

# Flowering Life-History Strategies Differ between the Native and Introduced Ranges of a Monocarpic Perennial

Jennifer L. Williams\*

Division of Biological Sciences, University of Montana, Missoula, Montana 59812; and National Center for Ecological Analysis and Synthesis, Santa Barbara, California 93101

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**ABSTRACT:** Life-history theory makes several key predictions about reproductive strategies on the basis of demographic vital rates, particularly the relationship between juvenile and adult survival. Two such predictions concern the optimal time to begin reproducing and whether semelparity or iteroparity is favored. I tested these life-history predictions and explored how they might differ between the native and introduced ranges of the monocarpic perennial *Cynoglossum officinale*. I first compared vital rates between ranges. I then used these vital rates to parameterize integral projection models to calculate the population growth rate ( $\lambda$ ) and net reproductive rate ( $R_0$ ) as surrogates for fitness to compare strategies within and between ranges. I found that both survival and growth were higher in the introduced range, where size at flowering was larger and iteroparity was much more common than in the native range. The observed and predicted strategies for size at flowering were similar in the native range. In the introduced range, however, even though plants flowered at a larger size, the observed size was not as large as the optimum predicted by  $\lambda$  or the higher optimum predicted by  $R_0$ . Iteroparity conferred higher fitness in both ranges, as measured by both fitness metrics, suggesting that severe constraints, potentially specialist herbivores, prevent this strategy from becoming more common in the native range.

**Keywords:** demography, exotic plant, integral projection model, iteroparity, life-history evolution, semelparity.

## Introduction

A long-standing puzzle for life-history theory has been under what conditions are semelparity and iteroparity favored in nature (Cole 1954; Roff 1992). Juvenile survival relative to adult survival has been argued as the key factor that shifts the optimal timing of each strategy (Charnov and Schaffer 1973). Variation in survival also affects the timing of when an individual, either semelparous or it-

eroparous, should first begin to reproduce. A large body of theoretical work has led to a rich set of predictions about when semelparity or iteroparity should be evolutionarily advantageous and the optimal time to begin reproducing (Hart 1977; Roff 1992; Klinkhamer et al. 1997; Metcalf et al. 2003).

The flowering strategies of monocarpic plants are useful for testing the predictions of life-history theory for two main reasons. First, although reproduction is fatal in monocarpic plants, individuals can live for one to many years before flowering. Thus, one can ask, at what age or size of flowering is fitness optimized? The “decision” of when to flower can be influenced by the benefits of growing another year—that is, having more energy to devote to reproduction—but also by the costs of waiting too long and potentially dying before reproduction (Metcalf et al. 2003; Rose et al. 2005). Second, individuals of some species that are classified as monocarpic may not be strictly monocarpic and may vary the number of times they flower (Hart 1977; Metcalf et al. 2003). A few studies have documented heritable variation for both when to flower and the number of times to flower, as well as significant genetic variance for plasticity (Law et al. 1977; Wesselingh et al. 1997; Johnson 2007). Thus, both life-history features are capable of responding rapidly to selection and evolving in ways that optimize fitness.

A key prediction of life-history theory is that the optimal number of times to flower (i.e., whether to be annual, biennial, or perennial) should change when environmental circumstances lead to differences between juvenile and adult survival (Hart 1977; Klinkhamer et al. 1997). Iteroparity should be favored when adult survival is greater than juvenile survival and semelparity when the opposite is true (Charnov and Schaffer 1973; Schaffer and Gadgil 1975). These basic predictions also commonly hold true when stochastic variation and density dependence in vital rates are considered (Bulmer 1985; Ranta et al. 2002; Wilbur and Rudolf 2006). In addition to intraspecific variation across habitats or regions, individuals may vary in their

\* Present address: National Center for Ecological Analysis and Synthesis, Santa Barbara, California 93101; e-mail: jwilliams@nceas.ucsb.edu.

life-history strategies within populations. This variation suggests that environmental differences across years may be important, leading to one strategy being favored in some years but not in others (e.g., Price et al. 1988).

Species introductions provide excellent opportunities for examining the predictions of life-history theory because selection pressures can change dramatically between the native and introduced ranges. One such factor concerns natural enemy pressure (Elton 1958; Keane and Crawley 2002). Introduced species are often thought to escape from their specialist enemies (Elton 1958), a hypothesis that has received increasing empirical support (Mommott et al. 2000; Wolfe 2002; Mitchell and Power 2003; Torchin et al. 2003; Jakobs et al. 2004). Release from enemy pressure may lead to changes in both individual growth and survival, although this is less well documented (but see Reinhart et al. 2003; DeWalt et al. 2004). Life-history theory makes two central predictions about how enemy escape might influence flowering within a monocarpic species when it alters the probability of survival. First, if the increase in adult survival is sufficiently large between the native and introduced range, it could tip the optimal strategy from semelparity to iteroparity (Klinkhamer et al. 1997). Second, increased survival could lead to increased optimal size at flowering within introduced populations. Without genetic constraints, selection might favor a shift from semelparity in a plant's native range, where it is subject to mortality from specialist enemies, to iteroparity, where plants escape from enemies in the introduced range (Müller-Schärer et al. 2004). Although several monocarpic species have been anecdotally observed to be partially iteroparous where they are introduced, rigorous assessments of this prediction are still lacking (Müller-Schärer and Steinger 2004). So too are determinations of how threshold flowering size differs between native and introduced genotypes of monocarps.

One approach to testing life-history theory is to employ demographic analyses to examine underlying vital rates and to explore how changes in these vital rates might influence particular life-history solutions (Metcalf and Pavarad 2007). Predictions about which life-history strategy should be favored under different ecological circumstances can be made by quantifying variation in vital rates. Further, vital rates can be used to parameterize population models, which can yield an estimate of the population growth rate ( $\lambda$ ) and the net reproductive rate ( $R_0$ ), or the mean expected number of offspring a newborn will produce in its lifetime, which can both be used as surrogates of individual fitness (Mylius and Diekmann 1995; van Tienderen 2000; Roff 2008). The particular life-history attributes that maximize these measures of fitness can then be explored (Rees and Rose 2002; Metcalf et al. 2003; Rose et al. 2005; Hesse et al. 2008).

Here I compare the demography of the facultative monocarp houndstongue *Cynoglossum officinale* L. (Boraginaceae) in its native and introduced ranges. I explore how variation in vital rates across ranges influences optimal flowering strategies and then ask how observed life-history strategies differ from predicted optima. At a basic level, we know very little about how demography differs between an invader's native and introduced ranges (but see Grigulis et al. 2001; Paynter et al. 2003; Hyatt and Araki 2006). Several features make *C. officinale* an interesting system in which to explore these issues. First, previous research in the native range has demonstrated that plants may spend one to several years as vegetative rosettes before flowering (de Jong et al. 1990). Variation in the size at flowering in this species exhibits both measurable genetic and genetic-by-environmental variation (Wesselingh et al. 1997). Second, additional research in Europe has shown that specialist herbivore pressure can decrease fecundity and, ultimately, survival (Prins et al. 1992; Klinkhamer et al. 1997). Moreover, while the vast majority of native plants die after they flower, a very small percentage may flower again during the following year (de Jong et al. 1990). If the absence of these specialist herbivores in the introduced range and other changes in the biotic and abiotic environments lead to differences in vital rates, theory predicts that a shift in life history should be favored.

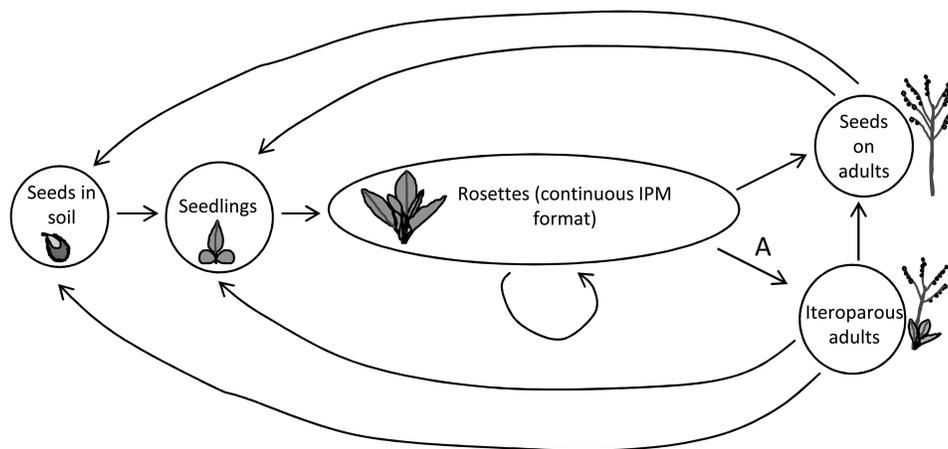
I address the following questions: (1) How do vital rates differ between the native and introduced ranges of *C. officinale*? (2) Given vital rates in both ranges, what is the optimal threshold flowering size or number of flowering times (i.e., semelparity vs. iteroparity) in each range? (3) Do observed flowering strategies match these predictions?

## Methods

### Study System

*Cynoglossum officinale* is native to Europe, where it grows in disturbed sites, open woodlands, meadows, and sand dunes (de Jong et al. 1990). It was first introduced to North America in the mid-nineteenth century as a feed contaminant and is now present across the United States and southern Canada, where it is particularly common in forest clear-cuts and overgrazed rangelands (Upadhyaya et al. 1988). It is classified as a noxious weed in six U.S. western states, where it occurs at high density (Upadhyaya et al. 1988).

*Cynoglossum officinale* is a self-compatible, facultatively monocarpic perennial (de Jong et al. 1990) that forms a rosette of basal leaves in its first year after germinating in early spring, overwinters as a rosette and taproot, and then bolts and flowers in the late spring or summer of its second or later years (fig. 1). Plants require a cold period to initiate



**Figure 1:** Life-cycle diagram of *Cynoglossum officinale*. Circles represent stages in the life cycle, and arrows represent yearly transition probabilities. In the native range, the transition marked “A” occurs at an extremely low probability. IPM = integral projection model.

flowering, but whether plants flower during their second summer depends on individuals attaining a threshold flowering size (de Jong et al. 1998), which is both environmentally and genetically determined (Wesselingh et al. 1997). Each flower produces fruits consisting of up to four large nutlets that are barbed and dispersed on mammal fur; all seeds germinate within 2 m of adult plants unless they are dispersed (Boorman and Fuller 1984). Plants invest all of their stored energy into seed production, with vegetative size before flowering positively and highly correlated with seed production (de Jong and Klinkhamer 1988). Seeds require cold stratification to break dormancy (van Breemen 1984). Although most native plants die after they flower, a tiny percentage of individuals may flower a second time in the subsequent year, after which they die (de Jong et al. 1990). To survive after a first bout of flowering, plants must keep at least one meristem vegetative, so that they can retain basal rosette leaves during the growing season. As such, these plants are easy to identify because they have both flowering stalks and basal leaves at the end of the summer.

*Mogulones cruciger*, a specialist root-boring weevil that is present only in the native range, preferentially attacks large rosettes and flowering plants and can reduce their seed set (Prins et al. 1992). Adult *M. cruciger* lay their eggs in late fall or early spring, and larvae are present in roots during the entire growing season (Schwarzlaender 1997). *Cynoglossum officinale* is also attacked by a specialist stem-boring weevil and two leaf-feeding flea beetles (Schwarzlaender 2000; M. Schwarzlaender, personal communication).

#### Demographic Monitoring

From 2004 to 2007, I monitored the fate of marked *C. officinale* individuals within three populations located in the center of both the native and introduced ranges (fig. A1 in the online edition of the *American Naturalist*). I selected study populations that occurred in broadly representative habitats and that grew at densities reflecting the average density in each range. I also chose sites within the native and introduced ranges, to minimize climatic differences so that differences between ranges would not be obscured by differences in climate. In the native range, I selected populations located within 100 km of Halle, Saxony-Anhalt, Germany. These populations were in the rain shadow of the Harz Mountains of central Germany and thus experienced a drier climate, more similar to that in the intermountain West of the United States, than other populations in central Europe might experience (Williams et al. 2008). Two populations grew in open grassland, and one occurred in an open *Robinia* and *Quercus* woodland, with an understory dominated by *Bromus sterilis*. In the introduced range, study populations were within 120 km of Missoula, Montana. Two of the populations occurred in grassland dominated by native perennial bunch grasses. The third population grew in a former clear-cut that was dominated by native grasses and forbs. Specialist insects, including *M. cruciger*, were present at all three sites in the native range but not at any of the sites in the introduced range (Williams 2008).

At each site, I followed the demographic fate of all individuals in two 1 × 10-m transects that included at least 100 plants. These transects were lengthened to include

enough individuals in the native range, where densities were lower. New seedlings were marked in the spring (April in Germany, May in Montana) and were uniquely tagged the following summer, when they were 1-year-olds. In summer, the size of all plants was recorded by counting the number of leaves and measuring the length of the longest leaf. At this time (early July in Germany, late July in Montana), the plants had set seed, and the number of seeds produced was estimated by counting the number of inflorescence branches, known as cymes (number of seeds =  $\exp[1.882 + 1.229 \times \log(\text{number of cymes})]$ ;  $R^2 = 0.78$ ,  $F_{1,297} = 1,028.0$ ,  $P < .001$ ).

To more closely examine the transition from seed to seedling, as well as the longevity of seeds in the seed bank, I initiated a seed addition experiment at all six sites in late summer 2004. Details of this experiment are reported elsewhere (Williams et al., forthcoming). In brief, I added 80 seeds from locally collected sources to  $25 \times 25$ -cm plots in both 2004 and 2005, with six replicates in the first cohort and eight in the second. I followed the germination and the fate of seedlings through summer 2007 in plots with seeds added, as well as in those with no seeds added.

#### Life-History Monitoring

To document the proportion of *C. officinale* flowering more than once, I used belt transects (50 m  $\times$  2 m) that sampled at least 50 plants in 11 populations in the native range and nine populations in the introduced range (see fig. A1 for population locations). I expanded the number of sites beyond the three used for detailed demographic analysis, to more adequately assess variation in life-history strategy within a range. These populations spanned 700 km in the native range, from Hungary to Germany, and 500 km in the introduced range, across the state of Montana. The presence of iteroparity has also been observed at other locations in the introduced range, including Idaho and southern British Columbia (M. Schwarzlaender, personal communication). I recorded the size and status of all live and dead flowering plants at these 20 sites in 2004 or 2005. From these data, I calculated the proportion of iteroparous plants in populations in each range.

To investigate the total seed set of iteroparous plants, I marked 40 iteroparous plants at each of the three study sites in Montana in 2005 and 2006. I assessed reproduction by counting the number of inflorescence branches in the year the plants were marked and followed their fate and reproductive output in the next year (2006 or 2007). Since iteroparity is extremely rare in the native range, I was unable to follow plants there.

#### Data Analysis

I compared the probability of iteroparity between ranges by using a generalized linear model with a binomial error distribution. I compared total lifetime seed production of semelparous and successful iteroparous plants in the introduced range using an ANOVA that controlled for year and site. To evaluate the difference in the distribution of sizes of vegetative plants between ranges, I used a non-parametric Mann-Whitney test.

I used generalized linear models to examine the differences in vital rates between the native and introduced ranges. Specifically, I examined the differences in size-specific survival, growth, probability of flowering, and fecundity; the size of new adults (1-year-olds); and the probabilities of establishment and seedling survival. Size was measured as the number of leaves  $\times$  the length of the longest leaf and was then log transformed. This composite variable was the best predictor of aboveground biomass ( $R^2 = 0.95$ ,  $F_{1,98} = 1,788.1$ ,  $P < .001$ ), was easy to measure in the field, and gave the best prediction for survival. To compare vital rates between ranges, range (native or introduced) was treated as a fixed effect, and population nested within a range was treated as a random effect; significant differences between ranges then indicated that vital rates differed between the regions where the field sites were located. I included year as a random effect to examine differences in environmental stochasticity, as well as interactions between size, year, and range. I compared these models to a set of models where range was excluded and population and year were fixed effects; when the latter models provided a better fit to the data, they were used to estimate parameters for the population models. Best-fit models were selected using the Akaike Information Criterion. Analyses were done in SAS (ver. 9.1.; SAS Institute, Cary, NC) with the MIXED procedure for growth, fecundity, size of new adults, and probabilities of seedling establishment and survival and with the LOGISTIC and GLIMMIX procedures for the probabilities of survival and flowering.

Statistical significance for all fixed factors was determined by Type III *F*-tests and for all random factors by log-likelihood ratio tests. In all analyses, the size and number of cymes were log transformed, and probabilities were arcsine square root transformed to meet assumptions of equal variance.

#### Model Structure

I used integral projection models (IPMs) to calculate  $\lambda$  and  $R_0$  as surrogates for the individual fitness of life-history strategies at each site, both for considering a range of flowering sizes and for comparing semelparity with it-

eroparity. Integral projection models are similar to size-based demographic matrix models, but they use continuous relationships between size and vital rates rather than dividing the population into discrete size classes (Easterling et al. 2000; Ellner and Rees 2006). They are better suited for examining life-history differences that vary continuously with plant size than are traditional stage-based matrix models, and they have recently been used for this reason to explore the optimal threshold flowering size in semelparous plants (Rees and Rose 2002; Metcalf et al. 2003; Rose et al. 2005; Hesse et al. 2008; Kuss et al. 2008).

Here I incorporate four discrete stages into the IPM framework: three discrete early-life stages for current-year seed production, seeds in the soil, and seedlings, as well as one class for iteroparous plants (fig. 1; Rees et al. 2006; Hesse et al. 2008). A separate class for seedlings was necessary because seedling size was not a good predictor of survival or growth (J. L. Williams, unpublished data).

The continuous part of the model describes the distribution of adult vegetative plants of size  $x$  at time  $t$  ( $n(x, t)$ ) and predicts the proportion of individuals of size  $y$  in time  $t + 1$  by

$$n(y, t + 1) = \int_{\Omega} \{s(x)[1 - p_f(x)]g(y, x)\}n(x, t)dx + p_{SR}f_r(y)R(t), \quad (1)$$

where  $n(y, t + 1)$  is the number of individuals of size  $y$  in time  $t + 1$ ,  $s(x)$  is the survival of individuals of size  $x$ ,  $p_f(x)$  is the probability of plants of size  $x$  flowering, and  $g(y, x)$  is the size  $y$  an individual of size  $x$  will be in  $t + 1$ . In the simplest form of the model, where all plants are semelparous, vegetative plants that flower in  $t + 1$  do not survive reproduction and are thus removed from the population (the incorporation of iteroparity is described in eq. [5]). This function is integrated over all possible sizes ( $\Omega$ ). The second term is for new adults entering the population, where  $p_{SR}$  is the probability of a seedling becoming an adult,  $f_r(y)$  is the size distribution of 1-year-olds, and  $R(t)$  is the number of recruits at time  $t$ .

New seedlings in  $t + 1$  (recruits, described by  $R(t + 1)$ ) can come either from seeds in the seed bank or from seeds produced at time  $t$ :

$$R(t + 1) = p_{eS}S(t) + p_{eSB}B(t), \quad (2)$$

where  $p_{eS}$  and  $p_{eSB}$  are the probabilities of seeds establishing from seeds produced at time  $t$  and from seeds in the seed bank, respectively, and  $S(t)$  and  $B(t)$  are the number of seeds produced in the current year and in the soil seed bank, respectively.

Seeds exist in the model in one of two states. They can

be either on the dead stalks of flowering plants that were vegetative in the previous year or in the soil. The number of seeds that vegetative rosettes at time  $t$  will produce at time  $t + 1$  (flowering occurs during this interval) can be described by

$$S(t + 1) = \int_{\Omega} s(x)p_f(x)f_n(x)n(x, t)dx. \quad (3)$$

That is, seed production by an individual of size  $x$  is equal to the probability of survival  $\times$  probability of flowering  $\times$  size-specific fecundity  $f_n(x)$  (Ellner and Rees 2006). This is multiplied by the number of individuals of size  $x$  and integrated over  $\Omega$  to calculate total seed production.

If seeds do not germinate in the year after they are produced, they can remain in the seed bank until the next year:

$$B(t + 1) = (1 - p_{eS})S(t). \quad (4)$$

For *C. officinale*, most seeds germinate the year after they are produced, and a smaller proportion germinates in the second year. However, the probability of surviving in the seed bank for multiple years is 0 in some populations and very close to 0 in others ( $>1\%$ ), so the model does not allow for seed bank persistence.

The fecundity equation can be modified to incorporate the contribution of iteroparous plants:

$$f(x) = s(x)p_f(x)[(1 - p_{itero})f_n(x) + p_{itero}f_{itero}(x)], \quad (5)$$

where  $p_{itero}$  is the probability that a flowering plant will be iteroparous and  $f_{itero}(x)$  is the size-specific fecundity of an iteroparous plant in the first year it flowers. Iteroparous plants contribute seeds in the following year (average fecundity of  $f_{itero}$ ) if they survive to reproduce again ( $s_{itero}$ ). In the model, all iteroparous plants that survive to reproduce are given the same fecundity because of a lack of data necessary to estimate a size-specific function. Following what was observed in the field, where the probability of flowering three times was extremely low, the model allows plants to flower only twice.

To estimate the probability of seedlings becoming 1-year-olds, I used data from marked plants in the demography transects at each site. I calculated survival in each 1-m<sup>2</sup> plot and then took the average across all plots at each site for each yearly transition. The estimates for the probability of establishment came from the seed-addition experiment. This experiment included a disturbance treatment, where recruitment was much higher in both ranges. For the simulations, I used a weighted average of rates in disturbed and undisturbed plots, assuming 15% distur-

bance, the average observed in the field (Williams et al., forthcoming). In each plot, I calculated the proportion of seeds that germinated and survived to the summer census in the following year and then averaged across all plots within each site to estimate the proportion of seeds that became seedlings (2004–2005 and 2005–2006). To estimate the proportion of seeds germinating from the soil seed bank, I calculated the proportion of seeds that germinated and survived in the second summer out of the total number that did not germinate in the first year (i.e., for seeds added in 2004, the number of seedlings that established in 2006 divided by the number of seeds that did not germinate in 2005). This estimate of  $p_{\text{esB}}$  (the probability of establishment from the soil) includes both survival of seeds in the soil and the probability of germinating and surviving as a seedling.

#### Model Simulations and Analyses

An IPM generates an approximating matrix, from which properties of a more traditional stage-based matrix can be calculated, such as  $\lambda$ ,  $R_0$ , and vital-rate sensitivities and elasticities (Cochran and Ellner 1992; Easterling et al. 2000; Caswell 2001; Morris and Doak 2002; Ellner and Rees 2006). The number of size categories in the approximating matrix is determined by choosing the smallest matrix size that generates the same values as larger matrices (I used 50 classes). I used parameter estimates from the best-fit models for survival, growth, probability of flowering, fecundity, and size of 1-year-old plants (table A2 in the online edition of the *American Naturalist*) along with the estimates of seedling transitions to create 12 different matrices, one for each site in each of the three yearly transitions (2004–2005, 2005–2006, and 2006–2007; table A3 in the online edition of the *American Naturalist*). The numerical solution of an IPM with both discrete and continuous stages is described in detail by Rees et al. (2006), and the details of the calculation for  $R_0$  are described by Cochran and Ellner (1992), Caswell (2001), and Ellner and Rees (2006).

To estimate the predicted flowering size in each range based on current demographic rates, I ran simulations to calculate the intercept of the probability-of-flowering function ( $c_0$ ) that maximized fitness, as measured by  $\lambda$  or  $R_0$ . Both can be used as surrogates of individual fitness, with  $\lambda$  being appropriate when density-dependent processes are not acting and  $R_0$  when they are (Mylius and Diekmann 1995; Roff 2008). Although I detected no density dependence in seedling recruitment or survival (J. L. Williams, unpublished data), here I present results with the use of both metrics of fitness. I calculated  $\lambda$  and  $R_0$  for a range of median threshold sizes (the size at which >50% of plants flower), using parameter estimates from

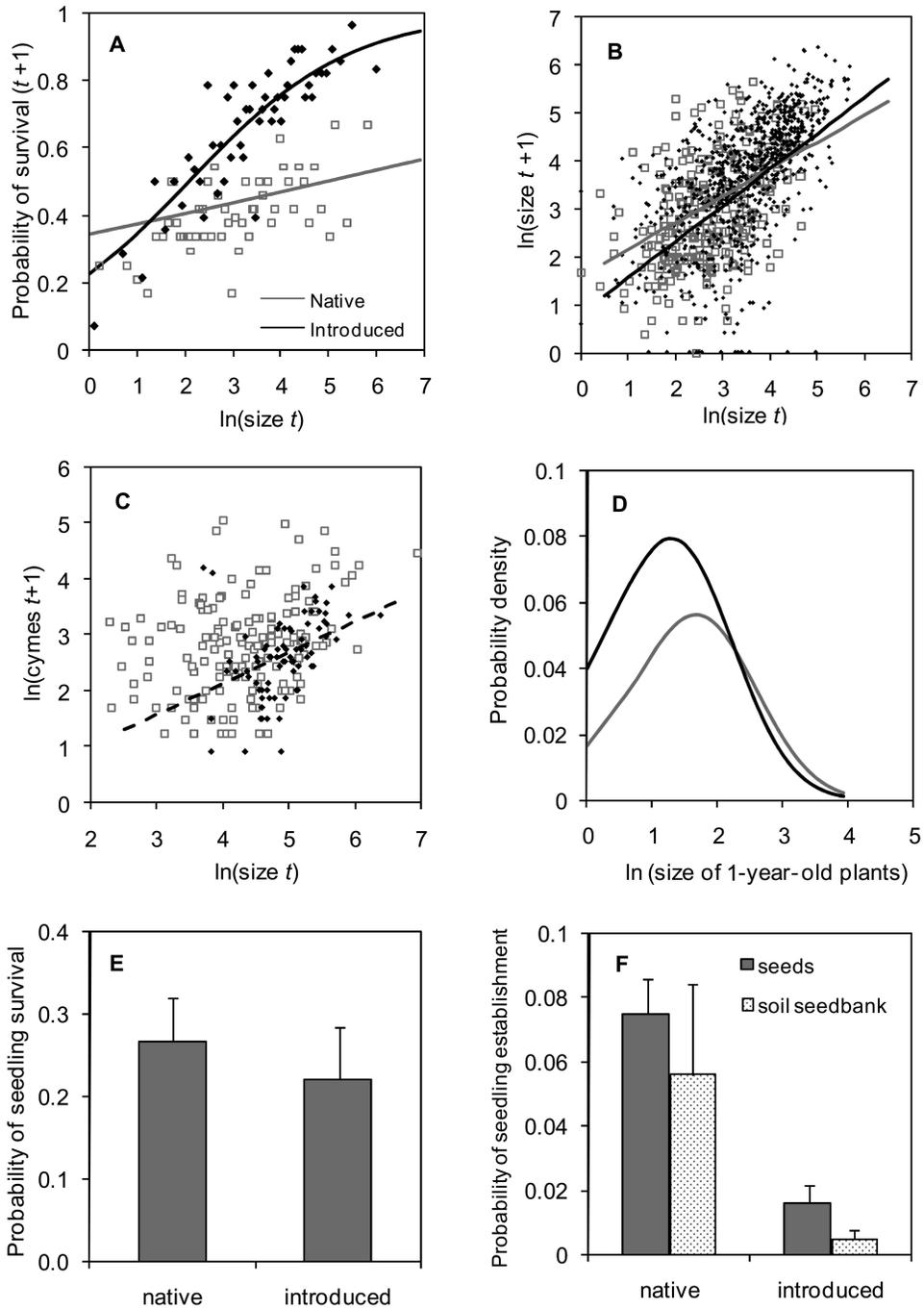
each site in each year. Since the slope of the probability-of-flowering function was constant across sites and years, I altered the intercept to correspond with median threshold size. I averaged  $\lambda$  or  $R_0$  across all site  $\times$  year combinations in each range (nine total) to calculate the average optimum for the native and introduced ranges. To make interpretation easier, I present relative fitness by scaling  $\lambda$  or  $R_0$  as a percentage of the maximum. I then compared the observed median threshold size to the size that maximized  $\lambda$  or  $R_0$ .

To evaluate the advantage of the iteroparous and semelparous life-history strategies, I ran simulations in both deterministic and stochastic environments for each site. First, I compared  $\lambda$  and  $R_0$  for a population of individuals where the probability of iteroparity was either 0 or 1 for each site in each year. In the native range, where iteroparity is extremely rare, I used values from the introduced range for  $s_{\text{itero}}$  and  $f_{\text{itero2}}$ . Second, I included temporal stochasticity at each site by choosing one matrix through a random draw in each year (with equal probability), multiplying that matrix by a vector from the previous year to calculate a new population size and log growth rate, and then rescaling the vector to 1 (Morris and Doak 2002). After 50,000 iterations, stochastic  $\lambda$  was calculated by taking the mean of the log growth rate from each iteration. I started the stochastic simulations by using the stable stage distribution vector from the 2005–2006 matrix. I compared the absolute differences in  $\lambda$  and  $R_0$  at each site where the probability of iteroparity was either 0 or 1, using paired  $t$ -tests. All matrix simulations and analyses were done using Matlab (release 14; MathWorks, Natick, MA).

## Results

### Vital-Rate Difference between Ranges

Adult survival and growth rate were, on average, higher in populations in the introduced range than in those in the native range (fig. 2A, 2B; table 1). Fecundity, as measured by the number of cymes (flowering branches) produced, had the same relationship to size in both ranges (fig. 2C; table 1). Both seedling survival and the size of new adults (1-year-olds) entering the population did not differ significantly between ranges (fig. 2D, 2E; table 1), but the probability of seedling establishment was higher in the native range (fig. 2F; table 1). All vital rates differed significantly across sites and years, except for fecundity, the probability of flowering, and the probability of establishment from seeds, which did not vary among years (table A2). Finally, the median size of vegetative plants was greater in the introduced range (median  $\log(\text{size}) = 3.06$ ) than in the native range (median  $\log(\text{size}) = 2.71$ ;  $Z = -5.67$ ,  $P < .001$ ).



**Figure 2:** Relationships between size and probability of survival (A), growth (B), and fecundity (C). Lines show best-fit model predictions for the native (gray) and introduced (black) ranges of *Cynoglossum officinale*. Open squares indicate plants from the native range; filled diamonds indicate those from the introduced range. A, Data have been binned into 50 equal segments for display. C, Dashed line indicates the average slope (no difference between ranges). D, Probability density of 1-year-old adults. E, F, Differences in seedling survival and establishment, respectively, between ranges.

**Table 1:** Differences in vital rates between the native and introduced ranges of *Cynoglossum officinale*

Vital rate	Introduced			
	native	F	df	P
Survival	>	5.11	1, 2,571	.024
Growth rate	>	11.05	1, 1,057	<.001
Fecundity	=	1.35	1, 4.13	.31
Size of 1-year-old adults	=	.39	1, 4.05	.58
Probability of seedling survival	=	.28	1, 3.78	.62
Probability of seedling establishment (from seeds)	<	14.06	1, 4	.020
Probability of seedling establishment (from soil seed bank)	=	3.82	1, 3.98	.12

Note: Symbols (<, >, =) indicate the direction of the relationship between the introduced and native ranges. Significance tests are from best-fit models with population (range) treated as a random factor, except for survival and individual growth rate.

### Threshold Flowering Size

I used IPMs to calculate the threshold size that maximized  $\lambda$  or  $R_0$ , as measures of inclusive fitness. In the native range, both  $\lambda$  and  $R_0$  were highest for plants flowering at an intermediate size; however, this varied among years for each site, such that in some years the optimal size was either much smaller or much larger (figs. 3A, A2 in the online edition of the *American Naturalist*). In the introduced range, the largest sizes always conferred the highest fitness when measured by  $\lambda$  (fig. 3B). When  $R_0$  was the metric of fitness, two average optima were observed, one at the very smallest size and a second higher one at a large size, although not as large as that for  $\lambda$  (fig. A2). How did actual patterns in threshold flowering size correspond to these predictions? In general, threshold flowering sizes were close to the predicted optimum in the native range, although  $\lambda$  overestimated the observed value and  $R_0$  underestimated it (figs. 3A, A2). In the introduced range, plants flowered, on average, when they were bigger than those in the native range, although this result was not significant ( $F_{1,4} = 5.35$ ,  $P = .082$ ; fig. 3C). Plants in the introduced range did not flower at a size as large as the predicted optima (figs. 3B, A2).

### Degree of Semelparity versus Iteroparity

Although a few individuals in the native range flowered more than once, in general, the vast majority of plants were semelparous (mean percentage of iteroparous plants  $\pm$  SE: 0.99%  $\pm$  2.98%). In contrast, despite substantial site-to-site variation in the introduced range (mean percentage of iteroparous plants  $\pm$  SE: 18.9%  $\pm$  13.1%; range: 2%–45%), the probability of iteroparity was significantly higher in the introduced than in the native range ( $z_{18} = 10.21$ ,  $P < .001$ ).

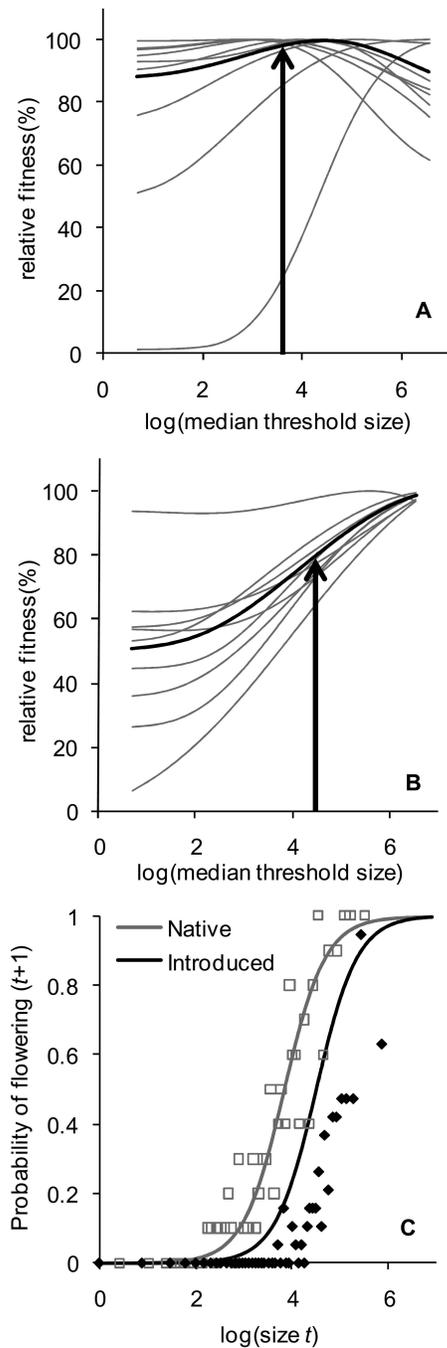
If individuals flowered twice, their total lifetime seed production was higher than that of semelparous plants (fig. 4A;  $F_{1,210} = 28.53$ ,  $P < .001$ ). However, of those marked individuals in the introduced range that had basal

rosette leaves in addition to a flowering stalk, which is indicative of iteroparity, not all survived to flower in the second year (range in survival probability: 0.4–0.6). If potentially iteroparous plants did not survive, they produced only half as many seeds in their first year of reproduction as semelparous plants produced (fig. 4A). Total fecundity of iteroparous plants did not differ among sites or years (year:  $F_{1,90} = 2.54$ ,  $P = .11$ ; site:  $F_{2,210} = 2.50$ ,  $P = .085$ ).

The comparison of total seed production between strategies does not take into account the advantage of producing offspring earlier in an individual's lifetime. I compared the fitness of semelparity and iteroparity, using  $\lambda$  and  $R_0$ . Iteroparous plants had higher fitness in comparison to strictly semelparous plants in all populations, except for one in the native range, as measured by  $\lambda$  for simulations run in both ranges (fig. 4B; deterministic  $\lambda$ :  $t_{17} = 2.88$ ,  $P = .01$ ; stochastic  $\lambda$ :  $t_5 = 5.56$ ,  $P = .003$ ). This result also held for  $R_0$ , although it was significant only when seedling recruitment and survival parameters from the disturbance scenario were used (fig. 3C;  $R_0$  control:  $t_{17} = 1.56$ ,  $P = .068$ ;  $R_0$  disturbance:  $t_{17} = 2.49$ ,  $P = .012$ ). The fitness advantage of  $\lambda$  was higher in a stochastic environment than in the deterministic environment in both ranges (fig. 4B; comparison of delta  $\lambda$ :  $t_5 = 4.14$ ,  $P = .009$ ). Average values of deterministic  $\lambda$  for semelparous populations ranged from 0.51 to 0.80 (range: 0.33–1.16), and those of  $R_0$  ranged from 0.01 to 0.81 in the control treatment (low disturbance, range: 0.001–1.65).

### Discussion

Life-history theory makes several predictions about optimal reproductive strategies on the basis of the relationship between the relative survival and growth rates of adults and juveniles (Charnov and Schaffer 1973; Schaffer 1974; Hart 1977). Surprisingly few empirical tests exist that use demographic data in these life-history theory predictions. I found increases in adult survival and individual growth rates in *Cynoglossum officinale* between its native range in



**Figure 3:** Relationship between threshold size and relative fitness (measured by population growth rate,  $\lambda$ ) in the native (A) and introduced (B) ranges. Black lines show average relationship, and gray lines show yearly estimates for each site (three yearly transitions  $\times$  three sites in each range). Arrows show observed average median threshold size in each range. C, Observed probability of flowering in each range; median threshold size occurs when the probability of flowering is 0.5. Data were binned into 50 equal segments for display (*open squares*, plants from the native range; *closed diamonds*, those from the introduced range).

central Europe and its introduced range in intermountain western North America (table 1). This intraspecific variation in vital rates leads to interesting consequences for how the predicted optimal and observed strategies of when and how many times to flower have changed between ranges. The shifts in life history following the introduction to a new range, where both biotic and abiotic selection pressures are different, support theoretical predictions. These shifts also have important implications for the success of this plant where it is introduced.

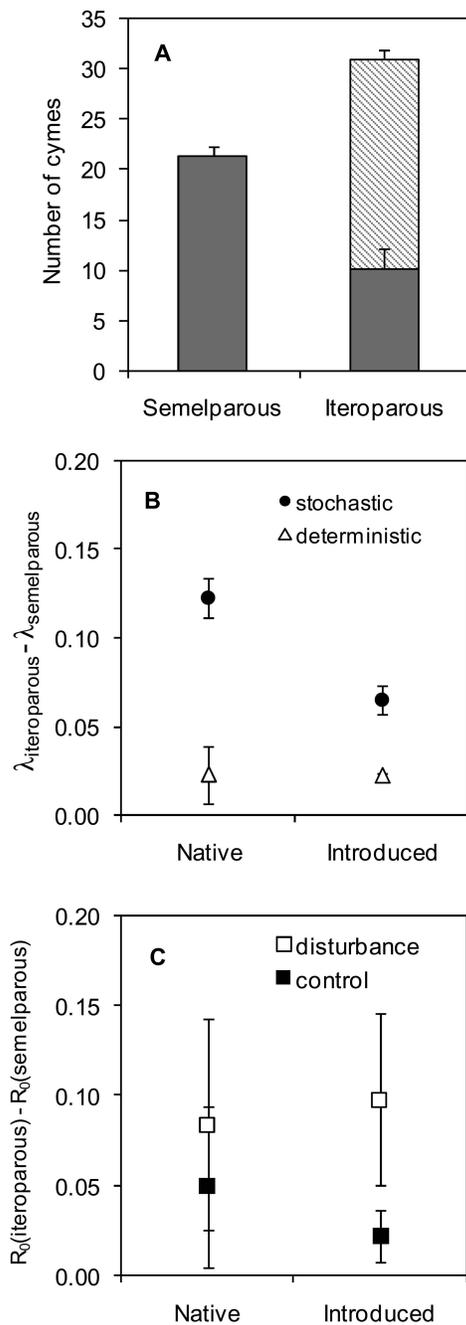
#### *Shifts in Life History between Ranges*

The differences in the size at which plants flower in the native and introduced ranges reflect what might be predicted if selection were operating to optimize fitness and there were no constraints on the evolution of life-history traits. Although different optima were predicted for each site in each year, reflecting variation in vital rates, on average, the median threshold flowering size of plants in the native range was near the optimal predicted strategy for both measures of fitness (figs. 3A, A2). In contrast, in the introduced range, where survival was higher, both observed and predicted median threshold sizes (as measured by  $\lambda$ ) were higher than those in the native range (fig. 3B, 3C). Although  $R_0$  led to the prediction of two optima, the higher optimum corresponded to the larger size, similar to that predicted by  $\lambda$ . This result of delayed maturity corresponding with increased survival follows the basic theoretical predictions (Roff 1992). These results also concur with a study in the native range of *C. officinale* that found that plants flowered at larger sizes at sites where survival and relative growth rates were higher (Wesselingh et al. 1997).

The life-history shift from semelparity to iteroparity also matches theoretical predictions. The observed higher survival of young plants in the native range compared with that of those in the introduced range fits theoretical predictions that semelparity is favored when juvenile survival is high relative to adult survival (Charnov and Schaffer 1973; Klinkhamer et al. 1997). However, I found that, in both ranges, a population of iteroparous individuals would have higher lifetime fitness than that of a population of semelparous individuals, as measured by  $\lambda$  and  $R_0$  (fig. 4B, 4C). The predicted advantage of iteroparity in two of three populations in the native range, where it is rare, suggests severe constraints on this strategy.

#### *Biotic and Abiotic Factors That Contribute to Life-History Shifts*

Several ecological factors, both biotic and abiotic, likely contribute to the observed differences in vital rates be-



**Figure 4:** A, Fecundity (number of cymes) of semelparous and iteroparous plants; solid bars show fecundity in the first year and dashed bar in the second year. B, Effects of iteroparity on total individual fitness, as measured by the difference in the population growth rate ( $\lambda$ ) of populations of exclusively semelparous or iteroparous plants (mean  $\pm$  1 SE for three populations in each range) for both deterministic and stochastic scenarios. C, Effects of iteroparity on total individual fitness, as measured by the difference in the net reproductive rate ( $R_0$ ) of populations of exclusively semelparous or iteroparous plants (mean  $\pm$  1 SE for nine site  $\times$  year combinations in each range) for control and disturbance scenarios, which altered rates of seedling recruitment and survival.

tween ranges and thus affect the resulting differences in life-history strategy. One potentially driving factor is the presence of the specialist root-boring weevil *Mogulones cruciger* in the native range but not yet in the study area in the introduced range. Adult weevils are known to preferentially choose large rosettes on which to lay their eggs; many of these large rosettes flower, and larval feeding causes a reduction in plant fecundity (Prins et al. 1992). It has also been suggested that if weevil-infested plants did not die after flowering, they would be too damaged to survive into the next year (Klinkhamer et al. 1997). Thus, weevils may exert strong selection on plants to flower at a smaller size, since small plants are more likely to grow undetected. Rose et al. (2005) demonstrated a similar pattern in the monocarpic thistle *Cirsium canescens*, where introduced seed-feeding weevils preferentially chose large plants and thereby selected for a smaller optimal flowering size. Attack by *M. cruciger* and other specialist insects in the native range may also constrain iteroparity from increasing in frequency. Thus, even if a plant that flowered once were to save energy in a side rosette for a second bout of reproduction, the probability of that plant surviving given the presence of *M. cruciger* is likely extremely low.

Variation in the frequency of iteroparity among introduced populations suggests that abiotic factors may also contribute to the shifts in life history. The predictions for how environmental stress should shape reproductive strategy are dependent on how stress affects young versus old life stages (Hart 1977). Lesica and Young (2005) found that semelparity in *Arabis fecunda* was more common in environments with lower water availability. In contrast, in *Oenothera biennis*, Johnson (2007) found that biennials were more common in moderately productive environments but that an annual strategy was favored in areas of both low and high productivity. *Cynoglossum officinale* faces very dry summers where it is invading in the intermountain West of the United States. In contrast, summer rain is common where it is native in central Europe. This difference in midsummer moisture may explain the differential survival of early life stages in the introduced range (fig. 2E) compared with late life stages (fig. 2A), which are less affected by summer drought (J. L. Williams, unpublished data). Such differential juvenile versus adult survival should favor iteroparity (Klinkhamer et al. 1997). Another factor contributing to variation in iteroparity may be fluctuating selection due to the variation in survival of iteroparous plants to reproduce twice, since higher lifetime fecundity is conferred only when plants survive. If some populations have higher background levels of survival to the second year, one might expect to see a greater frequency of iteroparous plants there.

Although I have focused on average differences between

ranges to examine overall changes in flowering life-history strategies, most vital rates varied across sites within each range as well as among years. Theory predicts that temporal variation should lead to fluctuating selection for optimal threshold size and that different optima should be found in different years (Childs et al. 2004; Sletvold and Grindeland 2007). Indeed, the optimality models support this prediction, but I found no variation in the observed median threshold size between years. This suggests that different optima may be favored depending on environmental conditions, but plants are unable to immediately respond to these changes. Across all sites, establishment of new plants and survival of seedlings to 1-year-old adults also varied among years; most sites had at least one year where recruitment was very close to 0 because of very low survivorship to summer following spring germination. Yearly variation in vital rates led to some years with very low  $\lambda$  and  $R_0$ , but, at least in the near term, populations are unlikely to become extinct because of higher values in favorable years. Variation in the success of early life stages across years may also contribute to the advantage iteroparity confers as a bet-hedging strategy (Wilbur and Rudolf 2006). I found that iteroparity increases fitness more in a variable environment than in a constant environment (fig. 4B). For a plant that has a short-lived seed bank, such as *C. officinale*, spreading the risk of poor recruitment across multiple years is advantageous.

The mechanism for the observed life-history shifts is not possible to discern from field-monitoring data. However, it is known that the threshold flowering size can be affected by both genetic and environmental contributions (Wesselingh et al. 1997). Yet whether the shifts in life history I observed are due to adaptive evolved responses to differential selection pressures across ranges or to phenotypic plasticity is unclear. Founder effects may also be important. Recent genetic analyses of neutral markers from populations collected from both ranges indicate that allelic diversity and average heterozygosity are lower among individuals from introduced populations than among those from native populations (J. L. Williams, unpublished data). Common-garden experiments also suggest that founder effects occurred during the introduction of *C. officinale* (Williams et al. 2008), but the role they play in the life-history shifts depends on the strength of genetic control over iteroparity and flowering size.

#### *Implications of Life-History Shifts for the Success of an Exotic Plant*

This is the first time a life-history shift from semelparity to iteroparity has been explicitly documented in an invasive plant, although authors have speculated that such a shift might occur after a plant escapes from its specialist

insects (Müller-Schärer and Steinger 2004). If the life-history shifts in *C. officinale* are influenced by its escape from specialist insects, they provide an example of another mechanism by which herbivores may influence population dynamics via their influence on life-history strategy. This is in contrast to the direct effects of herbivore consumption on plant size or fecundity that are typically examined, with inferred consequences for population growth (Maron and Vilà 2001; DeWalt et al. 2004). Thus, rather than an immediate release from enemies leading to increased success in the introduced range, the differential selection pressures might lead to evolution of a trait that contributes to higher population growth. This life-history response, which would be expected to evolve over time, may then be an indirect way that escape from enemies leads to success of an invader. The results presented here cannot rule out the role that founder effects and phenotypic plasticity play in this process, but these data imply the strong potential that genetic shifts have occurred since initial introduction.

Finally, much attention on invasive species has focused on the sometimes observed larger sizes of organisms in recipient communities than in the communities where they are native (Crawley 1987; Thébaud and Simberloff 2001; Grosholz and Ruiz 2003). In plants, an increasing body of work has examined whether these changes in phenotype across ranges are the result of rapid evolution (reviewed in Bossdorf et al. 2005). I found that the size distribution of nonflowering *C. officinale* was shifted to include more larger plants in introduced populations, where the median size was greater than that in native populations. Additionally, in broader-scale surveys across both ranges, flowering plants produced more cymes in introduced populations than in native populations (J. L. Williams, unpublished data). These results differ from previous common-garden studies, where *C. officinale* from introduced populations were larger and more fecund in one environment, but the opposite was true in a second common garden in a different environment (Williams et al. 2008). The driver of these differences in phenotype in natural populations across ranges may be different from the defense-growth trade-off that has been proposed in previous work (Blossey and Nötzold 1995). Vegetative *C. officinale* are larger in the introduced range than in the native range because they flower at a larger size in North America than in Europe. This larger size at flowering, in turn, leads to greater seed production in North America than in Europe. This life-history difference has important consequences for the success of *C. officinale* because, along with the shift to iteroparity, it leads to the potential for increased population growth. Future studies should not ignore the importance that life-history strategies, whether they are controlled by enemies or other abiotic factors,

may play both in the success of introduced plants and, more generally, in plant population dynamics.

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