

Integral projection models show exotic thistle is more limited than native thistle by ambient competition and herbivory

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Citation: Tenhumberg, B., T. Suwa, A. J. Tyre, F. L. Russell, and S. M. Louda. 2015. Integral projection models show exotic thistle is more limited than native thistle by ambient competition and herbivory. *Ecosphere* 6(4):69. <http://dx.doi.org/10.1890/ES14-00389.1>

Abstract. Both competitors and natural enemies can limit plant population growth. However, demographic comparisons of the effects of these interactions on introduced versus co-occurring, related native species are uncommon. We asked: (1) does plant competition, insect herbivory, or their combination reduce population growth rate, $\log \lambda$, of the Eurasian thistle *Cirsium vulgare* sufficiently to explain its limited invasiveness in western tallgrass prairie; and (2) how do the effects of these interactions compare to those for *C. altissimum*, its co-occurring, synchronously-flowering native congener? We developed integral projection models (IPMs) to estimate $\log \lambda$ for both species, using parameter estimates from field experiments. Our models predicted that the growth potential (growth rate at minimal competition and herbivory) for the introduced thistle ($\log \lambda = 3.5$ (2.5, 4.6)) was twice as large as for the native thistle ($\log \lambda = 1.6$ (0.4, 3.1)); however, a high level of competition and ambient insect herbivory together reduced $\log \lambda$ to similar values for both thistle species (*C. vulgare*: $\log \lambda = -1.3$ (-2.4, -0.3) vs *C. altissimum*: $\log \lambda = -0.9$ (-1.4, -0.3)). This suggests that the introduced thistle was more affected by competition and insect herbivory. For the introduced thistle, neither competition nor insect herbivory alone led to negative $\log \lambda$. In contrast, for the native thistle, high competition alone also led to negative population growth ($\log \lambda = -0.8$, percentile limits do not overlap with zero). Ambient herbivory alone prevented the spread for both thistle species (percentile limits include zero). Overall, the results show that interspecific competition followed by ambient levels of insect herbivory strongly constrained $\log \lambda$ for both thistles, limiting *C. vulgare* invasiveness and *C. altissimum* abundance. The outcome highlights the importance of synergy between the two biological interactions in limiting plant population growth. Improved understanding of mechanisms limiting $\log \lambda$ for weedy plants enhances our ability to predict when biotic resistance will contribute to invasive plant species management.

Key words: biotic resistance; *Cirsium altissimum*; *Cirsium vulgare*; congeneric species; enemy release hypothesis; exotic species; integral projection model; invasive plants; Nebraska; population growth rate; thistle.

Received 14 October 2014; revised 5 December 2014; accepted 22 December 2014; final version received 10 March 2015; **published** 28 April 2015. Corresponding Editor: D. P. C. Peters.

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INTRODUCTION

Most plant introductions fail, and species that do establish typically remain at low densities (Rejmánek 1989, Williamson and Fitter 1996, Mack et al. 2000). This is surprising because introduced species generally leave their co-evolved competitors and natural enemies behind. For instance, compared to their conspecifics within the home range, introduced plants in a new range averaged 84% fewer fungi, 25% fewer virus infections (Mitchell and Power 2003), as well as significantly less herbivory, resulting in larger energy allocation to growth and reproduction (Liu and Stiling 2006, Hawkes 2007, Chun et al. 2010).

On the other hand, introduced species inevitably encounter novel competitors and natural enemies in their new habitats (Mitchell et al. 2006). Some of these new antagonists may be pre-adapted, or evolve rapidly, to compete with or to consume the introduced plants (Maron et al. 2004, Parker and Hay 2005). Elton (1958) was among the first to recognize the potential importance of novel biotic interactions within the introduced range in the outcome of biological invasions. Elton's "biotic resistance hypothesis" posits that native communities often limit the colonization, establishment, and spread of introduced species through intense antagonistic interactions (Crawley 1997, Keane and Crawley 2002).

The evidence to date suggests that, although new biological interactions reduce individual performance and establishment probability of introduced species in some cases, on average new interactions are not strong enough to prevent population establishment, growth and spread (Levine et al. 2004). However, current studies do not adequately assess the role of biotic resistance in limiting invasiveness of introduced plants for at least two reasons. First, most studies have focused on evaluating a single biotic interaction (i.e., competition or herbivory) on the performance of individuals of the introduced species (but see Zou et al. 2008, Suwa et al. 2010, Huang et al. 2012, Suwa and Louda 2012). Single interactions are seldom sufficient to explain species dynamics; the simultaneous effects of multiple key interactions on performance of an introduced species usually need to be examined (Lau and Strauss 2005, Mitchell et al. 2006, Parker

and Gilbert 2007). For example, the effects of interspecific competition and herbivory on plant performance may not be independent; interactions could either magnify or lessen the effect of either interaction alone (Harper 1977, Rand 2003).

Second, the influence of biotic interactions on the rate of invasion ultimately depends upon their effect on the plant population growth rate, rather than on individual plant performance (Maron and Vilà 2001, Liu and Stiling 2006, Ramula et al. 2008). Most studies quantifying the effect of competitors or consumers examine only a subset of performance traits (e.g., biomass, number of seeds) or vital rates (e.g., emergence rate, survival), rather than population growth rate. Yet, the contribution of specific traits, or specific vital rates, to the population growth rate can vary dramatically (Caswell 2000). Estimating impact on vital rates and population growth rates requires long-term demographic data or demographic models based on experimental estimates of demographic parameters (Maron and Vilà 2001, Halpern and Underwood 2006); such data or models are seldom available.

In this study, we used mathematical models to synthesize our empirical work on this system in order to estimate the combined effects of experimentally modified interspecific competition and insect herbivory on population growth rates of Eurasian *Cirsium vulgare* Savi Tenore (Bull or Spear thistle), a known invasive species worldwide (Julien and Griffiths 1998), and on its native, co-occurring, synchronously-flowering congener, *C. altissimum* (L.) Spreng (Tall thistle). This modeling effort is distinguished from our previous work on this system in that it is the first quantification of effects of insect herbivory and interspecific competition on populations of both species using the same modeling framework; hence, it provides the best comparison of the population limiting effects of these factors. Such comparisons between introduced and native congeners are useful for identifying factors that may promote or limit invasiveness (Mack 1996, Agrawal and Kotanen 2003). Both interspecific competition and insect herbivory can reduce plant vital rates, influencing population growth either independently (Newingham and Callaway 2006, Doyle et al. 2007) or interactively (Parmesan 2000, Russell et al. 2010). Data for our model

parameters come from our published field experiments that manipulated both interspecific competition and insect herbivory for these species (Suwa et al. 2010, Rose et al. 2011, Suwa and Louda 2012).

Using integral projection models (IPMs), we addressed two specific questions: (1) does competition from the resident plant community, herbivory by native insects, or their interaction significantly reduce the population growth rate of the introduced *C. vulgare* and (2) how do the effects of these biotic interactions on *C. vulgare* compare to their effects on the co-occurring native *C. altissimum*? Given the limited occurrence of *C. vulgare* in our region (Andersen and Louda 2008), we expected that population growth rates of the introduced *C. vulgare* would be impacted more severely by resident competitors and native insect herbivores than the population growth rates of the related native thistle.

METHODS

Study system

C. vulgare (Bull thistle), a native of Eurasia, is considered a problematic, invasive species in many countries (Julien and Griffiths 1998). Its most common congener in western tallgrass prairie, *C. altissimum* (Tall thistle), is native to the central and eastern United States (Kaul et al. 2006). These thistles have similar habitat requirements, typically growing in disturbances in prairie and old fields, and along roadsides. Both species are monocarpic, short-lived perennials reproducing only by seed (Guretzky and Louda 1997, Kaul et al. 2006); and, they share a similar, late-season flowering phenology (Louda and Rand 2002). Studies show that 96% of the native thistle-feeding arthropod fauna found on the native *C. altissimum*, including the most abundant thistle specialists, also feed on *C. vulgare* (Takahashi 2006). Introduced thistle-feeding insects are rare in this system (Takahashi 2006).

C. vulgare is uncommon, about 100-times less frequent than the relatively sparse *C. altissimum*, on transects in the western tallgrass prairie (Andersen and Louda 2008). Previous studies found that native insects limit seed production and subsequent seedling density of both thistle

species (e.g., Louda and Rand 2002, Russell et al. 2010, Eckberg et al. 2012), as well as population growth rate of *C. vulgare* under some conditions (Eckberg et al. 2014).

Integral projection model

To estimate population growth rates for both species, we constructed integral projection models (IPMs). In these models, we treated plant size as a continuous variable, and time as a discrete variable with a time step of one year (e.g., Easterling et al. 2000, Ellner and Rees 2006). We did not include a seed bank because of the very low frequency of *Cirsium* spp. seed survival within the seed bank (Potvin 1988, Tenhumberg et al. 2008; F. L. Russell, unpublished data).

Since time was discrete, the start and end of the models' time interval (population census) needed to be specified. Here, we envisioned the population census to be in late spring after overwintering seeds have germinated and all plants are still rosettes of size x (Fig. 1). After the population census, plants either flowered and died (as monocarpic species), with probability $p_f(x)$, or remained non-flowering vegetative rosettes. Flowering plants survive to the end of the season, or non-flowering plants survive to the next census, with probability $p_s(x)$. Compared to the juvenile rosette plants that remained vegetative, the plants that flowered (bolted and died) developed a much larger biomass, including an elongated stem with more leaves and multiple flower heads. We used two specific, empirically-derived growth functions, one for juvenile rosette plants ($g_0(y, x)$) and one for bolting adult plants ($g_1(x', x)$). Seed production, $S(x')$, was estimated as a function of bolting adult plant size x' . Viable seeds germinated, emerged, and developed into small juvenile plants with probability p_e before the next population census. We did not keep track of plant age; thus, in the models a very small plant could be either a seedling or a one-year old plant that did not grow much from one year to the next.

Let $n(x, t)$ describe the size distribution of each thistle population at time t , and m and M specify the range of possible sizes ($x \in [m, M]$). Then, the thistle population in the next time step, $t + 1$, is

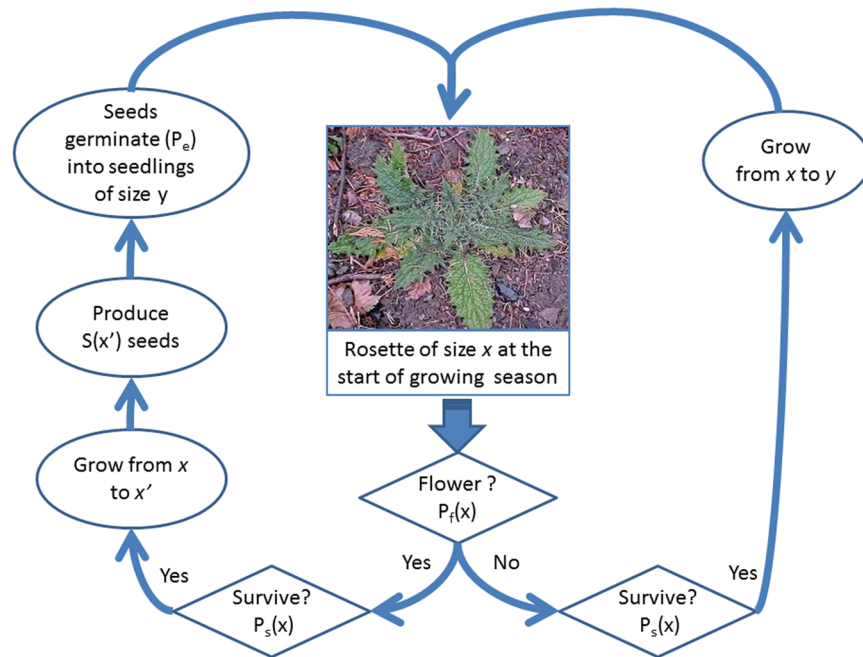


Fig. 1. Overview of *Cirsium* integral projection models. A juvenile rosette plant of size x survived with probability $p_s(x)$ and developed into an adult, bolting plant with probability $p_f(x)$. The growth function $g_1(y, x')$ determined the size x' of the bolting plant which produced $S(x')$ seeds. Seeds germinated in the spring with probability p_e and developed into y sized plants with probability $p_d(y)$. Plants that remained juvenile for another year developed a smaller biomass than bolting plants; and their size y at the end of the time interval is determined by the growth function $g_0(y, x)$.

$$\begin{aligned}
 n(y, t+1) &= \int_m^M \left[\left((1 - p_f(x)) g_0(y, x) p_s(x) n(x, t) + \right. \right. \\
 &\quad \left. \left. p_f(x) g_1(x', x) p_s(x) \left(S(x') p_e p_d(y) n(x, t) \right) \right] dx \right. \\
 &\quad \text{(Vegetative Plants)} \\
 &\quad \text{(New Recruits)}
 \end{aligned}$$

where $p_d(y)$ specifies the probability that the developing seedling will be size y .

Model analysis

We estimated the asymptotic population growth rate by computing the dominant eigenvalue (λ) of the IPMs (Easterling et al. 2000, Ellner and Rees 2006). For each of the 12 experimental treatments used to parameterize the models (detailed below), we calculated a distribution of λ -values using parametric boot-

strapping (Clark 2007; 500 runs for each of the 12 environmental conditions). For each λ -value distribution, we determined the median, as well as the 5th and 95th percentile limits. In general, a population grows if $\log \lambda > 0$ (so, $\lambda > 1$), and declines if $\log \lambda < 0$ (so, $\lambda < 1$). Conservatively, we interpreted the result to be population stasis if either percentile limit of the log λ -value distribution included zero. We considered population growth rates between experimental treatments to be different if either percentile of one log λ -value distribution did not overlap with the median of the other log λ -value distribution. We could not calculate t-statistics to compare the effect of the different treatments because the predicted means are derived from combinations of several statistical models, and as a result the degrees of freedom are unknown. We interpret the percentile limits analogous to confidence limits and use them to infer statistical differences. According to Wolfe and Hanley (2002), and Goldstein and Healy (1995) two treatments can be considered

statistically different if confidence limits are not overlapping, and they are not statistically different if confidence limits overlap the mean of the other treatment; it is unclear if two treatments are significantly different if confidence limits overlap, but not with the means (Goldstein and Healy 1995, Wolfe and Hanley 2002). To be conservative, we considered overlapping percentile limits that did not overlap with the median as not statistically different.

Data used to estimate model parameters

To estimate model parameters, we used published data from three of our previous experiments. Insect herbivory reduction treatments were similar among all three experiments; and, all three studies were conducted in restored tallgrass prairie/old fields in eastern Nebraska between 2006 and 2008 (see below).

Effects of competition and herbivory on growth and survival.—For both thistle species, survival and growth data came from the experiment described in Suwa and Louda (2012). This experiment was conducted at a site near Lincoln, Nebraska, and included three levels of interspecific competition and two levels of insect herbivory on a total of 174 plots (50 cm × 25 cm), to each of which 400 locally collected seeds of either *C. vulgare* or *C. altissimum* had been added. Interspecific competition levels were manipulated two months before the experimental seeds were sown (5–10 November 2006) by altering cover of ambient vegetation with spot application of herbicide to achieve three levels of competition: high (ambient, control, 65–90% cover); medium (reduced to 25–35% cover); and low (reduced to 0–5% cover). Insect herbivory was reduced on a subset of the plots within each competition treatment for each species by spraying a non-systemic insecticide every 20 d during two growing seasons (27 April 2006 to 15 September 2007). The remaining plots in each competition treatment were controls, and sprayed only with an equivalent amount of water.

Effects of the interactions on seed production.—Because adult plant seed production was not recorded in Suwa and Louda (2012), we supplemented these data with data from two other parallel experiments. For *C. vulgare* seed production, we used data from the experiment (Suwa et al. 2010) that compared focal plant reproductive

performance under two levels of interspecific competition (ambient, reduced) and two levels of herbivory (ambient, reduced) for established juvenile rosettes (diameter >15 cm) that were likely to become bolting and flowering adults within the season. In half of the plots, competition was reduced to a level comparable to the medium competition treatment described above (25–35% cover) (N = 148 plots in 2006; N = 80 plots in 2007). Competition was reduced by clipping the vegetation at ground level and by painting the clipped vegetation with a non-selective herbicide monthly during each growing season. The other half of the plots were unmanipulated, ambient competition controls (65–90% cover). In half the plots of each competition treatment, we reduced herbivory on the focal *C. vulgare* rosette by spraying it with a non-systemic insecticide-in-water; focal plants used in control plots were sprayed only with water (Suwa et al. 2010). For IPMs, we assumed that seed production by plants of a given size was similar under low and medium competition, an assumption consistent with field observations (S. M. Louda, unpublished data). For *C. altissimum* seed production, we used data from an experiment (Rose et al. 2011) that involved treating half of all the naturally occurring *C. altissimum* rosette plants that were initiating bolting with non-systemic insecticide at 2–3 week intervals over their flowering season. The remaining plants were sprayed with an equal volume of water. Treatments were imposed from late June through the end of the growing season in early October (N = 159 plants in 2006, N = 145 plants in 2007). Since competition was not manipulated in this experiment, for the model we assumed that seed production of thistles of a given size was not influenced by competition, as above. Thus, the effect of competition on seed production included in the models here was exclusively related to the effect of competition on plant growth and size, a conservative estimate of biotic interaction effects.

Plant size.—Plant size was estimated as above-ground leaf biomass, a continuous variable. For adult plants, leaf biomass was measured at the end of the experiment by destructive sampling (Suwa and Louda 2012). For younger plants, we counted the number of leaves and estimated biomass using a regression between log-trans-

formed number of leaves and log-transformed biomass from the destructive sampling. We expressed all vital rates as functions of log plant biomass.

Statistical analysis

All statistical analyses were performed with the statistical package R version 2.5.3 (R Core Development Team 2010). We analyzed the data for *C. vulgare* and *C. altissimum* performance separately, using generalized linear mixed models, or nonlinear mixed models, with vital rates (annual change in size, survival, and fecundity) as response variables. The set of explanatory variables included: plant size, level of competition and level of insect herbivory, and whether a plant bolted and flowered in its second year. Block and plot were included as random effects. We used a Poisson error distribution for models estimating plant growth and seed production, and a binomial error distribution for calculating the probability of flowering in the next year, the probability of surviving until the next year, and the probability that a seed will germinate and survive until the next population census.

Seed production of plants had a strongly bimodal distribution, since many flowering plants did not succeed in maturing any potentially viable seeds. So, we first used a binomial mixed model to calculate the probability of producing zero seeds. Then, we analyzed the seed production data of those plants that produced at least one potentially viable seed, using a linear model with the log-transformed number of seeds as the response variable. The number of seeds and plant sizes (number of leaves or plant biomass) were log-transformed for the statistical analysis.

Model averaging using the Bayesian information criterion (BIC)

Including all possible interactions and combinations of random and fixed effects for the growth model would have resulted in an extremely large, unwieldy model set. Including too many models increases model selection uncertainty leading to poor precision in our predictions, while including too few models risks overlooking important interactions between the covariates leading to biased predictions. In order to keep the model set to a reasonable size, we

first selected the random effects that had to be included, using a model with only main fixed effects (no interactions), i.e., plant size, insect herbivory treatment level, competition treatment levels, and whether a plant was going to bolt and flower. Because the population model was size structured we only included models involving size and one other main effect, and samples across the space of models involving three or four main effects. Further we evaluated a range of plausible combinations of fixed effects and two way interactions; considering all combinations of the 6 possible two way interactions together with all four main effects would have led to 64 models for each thistle species, which was still too large a model set. Note, those models that did include interactions had relatively low statistical support (BIC weights <10%). Thus, our final growth model set consisted of 35 models for each species (see Appendix for details). For all remaining statistical models, it was feasible to evaluate all combinations of main effects and pairwise interactions, because whether or not a plant bolted was not an issue. All combinations of size, herbivory and competition led to 18 models. In some cases we had fewer models because either herbivory or competition had not been manipulated in that particular experiment.

We used model averaging (Burnham and Anderson 2002) to predict the vital rates as a function of the explanatory variables because our goal was predicting vital rates for different levels of competition and insect herbivore pressure, and model averaging minimizes the combination of bias and estimation variance to achieve the best predictive power (Shmueli 2010). Specifically, we first estimated the parameters of each model, and then predicted the values of the life history parameter for all conditions for each model. The predictions from a model were multiplied by the BIC weight associated with that model, and then we summed the weighted predictions to obtain a model averaged prediction for that life history parameter. To avoid underestimating the uncertainty associated with model selection in predicting the population growth rate, we included all models in the vital rates estimates used in the IPMs. In a few cases there was a single best model, but for consistency we used model averaging throughout the paper. Models with low weight make a small contribution to the

Table 1. Bayesian Information Criterion (BIC) weights of fixed effects with model weights $\geq 10\%$. Complete list of statistical models included in model averaging is presented in the Appendix. S = plant size, H = insect herbivory treatment levels, C = interspecific competition treatment levels, B = bolting (adult, flowering) plant, No. seeds/seeds = number of seeds per plant that produced seed, k = number of parameters (including the intercept).

Vital rate	Species	Model	k	Log likelihood	ΔBIC	w
Growth	<i>C. vulgare</i>	S + B	3	-378.8	0	0.79
		S + H + B	4	-377.9	3.84	0.12
Survival	<i>C. altissimum</i>	S + H + B	6	-657.4	0	0.98
	<i>C. vulgare</i>	S + H	5	-428.6	0	0.83
		S + H + C	7	-423.9	4.08	0.11
	<i>C. altissimum</i>	H	4	-481.4	0	0.82
		S + H	5	-479.7	3.20	0.17
P(flowering)	<i>C. vulgare</i>	S	3	-139.5	0	0.84
	<i>C. altissimum</i>	S + C	5	-230.4	0	0.88
P(seeds)	<i>C. vulgare</i>	S	3	-31.6	0	0.90
	<i>C. altissimum</i>	S + H	5	-247.8	0	0.90
No. seeds/seeds	<i>C. vulgare</i>	S + H	6	-180.0	0	0.35
		S + H + S:H	7	-177.6	0.186	0.32
		S	5	-183.0	0.668	0.25
	<i>C. altissimum</i>	S + H	5	-272.4	0	0.75
		S + H + S:H	6	-271.3	2.80	0.19
	<i>C. vulgare</i>	C	5	-598.9	0	0.77
		C + H + H:C	8	-594.0	3.62	0.13
Recruitment	<i>C. vulgare</i>	C + H	6	-598.7	4.01	0.10
		C + H + H:C	8	-431.0	0	0.99
	<i>C. altissimum</i>	C + H + H:C	8	-431.0	0	0.99

averaged response. For estimating the standard error of each of these predictions, we used the delta method (Powell 2007) because each prediction was a sum of random variables (the coefficients in each model). This standard error is the population standard error because it does not include the variance attributed to random effects, but only the variance from the estimated population level fixed effects.

RESULTS

Vital rates

Complete statistical models are presented in the Appendix (Tables A1–A6). Generally, the statistical models with fewer parameters provided similar explanatory power to the models with more parameters (indicated by small ΔBICs). To characterize the most influential effects, we discuss only those statistical models with $\geq 10\%$ of the BIC weights (Table 1); however, for the IPMs, all models were used.

For the introduced *C. vulgare* (Table 1), the change in plant size (growth) from one year to the next was most influenced by the main effects of plant size, plus whether a plant was going to bolt and flower. Plant survival was most influenced by herbivory level plus plant size; whether

or not a plant flowered did not affect survival probability. The probabilities of both a plant flowering, and of a flowering plant producing seed, were best predicted by models that included only the main effect of plant size. For plants that produced seeds, the number of potentially viable seeds was best explained by models that included the main effects of both plant size and herbivory level plus the interaction of size and herbivory. Recruitment was most strongly influenced by level of interspecific competition.

For the native *C. altissimum* (Table 1), the change in plant size from one year to the next was best predicted by the plant growth model that included the three main effects: insect herbivory level, plant size in the previous year, and whether a plant was going to bolt and flower. Plant survival was best explained by insect herbivory level only. The probability of flowering was best predicted by the main effects of plant size and competition level. The probability of a flowering plant producing seeds, as well as the total number of potentially viable seeds produced if a plant produced any seed, were best explained by the main effects: plant size and insect herbivory level. Recruitment was strongly influenced by a combination of: compe-

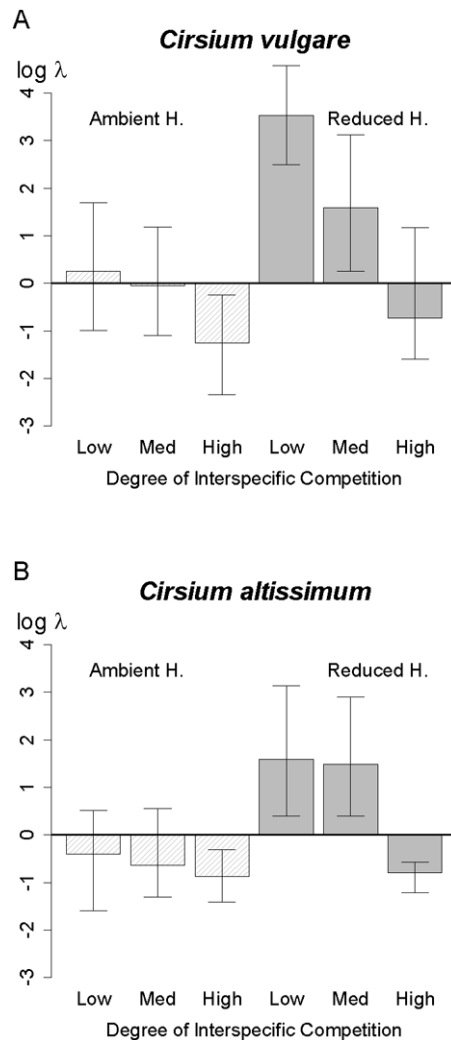


Fig. 2. Median population growth rates ($\log \lambda$; zero = stable) of *C. vulgare* and *C. altissimum* at three levels of interspecific competition (low = 0–5%, medium = 25–35%, and high = 65–90% [ambient]), when insect herbivory is either ambient (high) level (light grey bars) or experimentally reduced level (dark grey bars). Tick lines on each bar indicate 5th and 95th percentiles of bootstrapped $\log \lambda$ -value distributions.

tition level, insect herbivory level, and interaction between these two factors.

Overall, insect herbivory and interspecific competition strongly influenced more vital rates of the native thistle than of the introduced thistle (Table 1). While insect herbivory influenced seed production and survival for both thistle species, herbivory also influenced plant growth of the

native *C. altissimum*. Competition affected recruitment in both species, and also flowering probability in *C. altissimum*. Thus, both interactions influenced plant vital rates similarly, but with several additional effects on the native versus on the introduced thistle.

Predicted population growth rates

The model predictions were qualitatively similar for both *Cirsium* species (Fig. 2). For both thistles, populations declined ($\log \lambda < 0$) with ambient levels of both insect herbivory and high levels of interspecific competition (65–90% vegetation cover). Reduced herbivory with ambient competition leads to population stasis for the *C. vulgare* but population decline for *C. altissimum*. Population stasis (where 5th and 95th percentiles included zero) occurred for *C. altissimum* with ambient insect herbivory at reduced levels of interspecific competition (low or medium: 0–35% cover). Finally, populations of both species grew ($\log \lambda > 0$) when both insect herbivory and interspecific competition were reduced.

Evaluation of the magnitude of reduction in average population growth rate caused by competition and by herbivory suggested that the two interactions together had a greater impact on the population growth of the introduced *C. vulgare* than on the native *C. altissimum*, for two reasons. First, the difference in median $\log \lambda$ between ambient and reduced herbivory levels at low and high competition levels was larger for the introduced *C. vulgare* than for the native *C. altissimum* (Fig. 2; Appendix: Table A7). Reducing insect herbivory increased $\log \lambda$ for *C. vulgare* by 3.28 at low competition, 1.64 at medium competition, and 0.53 at high competition. By comparison, reducing herbivory only increased $\log \lambda$ for *C. altissimum* by 2.00 at low competition, 2.12 at medium competition and 0.07 at high competition. These results demonstrate that competition level influenced the magnitude of the herbivore effect, and more so for the introduced species than for the native species.

Second, the same pattern held for $\log \lambda$ between all three competition levels within each herbivory level. The difference in median $\log \lambda$ between the high, medium and low competition levels within each herbivory level was larger in *C. vulgare* than for *C. altissimum* (Fig. 2; Appen-

dix: Table A7). Reducing competition from high to low increased $\log \lambda$ for *C. vulgare* by 1.52 with ambient herbivory and by 4.27 with reduced herbivory, whereas reducing competition similarly for *C. altissimum* increased $\log \lambda$ by only 0.48 at ambient herbivory and by 2.41 with reduced herbivory. This contrast provides a basis for the inference that competition had a larger impact on the introduced *C. vulgare* than on the native *C. altissimum*. Thus, overall, we found that the biotic interactions had a greater negative effect on population growth rate of the introduced thistle than of the native thistle.

DISCUSSION

Competition and herbivory together limit introduced C. vulgare population growth

A primary objective of invasive species research is to identify the conditions that limit these species' population growth and spread. Although the spread of an introduced species can be limited by negative interactions within the recipient native community (Levine et al. 2004), we know of only one previous model (Dauer et al. 2012) that evaluated how simultaneous biotic interactions influenced the population growth rate of an introduced, potentially invasive plant. Further, few studies have combined experimental manipulations of competition and population modeling to quantify strong effects of interspecific competition in suppressing population growth of a perennial plant (see Gustafsson and Ehrlén 2003, Fréville and Silvertown 2005, Dauer et al. 2012).

Our results suggest that population decline of the known invasive thistle, *C. vulgare*, requires ambient (high) levels of both interspecific competition and insect herbivory; however, ambient levels of interspecific competition or insect herbivory alone are sufficient to produce population stasis of *C. vulgare*, preventing its spread. This finding is consistent with the bulk of previous experimental studies that examined the effects of insect herbivory on plant performance and population growth rate (Louda and Potvin 1995, Hamback and Beckerman 2003, Miller et al. 2009, Schutzenhofer et al. 2009, Rose et al. 2011). Ruderal species, including thistles, often depend upon temporary refuges from competition provided by disturbances in order

to experience population growth (Harper 1977, Crawley 1997). For *C. vulgare* in our region, given the temporal variation in insect numbers (Takahashi 2006), high competitive pressure in relatively undisturbed sites (e.g., 60–95% cover) will be important in decreasing recruitment success and, so, limiting population growth. Our results suggest that ambient insect herbivory in this system closes the window of opportunity provided by disturbances. Actions that increase or maintain the competitive environment experienced by weeds should be powerful tools in slowing their population growth and spread.

The other studies on *C. vulgare* in tallgrass prairie generally support our finding that native insect herbivores can suppress population growth rates of this introduced weed. For example, Louda and Rand (2002) and Andersen and Louda (2008) reported extensive insect herbivory on *C. vulgare* in tallgrass prairie. Further, the median population growth rates ($\log \lambda = 0.4$ with ambient herbivory; $\log \lambda = 1.5$ with reduced herbivory) predicted by the matrix model of Tenhumberg et al. (2008) fall within the 5th and 95th percentiles of the low and medium competition levels of our study presented here. However, in contrast to this study, only 1% of the bootstrapped models with ambient herbivory in the previous study predicted a *C. vulgare* population growth rate of $\log \lambda \leq 0$ in the matrix model, which suggested that ambient insect herbivory was not sufficient to halt *C. vulgare* population growth. That matrix model, however, used early data on this ecosystem supplemented by data from the literature for missing parameter values. Thus, one hypothesis is that including parameter estimates derived from different countries introduced large parameter uncertainty that led to an overestimation of the predicted *C. vulgare* population growth rates in this ecosystem. An alternative hypothesis is that the intensity of herbivory may have varied between studies, since there can be large spatiotemporal variation in the impact of insect herbivory on *C. vulgare* vital rates (e.g., Eckberg et al. 2012). In any case, the cumulative evidence clearly shows that ambient levels of interspecific competition and insect herbivory together are able to limit *C. vulgare* population growth rate in the western tallgrass prairie region.

Effects of biotic interactions on the introduced thistle vs. on the native thistle

Since *C. vulgare* is an introduced species, with less time to adapt to competition and herbivory pressures in eastern Nebraska than its native congener *C. altissimum* has had and since *C. vulgare* is less abundant than *C. altissimum* (Andersen and Louda 2008), we asked whether the interactions would reduce population growth rate of *C. vulgare* more than that of *C. altissimum*. Our models suggest that *C. vulgare* suffered somewhat more from interspecific plant competition and insect herbivory than did *C. altissimum*. Within each level of herbivory, interspecific competition from the resident plant community had a greater negative effect on the population growth rate of the introduced *C. vulgare* than on the native *C. altissimum* (Appendix: Table A7). This result likely reflects both lower juvenile survival and lower proportion flowering successfully by *C. vulgare* than by *C. altissimum* with ambient levels of herbivory, as well as smaller size (biomass) and lower flowering success by *C. vulgare* than *C. altissimum* with reduced herbivory (Suwa and Louda 2012). One hypothesis to explain smaller size and lower flowering success of *C. vulgare* than *C. altissimum* even with reduced herbivory is that *C. vulgare* is less adapted to interacting with tallgrass prairie plant species than its native congener, *C. altissimum*. This result is consistent with several experiments with another species that found competition had a larger negative effect on population vital rates of an introduced species than of its related, co-occurring native species (Garcia-Serrano et al. 2007). Our study here, however, contributes new information by having the modeling based on experimental data to compare the effects of competition on population growth rate in relation to the level of herbivory for an introduced species vs. its co-occurring, native congener.

At both ambient (high) and experimentally reduced (medium/low) levels of plant competition, insect herbivory reduced the population growth rate of *C. vulgare* more than that of native *C. altissimum*. One explanation for this effect is that juvenile rosettes of *C. vulgare* experience more herbivory than do those of *C. altissimum* (Suwa and Louda 2012). These results are consistent with several other studies that found herbivory on an introduced species was greater

than that on its native congener in the habitat (Agrawal and Kotanen 2003, Liu and Stiling 2006, Stricker and Stiling 2012). This result is also consistent with the hypothesis that defenses against herbivory in an introduced species are absent or lower than in the resident, co-evolving native congener (e.g., Crawley 1997). Overall, the introduced *C. vulgare* was more affected by both plant competition and insect herbivory than was the native *C. altissimum*.

Management applications

It is useful to know that some potentially invasive species can be constrained by resistance from the resident community when managing native ecosystems. Our study also demonstrates the value of considering multiple, simultaneous factors to drive population decline in a weedy plant. The implication is that maintaining, and perhaps enhancing, components of biotic resistance could be one tool for invasive species control. Competition in grasslands can be increased by both enhancing recruitment of native competitors by seeding them in, as well as reducing frequency or intensity of disturbance that opens invasible space. Also, insect herbivory of the type recorded here can be maintained by conserving non-problematic native plant populations, such as the native thistle, as sources of herbivore antagonists of the introduced thistle. When disturbances are required, for example fire in tallgrass prairie, then ensuring that native herbivores are present to quickly recolonize an area minimizes the opportunity for non-natives to establish. In sum, based on our results, managing *C. vulgare*, and potentially similar weedy species, will require the combined effects of both interspecific competition and insect herbivory, comparable to the ambient levels here.

Conclusion: competition and herbivory provide biotic resistance

The goal of this study was to test the hypothesis that biotic factors limit population growth of the introduced thistle, *C. vulgare*, and to compare the effects of those interactions with those on its native congener, *C. altissimum*, within western tallgrass prairie. With a combination of manipulative experiments and IPMs, we found that the combined effect of interspecific plant competition and native insect herbivory from the

resident community additively reduced population growth rate of both species, and limited both invasiveness of *C. vulgare* and the abundance and, so weediness, of *C. altissimum* in tallgrass prairie. The outcome highlights the importance of maintaining multiple biological interactions in native communities as a limit on plant invasiveness. Improved understanding of biotic mechanisms limiting $\log \lambda$ for potentially invasive species and for their native relatives increases our ability to predict when biotic resistance is likely to contribute to invasive plant species management.

ACKNOWLEDGMENTS

We thank B. Seth for encouraging our research at the Pioneers Park Nature Center, plus the University of Nebraska Recreation Department and Nebraska Game and Parks Commission for facilitating our work and field experiments at the Pioneers Park. Partial support for this research was provided by: J. E. Weaver Grant from The Nature Conservancy–Nebraska Chapter, a John Davidson Scholarship, University of Nebraska–Lincoln (UNL) Initiative for Ecological and Evolutionary Analysis, UNL School of Biological Sciences Special Funds, and The Center for the Great Plain Studies to T. Suwa; and, by N.S.F. grant DEB 0532018 and U.S.D.A. grant NRI-2005-35320-15379 to F. L. Russell and S. M. Louda. This is KBS contribution #1726. F. L. Russell, S. M. Louda; and T. Suwa provided empirical data that were analyzed statistically by B. Tenhumberg and A. J. Tyre; B. Tenhumberg conducted the mathematical modeling, and all four authors contributed to the writing of the manuscript.

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SUPPLEMENTAL MATERIAL

APPENDIX

Procedure used to create a priori model sets

For predicting growth including all possible combinations of main effects and two way interactions created too many models. Thus, we evaluated a range of plausible combinations of fixed effects and interactions. Because the population model is size structured, we only included models with the size variable. When including interactions, we preferentially included interactions with size for the same reason. The model set is bounded by a null model with no covariates and a global model containing all four main effects and their two way interactions (two models).

The first group of models contained all combinations of the main effects without interactions that included the size variable (eight models). The second group of three models included size and one other effect, plus their two way interaction. The third group of models included size and two of the other three main effects, plus both two-way interactions involving size. The fourth group of models included the same three main effect models plus all three two-way interactions (three models). The final set of

models included all four main effects and then various combinations of two way interactions. First, we added each possible single interaction to the four variable model (six models). Second, we included all possible combinations of five two-way interactions (six models). Finally, third, we evaluated four models with three interaction terms: a model with interactions between herbivory, competition and bolting; a model with interactions between size, herbivory and bolting; a model with interactions between size competition and bolting; and, a model with interactions between size, herbivory and competition (four models).

For all remaining statistical models for parameters besides growth, it was feasible to evaluate all combinations of main effects and pairwise interactions, since whether a plant bolted was not an issue. All combinations of size, herbivory and competition led to 18 models. In some cases, we had fewer models because either herbivory or competition were not manipulated in that particular experiment.

Table A1. List of statistical models included in model averaging of thistle growth. Cv = *C. vulgare* (Bull thistle), Ca = *C. altissimum* (Tall thistle), k = number of parameters (including the intercept), loglik = log-likelihood; dbic = difference in Bayesian Information Criterion (BIC), wbic = BIC weights, S = plant size, H = insect herbivory treatment levels, C = interspecific competition treatment levels, B = bolting (adult, flowering) plant, 1 = model uses vital rate averaged over all treatments.

Species	Models	k	loglik	dbic	wbic
Cv	S + B	3	-378.79	0	0.78723
	S + H + B	4	-377.91	3.84304	0.11524
	S + B + S:B	4	-378.16	4.34353	0.08973
	S + C + B	5	-378.06	9.73086	0.00607
	S + H + B + S:H + S:B	6	-377.35	13.8983	0.00076
	S + H + C + B	6	-377.5	14.2045	0.00065
	S + H + B + S:H + S:B + H:B	7	-376.3	17.3894	0.00013
	S + H + C + B + S:B	7	-377.02	18.8369	6.39E-05
	S + H + C + B + H:B	7	-377.12	19.0321	5.80E-05
	S + H + C + B + S:H	7	-377.48	19.76	4.03E-05
	S + H + C + B + C:B	8	-375.17	20.7241	2.49E-05
	S + H + C + B + H:C	8	-376.6	23.5915	5.93E-06
	S + H + C + B + S:C	8	-377.39	25.1532	2.72E-06
	S + C + B + S:C + S:B	8	-377.52	25.4128	2.39E-06
	S + H + C + B + S:H + S:B + H:B	9	-376.08	28.136	6.12E-07
	S + C + B + S:C + S:B + C:B	10	-373.55	28.6711	4.68E-07
	S + H + C + B + H:C + H:B + C:B	11	-372.2	31.5558	1.11E-07
	S + H + C + B + S:C + S:B + C:B	11	-373	33.1655	4.95E-08
	S + H + C + B + S:H + S:B + H:C + H:B + C:B	13	-368.36	35.0584	1.92E-08
	S + H + C + B + S:C + S:H + S:B + H:B + C:B	13	-370.4	39.1352	2.50E-09
	S + H + C + B + S:C + S:H + H:C	11	-376.02	39.1879	2.44E-09
	S + H + C + B + S:C + S:B + H:C + H:B + C:B	14	-367.97	39.8726	1.73E-09
	S + H + C + B + S:C + S:H + S:B + H:C + H:B + C:B	15	-367.69	44.9051	1.40E-10
	S + H + C + B + S:C + S:H + S:B + H:C + C:B	14	-370.71	45.3432	1.12E-10
	S + H + C + B + S:C + S:H + S:B + H:C + H:B	13	-373.94	46.2261	7.21E-11
	S + H + C + B + S:C + S:H + H:C + H:B + C:B	14	-372.12	48.168	2.73E-11
	S	2	-460.12	157.075	6.13E-35
	S + C	4	-455.5	159.026	2.31E-35
	S + H	3	-459.95	162.328	4.44E-36
	S + H + C	5	-455.45	164.502	1.50E-36
	S + H + S:H	4	-459.27	166.554	5.36E-37
	S + C + S:C	6	-453.99	167.18	3.92E-37
	S + H + C + S:C + S:H	8	-453.3	176.988	2.91E-39
	S + H + C + S:C + S:H + H:C	10	-453.19	187.935	1.22E-41
	1	1	-510.55	252.351	1.26E-55
Ca	S + H + B	6	-657.37	0	0.97907
	S + H + B + S:H + S:B	8	-655.48	8.39316	0.01473
	S + H + C + B	8	-656.88	11.1939	0.00363
	S + H + C + B + S:H	9	-654.95	13.4167	0.0012
	S + H + B + S:H + S:B + H:B	9	-655.2	13.9113	0.00093
	S + H + C + B + S:B	9	-656.75	17.0107	0.0002
	S + H + C + B + H:B	9	-656.79	17.0945	0.00019
	S + H + C + B + C:B	10	-656.16	21.9197	1.70E-05
	S + H + C + B + H:C	10	-656.28	22.1679	1.50E-05
	S + H + C + B + S:C	10	-656.45	22.5117	1.27E-05
	S + B	5	-672.39	23.9578	6.14E-06
	S + H + C + B + S:H + S:B + H:B	11	-654.7	25.098	3.47E-06
	S + B + S:B	6	-672.2	29.675	3.52E-07
	S + C + B	7	-670.84	33.034	6.57E-08
	S + H + C + B + S:C + S:H + H:C	13	-653.65	35.1562	2.27E-08
	S + H + C + B + S:C + S:B + C:B	13	-655.05	37.9569	5.61E-09
	S + H + C + B + H:C + H:B + C:B	13	-655.53	38.9241	3.46E-09
	S + H + C + B + S:H + S:B + H:C + H:B + C:B	15	-652.7	45.4299	1.34E-10
	S + H + C + B + S:C + S:H + S:B + H:B + C:B	15	-653.49	46.9974	6.10E-11
	S + H + C + B + S:C + S:H + S:B + H:C + H:B	15	-653.5	47.0369	5.98E-11
	S + C + B + S:C + S:B	10	-669.93	49.4614	1.78E-11
	S + H + C + B + S:C + S:H + H:C + H:B + C:B	16	-652.45	51.0212	8.16E-12
	S + H + C + B + S:C + S:H + S:B + H:C + C:B	16	-652.51	51.1263	7.74E-12
	S + H + C + B + S:C + S:B + H:C + H:B + C:B	16	-654.32	54.7489	1.27E-12
	S + H + C + B + S:C + S:H + S:B + H:C + H:B + C:B	17	-652.33	56.857	4.41E-13
	S + C + B + S:C + S:B + C:B	12	-668.83	59.4333	1.22E-13
	S + H + C	7	-791.6	274.556	2.35E-60

Table A1. Continued.

Species	Models	k	loglik	dbic	wbic
	S + H	5	-799.12	277.413	5.64E-61
	S + H + S:H	6	-796.5	278.27	3.67E-61
	S	4	-804.37	281.837	6.18E-62
	S + C	6	-799.05	283.373	2.86E-62
	S + H + C + S:C + S:H	10	-788.53	286.656	5.55E-63
	S + C + S:C	8	-798.92	295.269	7.48E-65
	S + H + C + S:C + S:H + H:C	12	-786.98	295.73	5.94E-65
	1	3	-891.17	449.352	2.60E-98

Table A2. List of statistical models included in model averaging of thistle survival. Cv = *C. vulgare* (Bull thistle), Ca = *C. altissimum* (Tall thistle), k = number of parameters (including the intercept), loglik = log-likelihood; dbic = difference in Bayesian Information Criterion (BIC), wbic = BIC weights, S = plant size, H = insect herbivory treatment levels, C = interspecific competition treatment levels, 1 = model uses vital rate averaged over all treatments.

Species	Models	k	loglik	dbic	wbic
Cv	S + H	5	-428.593	0	0.830231
	S + H + C	7	-423.903	4.079979	0.107955
	S + H + S:H	6	-428.592	6.727979	0.028723
	H + C	6	-428.611	6.772993	0.028084
	S + H + C + S:H	8	-423.847	10.69784	0.003946
	S + H + C + S:C	9	-422.537	14.80768	0.000506
	S + H + C + H:C	9	-423.319	16.37099	0.000231
	H	4	-440.735	17.55855	0.000128
	S	4	-440.886	17.85519	0.00011
	H + C + H:C	8	-428.071	19.15482	5.75E-05
	S + H + C + S:C + S:H	10	-422.518	21.49965	1.78E-05
	S + H + C + S:H + H:C	10	-423.201	22.86459	9.00E-06
	S + H + C + S:C + H:C	11	-422.378	27.9497	7.08E-07
	S + C	6	-439.592	28.72685	4.80E-07
	S + H + C + S:C + S:H + H:C	12	-422.364	34.6515	2.48E-08
	S + C + S:C	8	-437.859	38.72218	3.24E-09
	C	5	-448.008	38.83656	3.06E-09
	1	3	-455.662	40.68222	1.22E-09
Ca	H	4	-481.422	0	0.819971
	S + H	5	-479.652	3.204552	0.165173
	H + C	6	-479.611	9.870769	0.005894
	S + H + S:H	6	-479.651	9.949838	0.005665
	1	3	-490.783	11.97371	0.002059
	S	4	-488.536	14.22765	0.000667
	S + H + C	7	-478.864	15.12138	0.000427
	H + C + H:C	8	-477.499	19.13952	5.72E-05
	S + H + C + S:C	9	-474.207	19.30144	5.28E-05
	S + H + C + S:H	8	-478.863	21.86732	1.46E-05
	C	5	-489.21	22.32108	1.17E-05
	S + H + C + H:C	9	-476.94	24.76684	3.43E-06
	S + H + C + S:C + S:H	10	-474.197	26.0275	1.83E-06
	S + C	6	-487.962	26.57267	1.39E-06
	S + C + S:C	8	-482.427	28.99529	4.15E-07
	S + H + C + S:C + H:C	11	-472.609	29.59728	3.07E-07
	S + H + C + S:H + H:C	10	-476.82	31.27445	1.33E-07
	S + H + C + S:C + S:H + H:C	12	-472.53	36.18574	1.14E-08

Table A3. List of statistical models included in model averaging of thistle flowering probability. Cv = *C. vulgare* (Bull thistle), Ca = *C. altissimum* (Tall thistle), k = number of parameters (including the intercept), loglik = loglikelihood; dbic = difference in Bayesian Information Criterion (BIC), wbic = BIC weights, S = plant size, H = insect herbivory treatment levels, C = interspecific competition treatment levels, B = bolting (adult, flowering) plant, 1 = model uses vital rate averaged over all treatments.

Species	Models	k	loglik	dbic	Wbic
Cv	S	3	-139.468	0	0.836828
	S + C	5	-135.993	4.560017	0.085594
	S + H	4	-139.34	5.498842	0.053528
	S + H + S:H	5	-137.686	7.947145	0.015737
	S + H + C	6	-135.866	10.06252	0.005465
	S + H + C + S:H	7	-134.18	12.44619	0.00166
	S + C + S:C	7	-134.629	13.34342	0.00106
	S + H + C + S:C	8	-134.52	18.88134	6.65E-05
	S + H + C + H:C	8	-135.014	19.87027	4.05E-05
	S + H + C + S:C + S:H	9	-133.063	21.72453	1.60E-05
	S + H + C + S:H + H:C	9	-133.994	23.58655	6.32E-06
	S + H + C + S:C + H:C	10	-134.163	29.67982	3.00E-07
	S + H + C + S:C + S:H + H:C	11	-133.058	33.22582	5.10E-08
	H + C	5	-170.317	73.22512	1.05E-16
	C	4	-173.399	73.6293	8.59E-17
	1	2	-183.766	82.84589	8.57E-19
	H + C + H:C	7	-169.396	82.90099	8.34E-19
	H	3	-182.32	85.71322	2.04E-19
Ca	S + C	5	-230.427	0	0.884341
	S	3	-239.604	5.945243	0.045251
	S + H + C	6	-230.381	6.112943	0.041611
	S + C + S:C	7	-227.87	7.295202	0.02304
	S + H	4	-239.531	12.00237	0.002189
	S + H + C + S:H	7	-230.238	12.03011	0.002159
	S + H + C + S:C	8	-227.819	13.39846	0.001089
	S + H + C + H:C	8	-229.848	17.45535	0.000143
	S + H + S:H	5	-239.387	17.92063	0.000114
	S + H + C + S:C + S:H	9	-227.788	19.5406	5.05E-05
	S + H + C + S:H + H:C	9	-229.758	23.48063	7.04E-06
	S + H + C + S:C + H:C	10	-227.374	24.91603	3.44E-06
	S + H + C + S:C + S:H + H:C	11	-227.357	31.08659	1.57E-07
	C	4	-249.811	32.56271	7.51E-08
	H + C	5	-249.74	38.6259	3.62E-09
	H + C + H:C	7	-249.394	50.34323	1.03E-11
	1	2	-269.375	59.28176	1.19E-13
	H	3	-269.292	65.32017	5.79E-15

Table A4. List of statistical models included in model averaging of the probability of zero seed production by a bolting plant. Cv = *C. vulgare* (Bull thistle), Ca = *C. altissimum* (Tall thistle), k = number of parameters (including the intercept), loglik = log-likelihood; dbic = difference in Bayesian Information Criterion (BIC), wbic = BIC weights, S = plant size, H = insect herbivory levels, C = interspecific competition levels, B = bolting (adult, flowering) plant, 1 = model uses vital rate averaged over all treatments.

Species	Models	k	loglik	dbic	wbic
Cv	S	3	-31.6224	0	0.897102
	S + C	4	-31.6198	4.658206	0.087363
	S + C + S:C	5	-31.2495	8.580955	0.012289
	1	2	-39.677	11.44559	0.002934
	C	3	-39.586	15.92719	0.000312
Ca	S + H	5	-247.797	0	0.903723
	S + H + S:H	6	-246.98	4.506147	0.094959
	H	4	-257.709	13.68363	0.000965
	S	4	-258.719	15.70379	0.000352
	1	3	-269.309	30.74354	1.91E-07

Table A5. List of statistical models included in model averaging of the number of seeds produced per bolting plant. Cv = *C. vulgare* (Bull thistle), Ca = *C. altissimum* (Tall thistle), k = number of parameters (including the intercept), loglik = loglikelihood; dbic = difference in Bayesian Information Criterion (BIC), wbic = BIC weights, S = plant size, H = insect herbivory levels, C = interspecific competition levels, B = bolting (adult, flowering) plant, 1 = model uses vital rate averaged over all treatments.

Species	Models	k	loglik	dbic	wbic
Cv	S + H	6	-180.048	0	0.348186
	S + H + S:H	7	-177.561	0.185862	0.317287
	S	5	-182.961	0.667831	0.249341
	S + H + C	7	-179.882	4.828335	0.031142
	S + H + C + S:H	8	-177.454	5.130625	0.026774
	S + C	6	-182.771	5.446251	0.022865
	S + H + C + H:C	8	-180.49	11.20266	0.001286
	S + H + C + S:H + H:C	9	-178.154	11.69017	0.001008
	S + H + C + S:C	8	-180.987	12.19636	0.000782
	S + H + C + S:C + S:H	9	-178.494	12.37023	0.000717
	S + C + S:C	7	-183.921	12.90504	0.000549
	S + H + C + S:C + H:C	9	-181.512	18.40539	3.51E-05
	S + H + C + S:C + S:H + H:C	10	-179.171	18.88367	2.76E-05
	H + C	6	-260.95	161.8052	2.55E-36
	H	5	-264.165	163.0765	1.35E-36
	C	5	-265.097	164.9387	5.32E-37
	1	4	-268.353	166.2929	2.70E-37
	H + C + H:C	7	-261.162	167.3879	1.56E-37
Ca	S + H	5	-272.392	0	0.754721
	S + H + S:H	6	-271.273	2.80399	0.185741
	H	4	-277.46	5.091624	0.059177
	S	4	-282.606	15.38351	0.000345
	1	3	-288.159	21.44739	1.66E-05

Table A6. List of statistical models included in model averaging of recruitment probability. Cv = *C. vulgare* (Bull thistle), Ca = *C. altissimum* (Tall thistle), k = number of parameters (including the intercept), loglik = loglikelihood; dbic = difference in Bayesian Information Criterion (BIC), wbic = BIC weights, S = plant size, H = insect herbivory levels, C = interspecific competition levels, B = bolting (adult, flowering) plant, 1 = model uses vital rate averaged over all treatments.

Species	Models	k	loglik	dbic	wbic
Cv	C	5	-598.908	0	0.770172
	C + H + H:C	8	-594.018	3.616345	0.126272
	C + H	6	-598.682	4.013013	0.103556
	1	3	-745.139	283.5299	2.08E-62
	H	4	-744.919	287.5562	2.78E-63
Ca	C + H + H:C	8	-430.998	0	0.999995
	C	5	-450.031	24.66914	4.40E-06
	C + H	6	-449.883	28.83785	5.47E-07
	1	3	-579.655	274.984	1.94E-60
	H	4	-579.483	279.1066	2.47E-61

Table A7. Population growth rate, $\log \lambda$, for different levels of insect herbivory at each level of competition. The numbers in brackets indicate 5th and 95th percentile limits of bootstrapped $\log \lambda$ -value distributions. “Max Competition Effect on $\log \lambda$ ” indicates the difference in $\log \lambda$ values between the ambient high and reduced low competition treatments ($\log \lambda_{\text{ambient high competition}} - \log \lambda_{\text{low reduced competition}}$).

Competition level	<i>C. vulgare</i>		<i>C. altissimum</i>		Herbivory effect on
	Ambient herbivory	Reduced herbivory	Ambient herbivory	Reduced herbivory	
Ambient, high	−1.27 (−2.35, −0.25)	−0.74 (−1.59, 1.18)	−0.88 (−1.42, −0.32)	−0.81 (−1.22, −0.57)	exotic > native
Medium, reduced	−0.05 (−1.11, 1.18)	1.59 (0.25, 3.13)	−0.64 (−1.32, 0.55)	1.48 (0.40, 2.90)	native > exotic
Low, reduced	0.25 (−1.00, 1.70)	3.53 (2.5, 4.58)	−0.4 (−1.59, 0.51)	1.6 (0.4, 3.14)	exotic > native
Max competition effect on $\log \lambda$	1.52	4.27	0.48	2.41	

Note: Competition levels are: ambient, high = 65–90% cover; medium, reduced = 25–35% cover; low, reduced = 0–5% cover.

SUPPLEMENT

Data files and R scripts for statistical analysis and integral projection modeling described in the main text (*Ecological Archives*, <http://dx.doi.org/10.1890/ES14-00389.1.sm>).