Acer rubrum	Native	<1	*Taraxicum officinale*	Exotic	<1
			Barbarea vulgaris	Exotic	<1
			Cardamine hirsuta	Exotic	<1

Table 2. Parameter estimates for the most parsimonious general linear mixed-effects model based on likelihood ratio tests for species cover and phenology response variables as explained by warming and species' origin at each site. All models included species as a random intercept. All parameters significantly different from zero are bolded. Positive origin effects indicate greater values for native species relative to exotic species. Interactions and additional treatments (insects, mammals) are only included when statistically significant (Appendix B).

Response	Northern Forest Clearing			Southern Old Agriculture Field		
	Estimate	Denom. df	95% CI	Estimate	Denom. df	95% CI
Species Cover						
Warmed	**0.62**	**122.14**	**(0.16, 1.07)**	-0.17	213.81	(-0.37, 0.02)
Origin	0.36	21.47	(-0.68, 1.42)	0.82	20.49	(-0.22, 1.92)
Warmed*Origin	**-0.69**	**122.14**	**(-1.38, -0.07)**			
Residuals		126			225	
Green-up						
Warmed	**-1.61**	**103.64**	**(-2.74, -0.52)**	0.29	251.98	(-2.87, 3.46)
Origin	6.86	18.1	(-0.69, 15.43)	**10.35**	**17.80**	**(2.23, 18.33)**
Residuals		115			262	
Flowering Time						
Warmed	**-2.18**	**84.19**	**(-4.02, -0.35)**	**2.42**	**211.24**	**(0.76, 3.88)**
Origin	-15.17	12.88	(-42.94, 9.79)	**37.14**	**18.94**	**(4.00, 70.88)**
Insects	**2.13**	**84.07**	**(0.41, 3.96)**			
Residuals		91			225	
Seed Set Time						
Warmed	0.82	81.09	(-1.98, 3.70)	0.89	183.53	(-2.26, 3.79)
Origin	-8.62	11.09	(-31.26, 14.66)	33.77	16.75	(-1.14, 65.48)
Residuals		87			195	

Table 3. Parameter estimates for the most parsimonious general linear mixed-effects model based on likelihood ratio tests for the herbivory response variables as explained by warming and species' origin at each site. All models included species as a random intercept. All parameters significantly different from zero are bolded. Positive origin effects indicate greater values for native species relative to exotic species. Interactions and additional treatments (insects, mammals) are only included when statistically significant (Appendix B).

Response	Northern Forest Clearing				Southern Old Agriculture Field			
	Estimate	SE	Z-Value	P-Value	Estimate	SE	Z-Value	P-Value
Amount Eaten								
Warmed	**0.68**	**±0.31**	**2.20**	**0.03**	**-0.70**	**±0.28**	**-2.51**	**0.01**
Origin	1.02	±0.84	1.21	0.23	**1.89**	**±0.63**	**3.00**	**<0.01**
Probability Attacked								
Warmed	0.07	±0.35	0.20	0.84	**-0.71**	**±0.23**	**-3.07**	**<0.01**
Origin	1.02	±0.84	1.21	0.23	**2.28**	**±0.54**	**4.22**	**<0.01**

517   **Figure Legends**

518   **Fig. 1** Species percent cover (mean ± 1SE) measured at the end of summer 2016 at the (a)

519   northern forest clearing and (b) southern old agriculture field. Shaded plots represent ambient

520   temperatures and white plots represent the warmed treatment. Data were measured for each

521   species in each plot at each site (n=24). Warming decreased average native cover, but increased

522   average exotic cover at the northern site (p<0.05).

523   **Fig. 2** Phenological responses measured for each species in each plot throughout the 2016

524   growing season at the northern site (left column) and southern site (right column). Shaded plots

525   represent ambient temperatures and white plots represent the warmed treatment. Boxplots

526   display the median (central line), 25th percentile (lower bound), 75th percentile (upper bound),

527   and smallest and largest value (ends of whiskers) no larger than 1.5x the interquartile range from

528   the upper and lower quartiles. An ANOVA (α=0.05) was run on each response's most

529   parsimonious model to determine significant differences between groups. Panels (a, b) show the

530   date where each species reached 50% of its maximum cover where warming led to earlier green-

531   up at the northern site, but not the southern site. Exotic species also greened-up earlier than

532   native species at the southern site, regardless of warming. This trend was also observed at the

533   northern site, although it lacked statistical significance. Panels (c, d) show the median date of

534   flowering, where warming led to earlier flowering at the northern site and delayed flowering at

535   the southern site. Native species also flowered later than exotic species at the southern site.

536   Panels (e, f) show the median date of seed set. No evidence was found for differences between

537   groups.

538   **Fig. 3** Percent of leaf eaten (Mean ± 1SE) at the end of summer 2016 at the (a) northern forest

539   clearing and (b) southern old agriculture field. Shaded plots represent ambient temperatures and

540   white plots represent the warmed treatment. Data were measured for four leaves on three

541   individuals of each species in each plot (n=12) for each site. An ANOVA ran on the most

542   parsimonious model shows warming increased the amount of leaf herbivory at the northern site

543   and decreased the amount of leaf herbivory at the southern site. Native species also experienced

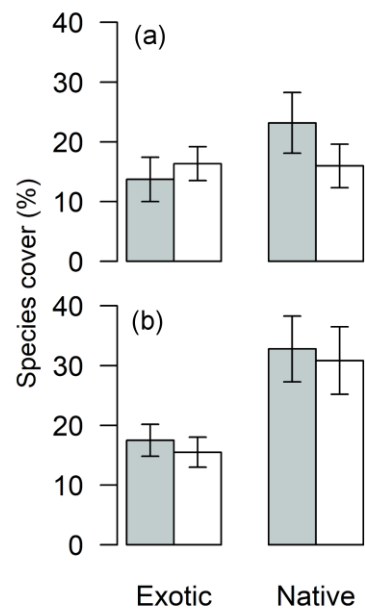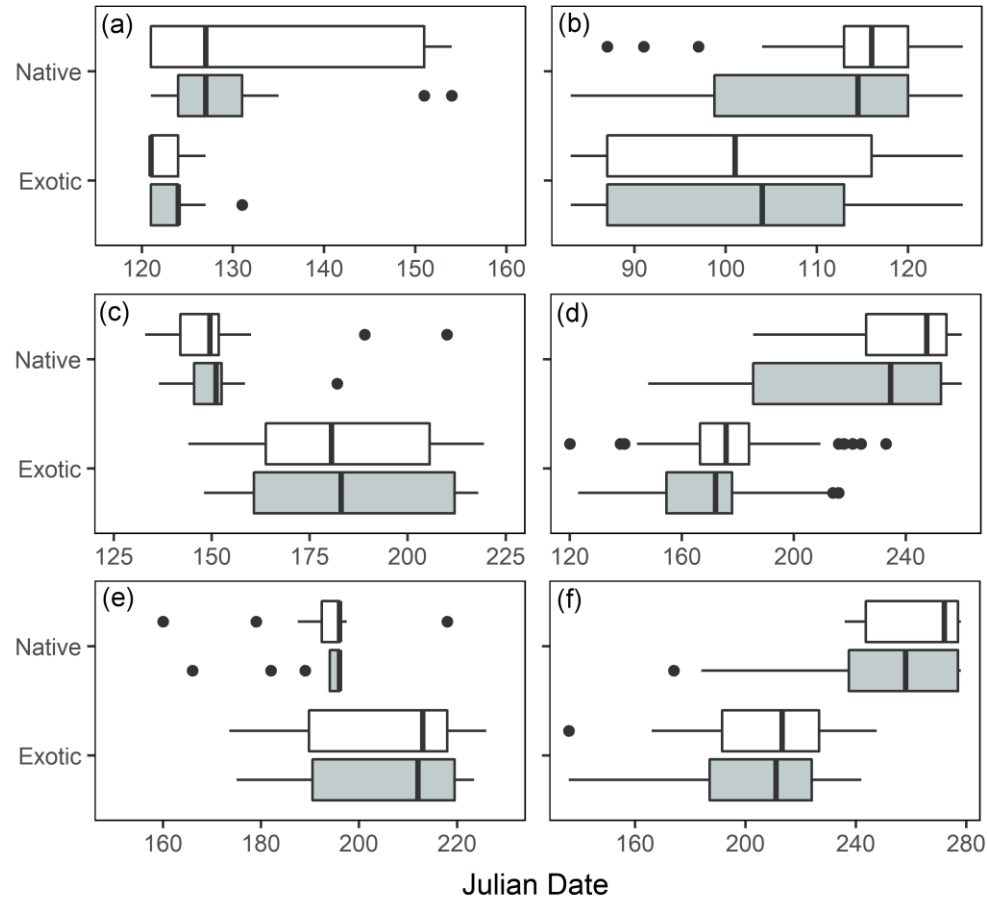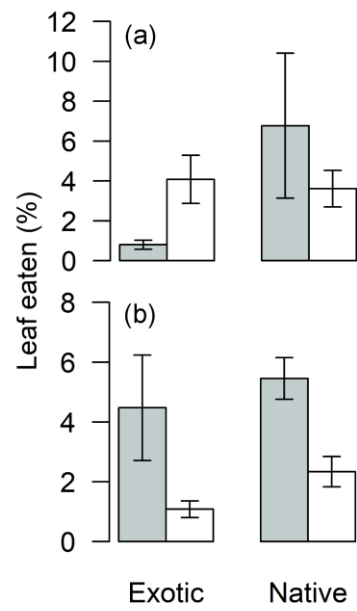544   a greater amount of herbivory than exotic species at the southern site.

Fig. 1

Fig. 2

Julian Date

Fig. 3

Electronic Supplemental Material

Appendix A. Locations of experimental sites.

Fig. S1 A. Map of mid-western United States with study site locations and 30-year temperature normal from 1981-2010 (PRISM Climate Group 2013). B. Open-top chamber experiment in southern old-agriculture field located at Kellogg Biological Station.
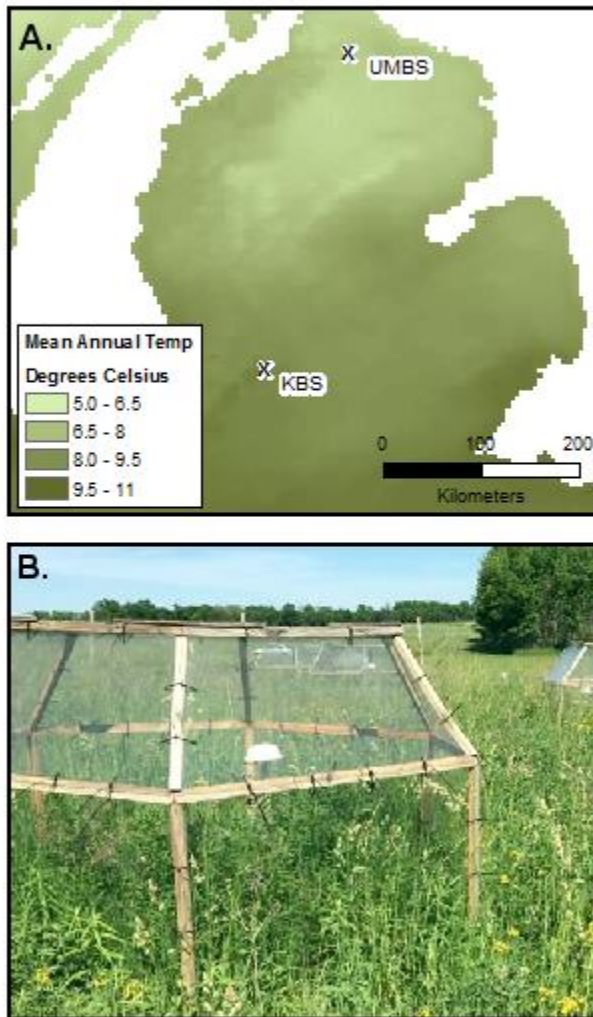
Appendix B. Additional experimental treatment methods for long-term herbivory experiment.

Additional Treatment Methods

As part of the long-term experiment, we reduced insect herbivory through the application of Merit-75 WP insecticide at a concentration of 0.031 g/L with 1.2 L applied for all insect exclusion plots at each site every 13-15 days while measurements were taken during the growing season (Bayer Environmental Science, Research Triangle Park, NC). An equal amount of water (1.2 L) was applied evenly across plots where insects were not reduced within the same treatment session in order to reduce any unequal effects of added water in the insecticide to the plants. All insecticide applications were performed to dry vegetation during early morning low-wind conditions and no precipitation in the following 24 hours. Care was taken to spray all plants across sub-canopies within each plot, such that ground dwelling plants also received treatment.

We also reduced small mammal herbivory by installing 91cm tall, 1.3 cm gauge mesh hardware cloth around 12 plots at each site at the beginning of the experiment. The cloth was buried 20-30 cm beneath the ground (Brown and Davidson 1977). The fencing was reinforced in Spring 2016 by attaching a second layer of hardware cloth along the ground to reduce plot access to burrowing mammals (Nutrient Network: A Global Research Cooperative, 2008). We tested the integrity of the fences during three separate 72-hour events at each site and in each year. During each sampling event we set Sherman live traps in the fenced and unfenced plots baited with peanut butter and oats (H. B. Sherman Traps, Tallahassee, FL: 6.5 2.0 × 2.5 cm). The traps were checked for captures and reset every 8 hours.

References (Appendix A)

Brown, J. H. and Davidson. D. W. (1977). Competition between seed-eating ants and rodents in desert ecosystems. *Science*, 196(4292), 880–882.

Nutrient Network: A Global Research Cooperative. (2008, March). "Building a Fence." University of Minnesota Department of Ecology, Evolution, and Behavior. Retrieved from http://www.nutnet.umn.edu/files/nutnet/NutNet_FenceBuilding.pdf

Appendix C. Summary of likelihood ratio tests (α=0.05) used to determine the most

parsimonious mixed-effects model at each site.

Table S1. Model comparisons and results for Species Cover, Emergence, Flowering Time, and Timing of Seed Set. All models included species identification as a random effect. Significant results listed in bold.

Fixed Model Comparisons	Northern Forest Clearing Summary Results	Southern Old Agriculture Field Summary Results
Species Cover (2015)		
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects+Mammals vs.	χ2=0.35; df=1;	χ2=0.90; df=1;
[M2]Cover~ Warmed+Origin+Warmed*Origin+Insects	P=0.55	P =0.34
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects vs.	χ2=0.30; df=1;	χ2=0.84; df=1;
[M2]Cover~Warmed+Origin+Warmed*Origin	P =0.58	P =0.36
[M1]Cover~Warmed+Origin+Warmed*Origin vs.	χ2=0.60; df=1;	χ2=2.46; df=1;
[M2]Cover~Warmed+Origin	P =0.44	P =0.12
Species Cover (2016)		
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects+Mammals vs.	χ2=0.10; df=1;	χ2=2.05; df=1;
[M2]Cover~ Warmed+Origin+Warmed*Origin+Insects	P =0.75	P =0.15
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects vs.	χ2=1.11; df=1;	χ2=0.04; df=1;
[M2]Cover~Warmed+Origin+Warmed*Origin	P =0.29	P =0.85
[M1]Cover~Warmed+Origin+Warmed*Origin vs.	**χ2=4.23; df=1;**	χ2=0.76; df=1;
[M2]Cover~Warmed+Origin	**P =0.04**	P =0.38
Emergence		
[M1]Emergence ~Warmed+Origin+Warmed*Origin+Insects+Mammals vs.	χ2=0.15; df=1;	χ2=1.73; df=1;
[M2]Emergence~ Warmed+Origin+Warmed*Origin+Insects	P =0.69	P =0.19
[M1]Emergence~Warmed+Origin+Warmed*Origin+Insects vs.	χ2=2.10; df=1;	χ2=1.07; df=1;
[M2]Cover~Warmed+Origin+Warmed*Origin	P =0.15	P =0.30
[M1]Emergence~Warmed+Origin+Warmed*Origin vs.	χ2=2.51; df=1;	χ2=1.75; df=1;
[M2]Emergence~Warmed+Origin	P =0.11	P =0.19
Flowering Time		
[M1]Flowering Time~ Warmed+Origin+Warmed*Origin+Insects+Mammals vs.	χ2=0.32; df=1;	χ2=0.33; df=1;
[M2]Flowering Time~ Warmed+Origin+Warmed*Origin+Insects	P =0.57	P =0.57
[M1]Flowering Time~ Warmed+Origin+Warmed*Origin+Insects vs.	**χ2=5.40; df=1;**	χ2=1.87; df=1;
[M2]Flowering Time~Warmed+Origin+Warmed*Origin	**P =0.02**	P =0.17
[M1]Flowering Time~Warmed+Origin+Warmed*Origin vs.	χ2=0.65; df=1;	χ2=0.37; df=1;
[M2]Flowering Time~Warmed+Origin	P =0.42	P =0.54
Timing of Seed Set		
[M1]Seed Set~ Warmed+Origin+Warmed*Origin+Insects+Mammals vs.	χ2=0.08; df=1;	χ2=0.05; df=1;
[M2]Seed Set~ Warmed+Origin+Warmed*Origin+Insects	P =0.78	P =0.82
[M1]Seed Set~Warmed+Origin+Warmed*Origin+Insects vs.	χ2=0.39; df=1;	χ2=0.32; df=1;
[M2]Seed Set~Warmed+Origin+Warmed*Origin	P =0.53	P =0.57
[M1]Seed Set~Warmed+Origin+Warmed*Origin vs.	χ2=0.00; df=1;	χ2=0.02; df=1;
[M2]Seed Set ~Warmed+Origin	P =0.95	P =0.89

Table S2. Model comparisons and results for Amount of Leaf Eaten and Probability of Attack.

All models included species identification and individual plant identification as random effects.

Significant results listed in bold.

Fixed Model Comparisons	Northern Forest Clearing	Southern Old Agriculture Field
	Summary Results	Summary Results
Leaf Herbivory (Amount of Leaf Eaten)		
[M1]Leaf Herbivory~Warmed+Origin+Warmed*Origin+Mammals vs.	$\chi2=2.43$; df=1;	$\chi2=1.41$; df=1;
[M2] Leaf Herbivory~Warmed+Origin+Warmed*Origin	P =0.12	P =0.24
[M1]Leaf Herbivory~Warmed+Origin+Warmed*Origin vs.	$\chi2=0.25$; df=1;	$\chi2=0.76$; df=1;
[M2]Leaf Herbivory~Warmed+Origin	P =0.62	P =0.38
Leaf Herbivory (Probability of Attack)		
[M1]Leaf Herbivory~Warmed+Origin+Warmed*Origin+Mammals vs.	$\chi2=0.38$; df=1;	$\chi2=1.70$; df=1;
[M2]Leaf Herbivory~Warmed+Origin+Warmed*Origin	P =0.53	P =0.19
[M1]Leaf Herbivory~Warmed+Origin+Warmed*Origin vs.	$\chi2=0.45$; df=1;	$\chi2=0.05$; df=1;
[M2]Leaf Herbivory~Warmed+Origin	P =0.50	P =0.81

Appendix D. Boxplots of individual species percent cover in warmed and ambient plots after two years of treatment. Boxplots display the median (central line), 25th percentile (lower bound), 75th percentile (upper bound), and smallest and largest value (ends of whiskers) no larger than 1.5x the interquartile range from the upper and lower quartiles. Triangles represent individual data points (e.g. one point = one plot). Species are arranged by origin and from most abundant to least abundant (left → right; top → bottom) at each site.

Fig. S2 Boxplots for individual native species' cover for native at the Northern Forest Clearing located at the University of Michigan Biological Station in Pellston, Michigan, USA.
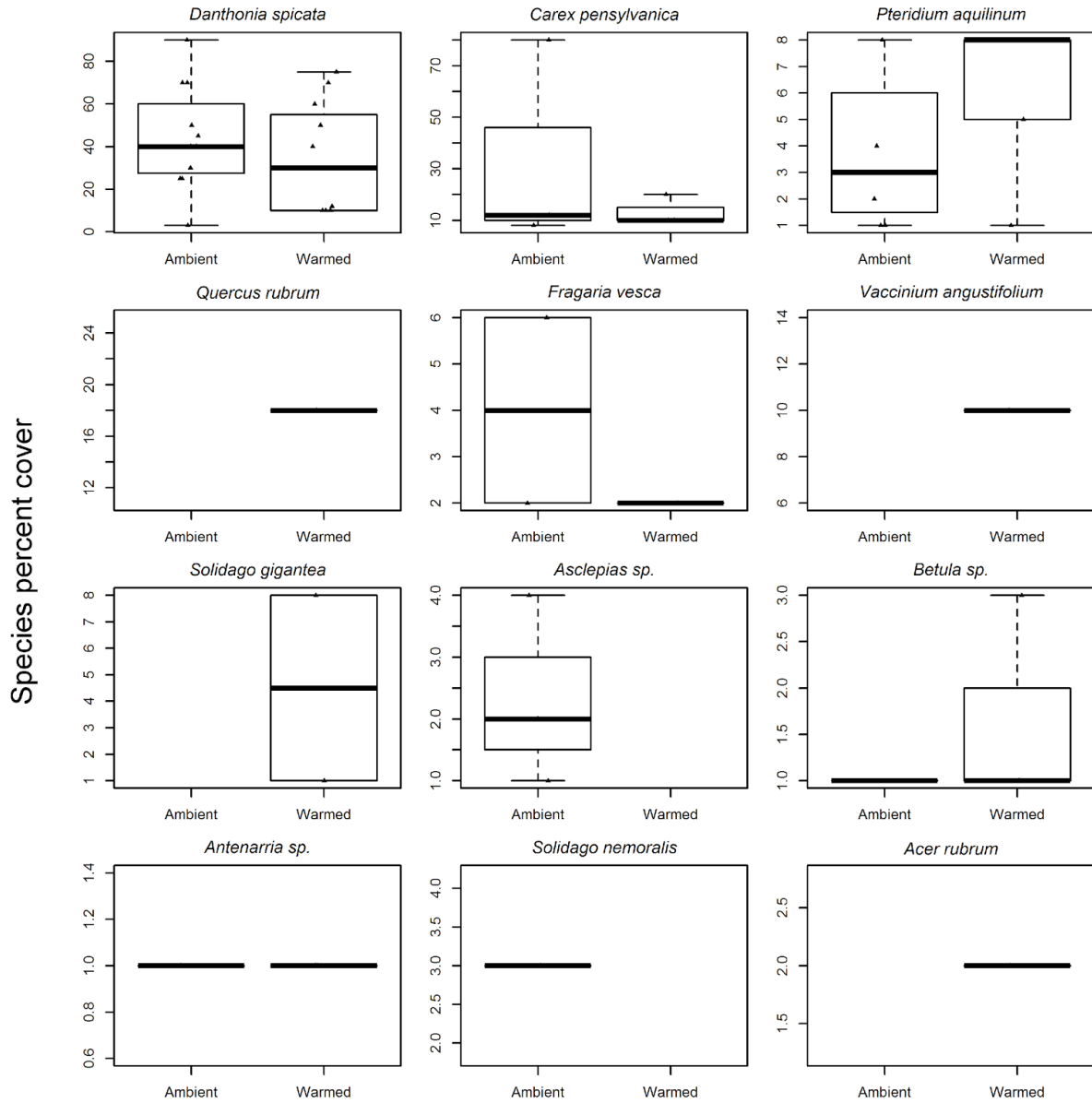
Fig. S3 Boxplots for individual exotic species' cover at the Northern Forest Clearing located at the University of Michigan Biological Station in Pellston, Michigan, USA.
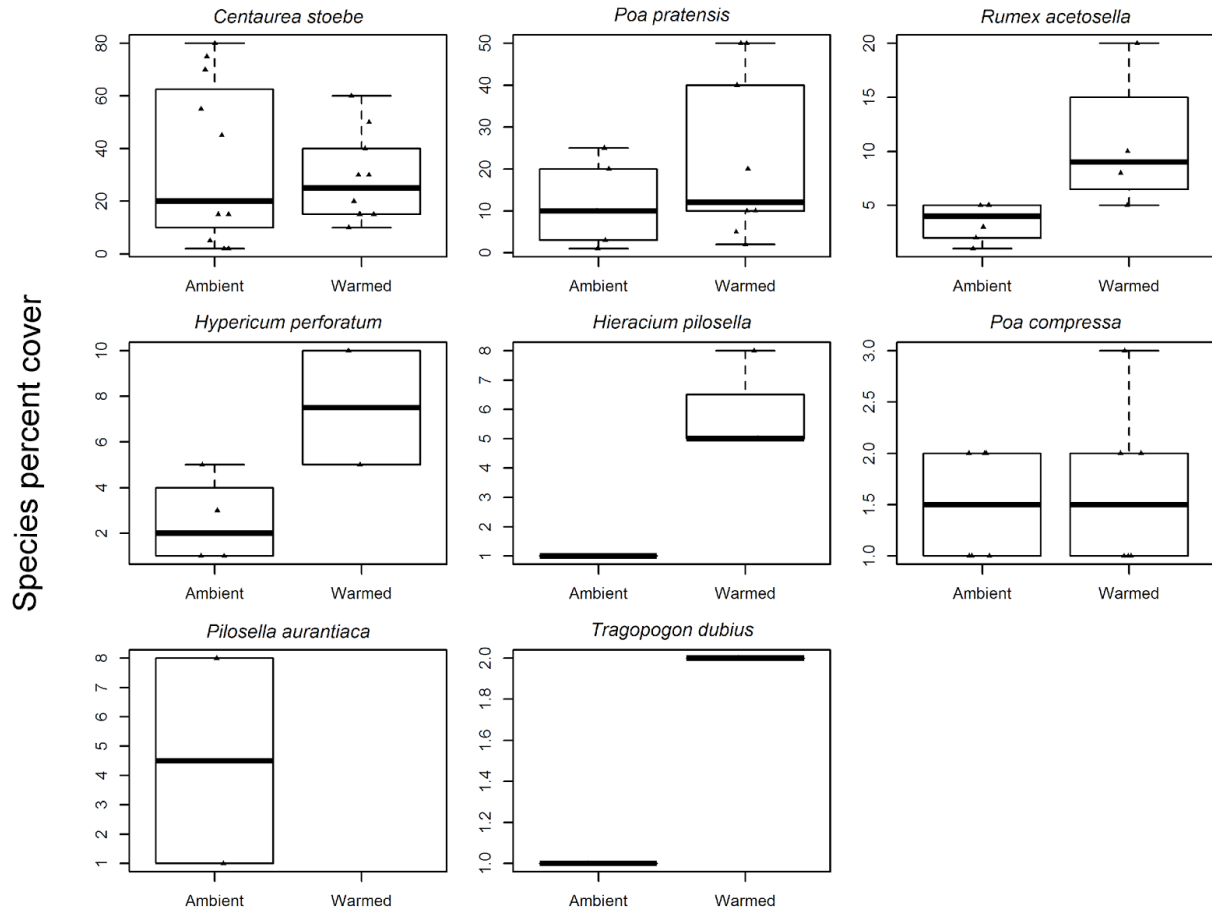
Fig. S4 Boxplots for individual native species' cover at the Old Agriculture Field located at Kellogg Biological Station in Hickory Corners, Michigan, USA.
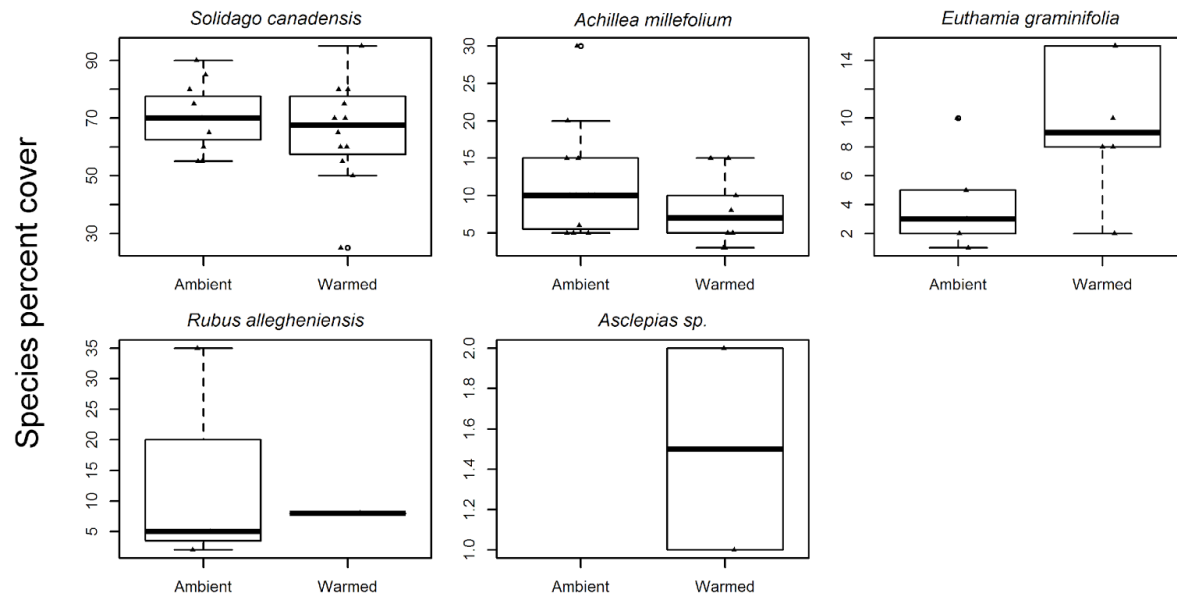
Fig. S5 Boxplots for individual exotic species' cover at the Old Agriculture Field located at

Kellogg Biological Station in Hickory Corners, Michigan, USA.