Monte Carlo analysis of parameter uncertainty in matrix models for the weed *Cirsium vulgare*

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Summary

1. Parameter uncertainty challenges the use of matrix models because it violates key assumptions underlying elasticity analyses. We have developed a matrix model to compare Monte Carlo methods with elasticity analyses for estimation of the relative importance of factors in the asymptotic population growth rate, λ, of *Cirsium vulgare* (spear thistle) in Nebraska, USA.
2. We calculated λ for a base model using 11 parameter estimates available for Nebraska populations plus eight extracted from the literature, causing parameter uncertainty. We then calculated λ for 10 000 alternative models using Monte Carlo parameter estimation; parameters were drawn from the full range of each parameter in the literature and partial rank correlation analysis (PRCC) was used to order the parameters by the magnitude of their effect on λ.
3. Monte Carlo analysis found that insect floral herbivory, affecting the regeneration transition, was the most important parameter affecting λ, whereas elasticity analyses suggested that the transition from small to medium size was the most significant. Statistical comparison, using PRCC vs. lower level elasticity (LLE), showed that the Monte Carlo analysis provided a more accurate assessment.
4. As λ > 1 in 99% of the model runs even with significant floral herbivory, we added two parameters influenced by weed management (probability of large thistles dying without producing seed and proportion of seeds that failed to germinate). Simulations that included reductions in these parameters, along with floral herbivory, led to λ < 1 in 17% of the runs, suggesting these three factors interact to produce the low densities observed for this invasive thistle in our study area.
5. *Synthesis and applications.* This study demonstrates the utility of the Monte Carlo approach for modelling weed dynamics with parameter uncertainty and multiple, potentially interacting, parameters. Invasive population growth by *C. vulgare* could be limited by a combination of weed management practices and the biotic resistance imposed by native floral herbivores.

Key-words: bull thistle, floral herbivory, partial rank correlation analysis, plant population dynamics, sensitivity analysis

Introduction

Matrix projection models are a prevailing tool for analysing the dynamics of stage-structured populations (Seno & Nakajima 1999; Ehrlén 2000; Caswell 2001; Mandujano *et al.* 2001). To be realistic, however, such models require multiple parameters, and one constraint on wider use is the availability of sufficient data to estimate model parameters. Integral projection models (Ellner & Rees 2006) often require fewer parameters, and

maximum likelihood and Bayesian methods can estimate missing or incompletely known parameters, using time series data (Hilborn & Mangel 1997; Gross, Craig & Hutchinson 2002). These methods, however, are difficult to implement; so additional ways to resolve high parameter uncertainty are needed for models to contribute to the management of weedy plants.

Perturbation analyses, used to rank the relative importance of factors influencing population growth rate, currently examine elasticity and sensitivity of matrix transition rates or parameter values (Caswell 2001). Such local perturbation analyses should be confined to examining the consequences of very small perturbations of single, well-known, independent parameters (Horvitz & Schemske 1995; Caswell 2001). Thus

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alternative methods are needed if there is parameter uncertainty, values vary widely or the effect of perturbation of one parameter is not independent of other values. Nevertheless, many authors suggest that elasticities give robust predictions of the effect of large changes in demographic parameters on the asymptotic population growth rate, λ (Caswell 2000; de Kroon, van Groenendael & Ehrlén 2000). For example, Caswell (2001) argued that 'although elasticities are local slopes, they do a good job of predicting the results of even relatively large (± 50% at least) perturbations'. As a consequence, the results of sensitivity or elasticity analyses are used to infer the effect of large perturbations and to derive management recommendations (Crooks, Sanjayan & Doak 1998; Fisher, Hoyle & Blomberg 2000; Hunt 2001).

We have used Monte Carlo methods, to assess the effect of large parameter uncertainty on matrix model predictions of λ, and partial rank correlation analysis (PRCC), to determine the relative importance of each contributing variable (Blower & Dowlatabadi 1994). PRCC results are comparable to elasticity but the Monte Carlo/PRCC approach is a global perturbation analysis, successfully applied to complex ecological models (Blower & Dowlatabadi 1994; Hilborn & Mangel 1997; Rushton *et al.* 2000a,b; Tenhumberg *et al.* 2004) but not previously to matrix models.

We focused on the relative importance of factors influencing the population growth rate of the Eurasian thistle *Cirsium vulgare* (Savi) Ten., a highly invasive monocarpic thistle (Julien & Griffiths 1998) and a noxious weed in nine USA states (http://plants.usda.gov/, accessed November 2005). Despite its presence for more than 50 years, *C. vulgare* occurs only at low densities in western tallgrass prairie in eastern Nebraska, USA, along rural roadsides and in perennial pastures (Stubbendieck, Friisoe & Bolick 1994; Andersen & Louda 2007). A high level of floral herbivory significantly reduces seed production in Nebraska (Louda 1999; Louda & Rand 2002) and weed management practices probably affect its demography in rural areas. Roadside vegetation is generally mowed early and late in the growing season, and intensive row-crop agriculture involves cultivation and herbicide application.

Our overall aim was to understand the factors that lead to the observed population stasis in this invasive thistle. Our first goal was to evaluate the relative contribution of floral herbivory to the *C. vulgare* population growth rate and to identify parameters still requiring additional local data. The parameters for the base matrix model were extracted from studies of local populations performed over the last 15+ years, supplemented by parameter estimates from the literature. As eight of the estimates had to be derived from foreign populations, parameter uncertainty was high; thus a second goal was to compare a global perturbation analysis using Monte Carlo simulations to the usual local sensitivity and elasticity analysis for evaluating relative parameter importance in this situation. Our third goal was to explore the consequences of weed management practices on λ, by including the proportions of bolting thistles that die before producing seed (increased by mowing) and seed germinating successfully (reduced by dispersal into intensively managed cropland) in the model.
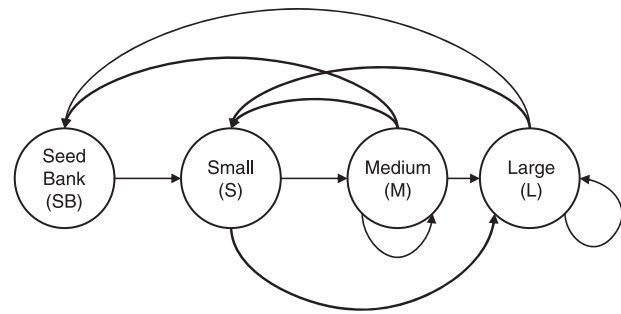

Fig. 1. Life cycle graph of the *Cirsium vulgare* population model. The arrows indicate transitions between the size-stage classes.

Methods

MATRIX MODEL STRUCTURE

We constructed stage-classified, pre-breeding census (late summer), birth-pulse matrix models (Caswell 2001) using annual time steps (Fig. 1). We modelled *C. vulgare* reproduction as a birth-pulse process because seed release occurs during a relatively short period near the end of the growing season (Barkley 1986). We assumed seed was produced and released after the population census. Seeds either die or overwinter; surviving overwintered seeds germinate and grow into small plants by the next census or they enter the seed bank. As survival of seeds in the soil for more than two winters is very low (van Breeman & van Leeuwen 1983), the seed bank consisted only of seeds that stayed in the soil for a second winter, after which we assumed that they either germinated or died. The model had four size-stage classes: seed bank (SB), small-sized plants (S; diameter < 10 cm, comprising mainly seedlings), medium-sized plants (M; diameter 11–20 cm) and large-sized plants (L; diameter > 21 cm), following Bullock, Hill & Silvertown (1994).

PARAMETER ESTIMATION, BASE MODEL

To calculate the elements, a_{ij}, of matrix **A**, we used 19 parameters suggested by the natural history of *C. vulgare* (Table 1 and Table 2). For example, the transition rate for plants from the small (S) to the medium (M) size class was calculated by multiplying four parameters: winter survival of small plants (*i*), proportion of small plants growing to a medium size (*a*), summer survival of medium-sized plants (*d*) and the proportion of medium-sized plants surviving insect foliage herbivory (*g*).

Where available, we used parameter estimates derived directly from *C. vulgare* populations in Nebraska to derive base values (Table 1; bold values). Values from the similar, co-occurring, native *Cirsium altissimum*, were used as second choice (Table 1; underlined values). Failing that, *C. vulgare* populations in other regions, both native and non-native, were used, taking the midpoint of the large range of values observed (Table 1). Our perturbation analysis to determine the effect of this parameter uncertainty assumed that there was no covariance between parameters; thus our results were biased towards an overestimation of the effect on λ.

Size-class transitions (a, b)

Local data on transition rates were supplemented with data for *C. vulgare* in Britain (Bullock, Hill & Silvertown 1994). It was found

Table 1. Life-history parameters of *Cirsium vulgare* (S, small plants; M, medium plants; L, large plants). Base values were used to calculate the transition rates in a matrix model of *C. vulgare* populations in eastern Nebraska, USA. Parameters derived directly from Nebraska populations of *C. vulgare* are in bold and from the related native *C. altissimum* are underlined (parameter values are rounded to 3 decimal points); other base parameters are the midpoint of the parameter range in the literature. The low and high points of the reported parameter range in the literature were used as lower and upper limits in the Monte Carlo simulations. Where we could not extract a parameter range from the literature (*n* = 5; indicated by *), we created a range by adding and subtracting 0·1 from the mean values; larger ranges would have resulted in some rates > 1·0. Estimates of summer survival (*c* – *d*) in the literature did not exclude leaf herbivory, making them conservative estimates that cause some underestimation of λ calculated in the Monte Carlo simulations. However, experiments used to estimate the base value for summer survival in Nebraska controlled for insect herbivory (insecticide application)

Variables	Symbol	Range* Low	Range* High	Base values
Probability of live plants graduating from S to M[1,13]	a	0·4	0·9	**0·9**
Probability of live plants remaining M (from M to M)[1]*	b	0·224	0·424	0·324
Summer survival of S[1,2,5,6,14]	c	0·2	0·94	**0·516**
Summer survival of M[1]	d	0·5	0·78	0·64
Summer survival of L[1,2]	e	0·7	0·99	0·85
Proportion of S surviving insect foliage herbivory[5]	f	0·25	0·63	**0·515**
Proportion of M surviving insect foliage herbivory[7]*	g	0·75	0·95	<u>0·85</u>
Proportion of L surviving insect foliage herbivory[7]*	h	0·65	0·85	<u>0·75</u>
Winter survival of S[3,13]	i	0·248	1·0	**0·248**
Winter survival of M[3]*	j	0·8	1·0	0·9
Winter survival of L[3]*	k	0·8	1·0	0·9
Flowering probability of L[6,8]	l	0·5	0·9	0·7
Flowering probability of M, as proportion of *l*[1,8,13]	m	0·2	0·65	**0·44**
Seed production of L[1,2,6,8,10]	n	8000	30 000	**22 119**
Seed production of M, as a proportion of that by L[14]	o	0·3	0·7	**0·5**
Seed survival of floral herbivory[2,8,9,10,11,13,14]	p	0·003	0·6	**0·058**
Survival of post-dispersal predation[1,8]	q	0·4	0·8	0·6
Germination rate[1,5,12,13,14]	r	0·06	0·8	**0·214**
Seed bank germination rate[1,4,8,12]	s	0·0	0·1	0·03

1, Bullock, Hill & Silvertown (1994); 2, de Jong & Klinkhamer (1986); 3, de Jong *et al.* (1987); 4, Doucet & Cavers (1996); 5, J. Eckberg, S. Louda & B. Tenhumberg, unpublished data; 6, Forcella & Wood (1986); 7, Guretzky & Louda (1997); 8, Klinkhamer, de Jong & van der Meijden (1988); 9, Louda (1999); 10, Louda & Rand (2002); 11, van Leeuwen (1983); 12, van Leeuwen (1987); 13, M. Takahashi & S. Louda, unpublished data; 14, Young (2003).

	Seed bank	Small	Medium	Large
Seed bank	0	0	*l m n o p q* (1 − *r*)	*l n p q* (1 − *r*)
Small	*c f s*	0	*l m n o p q r c f*	*l n p q r c f*
Medium	0	*a d g i*	*b d g j* (1 − *l m*)	0
Large	0	(1 − *a*) *e h i*	(1 − *b*) *e h j* (1 − *l m*)	*e h k* (1 − *l*)

Table 2. Parameters multiplied to calculate each size-class transition rate in the matrix model for *Cirsium vulgare*. Symbols are defined in Table 1

that, for plants that survived, 90% of the small-sized ones graduated into medium-sized plants, while 10% graduated into large-sized plants; 37·5% of the medium-sized plants remained in the medium size class, while 62·5% graduated to large-sized plants. Plant size reductions were not observed, so size regression was not included in our model; the transition from medium to small plants (Fig. 1) represented small-sized plants recruited from seed produced by medium-sized plants, seed that overwintered, germinated, survived and grew into the small size class by the next census date. All small-sized plants that did not die or grow into medium-sized plants were assumed to grow into large-sized plants.

Survival rates (c–k)

Survival of *C. vulgare* rosettes generally increases with size (de Jong & Klinkhamer 1986). For small plants (S), we recorded survival for

480 small seedling plants that germinated in 2004 in a seed-addition experiment in a prairie restoration (M. Takahashi & S. Louda, unpublished data) and 8066 seedlings that germinated in 2005 in an experiment to quantify spatial dynamics of the *C. vulgare*–insect herbivore interaction (J. Eckberg, S. Louda & B. Tenhumberg, unpublished data). For the 2004 cohort, 30·0% of the small (seedling) plants survived the summer; in addition, 24·8% of those remaining seedlings survived over the following winter. These survival rates included the effects of foliage herbivory. For the 2005 cohort, we found that, of the initial 3979 small (seedling) plants exposed to insect foliage herbivory (controls = no insecticide), 26·6% survived the summer; 51·6% in the insecticide-treated seedlings (*n* = 4087) survived the summer. So the proportion of small plants that died from foliage herbivory was 1 – the survival ratio of both experiments (1 – 0·266/0·516 = 0·485). For convenience, in this model we used the survival ratio (*f* = 0·266/0·516 = 0·515) such that the survival

rate of plants exposed to herbivores was calculated as $0.516 \times 0.515 = 0.266$. We set the range of f-values equal to the variation among subplots in 2005 (mean ± SD = 0.25–0.63).

For survival of medium- and large-sized plants, we used the midpoint of the published range to estimate these unknown rates. Guretzky & Louda (1997) found that foliage herbivory on *C. altissimum* reduced the survival of large rosettes by 25% but affected the survival of the medium-sized established rosettes less. To include such herbivory in the base model, we used a 15% reduction in survival for medium-sized plants and a 25% reduction for large-sized plants as our parameter estimates; we handled these as we did f for small plants (above).

Seed production rates (l–p)

The probability of flowering generally increases with *C. vulgare* rosette size and, in the indigenous environment, plants can take several years to reach flowering size (Klinkhamer, de Jong & van der Meijden 1988; Bullock, Hill & Silvertown 1994). However, in non-indigenous pastures in Queensland, Australia, *C. vulgare* was biennial (Forcella & Wood 1986). In Nebraska, 30.8% of the medium-sized rosettes in our experimental seed addition flowered in their second year (M. Takahashi & S. Louda, unpublished data). As no Nebraska data were available on the probability of flowering by large rosettes, we used the midpoint of the published range (Table 1 ; 70%, $l = 0.7$). To ensure that medium-sized plants always had a smaller probability of flowering than large ones in the Monte Carlo simulations, we created a parameter, m, and set $m = 0.44$, such that the flowering probability of medium-sized plants was constrained to 44% of the proportion of large-sized plants flowering (i.e. flowering of medium-sized plants: $lm = 0.7 \times 0.44 = 0.308$), consistent with the data available. Similarly, we also used the parameter o (Table 1) to constrain the calculation of seed production of medium-sized plants that flowered (below).

To estimate production of viable seed, we used data on seed initiation, floral herbivory and viable seeds recorded from 1997 to 1999 in the region (Louda 1999; Louda & Rand 2002; S. Louda, unpublished data). Individual *C. vulgare* plants initiated an average of 22 119 florets (SE 3521) and produced an average of 1285 viable seeds (SE 247); thus we set $n = 22\,119$. Reduction of seed by insect floral herbivory averaged 18 601 seeds plant^{-1} (84.1%) when strict criteria of definitive evidence of insect feeding were used (Louda & Rand 2002), and 94.2% if all of the evidence of probable damage by herbivores was included (S. Louda, unpublished data); we used the latter value ($P = 0.058$) as the maximum estimate of the effect of floral herbivory on viable seed production of populations in eastern Nebraska.

Germination rates (q–s)

Viable *C. vulgare* seeds falling on the ground are readily consumed or removed by seed predators such as rodents and ants; this post-dispersal seed predation and loss can be as high as 68% (Klinkhamer & de Jong 1988; Klinkhamer, de Jong & van der Meijden 1988). We used the midpoint of the range of values in the literature in our base model, leaving 60% of viable seeds escaping post-dispersal predation.

The recorded germination rate of *C. vulgare* in this region was highly variable. In 2004, for seeds planted in 50 × 50-cm plots along a habitat gradient, 3–42% of the seeds germinated (M. Takahashi & S. Louda, unpublished data). In 2005, for seeds planted in larger plots (2 × 2 m) across a larger spatial scale and multiple sites (70 plots,

~538 seeds added per plot), the estimated germination by *C. vulgare* across all plots was 21.4% (J. Eckberg, S. Louda & B. Tenhumberg, unpublished data). Because of the larger sample size and broad spatial representation, we used the latter estimate for our base model. The expected number of seeds produced per plant that survive to germinate in spring is quite low ($npq = 22\,119 \times 0.058 \times 0.6 = 769$), so it is unlikely that competition affects germination and early seedling survival (J. Eckberg, S. Louda & B. Tenhumberg, unpublished data). Therefore we assumed that recruitment was density independent.

PERTURBATION ANALYSES

We compared three methods for calculating the sensitivity of *C. vulgare* population growth rate to perturbation of model parameters. First, we calculated elasticity matrices (**E**) to assess the relative importance of small linear perturbations of individual matrix transitions (a_{ij}) for asymptotic population growth rate, λ, when other parameters were held constant (Caswell 2001). So, $E_{ij} = (a_{ij}/\lambda)(v_i w_j / <\mathbf{w}, \mathbf{v}>)$, where v is the vector of scaled reproductive values, w is the scaled age distribution, and the bracket $< >$ indicates the scalar product.

Second, because the calculation of each matrix element used multiple parameters, we also calculated the elasticity for specific components of the matrix entries, the lower level elasticities (LLE; Caswell 2001). The lower level elasticity of parameter X (LLE$_X$) is calculated as the weighted sum of the sensitivities ($S_{ij} = v_i w_j / <\mathbf{w}, \mathbf{v}>$) of those matrix elements that are influenced by X; thus, $\text{LLE}_x = (x/\lambda)\sum_{i,j} S_{ij}(\partial a_{ij}/\partial_x)$. Lower level elasticity values also assess the effect of small linear perturbations of single parameters; however, in contrast to elasticity values of the matrix entries, lower level elasticity values are not required to add up to 1.

Thirdly, we performed a Monte Carlo sensitivity analysis, given the uncertainty imposed by multiple estimated parameters and the possibilities of parameter interactions and non-linearities in response to larger perturbations associated with weed population dynamics. We used a Latin Hypercube (Blower & Dowlatabadi 1994) to produce 10 000 random parameter combinations, with each parameter drawn (sampling without replacement) from a uniform distribution bounded by the lowest and highest values in the *C. vulgare* literature (Table 1). According to Blower & Dowlatabadi (1994), the minimum number of simulations required for Latin Hypercube sampling is $^3/_4K$, given K equals the number of uncertain variables. In our case $K = 19$ or 21, so the number of simulations we used is orders of magnitude higher. No information exists on the true distribution of parameter values, and with the lack of such knowledge our uniform distribution is justifiable (Hilborn & Mangel 1997). Alternate distributions led to similar results (see Tables S1 and S2 in the Supplementary material). The only exception in this parameterization was that we excluded an unusually low estimate for seed reduction by floral herbivory (19%) from a non-native locale, Australia (Forcella & Wood 1986).

Thus the Monte Carlo analysis consisted of 10 000 unique parameter combinations in which all parameters varied simultaneously; we calculated λ-values for each parameter combination. Because input variables were not normally distributed and the outcome variables were generally non-linear functions of the input variables, non-parametric tests of ranked data were necessary (Conover 1980). We calculated partial rank correlation coefficient (PRCCs) as in Blower & Dowlatabadi (1994) to determine the statistical relationship of each parameter to the estimate of λ (Conover 1980) and the relative importance of each variable (Blower & Dowlatabadi 1994). This

Table 3. Matrix projection model of *Cirsium vulgare* in eastern Nebraska, USA, using base values (Table 1). Estimated asymptotic population growth rate $\lambda = 1.538$

	Matrix transition rates				Elasticity matrix			
	Seed bank	Small	Medium	Large	Seed bank	Small	Medium	Large
Seed bank	0·000	0·000	93·149	423·404	0·000	0·000	0·010	0·016
Small	0·008	0·000	6·752	30·689	0·026	0·000	0·146	0·219
Medium	0·000	0·121	0·110	0·000	0·000	0·295	0·023	0·000
Large	0·000	0·016	0·267	0·171	0·000	0·096	0·139	0·029

procedure enabled us to determine the independent effect of each parameter, even with unknown levels of correlation among parameters (Conover 1980).

EXAMINATION OF VARIATION IN TWO PARAMETERS AFFECTED BY WEED MANAGEMENT

The initial analyses above fell short of fully explaining the low population densities of *C. vulgare* observed in eastern Nebraska; therefore, we asked whether reduction in seed production and regeneration, the aim of local land management practices, could interact with biological factors to limit λ. We considered the probability of large plants surviving to flower and set seed (*e*), which is reduced by roadside mowing, and the probability of successful seed germination (*r*), which is reduced in croplands by intensive weed management.

Thus, as a first approximation, we explored how much *e* and *r* would have to be reduced in order to produce $\lambda \leq 1$ at various levels of floral herbivory. To do so, we defined two new parameters, the proportion of large flowering plants dying early (*u*), for example in response to mowing, and the proportion of seed lost to unsuitable habitat (*v*), for example into cropland, such that the new proportion of large plants surviving the summer was $e(I - M)$ and the new germination rate was $T(I - V)$. We varied *u* and *v* simultaneously between 0 and 1·0, assuming all other parameters were those in the base model (where *u* and *v* = 0, by definition). By varying these two parameters between 0 (no effect) and 1·0 (where all bolting thistles died or no seeds germinated), we could quantify the effects, examine the parameter interactions and calculate the relative importance of such variation to the estimated λ, given the parameter uncertainties, for varied levels of floral herbivory.

Finally, we used a Monte Carlo perturbation analysis to explore the sensitivity of λ to variation in *u* and *v*, and determine the relative contribution of these parameters to the population growth rate in the presence of uncertainty in the 19 other model parameters. The outcomes were viewed as predictions for further testing.

Results

COMPARATIVE ANALYSIS OF PARAMETER INFLUENCE ON λ

We analysed the matrix model (Fig. 1) using base parameter values (Table 1) that represented the current best estimates of vital rates for *C. vulgare* populations in eastern Nebraska. The estimate of the asymptotic population growth rate (λ) for this model (Table 3) was 1·538, suggesting an annual population increase of 53·8%, much higher than observed. With floral herbivory set to zero, λ was even higher (5·20; analysis not shown).

Elasticity analysis suggested that small changes in the transition from small- to medium-sized plants had the greatest impact on the base model estimate of λ. This transition was influenced by the proportion of plants growing from small to medium size (*a*), winter survival of small-sized plants (*i*), summer survival of medium-sized plants (*d*) and the proportion of medium-sized plants surviving insect foliage herbivory (*g*) (Table 2). Two of these parameter estimates (*a*, *i*) were from *C. vulgare* populations in eastern Nebraska and one (*g*) was an estimate from the co-occurring native *C. altissimum*. The second most important transition was recruitment, represented by the large-plant to small-plant transition (Table 3). This transition involved seven parameters (Table 2), of which five (*n*, *p*, *r*, *c*, *f*) were based on direct data from *C. vulgare* populations in Nebraska (Table 1) whereas two (*l*, *q*) had been estimated from the literature.

We then analysed the effect of perturbing single-component parameters using LLE. The sign of the LLE values indicates whether λ increases or decreases as a parameter increases; the larger the absolute value, the higher its influence on λ. The highest absolute LLE value was $a = -0.571$ (Table 4), suggesting growth from small to medium size influenced λ the most. Further, λ decreased as the proportion of plants growing from small to medium size (*a*) increased (1 − *a* is the proportion of plants growing to large size, with the highest seed production). Other parameters with high (and identical) absolute LLE values were: seed surviving floral herbivory (*p*); summer and winter survival of small-sized plants (*c*, *i*); seed production of large plants (*n*); proportion of small plants surviving insect foliage herbivory (*f*); and survival of post-dispersal predation (*q*). These parameters are all in life-history loops that determine recruitment (M → SB, M → S, L → SB, L → S), but other parameters in these loops had much smaller LLE values (0·251 and 0·085 for *l* and *m*).

Results from the $PRCC_1$ of the Monte Carlo Latin Hypercube perturbation are shown in Table 4 and Fig. 2. Only 1% of the simulations, which encompassed 10 000 different random parameter combinations across the reported range of each parameter in the literature, predicted a population growth rate of $\lambda = 1$. In this analysis, λ was most sensitive to insect floral herbivory ($PRCC_1 = 0.871$) but it was not sufficient to completely halt *C. vulgare* population growth in the model. Other parameters with high $PRCC_1$ values (> 0·5) were: germination rate (*r*, $PRCC_1 = 0.796$); summer and winter survival of small plants (*c*, *i*; $PRCC_1 = 0.680$ and 0·646, respectively); and seed production of large plants (*n*, $PRCC_1 = 0.633$). We had field-based estimates for all of the

Table 4. LLE and PRCC of each parameter with λ, where λ compared by PRCC were calculated in two Monte Carlo sensitivity analyses (10 000 different parameter combinations each). The absolute values of LLE and PRCC indicate the estimated relative importance of each variable to λ (absolute values in the upper 80th percentile in bold). In PRCC1, the first two parameters (u, v) were set to 0, whereas in PRCC2 these parameters were also varied (0–1) (see text)

| Variables	LLE	PRCC$_1$	PRCC$_2$
Reproductive failure of L flowering plants (mowed) (u)			**−0·743**
Recruitment reduction by unsuitable habitat (crops) (v)			**−0·736**
Seed survival of floral herbivory (p)	**0·391**	**0·871**	**0·736**
Germination rate (r)	0·358	**0·796**	**0·608**
Summer survival of S (c)	**0·391**	**0·680**	**0·481**
Winter survival of S (i)	**0·391**	**0·646**	0·455
Seed production of L (n)	**0·391**	0·633	0·451
Proportion of S surviving insect foliage herbivory (f)	**0·391**	0·491	0·329
Survival of post-dispersal predation (q)	**0·391**	0·401	0·258
Flowering probability of L (l)	0·251	0·324	0·166
Summer survival of L (e)	0·264	0·186	0·140
Probability to graduate from S to M (a)	**−0·571**	−0·458	−0·133
Proportion of L surviving insect foliage herbivory (h)	0·264	0·145	0·106
Seed production of M as a proportion of L (o)	0·156	0·142	0·068
Seed bank germination rate (s)	0·026	0·022	0·048
Summer survival of M (d)	0·318	0·077	0·047
Flowering probability of M as proportion of L (m)	0·085	0·141	0·038
Proportion of M surviving insect foliage herbivory (g)	0·318	0·065	0·034
Winter survival of M (j)	0·161	−0·003	0·021
Probability of remaining in M (from M to M) (b)	−0·044	0·007	−0·011
Winter survival of L (k)	0·029	−0·003	−0·004
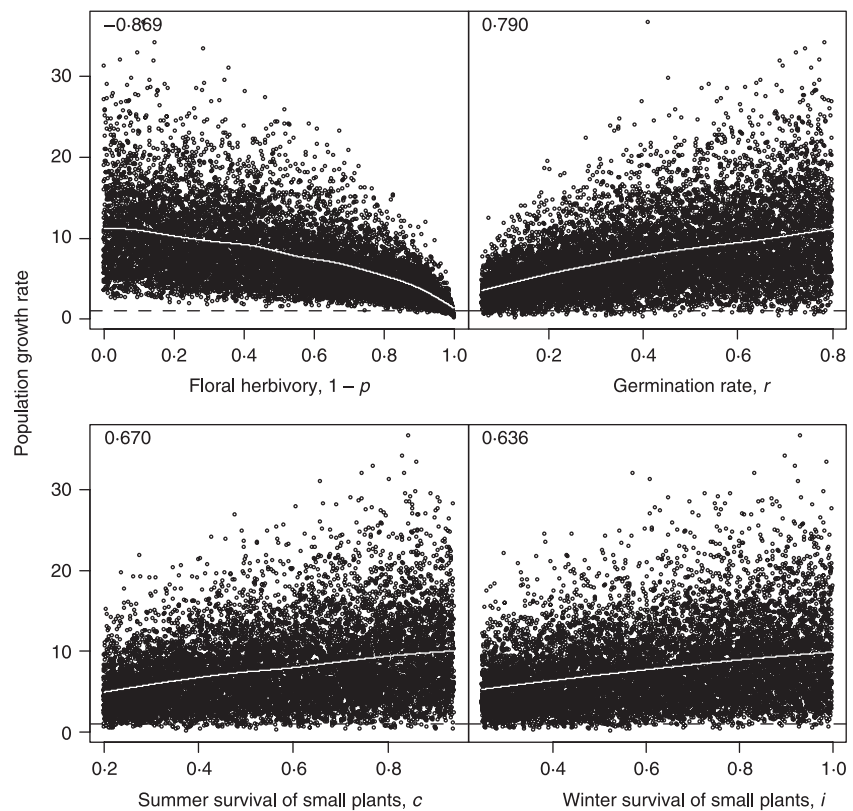
Fig. 2. Population growth rate (λ) as a function of seed mortality (proportion of seeds destroyed) as a result of insect floral herbivory ($1 - p$), germination rate (r), summer survival of small plants (c) and seed production of large plants (n). The corresponding PRCC are in the upper corner of each plot. Smooth spline fits through the cloud of points illustrate the pattern in effect of each parameter on λ (dashed lines, λ = 1).

important parameters emerging from this analysis (Table 1). In contrast to LLE, PRCC analysis differentiated among parameters in the important life-history loops; for example, the PRCC values of the parameters in the transition L → S are as follows: 0·871 (p), 0·796 (r), 0·68 (c), 0·633 (n), 0·491 (f), 0·401 (q), 0·324 (l).

Finally, we compared the LLE from the local analysis with PRCC$_1$ values from the global analysis. The eight parameters with the highest PRCC$_1$ values also had very high LLE values. However, the relationship between PRCC$_1$ and LLE was non-linear, with LLE appearing to loose resolution at the upper end of variation. PRCC$_1$ indicated

substantial differences in impact between the most important parameters ranked by LLE. For example, germination rate had the second highest $PRCC_1$ value but was ranked eighth by the LLE analysis. Also, the parameter with the highest LLE value was ranked seventh by $PRCC_1$. Thus both statistical analysis and direct comparison showed that, when parameter uncertainty occurred and the effect of disturbance on multiple parameters was not independent, elasticity analysis erroneously identified parameters as highly important (false positive).

Conclusions of the PRCC analysis did not rely on the choice of parameter distribution. The PRCC values from Monte Carlo analyses using beta and normal distributions were similar to the ones assuming uniformly distributed parameter values (see Table S1, S2, and Fig. S1 in the Supplementary material). The parameter ranges for the most important parameter values (high PRCC values) were large; consequently, we explored the effect of variation in the range of parameter values on model predictions (see Figs S2–S4 in the Supplementary material). In general, the larger the parameter range, the smaller the average predicted population growth rates (see Fig. S2 in the Supplementary material). Furthermore, as expected, if the range was very small ($\pm 0.0001\%$ of the nominal value), the agreement with the LLE was very good (see Fig. S3a in the Supplementary material). However, there were two exceptions. Winter survival of small plants had the second highest elasticity value (LLE = 0·391) but a relatively small PRCC value (0·548); and the parameter with the highest absolute LLE value (LLE of the 'probability of live plants graduating from S to M' = –0·571) had only a medium-high absolute PRCC value (–0·759). These discrepancies indicated that local slopes can be dependent on the values of other model parameters (in the Monte Carlo analysis parameter values were varied simultaneously). Thus we found that the agreement between PRCC and LLE weakens with increasing range.

MONTE CARLO ANALYSIS OF VARIATION IN TWO REGENERATION PARAMETERS

In the second Monte Carlo analysis (10 000 parameter combinations), in which the additional parameters u and v varied 0–1, we found that increases in pre-reproductive mortality (u) and decreases in seed germination rates (v) could help limit population growth rate ($\lambda = 1$) over a range of parameter combinations at realistic levels of floral herbivory (p). In Fig. 3, the combinations of parameter values that restrict λ to < 1 are represented by the area above each contour line, representing a specific level of seed escape from floral herbivory (from half that observed, $p/2$, to three times observed, $3p$). In total, 17% of the 1000 simulation runs predicted population stasis or decline ($\lambda = 1$). In this analysis, the parameters u, v and p had the highest $PRCC_2$ values (Table 4) and the similar values suggested that they contributed equally to the limitation of *C. vulgare* population growth rate in the tallgrass prairie region of Nebraska.
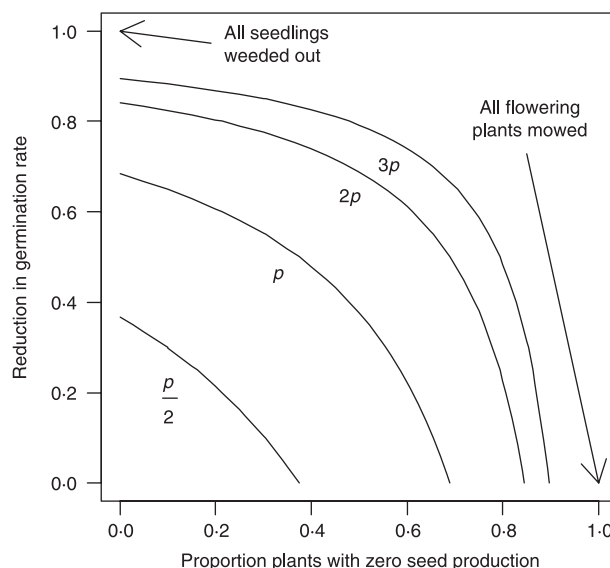

Fig. 3. Contour plots of the predicted combined effect of three parameters, floral herbivory, reproductive failure (increased by mowing) and reduced germination (increased by weed management in croplands), hypothesized to be important in determining the asymptotic population growth rate (λ) of *C. vulgare* thistle populations in Nebraska, USA. The contour lines represent parameter combinations where $\lambda = 1$ for different proportions of seeds escaping floral herbivory (p), with the observed proportion ($P = 0.058$) as well as half ($p/2 = 0.029$), twice ($2p = 0.116$) or triple ($3p = 0.174$) that base value. The area above each line indicates $\lambda < 1$, whereas the area below each line indicates $\lambda > 1$.

Discussion

DEMOGRAPHIC ANALYSIS WITH PARAMETER UNCERTAINTY

In theory, all of the transition rates needed to build a demographic matrix can be measured directly (16 transitions for a 4×4 matrix). However, in this study, as many others, we had to supplement local field data on transitions, and on processes affecting those transitions, with information from the literature. As data in the literature were from studies carried out for completely different purposes and in different locations (different countries), parameter uncertainties were large; also, we could not evaluate potential correlation among parameter values.

The reliability of local sensitivity and elasticity analyses given such parameter uncertainty is questionable. The range of possible parameter values is too large to meet the underlying assumptions, such as infinitesimally small changes in one parameter while all other parameters are held constant and independence of transitions. In fact, using methods adapted from robust control theory (transfer functions), Hodgson & Townley (2004) and Hodgson, Townley & McCarthy (2006) have demonstrated that the interpretation of sensitivity analysis can be quite misleading. One reason is that the response of λ to larger changes in parameter values is frequently non-linear. Further, even if the response of λ is linear for all parameters, there can be interplay between

the uncertainties in two parameters, such that management recommendations will depend upon whether there is uncertainty in one or both parameters (Deines *et al.* 2007).

As an alternative, we used a numerical global analysis (Monte Carlo) to deal practically with potentially large parameter uncertainty. Such analyses have been used for estimation of confidence intervals for λ but rarely for perturbation analyses. However, adding PRCC, as a statistical evaluation of the importance of each parameter to λ in a Monte Carlo analysis, allowed strong inference on the relative contribution of each parameter, even within important life-history loops. The results in this study show that Monte Carlo sensitivity analysis with PRCC, which does not require assumptions about parametric correlation coefficients, provides a quantitative determination of the relative importance of matrix parameters to λ and of their contribution to the limitation of a biological invasion.

In the global analysis, we found that λ was most closely correlated with floral herbivory (Table 4) rather than with the transition from small to medium size suggested by elasticity analyses (Table 3). Some parameters with low PRCC values had relatively high LLE values, demonstrating that LLE had a high false-positive error rate in identifying the predominant parameter(s) influencing λ. Thus this study supports suggestions that sensitivity and elasticity analyses are ambiguous in the presence of large parameter uncertainty (Hodgson & Townley 2004), which is often the case in weed management. Monte Carlo analysis provides an effective alternative approach to evaluating matrix model predictions of the relative importance of factors influencing the asymptotic population growth rate, λ, of weed populations.

EVALUATION OF PARAMETER INFLUENCE ON λ

The Monte Carlo analysis identified floral herbivore reduction of viable seed as the most significant naturally occurring constraint on *C. vulgare* population growth in the region ($PRCC_1 = 0.871$; Table 4). The estimates of parameters with the highest $PRCC_1$ values (> 0.41) were based on field data from Nebraska populations (compare Tables 1 and 2). Further, the actual parameter uncertainty was not as large as expected, as the small contribution of parameters with high uncertainty lowered the overall uncertainty in the predicted λ.

In addition, our analysis of the base model showed that observed levels of floral herbivory were not sufficient to explain fully the low population densities of *C. vulgare* observed in this region. If the eight parameter estimates from the literature (plus two from studies of the co-occurring native relative) were sufficient to model *C. vulgare* in Nebraska, seed loss to floral herbivores would have had to average 98·2% for λ = 1, more than that recorded (71–96·5%) (Louda & Rand 2002; S. Louda, unpublished data). Our model is deterministic and ignores temporal and spatial variation in parameter values, and deterministic models tend to overestimate population performance (Morris & Doak 2002). However, Doak, Gross & Morris (2005) found that, in the absence of 'good' data, deterministic models can provide better predictions

than stochastic ones. One hypothesis to explain this discrepancy is that our initial matrix model missed at least one mechanism critical for explaining the observed population stasis. This led us to explore the potential interaction of variation in two regeneration parameters affected by weed management practices with the floral herbivory.

MONTE CARLO ANALYSIS OF VARIATION IN TWO REGENERATION PARAMETERS

In a second Monte Carlo analysis, we evaluated the conditions under which reductions in two regeneration parameters targeted by weed management practices (mowing, cropland weed management) could result in thistle population control. We found that increased proportions of large plants dying before setting seed and seeds lost prior to germination, in combination with floral herbivory, predicted λ ≤ 1 for a wide range of values (Fig. 3). These results suggest that weed management practices that limit seed production and seedling establishment, added to the extensive floral herbivory, contribute to halting *C. vulgare* population growth in this region. Thus understanding the low *C. vulgare* abundance in eastern Nebraska, or the invasive potential of exotic plants in general, requires evaluation of the interaction of land management practices with other factors, such as biotic resistance. An important next step would be a direct test of the effect of land management practices on λ, and quantification of spatial patterns leading to the development of a spatially explicit model.

CONCLUSION

Ideally, studies of plant demography should include all necessary life-history parameters. However, limited time and funding, as well as logistical constraints, often lead to data sets that fall short of ideal. As a consequence, parameter uncertainty and interdependencies are common, particularly for invasive plants. Monte Carlo sensitivity analysis, along with PRCC, provides a robust numerical alternative to elasticity analysis in these cases. We found that the interactions between floral herbivory and two parameters that can be influenced by local weed management practices (survival to flowering and successful seed germination) predict population stasis across a wide range of parameter values, and probably explain the limited population growth and invasiveness of *C. vulgare* in Nebraska. This finding is consistent with the suggestion that multiple, interacting factors are generally needed for effective weed control (Shea, Thrall & Burdon 2000; Grigulis *et al.* 2001; Huwer *et al.* 2005).

Acknowledgements

References

Andersen, C.P. & Louda, S.M. (2007) Abundance of and floral herbivory on bull thistle in western tallgrass prairie. *Proceedings of the 20th North American Prairie Conference, Kearney, NE, 24–26 July 2006* (ed. J. Springer) in press.

Barkley, T.M. Ed. (1986) Flora of the Great Plains. *Great Plains Flora Association*, p. 1392. University Press of Kansas, Lawrence, KS.

Blower, S.M. & Dowlatabadi, H. (1994) Sensitivity and uncertainty analysis of complex models of disease transmission: an HIV model as an example. *International Statistical Review*, **62**, 229–243.

van Breeman, A.M.M. & van Leeuwen, B.H. (1983) The seed bank of three short-lived monocarpic species, *Cirsium vulgare* (Compositae), *Echium vulgare* and *Cynoglossum officinale* (Boraginaceae). *Acta Botanica Neerlandica*, **32**, 245–246.

Bullock, J.M., Hill, B.C. & Silvertown, J. (1994) Demography of *Cirsium vulgare* in a grazing experiment. *Journal of Ecology*, **82**, 101–111.

Caswell, H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**, 619–627.

Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer Associates Inc., Sunderland, MA.

Conover, W.J. (1980) *Practical Nonparametric Statistics*, 2nd edn. John Wiley and Sons Inc., New York, NY.

Crooks, K.R., Sanjayan, M.A. & Doak, D.F. (1998) New insights on cheetah conservation through demographic modeling. *Conservation Biology*, **12**, 889–895.

Deines, A., Peterson, E., Boekner, D., Boyle, J., Keighley, A., Kogut, J., Lubben, J., Rebarber, R., Ryan, R., Tenhumberg, B., Townley, S. & Tyre, A. (2007) Harvesting peregrine falcon populations: guaranteeing population growth under uncertainty. *Ecological Applications*, in press.

Doak, D.F., Gross, K. & Morris, W.F. (2005) Understanding and predicting the effects of sparse data on demographic analyses. *Ecology Letters*, **86**, 1154–1163.

Doucet, C. & Cavers, P.B. (1996) A persistent seed bank of the bull thistle *Cirsium vulgare*. *Canadian Journal of Botany–Revue Canadienne de Botanique*, **74**, 1386–1391.

Ehrlén, J. (2000) The dynamics of plant populations: does the history of individuals matter? *Ecology*, **81**, 1675–1684.

Ellner, S.P. & Rees, M. (2006) Integral projection models for species with complex demography. *American Naturalist*, **167**, 410–428.

Fisher, D.O., Hoyle, S.D. & Blomberg, S.P. (2000) Population dynamics and survival of an endangered wallaby: a comparison of four methods. *Ecological Applications*, **10**, 901–910.

Forcella, F. & Wood, H. (1986) Demography and control of *Cirsium vulgare* (Savi) Ten. in relation to grazing. *Weed Research*, **26**, 199–206.

Grigulis, K., Sheppard, A.W., Ash, J.E. & Groves, R.H. (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology*, **38**, 281–290.

Gross, K., Craig, B.A. & Hutchinson, W.D. (2002) Bayesian estimation of a demographic matrix model from stage-frequency data. *Ecology*, **83**, 3285–3298.

Guretzky, J.A. & Louda, S.M. (1997) Evidence for natural biological control: insects decrease survival and growth of a native thistle. *Ecological Applications*, **7**, 1330–1340.

Hilborn, R. & Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, NJ.

Hodgson, J. & Townley, S. (2004) Linking management changes to population dynamic responses: the transfer function of a projection matrix perturbation. *Journal of Applied Ecology*, **41**, 1155–1161.

Hodgson, D.J., Townley, S. & McCarthy, D. (2006) Robustness. Predicting the effects of life history perturbations on stage-structured population dynamics *Theoretical Population Biology*, **70**, 214–224.

Horvitz, C.C. & Schemske, D.W. (1995) Spatio-temporal variation in demographic transitions of a tropical understorey herb: projection matrix analysis. *Ecological Monographs*, **65**, 155–192.

Hunt, L.P. (2001) Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology*, **38**, 238–252.

Huwer, R.K., Briese, D.T., Dowling, P.M., Kemp, D.R., Lonsdale, W.M., Michalk, D.L., Neave, M.J.N., Sheppard, A.W. & Woodburn, T.L. (2005) Can an integrated management approach provide a basis for long-term prevention of weed dominance in Australian pasture systems? *Weed Research*, **45**, 175–192.

de Jong, T.J. & Klinkhamer, P.G.L. (1986) *Population ecology of the biennials* Cirsium vulgare *and* Cynoglossum officinale*: an experimental and empirical approach*. PhD Dissertation. University of Leiden, Leiden, the Netherlands.

de Jong, T.J., Klinkhamer, P.G.L., Nell, H.W. & Troelstra, S.R. (1987) Growth and nutrient accumulation of the biennials *Cirsium vulgare* and *Cynoglossum officinale* under nutrient rich conditions. *Oikos*, **48**, 62–72.

Julien, M.H. & Griffiths, M.W. (1998) *Biological Control of Weeds. A World Catalogue of Agents and their Target Weeds*, 4th edn. CABI Publishing, Wallingford, UK.

Klinkhamer, P.G.L. & de Jong, T.J. (1988) The importance of small scale disturbance for seeding establishment in *Cirsium vulgare* and *Cynoglossum officinale*. *Journal of Ecology*, **76**, 383–392.

Klinkhamer, P.G.L., de Jong, T.J. & van der Meijden, E. (1988) Production, dispersal and predation on seeds in the biennial *Cirsium vulgare*. *Journal of Ecology*, **76**, 403–414.

de Kroon, H., van Groenendael, J. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology*, **81**, 607–618.

van Leeuwen, B.H. (1983) The consequences of predation in the population biology of the monocarpic species *Cirsium palustre* and *Cirsium vulgare*. *Oecologia*, **58**, 178–187.

van Leeuwen, B.H. (1987) *An explorative and comparative study on the population ecology of* Cirsium arvensis, C. palustre, *and* C. vulgare. PhD Dissertation. University of Leiden, Leiden, the Netherlands.

Louda, S.M. (1999) Ecology of interactions needed in biological control practice and policy. *Bulletin of the British Ecological Society*, **29**, 8–11.

Louda, S.M. & Rand, T.A. (2002) Native thistles: expendable or integral to ecosystem resistance to invasion? *The Importance of Species: Perspectives on Expendability and Triage* (ed. S.A. Levin), pp. 5–15. Princeton University Press, Princeton, NJ.

Mandujano, M.C., Montana, C., Franco, M., Golubov, J. & Flores-Martinez, A. (2001) Integration of demographic annual variability in a clonal desert cactus. *Ecology*, **82**, 344–359.

Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology; Theory and Practice in Conservation Biology*. Sinauer Associates Inc., Sunderland, MA.

Rushton, S.P., Barreto, G.W., Cormack, R.M., Macdonald, D.W. & Fuller, R. (2000a) Modelling the effects of mink and habitat fragmentation on the water vole. *Journal of Applied Ecology*, **37**, 475–490.

Rushton, S.P., Lurz, P.W.W., Gurnell, J. & Fuller, R. (2000b) Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK. *Journal of Applied Ecology*, **37**, 997–1012.

Seno, H. & Nakajima, H. (1999) Transition matrix model for persistence of monocarpic perennial plant populations under periodically ecological disturbance. *Ecological Modelling*, **117**, 65–80.

Shea, K., Thrall, P.H. & Burdon, J.J. (2000) An integrated approach to management in epidemiology and pest control. *Ecology Letters*, **3**, 150–158.

Stubbendieck, J., Friisoe, G.Y. & Bolick, M.R. (1994) *Weeds of Nebraska and the Great Plains*. Nebraska Department of Agriculture, Bureau of Plant Industry, Lincoln, NE.

Tenhumberg, B., Tyre, A.J., Pople, A.R. & Possingham, H.P. (2004) Do harvest refuges buffer kangaroos against evolutionary responses to selective harvesting. *Ecology*, **85**, 2003–2017.

Young, L. M. (2003) *Native insect herbivory community provides resistance to invasive spread by an exotic thistle*. Masters University of Nebraska-Lincoln, Lincoln, NE.

Supplementary material

The following supplementary material is available for this article.

Table S1. PRCC values calculated from a Monte Carlo analysis assuming that all parameters follow a beta distribution

Table S2. PRCC values calculated from a Monte Carlo analysis assuming that all parameters follow a normal distribution

Fig. S1. Population growth rate (λ) as a function of seed mortality as a result of insect floral herbivory ($1 - p$), germination rate (r), summer survival of small plants (c) and seed production

of large plants (n), assuming that all parameters follow a beta distribution.

Fig. S2. The effect of parameter range on population growth rate.

Fig. S3. Correlation between LLE and PRCC calculated for different ranges around the nominal values.

Fig. S4. Correlation between LLE and PRCC calculated for different ranges around the midpoint of the reported range.

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