LETTER

Native insect herbivory overwhelms context dependence to limit complex invasion dynamics of exotic weeds

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Abstract

Understanding the role of consumers in density-dependent plant population dynamics is a long-standing goal in ecology. However, the generality of herbivory effects across heterogeneous landscapes is poorly understood due to the pervasive influence of context-dependence. We tested effects of native insect herbivory on the population dynamics of an exotic thistle, *Cirsium vulgare*, in a field experiment replicated across eight sites in eastern Nebraska. Using hierarchical Bayesian analysis and density-dependent population models, we found potential for explosive low-density population growth ($\lambda > 5$) and complex density fluctuations under herbivore exclusion. However, herbivore access drove population decline ($\lambda < 1$), suppressing complex fluctuations. While plant–herbivore interaction outcomes are famously context-dependent, we demonstrated that herbivores suppress potentially invasive populations throughout our study region, and this qualitative outcome is insensitive to environmental context. Our novel use of Bayesian demographic modelling shows that native insect herbivores consistently prevent hard-to-predict fluctuations of weeds in environments otherwise susceptible to invasion.

Keywords

Cirsium vulgare, demography, density-dependence, environmental context, hierarchical Bayesian model, insect herbivory, integral projection models, invasive species, population dynamics.

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INTRODUCTION

From the classic Green World Hypothesis to current studies of invasive plants, ecologists have studied and debated the role of insect herbivores in plant population dynamics (Hairston *et al.* 1960; Janzen 1970; Harper 1977; Colautti *et al.* 2004). The effects of herbivores on individual plant performance are well-established (Crawley 1989) and there are examples of insects being used as effective biocontrol agents of weedy plants (Landis *et al.* 2003; Weed & Schwarzländer 2014), but whether insect herbivores generally limit plant population abundance remains a persistent question (Maron & Crone 2006; Myers & Sarfraz 2017). Answering this question requires scaling from individual- to population-level effects (Halpern & Underwood 2006; Maron & Crone 2006) and incorporating density-dependence, which can modify population-level impacts of herbivory (Underwood & Halpern 2012). Furthermore, effects of herbivory can be mediated by environmental context, including both abiotic (Mitchell *et al.* 2006; Weed & Schwarzländer 2014) and biotic conditions (Mitchell *et al.* 2006). Understanding how herbivory and density interact and how these effects vary across heterogeneous landscapes would advance understanding of biotic resistance to plant invasions (D'Antonio *et al.* 2001) and address the larger question of the role of consumers in plant population dynamics (Katz 2016).

Herbivory can interact with host plant density and modify the process of host plant density-dependence in several ways (Underwood & Halpern 2012; Myers & Sarfraz 2017). First, if plant populations experience negative density-dependence, enhanced vital rates (e.g. growth, survival and fecundity) of plants escaping herbivory may compensate for herbivore-induced mortality (Harper 1977). Thus, even if low-density population growth rates are reduced by herbivory, equilibrium population sizes might not be (Halpern & Underwood 2006). Second, herbivory itself may be density-dependent, with negative (i.e. resource dilution; Fagan *et al.* 2005, Kula *et al.* 2014) or positive (i.e. resource concentration; Bagchi *et al.* 2014; Comita *et al.* 2014) relationships between host plant density and herbivore attack. Finally, density may affect plants' tolerance to herbivory (He *et al.* 2014). Incorporating interactions between herbivory and host plant density is necessary to appropriately scale the effects of herbivory on individual vital rates to population-level effects (Halpern & Underwood 2006).

The importance of herbivory may also depend on other aspects of environmental context. Context-dependence is a pervasive feature of interspecific interactions (Bradley *et al.* 2003; Agrawal *et al.* 2007; Chamberlain *et al.* 2014). For example, herbivore effects on plants can be affected by vegetation type (Lambrinos 2002), proximity to stand edges (Lambrinos 2006), soil characteristics (Louda *et al.* 1987; von Euler

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et al. 2014), elevation (Miller *et al.* 2009) and other environmental gradients (Louda 1982, 1983; Lehndal *et al.* 2016). A variety of mechanisms, often unknown, could underlie context-dependent variability (Maron *et al.* 2014). Context-dependence in interaction outcomes poses challenges for general insights into the effects of herbivory on plant populations, arguing for spatially replicated experiments that integrate across contexts by sampling the distribution of environmental heterogeneity.

Hierarchical Bayesian statistical models provide powerful methods for incorporating spatial or temporal environmental heterogeneity into studies of population dynamics (Elderd & Miller 2016). They are well suited for hierarchically structured data (Gelman & Hill 2006), in which uncertainty can be partitioned into estimation error and process error – the latter being ecologically meaningful variation associated with sites or time periods. The distribution of process error can be determined even without mechanistic understanding of its underlying causes. We are aware of no previous studies that have taken this approach to quantify context-dependence in the effects of herbivory.

We combined field experiments with statistical and demographic modelling to study the combined roles of native insect herbivory and host plant density in the incipient invasion dynamics of exotic plants. Our work focused on the exotic thistle *Cirsium vulgare*, which is highly invasive in some regions of North America but not in our eastern Nebraska study region, where *C. vulgare* occurs at low densities (Andersen & Louda 2008). Previous work in this system suggests that native insect herbivores act as biotic control agents, suppressing invasiveness in *C. vulgare* (Takahashi 2006; Andersen & Louda 2008; Tenhumberg *et al.* 2008, 2015; Suwa *et al.* 2010; Eckberg *et al.* 2012, 2014; Suwa & Louda 2012). We build on these previous studies by assessing, for the first time, the population-level interactions between insect herbivory and host plant density, using a spatially replicated field experiment and hierarchical Bayesian integral projection models (IPMs; Ellner & Rees 2006) to integrate over the distribution of environmental contexts. We used Life Table Response Experiments (LTRE; Caswell 2001) to identify demographic mechanisms by which herbivory and density modified *C. vulgare* population growth, and simulations to ask how herbivores affect complex, density-dependent population dynamics. The unusual scale of spatial replication of our study (eight sites spanning 534 km^2) allows us to test whether herbivore-mediated biotic resistance is a general outcome, or whether effects of herbivory and host plant density are subject to the vagaries of environmental context. Specifically, we addressed the following questions: (1) How do herbivory and host plant density affect individual-level vital rates of *C. vulgare*?; (2) What are the low-density plant population growth rates and equilibrium densities expected in the presence and in the absence of herbivory?; (3) How do individual vital rates contribute to the overall influence of density and herbivory on population growth?; and (4) Does the suppression of *C. vulgare* invasion by native herbivores vary with environmental context?

METHODS

Study system

Cirsium vulgare L. is a short-lived monocarpic Eurasian thistle with a rosette growth form that, in our study region, typically flowers in the fall (August–October) after 2–3 years of vegetative growth (Suwa *et al.* 2010; Suwa & Louda 2012; Eckberg *et al.* 2014). *C. vulgare* is considered invasive in much of the USA and elsewhere (Klinkhamer & de Jong 1993). In eastern Nebraska, however, *C. vulgare* is sparse: a survey of roadside quadrats showed occurrence frequency to be < 1% (Andersen & Louda 2008). Takahashi (2006) observed 98 insect species feeding on *C. vulgare* in eastern Nebraska (including leaf, stem, phloem and floral feeders), most of which (76%) also feed on the native, phenologically synchronised congener *Cirsium altissimum* (Louda & Rand 2002; Takahashi 2006); 97% of identified insects feeding on *C. vulgare* were native (Takahashi 2006).

Experimental design

Our previous study, which focused only on seedling recruitment, provides full details for the experimental set-up (Eckberg *et al.* 2012). We summarise the most relevant information here. A single replicate of the experiment consisted of 14 3 × 1 m plots (divided into three 1-m^2 subplots) in a full factorial combination of seven seed addition densities (50, 100, 150, 200, 250, 300, or 350 seeds/m^2) and two herbivory treatments (insecticide for herbivore exclusion, water-only control). While each subplot received the same seed density, subplots differed in realised density due to variation in recruitment. We quantified realised plant density at the subplot scale and tracked the demography of individuals within each subplot. The 14 plots were established in a 30 × 60 m grid; adjacent plots were separated by 15 m. The design was replicated across eight sites in Lancaster County, Nebraska, USA, with one replicate at each site. All sites were at least 1.3 km apart. We selected uninvaded sites representative of the variation in grassland communities of eastern Nebraska, including five restored tallgrass prairies, one untilled remnant prairie and two grasslands dominated by Eurasian species (Eckberg 2008, Eckberg *et al.* 2012). The native *C. altissimum* was present at each site.

The experiment was run over three consecutive years. In April 2006, we introduced *C. vulgare* seeds to each subplot at the assigned density. We applied a pyrethroid insecticide, bifenthrin [diluted to 0.06% active ingredient (Control Solutions, Pasadena, TX, USA)], to the exclusion plots from seedling emergence (mid-May) to the end of the first growing season (September 2006), throughout the second growing season (late April–early September 2007), and at the beginning of the third growing season (late April–early May 2008). Spraying occurred at 3-week intervals except during bolting when rapidly elongating floral shoots were sprayed at 2 week intervals. To minimise non-target effects on pollinators we did not spray flower heads. We previously showed that bifenthrin does not directly affect *C. vulgare* survival or growth (Eckberg *et al.* 2012).

Data collection

To quantify *C. vulgare* density, we counted the total number of seedlings and rosettes per subplot ($N = 330$ subplots; six control subplots were excluded after herbicide application) in spring (May–June) 2006, 2007 and 2008. Counts reflected initial emergence in spring 2006, and surviving plants plus new seedlings recruiting from the seed bank in 2007 and 2008.

To quantify individual-level survival, growth and fecundity, we marked up to 10 seedlings per subplot ($N = 3274$ individuals across all sites) at the start of the first growing season (May–June 2006). For each plant, we recorded the total number of leaves and length of a midsized leaf. The product of leaf number and leaf length (mm) was highly correlated ($r^2 = 0.93$, $n = 35$) with plant biomass (g), based on measurements taken at a site not included in this study, so this product was used as the measure of size for the size-structured model. Survival and size of marked plants were recorded again in May 2007 and May 2008. Leaf herbivory (% leaf area loss from insect herbivory) was recorded at the end of the 2006 growing season by estimating leaf area removed; insecticide treatment significantly reduced leaf herbivory by > 90% (Eckberg *et al.* 2012).

Plots were checked regularly for flowering *C. vulgare*, which were monitored for flower head and seed production. We covered flower heads with mesh once florets turned brown to prevent seed dispersal and allow seed maturation prior to collection. This was done in 2007 (2 August–19 November) only because 2006 recruits did not flower in their first year and the experiment ended before flowering in 2008. In total, we collected 1145 mature flower heads from 80 plants. Flower-head size and seed viability varied throughout the flowering period, so we estimated seed production on each collection date for each flowering plant (average of 3.76 collection dates per plant); 40 total visits were made to bag and collect flower heads. To estimate seed number per plant for each collection date, we counted the total number of filled seeds in a median-sized flower head and multiplied this number by the total number of collected flower heads. Estimates of fecundity were therefore based on 26% of all flower heads produced (301 flower heads).

There were an additional 137 *C. vulgare* that flowered in 2007 but had not been initially marked. Following the protocols above, we collected all flower heads ($N = 1352$ flower heads) from these *C. vulgare*, and counted seeds for 495 flower heads.

Vital rate modelling

We built statistical models for five individual-level demographic processes: survival, growth, flowering, seed production by flowering plants and seedling recruitment (detailed methods presented in Appendix S1). All vital rates except recruitment were modelled as functions of plant size. As in previous studies of limited temporal duration (Rose *et al.* 2005; Miller *et al.* 2009; Bricker & Maron 2012), we combined data from the two interannual transitions, thus assuming no temporal variability. We fit the vital rate functions using generalised linear mixed-effects models in a hierarchical Bayesian framework. We fit full models for each vital rate function, including effects of size, herbivory, host plant density and all possible interactions. We modelled density effects based on total realised plant density at the subplot scale, summed over all sizes. To account for spatial variation in vital rates and effects of herbivory, we modelled random site-to-site variance by allowing the intercepts and herbivore treatment coefficients to vary by site (Appendix S1). We also fit random effects for plot nested within site and subplot nested within plot for intercepts, accounting for the non-independence of multiple observations at these smaller spatial scales. Seed production models did not include random effects for herbivore treatment coefficients because seed production under herbivore access was limited to one site; therefore, these models did not converge with random effects for herbivory. We fit all of the vital rate models in a single analysis to account for spatial covariance between vital rates (e.g. sites that are good for survival might also be good for growth or recruitment) and spatial covariance in the effects of herbivory on survival, growth, flowering and recruitment (Appendix S1).

The Bayesian approach provided mean estimates for all parameters, as well as posterior distributions, which gave us estimates of process error and estimation uncertainty in vital rates that could be passed to our populations models (Ghosh *et al.* 2012; Gelfand *et al.* 2013; Elderd & Miller 2016).

Effects of herbivory and plant density on population growth

We used size-structured IPMs to scale from individual- to population-level effects of herbivory on *C. vulgare* (detailed methods presented in Appendix S2). The IPM used the above vital rate models, as well as estimates of seedling size distribution, to calculate the density-dependent population growth rate, $\lambda(N)$, where N is total plant density, summed over the size distribution. This quantity gives the asymptotic population growth rate at density N, assuming the population is at its stable size distribution. The low-density growth rate is given by $\lambda(0)$ and the equilibrium population density N^* satisfies $\lambda(N^*) = 1$. Quantifying $\lambda(N)$ allowed us to identify the direction and strength of density dependence and its interactions with herbivory in a way that integrates across multiple vital rate responses (Fowler *et al.* 2006; Underwood & Halpern 2012), motivated by the hypothesis that density-dependent regulation can dampen the influence of herbivory. We calculated $\lambda(N)$ across the range of observed densities (0–150 plants/m^2). For each density, we calculated 95% credible intervals for $\lambda(N)$. We drew 1000 parameter values from the posterior distributions of the parameter means, which isolated estimation error from spatial process error. These results reflect the global mean across sites for the density-dependent growth rate $\lambda(N)$.

We used LTREs to decompose the overall effects of herbivory and plant density on the asymptotic population growth rate $\lambda(N)$ into contributions from individual vital rates (detailed methods presented in Appendix S3). We used regression-style LTRE (Caswell 2001) to decompose the effects of continuous variation in density. Because we found evidence for interactions between herbivory and density, the demographic effects of increasing density may differ under

herbivore access and exclusion. Therefore, we conducted separate LTREs for herbivore access and exclusion treatments. Similarly, we conducted a categorical LTRE to examine the vital rates contributions to the overall effect of insect herbivory on thistle population growth across the range of densities.

Spatial heterogeneity in effects of herbivory

We expanded our analysis of the population-level effects of insect herbivory in two ways to account for spatial process error driven by site-to-site variability, and to more realistically model density feedbacks that occur during population growth [which are ignored by the asymptotic growth rate $\lambda(N)$]. First, we estimated spatial variation in the low-density population growth rates, $\lambda(0)$, for the herbivore access and exclusion treatments. For the parameters that included site random effects, we drew 1000 parameter values from the multivariate normal distribution that describes spatial variation and covariation (Appendix S1, Eq. 6b).

Herbivory might affect not only equilibrium population size but also the qualitative behaviour of the population dynamics in ways that are not revealed by examination of $\lambda(N)$ (Eager et al. 2012). Therefore, our second approach to test the effect of herbivores on the population dynamics, accounting for density-dependent feedbacks and spatial process error, used simulations of the IPMs to project future population dynamics in the herbivore access and exclusion treatments. We started with a population of 50 seedlings/m^2 representing a new invasion (other starting densities and size distributions produced qualitatively similar results). Populations were projected 100 years into the future; longer simulations gave similar results. We first projected population dynamics using global mean parameter values, ignoring site-to-site variability, giving the expected population dynamics at the average site. We then tested for the generality of the effect of herbivores by estimating population trajectories across environmental contexts, sampling from the estimated distribution of spatial heterogeneity, following the methods above. Simulated populations sometimes reached an equilibrium density but other times showed complex fluctuations, so we calculated the frequency of each pattern across 100 samples of spatial heterogeneity. Aperiodic fluctuations were identified by calculating the Lyapunov exponent, which measures divergence of systems with nearly identical states (Caswell 2001). A Lyapunov exponent > 0 indicates chaotic dynamics.

Code to reproduce the analysis and full posteriors from the Bayesian models are provided in Appendices S5 and S6, respectively.

RESULTS

Effects of herbivory and plant density on vital rates

Individual plant growth was influenced by herbivory, including a size–herbivory interaction and an herbivory–density interaction (Fig. 1a). Herbivory depressed growth over most of the size distribution, particularly for large sizes. At the smallest sizes, the prediction of positive effects of herbivory

and density (in the herbivore access treatment) likely reflects the paucity of observations for small plants, combined with the linear functions being overwhelmed by negative effects of herbivory for most plant sizes. Local population density had a negative effect on growth for both treatments, especially at larger plant sizes (Fig. 1a).

Rosette survival was influenced by herbivory and a size–herbivory interaction (Fig. 1b). We included a quadratic term for size under herbivore access because survival appeared to peak at intermediate sizes in this treatment. We think this pattern reflects large plants initiating flowering but dying before producing a mature flower head. Under herbivore exclusion, large non-flowering plants had a nearly 100% probability of survival (Fig. 1b, solid points, black lines), but under herbivore access, survival never exceeded 60% (Fig. 1b, open points, grey lines). Density had a positive effect on survival in both treatments (Fig. 1b).

Flowering was influenced by the interaction of size, herbivory and density, with greater negative effects of herbivory at larger sizes (Fig. 1c). Under herbivore exclusion, the largest plants had a 100% probability of flowering (Fig. 1c, solid points, black line). Under herbivore access, the largest plants had 100% probability of flowering at high densities but 19% at low densities, and plants were unlikely to reach those sizes because of reduced growth and survival. Indeed, only four plants flowered in the herbivore access treatment across all sites, so the predicted flowering probabilities are accompanied by substantial uncertainty (Table 1 in Appendix S1).

Only three out of four flowering plants produced seeds under herbivore access, with a maximum of 105 seeds per plant (Fig. 1d, open points). Under herbivore exclusion, seed production ranged from 331 to 13 888 seeds per plant, with larger plants producing more seeds (Fig. 1d, solid points). The full model made unrealistic predictions (i.e. small plants producing nearly infinite numbers of seeds), likely because there were few observations for seed production under herbivore access (because so few plants reached flowering sizes). We instead used a model without density as a predictor in the IPM.

The probability of recruitment was 0.26 (95% CI: 0.08, 0.47) across all treatments, and was not affected by herbivory (Fig. 1e). All parameter values (means and 95% credible intervals), including variance components, are provided in Table 1 in Appendix S1.

Effects of herbivory and plant density on population growth

We first examined the density-dependent, asymptotic population growth rate, $\lambda(N)$, using global mean parameter values across all sites, accounting for estimation uncertainty (Fig. 2). According to the IPM predictions, C. vulgare populations were predicted to go extinct under herbivore access (Fig. 2, dashed line). The expected low-density population growth rate, $\lambda(0)$, was 0.18 (95% CI: 0.03, 0.85) (82% annual decline) and mean growth rate never reached $\lambda(N) \geq 1$ for any density. The upper 95% credible intervals on $\lambda(N)$ were < 1 for all densities. The LTRE showed weak positive density-dependence in population growth, driven by positive density-dependence in survival (Fig. 3a). Negative density-dependence in
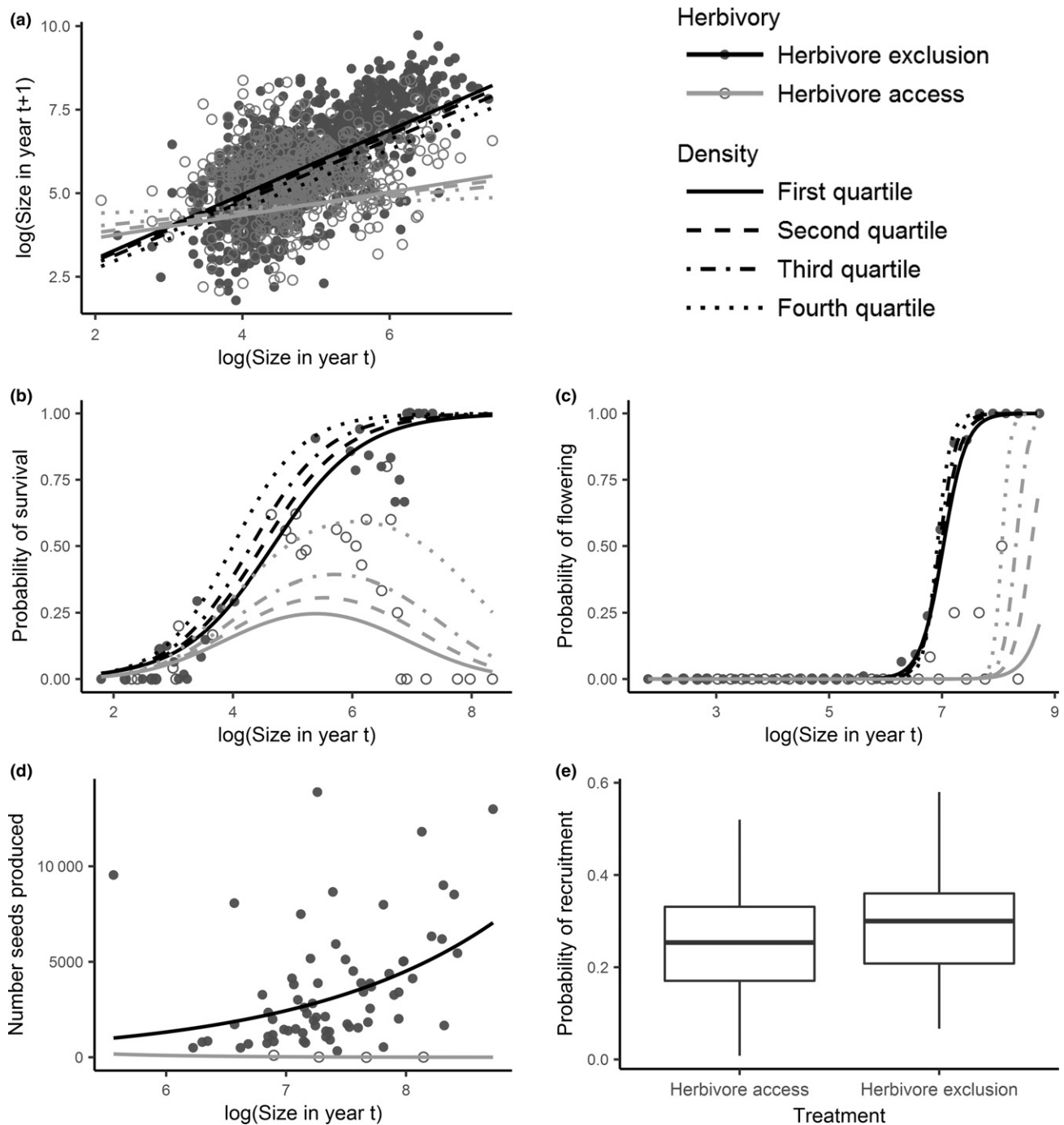
Figure 1 Vital rate functions for *Cirsium vulgare*. (a) Change in size from year t to year *t* + 1. (b) Size-dependent probability of survival. (c) Size-dependent probability of flowering. (d) Size-dependent seed production. (e) Probability of recruitment. Plots a, b, c and e show predictions for quartiles of realised plant density at the subplot scale (plants/m^2).

rosette growth and positive density-dependence in flowering contributed little to overall density-dependence in population growth (Fig. 3a). Seed production and recruitment functions did not include density-dependence (Fig. 1).

Alternately, under herbivore exclusion, the low-density population growth rate, λ(0), was *c*. 5.1 (95% CI: 2.5, 9.1), suggesting potential for explosive population growth, and growth rate declined with increasing density (Fig. 2, solid line). The estimation uncertainty surrounding λ(N) suggested

that population growth was positive [λ(N) > 1] across all densities. The LTRE showed positive density-dependence in survival at low densities, which weakened as density increased (Fig. 3b). In contrast to the herbivore access treatment (Fig. 3a), there was strong negative density-dependence in rosette growth, (Fig. 3b), which outweighed the positive density-dependence in survival, resulting in negative density-dependence overall, the strength of which increased with increasing density.
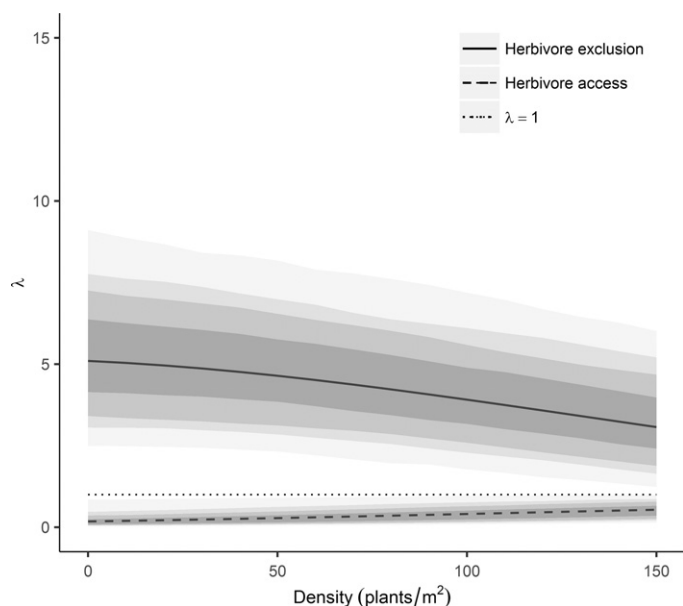
Figure 2 Density-dependent asymptotic population growth rate ($\lambda(N)$) of *Cirsium vulgare*. Lines show mean estimates and shaded areas show credible intervals (95, 85, 75, 50%) for estimation error. The dotted line shows $\lambda(N) = 1$.

Insect herbivores strongly reduced the population growth rate over the entire range of densities bases on 95% credible intervals, which did not overlap between treatments (Fig. 2; Fig. 3c). The LTRE showed that the negative effect of herbivores was driven most strongly by the reduction in seed production and growth (Fig. 3c). Negative effects on survival and flowering also contributed to the overall negative effect (Fig. 3c). The negative effect diminished with increasing density (Fig. 3c, solid line becomes less negative with increasing density), as negative density-dependence caused the herbivore-free population growth rate to decline (Fig. 3b).

Spatial heterogeneity in effects of herbivory

Under herbivore access, all combinations of parameters sampled from the distribution of site heterogeneity resulted in declining population growth rates at low densities (100% of λ (0)< 1; Fig. 4). Under herbivore exclusion, we found substantial spatial variation in $\lambda(0)$, with the distribution spanning λ (0) < 1 to $\lambda(0) \geq 40$ with a mean of 5.9 (Fig. 4). Thus, some sites were unlikely to support *C. vulgare* invasion for reasons unrelated to herbivory, but the majority would likely support explosive population growth of incipient invasions without herbivory. Herbivores, thus, are expected to suppress invasion at most sites in our study region, given our estimates of process variability in demography and herbivore effects.

Simulated population projections based on global mean parameter values (representing an average site) led to rapid extinction under herbivore access. Under herbivore exclusion, however, population projections showed aperiodic density fluctuations typical of populations with high low-density growth rates and strong negative density-dependence (Fig. S4-1). The population trajectories drawing from the

distribution of spatial heterogeneity were consistent with average outcomes (Fig. 5). Under herbivore access, there was population decline predicted in 99% of sites and logistic growth in the remaining 1%. The positive density-dependence under herbivore access likely explains why there were rare circumstances that led to positive growth although $\lambda(0) < 1$ for all parameter combinations. Under herbivore exclusion, where population growth rates were almost always positive, there was potential for diverse population behaviours. Most frequently, there were aperiodic (i.e. chaotic) fluctuations, as demonstrated by positive Lyapunov exponents (47% of sites), followed by apparently unbounded growth (37%) (Fig. 5). Less commonly, projections resulted in stable oscillations (7%), population decline (7%), or logistic growth (2%) (Fig. 5).

DISCUSSION

Our results demonstrate that native insect herbivores suppress the potential for complex population fluctuations of the exotic thistle *C. vulgare* throughout our study region. Across sites otherwise susceptible to invasion, insect herbivores reduced the population growth rate below replacement ($\lambda(0) < 1$) (Fig. 4) by affecting multiple demographic rates, especially seed production (Fig. 3). Density also played an important role in *C. vulgare* population dynamics, with herbivory altering the nature of the density-dependence. Under herbivore exclusion, there was negative density-dependence in population growth, but under herbivore access, there was weak positive density-dependence (Figs 2 and 3b). Negative density-dependence under herbivore exclusion weakened the overall effect of herbivory as density increased, as has been long hypothesised (Harper 1977) but rarely demonstrated. Nonetheless, the strong effect of herbivores overwhelmed negative density-dependence. As a counter-example to the assertion that insect herbivory is unlikely to prevent establishment of invasive plants (Levine *et al.* 2004), our results strongly suggest that native insect herbivores are indeed capable of preventing invasive population growth by *C. vulgare*, even in the face of density-dependence and spatial environmental heterogeneity.

Understanding how species interactions depend on environmental context is suggested to be one of the foremost questions in ecology (Agrawal *et al.* 2007; Maron *et al.* 2014). Our experimental design, including large-scale site replication, and the hierarchical Bayesian statistical approach were intended to estimate the distribution of environmental heterogeneity in demographic rates and associated effects of herbivory. In our framework, baseline demography and the demographic effects of herbivory were random variables that followed stochastic distributions and could co-vary across sites. This approach led to two important and novel insights. First, by sampling environmental heterogeneity, we demonstrated that suppression of invasive plant population growth by native insect herbivores is the 'global mean' outcome in our study region, and further, this outcome is not sensitive to context-dependent interaction outcomes. Our statistical inference tells us there are few sites in eastern Nebraskan grasslands where *C. vulgare* can escape eventual extirpation
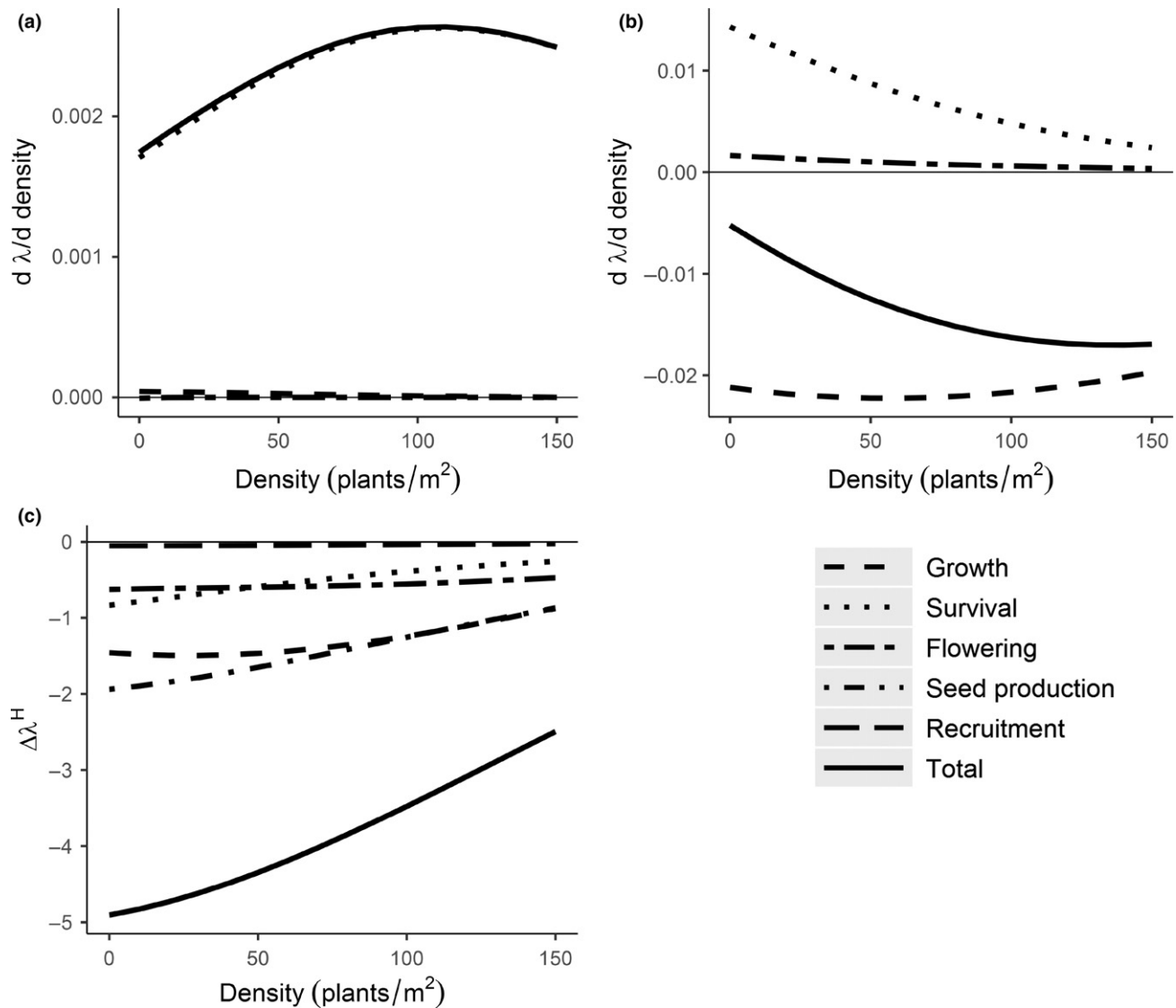
Figure 3 Results of life table response experiments showing the contribution of each vital rate to the change in population growth rate. Top panel shows the change in growth rate per unit change in density (d λ/d density) in (a) herbivore access and (b) herbivore exclusion treatments. Bottom panel (c) shows the difference in population growth rate between the herbivore access treatment and the herbivore exclusion treatment ($\Delta\lambda^H$) across a range of densities. The bold solid lines show the total effect of the treatments on λ (the sum of the contributions from all vital rates).

by insect herbivory, although at some sites, extinction is expected even in the absence of herbivores.

Second, our results demonstrate that native insect herbivory suppresses potential for the complex, chaotic population dynamics predicted when herbivores are excluded. We estimate that, in the absence of native insect herbivores, the majority of sites in our study region would be prone to aperiodic fluctuations or unbounded growth in *C. vulgare* density. The fluctuations are likely the result of high low-density growth rates combined with strong negative density-dependence, a combination known to give rise to complex dynamics (Costantino *et al.* 1997), including in invasive plants (Buckley *et al.* 2001; Pardini *et al.* 2011; Shyu *et al.* 2013). The prediction of unbounded growth suggests that negative density-dependence in population growth is weak at many sites. This outcome is consistent with the results of a recent meta-

analysis that found insect herbivores decrease population growth rates more strongly when there is potential for very high growth rates in the absence of herbivores (Katz 2016). Outbreaks of invasive organisms can be ecologically and economically damaging, and difficult to control (Mack *et al.* 2000; Simberloff *et al.* 2013). Suppression of hard-to-predict, potentially damaging oscillations in density may therefore be an under-appreciated ecosystem service provided by native insect herbivores in this system and possibly others.

Early theory asserted that insect predators may have minimal impact on plant population dynamics because, under negative density-dependence, plant populations can tolerate some losses to herbivory without a reduction in abundance (Harper 1977). However, our study adds to the growing body of literature (Louda & Potvin 1995; Maron 2001; Kauffman *et al.* 2006; Maron & Crone 2006) that suggests that consumers do
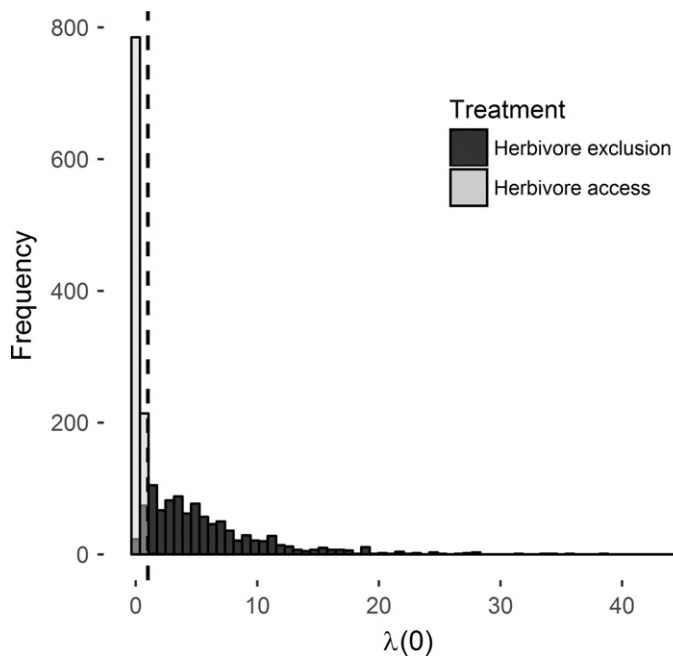
Figure 4 Distribution of low-density population growth rates ($\lambda(0)$) of *Cirsium vulgare*, sampling over estimated spatial heterogeneity in baseline demography and demographic effects of herbivores. Vertical dashed line shows $\lambda(0) = 1$.

could overwhelm the effects of herbivory, assuming populations could reach those densities. Although other studies have found effects of density on herbivore damage at the scale of individuals (Underwood & Halpern 2012), to our knowledge, our study provides the first direct, population-level test of Harper's classic hypothesis (Harper 1977).

Herbivore density and herbivore efficacy can also depend on plant density (Underwood & Halpern 2012). Although we did not directly measure herbivore densities, we found weak positive density-dependence in λ under herbivore access. We can therefore conclude that the resource concentration hypothesis, which predicts lower herbivory rates at low plant densities, is unlikely to be acting in our system, and there might be weak resource dilution (Stephens & Myers 2012). However, we cannot rule out the possibility that the positive density-dependence is instead due to higher tolerance of herbivory at high plant densities or potential changes in the density of interspecific competitors. Interactions between host plant and herbivore density might also explain why our model predicts *C. vulgare* persistence under herbivore access only rarely, although *C. vulgare* is still found in eastern Nebraska, albeit infrequently. If herbivore abundance is dependent on host plant abundance, it can lead to herbivore population cycles (Buckley *et al.* 2005; Abbott & Dwyer 2007). When *C. vulgare* populations are driven to very low densities or extinction, insect herbivore populations might decline or disperse in response, allowing *C. vulgare* population to rebound, as is often observed with specialist herbivores which are abundant on *C. vulgare* (Louda & Rand 2002). However, in this system, insect herbivores have alternate hosts, so tight coupling seems unlikely.

The reduction in population growth rate due to herbivory was most strongly driven by negative effects of herbivores on seed production (Fig. 3c). Although there was a reasonable
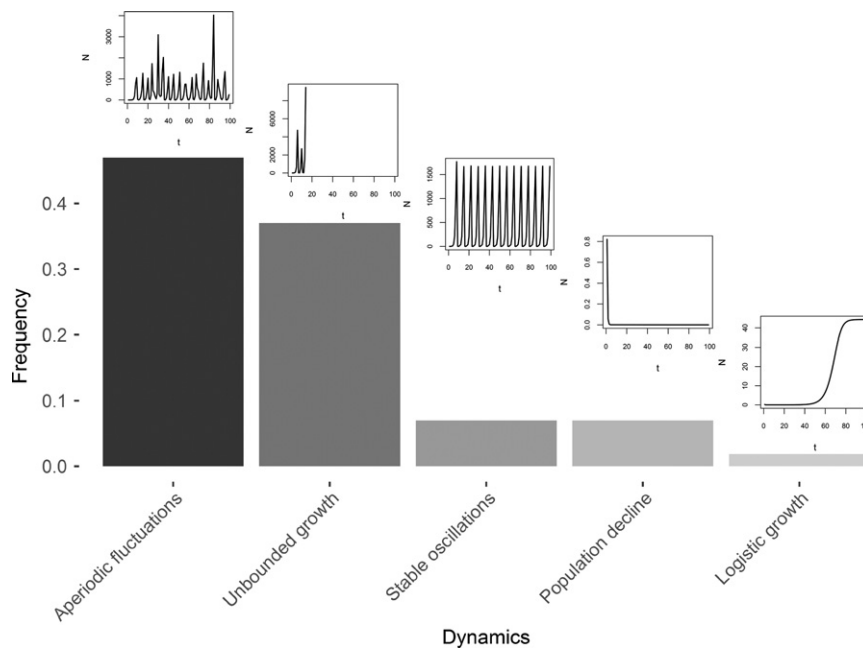
play an important role in plant population dynamics, even under strong density regulation. It is interesting to note, however, that under herbivore exclusion there was strong negative density-dependence, leading to a diminishing effect of herbivory as plant density increased (Fig. 2). Therefore, there is evidence that at high densities, negative density-dependence

Figure 5 Frequency of *Cirsium vulgare* population dynamics across samples of spatial heterogeneity for the herbivore exclusion treatment. Insets show examples of the change in total population size through time for each class of dynamics.

probability of flowering at large sizes under herbivore access, most plants were unable to reach those sizes due to reduced growth and higher mortality. The reservoir of natural enemies supported by native host plants may explain why seed predators were so effective in this system. Nebraska is home to native thistle species that harbour a variety of insect herbivores also suited to *C. vulgare* (Louda & Rand 2002; Takahashi 2006). Whether our results are representative of herbivore suppression of plant invasion will require further studies of systems with and without pre-adapted enemies, especially 'failed' invasions, which often go under-studied (Zenni & Nuñez 2013).

There are some limitations and caveats to our conclusions. First, while our experiment had extensive spatial replication, it covered a short timeframe, so there are likely environmental conditions that were not sampled during our experiment. However, other work conducted across more than two seasons in this system has found consistently strong herbivory (Louda & Rand 2002; Eckberg *et al.* 2014). Second, we were unable to fit random affects for the herbivory coefficient for seed production, so there might be some spatial variation in herbivory that was unaccounted for in our model. Third, we only selected uninvaded sites at which the native *C. altissimum* was present. Herbivory rates might be lower in sites that we did not sample, especially areas where the native tall thistle and its associated assemblage of thistle-feeding insects are absent. Studies at sites where *C. vulgare* was previously present have found weaker effects of herbivory on population growth (Tenhumberg *et al.* 2015) suggesting that *C. vulgare* may overwhelm the effects of herbivores and invade some environments. Finally, our results are most representative of disturbed grasslands, with reduced competition from other plants, because our experimental design included raking of soil and clipping of other plant species in the plots. However, these are the conditions most conducive to *C. vulgare* establishment (Suwa & Louda 2012; Tenhumberg *et al.* 2015), so while we may be overestimating the number of sites susceptible to invasion under herbivore exclusion, it is unlikely to change our conclusion that insects suppress *C. vulgare* in most environments where invasion would otherwise be possible.

CONCLUSION

Due to the complexities of density-dependence and context-dependence, the general role of insect herbivores in plant population dynamics remains uncertain. We show that biotic resistance to invasion provided by native insects can be a general result: insect herbivory was expected to drive the local extinction of *C. vulgare* in most environmental contexts. Although negative density-dependence weakened the effect of herbivory, the strong effect of herbivory overwhelmed negative density-dependence. By reducing the low-density growth rate and the strength of density-dependence, insect herbivores suppressed the potential for unpredictable oscillations in *C. vulgare* populations. Native insects can therefore play an important role in regulating plant populations and resisting invasion and complex dynamics by exotic plants.

AUTHORSHIP

JOE, SML and TEXM conceived and designed the experiment. JOE performed the field experiment and wrote the field methods section. SSB performed initial population growth modelling and analysis. ELS and TEXM designed analyses. ELS performed analyses and wrote manuscript. All authors edited the manuscript.

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