

Insect herbivory and propagule pressure influence *Cirsium vulgare* invasiveness across the landscape

JAMES O. ECKBERG,^{1,3} BRIGITTE TENHUMBERG,^{1,2} AND SVATA M. LOUDA¹

¹*School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588 USA*

²*Department of Mathematics, University of Nebraska, Lincoln, Nebraska 68588 USA*

Abstract. A current challenge in ecology is to better understand the magnitude, variation, and interaction in the factors that limit the invasiveness of exotic species. We conducted a factorial experiment involving herbivore manipulation (insecticide-in-water vs. water-only control) and seven densities of introduced nonnative *Cirsium vulgare* (bull thistle) seed. The experiment was repeated with two seed cohorts at eight grassland sites uninhabited by *C. vulgare* in the central Great Plains, USA. Herbivory by native insects significantly reduced thistle seedling density, causing the largest reductions in density at the highest propagule inputs. The magnitude of this herbivore effect varied widely among sites and between cohort years. The combination of herbivory and lower propagule pressure increased the rate at which new *C. vulgare* populations failed to establish during the initial stages of invasion. This experiment demonstrates that the interaction between biotic resistance by native insects, propagule pressure, and spatiotemporal variation in their effects were crucial to the initial invasion by this Eurasian plant in the western tallgrass prairie.

Key words: bull thistle; *Cirsium vulgare*; insect–plant interaction; invasive species; plant invasion; plant population dynamics; spear thistle; weed; weed dynamics.

INTRODUCTION

Understanding the dynamics of exotic plant invasions remains an important challenge in ecology. Propagule pressure is recognized as one of the most significant factors influencing nonnative species invasions (Eschtruth and Battles 2009, Simberloff 2009). As the number of nonnative plant propagules arriving increases, the probability of establishment and persistence in a new environment should be less affected by demographic stochasticity or Allee effects (Simberloff 2009). Propagules invading a new environment must also overcome abiotic and biotic resistance to establish a new plant population (Levine et al. 2004). Severe effects of native herbivores on nonnative plants are predicted by the new associations hypothesis, which posits that nonnative plants are evolutionarily naïve to native consumers (Parker et al. 2006). Indeed, mounting evidence shows that native herbivores reduce growth, reproduction, and density of nonnative plants (Maron and Vila 2001, Levine et al. 2004, Parker et al. 2006). For example, native jackrabbit (*Lepus californicus*) herbivory reduces fecundity and aboveground biomass and limits the local distribution of the invasive grass *Ehrharta calycina* in the coastal dunes of California (Cushman et al. 2011).

Herbivore pressure and its impact on nonnative plant performance can also intensify when insects spill over from native congeneric plants (Louda and Rand 2002, Suwa et al. 2010). While the outcome of nonnative plant introductions could be influenced by both propagule pressure and biotic resistance, little is known about the interaction or joint influence of these two processes across heterogeneous landscapes (D'Antonio et al. 2001).

We address this gap in our knowledge of propagule pressure and biotic resistance by herbivory. Specifically, we do not know whether biotic resistance is a density-dependent process, and if so, whether its impact on an invading plant varies with the number of arriving propagules. Density-dependent interactions could arise, for example, if herbivore pressure differs at varied densities of invading plants (Otway et al. 2005). Also, reductions in plant survival caused by herbivory could have no net impact on plant populations if the number of viable seeds arriving exceeds the microsite availability (Crawley 1997). Interactions between propagule pressure and biotic resistance also may be important to understanding the causes of failed invasions. Small incipient plant populations resulting from low propagule pressure may fail to establish if they are detected and attacked by generalist herbivores (Levine et al. 2004). However, too little information currently exists on biotic resistance, propagule pressure, and their interaction during the early stages of a plant invasion (Levine et al. 2004). Experiments that manipulate herbivory across a wide gradient of arriving propagules during the initial

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³ Present address: Department of Agronomy and Plant Genetics, University of Minnesota, 1991 Upper Buford Circle, Saint Paul, Minnesota 55108 USA.

E-mail: jeckberg@umn.edu

stages of an invasion are needed to provide new insights into the importance of this interaction to plant invasions.

The relative importance of propagule pressure and herbivory by native consumers is likely to vary across heterogeneous landscapes. This can result from spatial variation in generalist and specialist herbivore density or feeding activity (Louda and Rodman 1996, Lambrinos 2002, Miller et al. 2009), or from the interaction of herbivory with spatial heterogeneity in abiotic conditions and plant community composition (Lambrinos 2002). To date, our knowledge of propagule pressure and ecosystem factors influencing invasions across the landscape is based primarily on observational studies that substitute indirect (ship traffic) or nonindependent (distance to propagule source) measures for propagule pressure (Eschtruth and Battles 2009, Simberloff 2009). Few studies have experimentally manipulated both propagule pressure and biotic resistance across multiple resident communities, thus limiting our understanding of their relative importance or potential interaction across landscapes.

The aim of this study was to experimentally quantify the independent and joint effects of propagule pressure and native insect herbivory on seedling establishment by the Eurasian plant *Cirsium vulgare* (Savi) Ten. (bull thistle, spear thistle) across the spatial variation represented by multiple grassland sites in the western tallgrass prairie region in eastern Nebraska, central Great Plains, USA. Despite the invasive status of *C. vulgare* in most of the United States, including the neighboring states of Colorado and Iowa, *C. vulgare* populations remain sparse in eastern Nebraska (Louda and Rand 2002, Andersen and Louda 2008), and it is not listed as noxious in Nebraska (USDA 2011). Native insect herbivores limit *C. vulgare* seed production in eastern Nebraska (Louda and Rand 2002, Suwa et al. 2010), and there is strong seed limitation in populations of native *Cirsium* species (Louda and Potvin 1995, Russell et al. 2010). The seedling dynamics of *C. vulgare* in the tallgrass region thus represent a good model system with which to explore the interactions between propagule pressure and insect herbivory in the early establishment of a nonnative plant.

We experimentally reduced herbivory on seedlings across a range of seed inputs (seven densities) for two seed cohorts introduced into eight previously uninvaded grassland sites. Because *C. vulgare* is a disturbance specialist (Suwa and Louda 2012), we provided a mechanical disturbance prior to planting the seeds. Our study tests two main questions focused on the initial seedling establishment stage of a nonnative plant invasion. First, what are the independent and joint effects of propagule pressure and insect herbivory on establishment of *C. vulgare* in this region? Second, how do these effects vary across multiple resident communities? The results are of both basic and applied interest.

METHODS

Natural history

The Eurasian thistle, *C. vulgare* (see Plate 1), is a short-lived, monocarpic perennial species that grows as a rosette until its single, lifetime flowering event. In eastern Nebraska, flowering and seed set usually occurs in two to three years during July–September (J. O. Eckberg, B. Tenhumberg, and S. M. Louda, *unpublished data*). Germination (21.4% on average) usually occurs during the following spring in eastern Nebraska (Tenhumberg et al. 2008). This study focused on seedling establishment, from spring germination (April) to the end of the first growing season (late September–early October).

Native insect herbivores feed extensively on *C. vulgare* in the tallgrass prairie region of Nebraska, and the seedling stage is vulnerable to >46 species of native, primarily generalist, defoliating and sap-feeding insects in the study region (Takahashi 2006).

Study sites

The experiment was conducted at eight grassland sites in Lancaster County, eastern Nebraska, USA, and it involved two annual seed cohorts (2006, 2007). Grassland sites were at least 1.3 km apart (mean = 6.5 km; maximum = 13.6 km; map in Eckberg [2008]). The eight sites are representative of currently uninvaded, contemporary grasslands in eastern Nebraska; and the sites included six native tallgrass prairies (sites 1–5, 7) and two grasslands dominated by Eurasian grasses (sites 6, 8) (Eckberg 2008).

Treatments

The factorial experiment included seven levels of seed addition and two levels of herbivory (insecticide-in-water, water-only control). Each year, we introduced *C. vulgare* seeds at seven densities: 50, 100, 150, 200, 250, 300, or 350 seeds/1-m² subplots in 3 × 1 m plots (150, 300, 450, 600, 750, 900, or 1050 total seeds/3-m² plot). All *C. vulgare* seeds added in this experiment were from naturalized plants in eastern Nebraska (Appendix A). We used the ratio of seed count to seed biomass to allocate the appropriate number of seeds to each 1-m² subplot (Appendix A). To establish seed addition treatments, we disturbed the soil by raking, seeded each subplot separately, and returned the raked litter to the subplot (4–23 April in both 2006 and 2007). Thus, we established two successive seed cohorts per site ($n = 14$ 3-m² plots/site at eight sites in each of two years; Appendix A). In 2006 (first cohort), we randomly interspersed treatment plots across a 30 × 60 m grid; individual plots were separated by 15 m. In 2007 (second cohort), we randomly interspersed treatment plots into the interstitial area between the first-cohort plots; and second-cohort plots also were separated by 15 m and were ≥10.5 m from any first-cohort plot.

To reduce herbivory, we sprayed the insecticide bifenthrin (pyrethroid insecticide, diluted as recom-

mended to 0.06% active ingredient [Control Solutions, Pasadena, Texas USA]) on aboveground plant structures on entire 3-m² plots at three-week intervals from seedling emergence (late April–mid May) through the growing season (September) in both years. Because bifenthrin is not a systemic insecticide, it is unlikely that the treatment influenced root herbivores. Insecticide application to entire plots may have reduced herbivory on background vegetation (primarily grass). However, we clipped the background vegetation, maintaining ~25 cm height in both spray treatments, in order to minimize potential positive effects of treating background vegetation with insecticide (Appendix A). We sprayed control plots with water-only on half of the spray dates to control for any effects of added water; moisture from both spray treatments usually dried in 10–20 minutes (J. O. Eckberg, *personal observation*). A separate greenhouse test ($n = 20$ per spray treatment) demonstrated that the rate of bifenthrin used in the field had no direct effects on *C. vulgare* seedling growth rate ($P = 0.484$) or survival ($P = 0.996$) (Appendix A).

Measurements

We counted seedlings in 1-m² subplots of each 3-m² plot in both early season (early–mid June) and late season (mid September–October) for both seed cohorts (in 2006, $N = 330$ subplots; in 2007, $N = 336$ subplots).

To further quantify seedling survival, growth and herbivory, we marked and measured a subset of 10 seedlings per subplot on average (30 plants/3-m² plot; total $N = 3274$ and 3338 seedlings in the 2006 and 2007 cohorts, respectively). At each site, we marked half of this subset (late May–early June) and then returned to mark the second half later (mid–late June). Given the time required to mark and measure seedlings, this approach minimized site-to-site disparities caused by variation in initial measurement time. At the end of each season (mid-September–mid-October), for marked seedlings we recorded both survival and the number of leaves and length of a medium-sized leaf on survivors (in 2006, $N = 1987$; in 2007, $N = 1774$). To estimate size, we multiplied the number of leaves by the length of the medium-sized leaf. This variable was highly correlated with plant biomass (measured in grams) ($r^2 = 0.93$, $N = 35$). Herbivory was measured on a subset of the marked survivors in 2006 ($N = 215$) and all marked survivors in 2007 ($N = 1774$); to do so, we visually estimated the total percentage of leaf area removed by insect feeding.

Statistical analyses

Herbivory, survival, size, and density.—A Bayesian hierarchical model with uninformative priors was developed, using WinBUGS (version 1.4.3; Lunn et al. 2000) in the statistical package R. One key advantage of Bayesian statistics and Markov Chain Monte Carlo method was that credible intervals could be generated for random effects; there are no efficient methods to generate confidence intervals for random effects in a

generalized linear mixed model. Further, because we use noninformative prior distributions, the results can be interpreted similarly as a generalized linear mixed model (McCarthy 2007). We analyzed the fixed effects of propagule input ($N = 7$ levels), insect herbivory ($N = 2$), and their interaction on end-of-season seedling survival, density, size, and percentage of total leaf damage on surviving seedlings (R Development Core Team 2005, McCarthy 2007). The unit of observation for plant size (log-transformed), percent total leaf damage (log-transformed proportion), and survival was the individual marked seedling; and the unit of observation for seedling density (not transformed) was the 1-m² subplot. Site, year, and plot were included as random effects. Estimating standard deviation for year-to-year variation was difficult because only two years were included in the study. We therefore incorporated cohort year ($N = 2$) and site ($N = 8$) into a single random effect to represent year–site variation. Plot (3 m²) was nested within year–site, and residual deviation was estimated between subplots (1 m²) or among individual marked seedlings, depending on the response variable (Appendix B). We included all interactions between fixed effects and the site–year random effects to estimate the spatiotemporal variation in fixed effects (Appendix B). The 95% credible intervals are the 2.5% and 97.5% quantiles from the sum of the posterior distributions of the site/year intercept, propagule input, and/or spray effect (Figs. 1, 2, and 4) or the posterior distribution of a single parameter (Appendix B) (McCarthy 2007). For each analysis we ran three independent chains for 50 000 iterations, discarding the first 2000 as burn-in, and thinning the remainder of the chain to every fifth sample. Convergence was confirmed by inspection of the Potential Scale Reduction Factors, \hat{R} (Brooks and Gelman 1998) for each sampled node. All models were run until $\hat{R} < 1.01$ for all nodes.

RESULTS

Main effects and spatiotemporal variation

The insecticide treatment significantly reduced herbivory (95% credible interval does not overlap with zero, Appendix B). Percentage of leaf damage decreased overall by >90%, representing significant reductions (72–96%) at all sites in both seedling cohorts (Appendix C). The insecticide treatment showed that herbivory significantly reduced the proportion of marked seedlings surviving (Appendix B), by 61% overall, with significant reduction at all sites in 2007 and the majority of the sites in 2006 (Fig. 1A). The effect of herbivory on seedling survival led to significantly reduced end-of-season juvenile density (Appendix B), 58% less overall, with significant effects at seven sites in 2007 and four sites in 2006 (Fig. 1B). Although herbivory reduced seedling survival and density in most sites, spatial variation in the magnitude of those impacts was large (Fig. 1). Herbivory also significantly reduced seedling size (Appendix B); seedlings were 53% smaller overall (Fig. 2), although

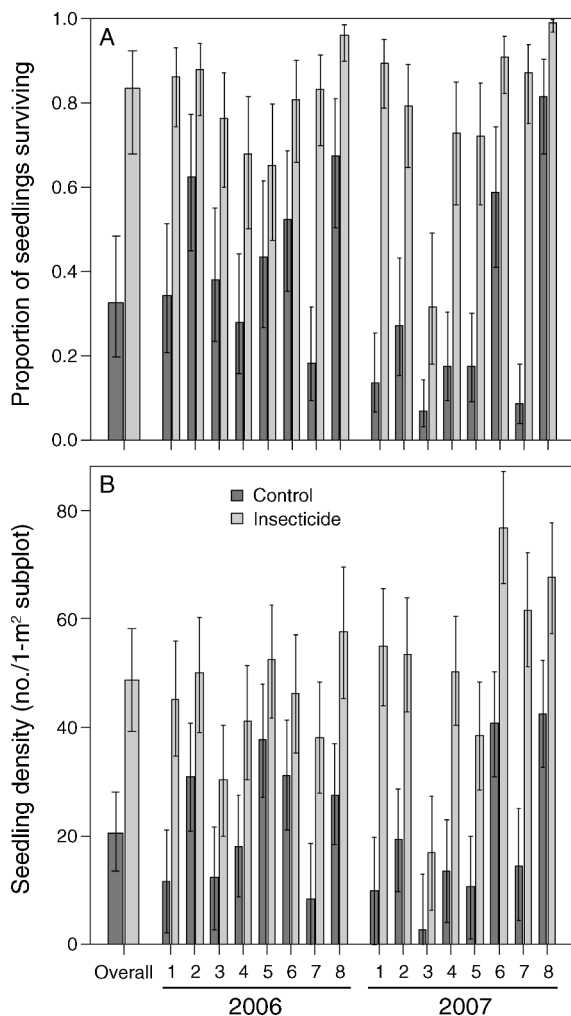


FIG. 1. Number (with 95% credible intervals) of *Cirsium vulgare* seedlings in each seed addition cohort (2006, 2007) at the end of the first growing season. The 95% credible intervals are the 2.5% and 97.5% quantiles from the sum of the posterior distributions of the site/year intercept and spray effect. (A) The proportion of marked seedlings surviving in each cohort ($N = 3274, 3338$ seedlings); (B) total density (number per 1-m^2 subplot within 3-m^2 plots; $N = 330, 336$ subplots) by spray treatment overall and for each site (sites 1–8). Dark bars are the water-only control treatment (ambient insect herbivory), and light-gray bars are the insecticide treatment (reduced insect herbivory).

many within-site differences between treatments were not statistically significant (Fig. 2).

Spatial variation occurred in the magnitude of the effect of herbivory on seedling survival (Fig. 1A). The variation was not correlated with percent leaf damage on survivors at the end of the season ($P = 0.89$, $R^2 = 0$). Instead, the variation was predicted by differences in plant size in the insecticide treatment, a proxy for other site-specific influences on seedling performance (Fig. 3). The effect of herbivory was greater at sites where those other factors were more limiting on seedling size (Fig. 3). Herbivory, other site factors influencing seedling size,

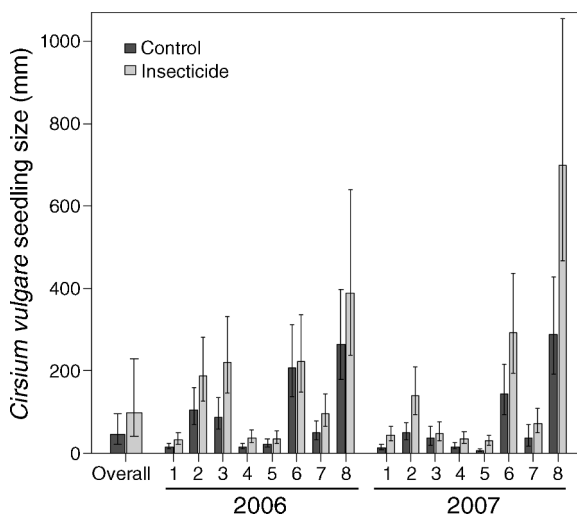


FIG. 2. Size (with 95% credible intervals) of surviving *Cirsium vulgare* marked seedlings in each seed addition cohort (2006, 2007) at the end of the first growing season ($N = 1987, 1774$ seedlings) by spray treatment overall and for each site (sites 1–8). The 95% credible intervals are the 2.5% and 97.5% quantiles from the sum of the posterior distributions of the site/year intercept and spray effect. Dark bars are water-only control treatment (ambient insect herbivory), and light-gray bars are insecticide treatment (reduced insect herbivory).

and their interaction predicted 79% of the year–site variation in seedling survival (Fig. 1A).

Interaction of seed density and herbivory

Seedling density increased with propagule input, but there was a significant herbivory \times propagule pressure

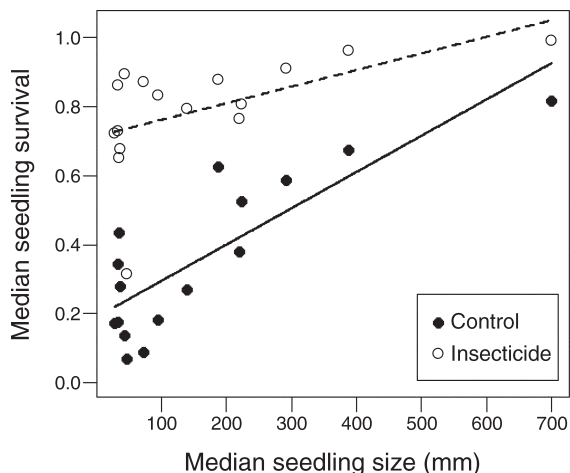


FIG. 3. Median *Cirsium vulgare* seedling survival per site–year combination vs. median seedling size of insecticide-treated seedlings (proxy for site–year-specific factors influencing seedling success, independent of herbivory) by spray treatment ($N = 8$ sites \times 2 years = 16). Regression analysis (adjusted $R^2 = 0.79$) showed significant effects on seedling survival from spray treatment ($P < 0.001$), site–year indexed as median seedling size ($P < 0.001$), and spray treatment \times site–year indexed as median seedling size ($P = 0.047$).

interaction (95% credible interval does not overlap with zero; Appendix B). Herbivory reduced the probability of seedling establishment (Fig. 4A), and greater reductions in seedling density occurred at higher propagule inputs (Fig. 4B). We did not find any significant herbivory \times propagule pressure interactions that suggest density-dependent effects of herbivory (Appendix B). Seedling survival increased significantly with propagule input (Appendix B). However, the effect was small (Appendix D), and it did not lead to higher seedling establishment rates at the subplot level (Fig. 4A). Seed density and herbivory influenced the proportion of plots that failed to establish (0 seedlings/1-m² subplot; see 95% credible intervals in Fig. 4). At low propagule inputs more plots failed to establish, and herbivory increased the rate of failure (Appendix E). Thus, the interaction of leaf herbivory, propagule input, and site-specific differences (indexed by median seedling size) strongly influenced *C. vulgare* recruitment over a large spatial scale.

DISCUSSION

Significant herbivore impact

The native assemblage of insect herbivores (Takahashi 2006) reduced seedling survival, size, and density of *C. vulgare* over a relatively large spatial scale, and for two experimentally introduced cohorts, in the western tallgrass prairie region (Figs. 1 and 2). Our study included more than twice the number of sites involved in most experimental tests of biotic resistance from herbivory (Levine et al. 2004), providing a larger, more representative estimate of biotic resistance across the region. This experiment thus provides strong support for the hypothesis that widespread biotic resistance can limit the early stages of a plant invasion (Louda and Rand 2002, Levine et al. 2004). Previous studies have illustrated that insect herbivory of *Cirsium* seedlings can cause a reduction in adult population sizes (Louda and Potvin 1995, Russell et al. 2010). Further, in a parallel study, we found that any subsequent compensatory density-dependent processes did not alter predictions for population size and dynamics suggested by the herbivory effects on the seedling stage (J. O. Eckberg, B. Tenhumberg, and S. M. Louda, *unpublished data*). Native insect herbivory also impacts later life stages of *C. vulgare*, reducing rosette survival, probability of flowering, and seed production (Louda and Rand 2002, Suwa et al. 2010, Suwa and Louda 2012), all of which can reduce population growth rate. For instance, floral herbivory can reduce the population growth rate of *C. vulgare* by 70% (Tenhumberg et al. 2008). The magnitude and spatial consistency of the herbivore effect on *C. vulgare* seedlings and other life stages may contribute to the low population densities of this known invasive weed in our region (Andersen and Louda 2008).

The high spatial regularity of the herbivory effects on *C. vulgare* seedlings, despite site-specific variation, likely resulted from a diverse assemblage of native insect herbivores, including multiple generalist species (Taka-

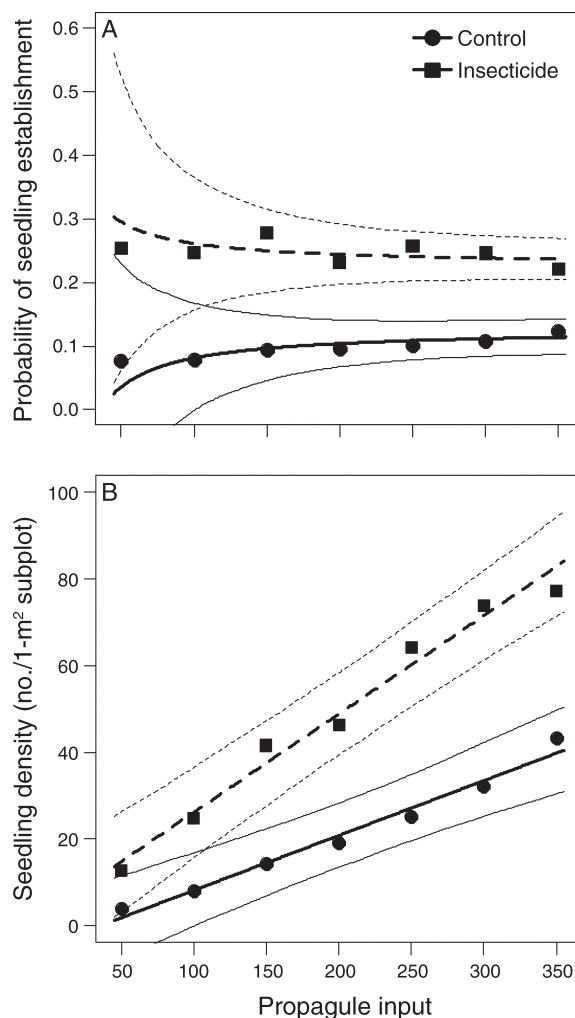


FIG. 4. (A) Probability of *Cirsium vulgare* seedling establishment (seedling density/propagule input) and (B) seedling density at the end of the growing season (number per 1-m² subplot, $N = 666$), in relation to propagule input (seven levels) and spray treatment (insecticide vs. water-only) (with 95% credible intervals) for eight sites and two annual seed cohorts (2006, 2007). The 95% credible intervals are the 2.5% and 97.5% quantiles from the sum of the posterior distributions of the propagule input and spray effect. Model equation and parameter estimates in part B: $Y = \beta_0 + \beta_1 P + \beta_2 H + \beta_3 PH + \epsilon$. (Key to symbols: P , Propagule input; H , Herbivory treatment [0 = control, 1 = insecticide]; ϵ , residual error); $\beta_0 = 20.7$, $\beta_1 = 12.7$, $\beta_2 = 28.0$, and $\beta_3 = 10.0$.

hashi 2006). The insect assemblage observed on *C. vulgare* parallels that of the more common native congener *C. altissimum*, which occurred at all sites, showing that native insects can rapidly expand their diet breadth to include *C. vulgare* (Takahashi 2006). Evidence shows that *C. altissimum* supports a diverse assemblage of native specialized insects that spill over and attack *C. vulgare*, an interaction that intensifies with proximity to *C. altissimum* (Louda and Rand 2002, Takahashi 2006, Andersen and Louda 2008). Generalist herbivory of *C. vulgare* seedlings can occur in either the



PLATE 1. (Left and right) Feeding damage on *Cirsium vulgare* leaf by *Systena hudsonias*; (inset) adult *S. hudsonias* (Forster) (Coleoptera: Chrysomelidae). Photo credit: Masaru Takahashi.

absence or presence of *C. altissimum*. However, a recent meta-analysis of the associational susceptibility hypothesis showed that usually the presence of neighboring palatable plants (i.e., *C. altissimum*), not diet breadth of the shared herbivores, led to greater insect herbivory and impacts on the focal plant (Barbosa et al. 2009). Therefore, the possibility that *C. altissimum* density contributes to patterns in herbivory effects on *C. vulgare* seedlings remains open for subsequent research. Further, Suwa and Louda (2012) observed greater herbivory and higher mortality due to herbivory for *C. vulgare* as compared to the native congener, *C. altissimum*. This is consistent with the observation that native herbivores, and their impacts on plant performance, are often more severe for nonnative plants than for the native congeners (Parker et al. 2006). The strong effects of herbivory in this study could be characteristic of situations where nonnative plants share a diverse assemblage of native generalist and specialist herbivores with a native congeneric plant species.

Role of propagule pressure

This study provides experimental evidence of the positive effects of propagule pressure on invader density across a wide range of arriving propagules (Fig. 4). Our experimental range of propagule input (150–1050 seeds/3 m² plot) encompassed and extended the mean propagule pressure expected from a single flowering *C. vulgare* exposed to herbivory, 382 seeds/plant (J. O. Eckberg, B. Tenhumberg, and S. M. Louda, *unpublished data*). Even the highest propagule density tested led to increases in seedling density (Fig. 4), consistent with observations of much larger seedling densities in a survey of two invaded grasslands in 2006 ($N = 16$ m² plots, J. O. Eckberg, *unpublished data*). Thus, these data are consistent with earlier studies showing strong seed limitation in native *Cirsium* populations (Louda and Potvin 1995, Russell et al. 2010). We extend the previous

studies here by demonstrating significant effects of propagule pressure in the early stage of a *C. vulgare* invasion.

Interaction between herbivory, propagule pressure, and spatiotemporal variation

One of the striking results of this study is the interaction and variation in the effects of herbivory and propagule pressure across the landscape. Consistent strong effects of herbivory on seedling survival, with little or no evidence of density dependence, led to larger reductions in seedling density as propagule pressure increased (Fig. 4B), damping the effect of increasing propagule pressure. Herbivory and propagule pressure effects on *C. vulgare* seedlings are likely to differ in disturbed (current study) vs. undisturbed grasslands. Interspecific competitors were shown to reduce *C. vulgare* seedling emergence, increase seedling mortality, and dramatically increase seedling mortality caused by herbivory (Suwa and Louda 2012). These findings are consistent with a recent study of the co-occurring native thistle, *C. altissimum* (Russell et al. 2010), and they suggest an important role of insect herbivory, rather than intraspecific density dependence, in constraining the effects of propagule pressure on thistle seedling density.

The strong and rapid effects of native insect herbivory on *C. vulgare* seedling populations at previously unoccupied sites suggest that insect herbivory exerts severe biotic resistance at the onset of plant invasion. In addition, there is high variation in the probability of seedling establishment at lower levels of propagule pressure (Fig. 4). Thus, the combined effects of herbivory and lower propagule pressure led to more failed invasions (Fig. 4 and Appendix E). Further, predispersal seed herbivory by native specialist insects is a primary constraint on propagule pressure, reducing seed production by 60–93% (Louda and Rand 2002,

Suwa et al. 2010). Their median estimate of predispersal seed predation (76.5%) combined with our 58% median reduction in seedling density indicates that herbivory can reduce lifetime fitness of *C. vulgare* by >90%. These results challenge the prevailing notion that abiotic constraints on plant physiology alone are likely to exclude nonnative plants from certain habitats (Levine et al. 2004), since they show that herbivory can increase the rate of failed invasions, especially when initial propagule pressure is low.

The effect of foliage herbivory on seedling survival and density varied among the sites, which differed in landscape position, site history, and plant community composition. This finding is consistent with reported variation in herbivore impact on native plant populations driven by differences among habitats, sites, and regions (Louda 1982, Louda and Rodman 1996, Miller et al. 2009). The implication is that community-level variation in biotic resistance can mediate spatial heterogeneity in the propagule pressure needed to establish a seedling. Depending upon the site and year cohort, between 39% and 509% more seeds were needed to establish a seedling because of biotic resistance posed by herbivores (Fig. 1B).

To examine the large spatiotemporal variation in the magnitude of herbivore effects on seedling survival, we used median *C. vulgare* seedling size in the insecticide treatment as a proxy for other, site-specific factors influencing seedling success, independent of herbivory. The results showed that fewer seedlings survived insect herbivory at sites where protected seedlings were smaller, and thus where other site-specific factors were more negative (Fig. 3). This suggests that environmental conditions influenced the magnitude of the herbivore effects on *C. vulgare* establishment, consistent with studies of other nonnative plants (Lambrinos 2002) and native plants (Louda 1982, Louda and Potvin 1995, Louda and Rodman 1996). This study extends such prior results by showing that apparent site-specific variation among multiple sites across a region can play a large role in the magnitude of herbivore-imposed biotic resistance. Further, our data suggest that studies that do not account for spatial heterogeneity in the magnitude of herbivory may over- or underestimate the role of biotic resistance in nonnative plant establishment.

Overall, this experiment shows that insect foliage herbivory is important in limiting the early establishment of *C. vulgare*. Herbivory also constrained the effect of increasing propagule pressure. And major spatiotemporal variation in the magnitude of herbivory occurred across multiple sites within a biogeographic region. The outcome provides greater insight into the complexity and dynamics of plant invasion.

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SUPPLEMENTAL MATERIAL

Appendix A

Additional details of methods: seed source, determination of seeding rates, plot establishment and maintenance, and greenhouse test of the direct effects of bifenthrin (*Ecological Archives* E093-157-A1).

Appendix B

Results from Bayesian hierarchical model with uninformative priors (*Ecological Archives* E093-157-A2).

Appendix C

Percentage of leaf damage on *Cirsium vulgare* (*Ecological Archives* E093-157-A3).

Appendix D

Survival of marked *Cirsium vulgare* seedlings (*Ecological Archives* E093-157-A4).

Appendix E

Observed proportion of *Cirsium vulgare* subplots with no seedling establishment (failed invasion) (*Ecological Archives* E093-157-A5).