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An experimental demographic approach to exotic plant success: Cynoglossum officinale in its native and introduced ranges

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AN EXPERIMENTAL DEMOGRAPHIC APPROACH TO EXOTIC PLANT SUCCESS: *CYNOGLOSSUM OFFICINALE* IN ITS NATIVE AND INTRODUCED RANGES

By

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An experimental demographic approach to exotic plant success: *Cynoglossum officinale* in its native and introduced ranges

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Invasive species often face novel abiotic and biotic environments with different selective regimes where they are introduced. How these changed conditions influence individual life-history traits, and what particular factors spur increases in population abundance in the introduced versus native range, are not well understood. I conducted parallel experiments in both the native and introduced ranges of a widespread plant invader in North America, houndstongue (*Cynoglossum officinale*). I combined these experimental results with demographic monitoring in each range, and population modeling, to explore how introduction has affected houndstongue demography and life-history evolution, and to determine the role of specialist herbivores and altered responses to disturbance in affecting plant population growth in both ranges.

From reciprocal common gardens in each range, I found substantial population-level plasticity in size and fecundity between native and introduced populations of houndstongue, but no significant genetically based differences in morphology. Differentiation of native populations in the magnitude of plasticity were much stronger than that of introduced populations, suggesting an important role for founder effects. From demographic data collected in each range, I found that both survival and growth were higher in the introduced range, where size at flowering was larger and iteroparity more common. Since iteroparity conferred higher fitness in both ranges, my results imply severe constraints on the evolution of this life-history strategy in the native range, potentially because specialist herbivores select for plants that flower only once. Finally, results from manipulative experiments at multiple sites in each range involving suppression of insect herbivore pressure and creation of small scale disturbances revealed several important results. First, specialist herbivores reduced plant size and fecundity in Germany, but generalist herbivores had no effect on plant performance in Montana. Second, in both ranges, seedling recruitment responded positively to disturbances, but seedling survival was more positively affected in Montana. Integrating these results into integral projection models of population growth suggest that while escape from enemies may contribute slightly to the increased abundance of houndstongue in North America, it is the differences in response to small disturbances that leads to higher abundance in the novel range compared to at home.

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CHAPTER 1

DIFFERENT GARDENS, DIFFERENT RESULTS: NATIVE AND INTRODUCED POPULATIONS EXHIBIT CONTRASTING PHENOTYPES ACROSS COMMON GARDENS

ABSTRACT

Invasive plants may respond through adaptive evolution and/or phenotypic plasticity to new environmental conditions where they are introduced. Although many studies have focused on evolution of invaders particularly in the context of testing the Evolution of Increased Competitive Ability (EICA) hypothesis, few consistent patterns have emerged. Many tests of the EICA hypothesis have been performed in only one environment; such assessments may be misleading if plants that perform one way at a particular site respond differently across sites. Single common garden tests ignore the potential for important contributions of both genetic and environmental factors to affect plant phenotype. Using a widespread invader in North America, *Cynoglossum officinale*, we established reciprocal common gardens in the native (Europe) and introduced range (North America) to assess genetically based differences in size, fecundity, flowering phenology and threshold flowering size between native and introduced genotypes as well as the magnitude of plasticity in these traits. In addition, we grew plants at three nutrient levels in a pot experiment in one garden to test for plasticity across a different set of conditions. We did not find significant genetically based differences between native and introduced populations in the traits we measured; in our experiments, introduced populations of *C. officinale* were larger and more fecund, but only in common garden experiments in the native range. We found substantial population-level plasticity for size, fecundity and date of first flowering, with plants performing better in a garden in Germany than in Montana. Differentiation of native populations in the magnitude of plasticity was much stronger than that of introduced populations, suggesting an important role for founder effects. We did not detect evidence of an evolutionary change in threshold flowering size. Our study demonstrates that detecting genetically based differences in traits may require measuring plant responses to more than one environment.

INTRODUCTION

Plants adapted to particular conditions in their home range are increasingly introduced into new areas, where conditions may differ. How exotic species cope with these novel environmental conditions in recipient communities is an area of growing interest in ecology (Blossey and Nötzold 1995; Hänfling and Kollman 2002; Maron et al. 2004; Sakai et al. 2001; Stockwell et al. 2003). Some have suggested that the lag time between the initial introduction and resulting spread of an invader might be the result of plants evolving adaptations to these new conditions (Byers et al. 2002; Lee 2002). A growing number of studies have tested this hypothesis and have found evidence for genetically based changes in phenotype in common gardens (Blair and Wolfe 2004; Bossdorf et al. 2005; Bossdorf et al. 2004; Joshi and Vrieling 2005; Leger and Rice 2003; Maron et al. 2004; Siemann and Rogers 2003; Stastny et al. 2005; van Kleunen and Schmid 2003; Wolfe et al. 2004). The hypothesis that motivated most of these studies, proposed by Blossey and Nötzold (1995), is that exotic plants released from their specialist natural enemies in the introduced range might be selected to reallocate energy away from producing costly defenses toward increased growth or reproduction (the evolution of increased competitive ability, or EICA, hypothesis). Such an evolutionary switch in energy allocation might give plants a competitive advantage in the introduced range. However, to date, results from tests of this hypothesis have been mixed. Some studies find that individuals are larger in introduced populations or that defenses are lower, others find the opposite result, and some studies have found no pattern at all (reviewed in Bossdorf et al. 2005).

A challenge in interpreting the results of tests of the EICA hypothesis is that, typically, plants are grown in only one common environment. For example, of the 26 studies that have compared phenotypes between native and introduced populations in common gardens (reviewed by Bossdorf et al. 2005), only five utilized common gardens in more than one environment and only two of those had common gardens in both the native and introduced ranges. Since Bossdorf et al. (2005), 18 additional EICA tests have been published, of which only three were performed in more than one common garden (Genton et al. 2005; Maron et al. 2007; Widmer et al. 2007). The use of only one garden can present problems in interpretation if there are substantial differences in phenotypic plasticity among ranges of origin, i.e. if there are genotype by environment interactions. For example, imagine the situation in which plants collected from introduced populations outperform those from native populations in one common garden, but the reverse is true in another common garden. In this case, data from only one garden might lead one to ascribe differences in performance between native and introduced populations wholly to genetically controlled shifts in plant phenotype, whereas in actuality, phenotypic differences between gardens would indicate a large genotype by environment interaction.

The potential problem of using only one common garden can be further exacerbated if there are large founder effects among introduced populations. Again, imagine the example where exotic genotypes outperform native genotypes of the same species in a single common environment. In this case, this result might be due to the fact that introduced populations were founded by a relatively small number of native genotypes. These introduced genotypes could have originated from a restricted set of native locales where they were adapted to local environmental conditions. If these original environmental conditions happen to be similar to those in the chosen common garden site, then these genotypes might outperform native genotypes. Because native genotypes may come from a greater diversity of populations, some of which experience very different climatic conditions than the garden site, on average, native populations might underperform introduced populations.

To help alleviate these issues, we performed a reciprocal common garden experiment in the native and introduced ranges to compare levels of fixed and plastic differences in phenotype among native and introduced populations of a widespread invasive plant of western North America, houndstongue (*Cynoglossum officinale* L. Boraginaceae). Here we describe experiments where we have used one common garden in each range (in Montana and Germany), but if the logistical challenges could be overcome, having more than one garden in each range would lend greater insight into the strength of genotype by environment interactions. In addition to field garden experiments, we also explicitly manipulated growing conditions (soil nutrient levels) in an outdoor pot experiment in the native range to further explore the magnitude of fixed versus plastic responses in the traits we measured in larger gardens, and to also determine whether threshold flowering size in this semelparous plant has increased in introduced populations. We use results from both the reciprocal field common garden and nutrient addition (pot) experiments to ask: have plant size, fecundity, date of initial flowering, and average plasticity for these three traits increased in populations of *C. officinale* between the native and introduced ranges? Furthermore, in the nutrient addition experiment: has the median threshold flowering size increased between native and introduced populations?

We quantified levels of plasticity among native and introduced genotypes across gardens because it has recently been proposed that selection should favor the evolution of greater plasticity among introduced populations (Richards et al. 2006). Although comparing average levels of plasticity for particular traits between native and exotic genotypes appears straightforward, in practice it can present difficulties. The traditional approach to estimating phenotypic plasticity has been to compare the response of genetically related individuals across multiple sites (Pigliucci 2001). However, in the case of natives vs. exotics, replicating genotypes at the individual, genetic family, population, and regional (native vs. introduced range) levels requires a number of samples that becomes logistically problematic. One solution to this, which we have adopted here, is to compare average differences in plasticity among native and introduced populations, where there are replicate individuals within each population, but not replicate individuals within replicate families within each population. This approach, while less precise than the traditional methods for estimating plasticity, can still be appropriate for comparing native and introduced populations (Muth and Pigliucci 2007; Richards et al. 2006). It is also necessitated, because any comparison of native and introduced phenotypes requires sampling genotypes from a sufficient set of populations across each range to ensure a representative sample of native and introduced genotypes. Only a few studies have explicitly tested for increased phenotypic plasticity using populations from both ranges (DeWalt et al. 2004; Kaufman and Smouse 2001; Maron et al. 2007; Muth and Pigliucci 2007; Bossdorf et al. in Richards et al. 2006).

We measured threshold flowering size to test the life history prediction that relative growth rate and the probability of mortality before reproduction dictate the optimal threshold size for flowering (Roff 1992; Wesselingh et al. 1997). If the probability of pre-reproductive mortality decreases in the introduced range, potentially due to escape from enemies, increased threshold flowering size between native and introduced populations might evolve.

MATERIALS AND METHODS

Houndstongue, *Cynoglossum officinale* L. (Boraginaceae), is native to Europe, where it grows in disturbed sites, open woodlands, meadows and sand dunes (de Jong et al. 1990). Its native range extends from the mountains of western Asia and eastern Europe west to the Netherlands, and north to southern Britain and Scandinavia; it is not present in the southern Mediterranean regions of Europe (de Jong et al. 1990). It was first introduced to North America in the mid-19th century as a feed contaminant and is now present across the U.S. and southern Canada, where it is particularly common in forest clearcuts and overgrazed rangelands (Upadhyaya et al. 1988). It is classified as a noxious weed in six western states, where it occurs at high density and is toxic to cattle and horses (Upadhyaya et al. 1988).

Cynoglossum officinale is a self-compatible, facultatively biennial forb (de Jong et al. 1990) that forms a rosette in its first year after germinating in the early spring, overwinters as a rosette and taproot, and then bolts and flowers in the summer of its second or later year, depending on plant size and environmental conditions. Whether or not plants flower at the end of 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 at the end of the summer consisting of up to four large nutlets. Plants invest all of their stored energy into seed production and then die, with vegetative size prior to flowering positively and highly correlated with seed production (de Jong and Klinkhamer 1988).

A specialist root-boring weevil, *Mogulones cruciger*, that is present only in the native range, preferentially attacks large rosettes and flowering plants, and can reduce seed set (Prins et al. 1992). In the native range, *C. officinale* is also attacked by a specialist stem-boring weevil and two leaf-feeding flea beetles (Schwarzlaender 2000, M. Schwarzlaender, pers. comm.). These specialists are not present in the introduced range, where herbivory by generalists such as Lepidopteron larvae and grasshoppers does not affect plant size or fecundity (J. Williams, unpublished data).

Field common gardens in the native and introduced ranges

We established common gardens in Missoula, Montana and Bad Lauchstädt, Germany (environmental conditions described in Table 2). The soil was tilled in both gardens in March 2004 prior to planting. In Montana, we applied the herbicide Roundup two weeks before tilling to remove existing weeds. We quantified soil nitrogen and carbon from 10 bulk soil samples (collected with a 3 cm diameter soil borer to a depth of 10 cm) from each garden in April 2006, at the conclusion of the experiment. Soil was sieved through 2 mm mesh and then ground in a Wiley mill using a 20 M screen. All samples were analyzed in a CN-Analyzer for %N, %C, C/N ratio and pH. Differences in mean values between the two gardens were evaluated using t-tests that assumed unequal variance between groups. Both gardens were fenced to keep out animals. In Germany, specialist root boring and leaf chewing insects (*Mogulones cruciger* and *Longitarsus* spp., respectively) were not present in the garden.

In 2003, we collected seeds from ten *C. officinale* populations in the native range (Europe) and introduced range (North America), respectively (Table 1). Seeds from each population were collected from 10-15 individuals, separated by at least 1 m. Ten maternal seed sources were randomly selected from each source population and seeds were put into cold stratification for six weeks starting in December 2003 to break seed dormancy. We planted seeds into small pots in greenhouses in Missoula, Montana and Bad Lauchstädt, Germany in early February 2004. Seeds were sown in a 1:1 mixture of compost and sand.

We planted the seedlings into the gardens in Germany on 1 April 2004 and in Montana on 18 April 2004. Each common garden was divided into ten blocks, with one plant from each family randomly assigned to block, for a total of 200 plants per garden (2 continents × 10 populations × 10 maternal families). Every plant in each garden had a sib in the other garden. In Montana, plants within blocks were spaced 0.75 m apart, with blocks separated by 1 m. In Germany, due to space constraints, plants within a block were spaced 0.5 m apart, with 0.9 m separating blocks. Seedlings were watered on the initial planting date, after which they received only ambient rainfall.

We quantified date of first flowering by recording the approximate day that the first flower completely opened on each plant; gardens were visited 2 – 3 times per week during the period of initial flowering. We assessed plant size at the end of the first growing season in fall 2004 by measuring the diameter and height of each rosette and calculating plant volume using the equation for a cylinder. The vast majority of plants in both gardens began flowering in spring 2005 and we harvested all plants after they had set seed in July 2005, but before plants died and released their seeds. In the Montana garden, we directly counted all seeds produced by each plant. In Germany, the plants were too large to count every seed. We therefore estimated fecundity by multiplying the number of inflorescences (cymes) on each plant by the average number of seeds per cyme. We estimated the average number of seeds per cyme by counting the number of seeds on each of 20 randomly selected cymes.

Nutrient experiment

To experimentally determine how variation in resource availability influences plant size, fecundity, date of first flowering and threshold flowering size, we also established an experiment where we manipulated fertilizer levels to create three different nutrient treatments. Seedlings were planted in 1 liter pots with a mixture of, by volume, 67% washed sand and 33% compost soil ("La Terra") and transferred to the experimental garden in Bad Lauchstädt, Germany, on 3 May 2004. Due to logistical constraints, we were only able to perform this experiment in one location. Pots were placed in experimental beds filled with bark mulch to protect them from extreme temperatures. The low nutrient treatment received no additional fertilizer, the medium nutrient treatment received half of the recommended dosage (3 g) and the high nutrient treatment received the recommended dosage of 6 g of slow-release fertilizer (Osmocote 8-9M). Six seed families from each of the 20 populations (10 from the native range and 10 from the introduced range) were randomly chosen for this experiment, as we did not have enough space to use all ten maternal families from each population. We planted one seedling from each family into each fertilizer treatment, so that each replicate consisted of three nutrient levels with one sib at each level. All plants in the nutrient experiment were watered when necessary, because the sand in the small pots dried out quickly. We assessed plant size at the end of the growing season in 2004 and date of first flowering and fecundity in 2005, using the same methods described above for the German common garden.

Statistical analyses

We used analyses of variance (ANOVAs) to examine differences between plants from the native and introduced ranges in plant volume, fecundity and date of first flowering for both experiments. We first ran one analysis to examine overall differences in these three traits, where we treated location of garden (Germany or Montana), range (native or introduced) and the interaction of garden × range as fixed factors, and population nested within range and garden × population nested within range as random factors (Proc GLM in SAS, SAS 9.1, SAS Institute, 2003). Since each garden represented a different environment, a significant main effect of garden indicates plasticity for that trait. A significant interaction between garden and range indicates that the magnitude of the plastic response is dependent on the range of population origin. We report the magnitude of plasticity for each range as the percent increase in the trait ($[(\text{trait}_{\text{Germany}} - \text{trait}_{\text{Montana}})/\text{trait}_{\text{Germany}}]*100$), calculated for each population and then averaged within range. Here we are considering plasticity at the population level, as an average across individuals from each population (Maron et al. 2007; Neubert and Caswell 2000; Richards et al. 2006), rather than in the strict sense, of at the genotype level. We used Tukey post hoc tests to test for significant differences in traits between native and introduced populations in each garden.

To test for among population differences in plasticity, we ran analyses separately for native and introduced populations. We treated garden as a fixed factor and population and garden × population as random factors (Proc GLM, SAS). A significant garden by population interaction indicates that populations within a continent vary in plasticity.

In the nutrient addition experiment, we used ANOVAs to examine both genetically-based and plastic differences in the three traits we measured. Here, we treated nutrient level (low, medium or high), range (native or introduced) and nutrient level × range as fixed factors and population nested within range and nutrient level × population(range) as random factors (Proc GLM, SAS).

To assess threshold flowering size, we used a logistic regression to examine the effect of size in 2004 and range (native or introduced), as well as their interaction, on the probability of flowering in 2005 (Proc Genmod, SAS). Median threshold size is determined as the size at which the probability of flowering is 0.5 (Wesselingh et al. 1997). We used Type III Likelihood Ratio tests to assess significance of the model factors in this analysis.

In all analyses of variance, statistical significance of fixed factors was tested using *F*-tests based on Type III sums of squares, where the error term was calculated from the appropriate combination of random effects. The appropriate denominator degrees of freedom for models with random factors were determined by Satterthwaite's approximation (Satterthwaite 1946). Plant volume and fecundity were natural log transformed in all analyses to meet model assumptions of equal variance.

RESULTS

Field common gardens in the native and introduced ranges

All of the plants in the common gardens on both continents either flowered in their second year or did not survive to flower at all. Survival in the German garden was high (90%) for both native and introduced populations. In the Montana garden, survival of plants from native European populations (77%) was significantly higher than that of plants from introduced North American populations (54%; $\chi^2_1 = 4.93$, $P = 0.026$).

Populations exhibited substantial plasticity in size and fecundity between gardens. In general, plants grown in Germany were much larger and produced more seeds than plants grown in Montana (Fig. 1d, e; Table 3). Introduced and native populations responded differently to the respective growing conditions across gardens, indicated by the significant range of origin by garden interaction (Table 3). Specifically, the magnitude of plasticity of introduced populations was greater, on average, than that of native populations. Introduced populations were, on average, 4659% larger and produced 2344% more seeds in the German garden compared to the Montana garden. This response was higher than that of native populations, which were, on average, 2912% larger and produced 1246% more seeds in the German garden compared to the Montana garden. Although, plants from populations in both ranges flowered earlier in the German garden, on average, we observed no differences in the magnitude of plasticity in flowering phenology between populations from the native and introduced ranges (Fig. 1f; Table 3).

Across gardens, populations exhibited differences in the magnitude of phenotypic plasticity for all traits measured (population(range) × garden was significant; Table 3). However, this significant population differentiation in plasticity was driven by significant differences among native populations. When plants from the native and introduced ranges were analyzed separately, we found no significant differences among introduced populations (population × garden interaction was not significant; plant volume: $F_{9,\,129} = 1.33$, $P = 0.23$; fecundity: $F_{9,\,124} = 1.41$, $P = 0.19$; day of first flowering: $F_{9,\,127} = 0.57$, $P = 0.82$). In contrast, plasticity in all traits was significantly different among native populations (significant population × garden interaction; plant volume: $F_{9,\,153} = 3.29$, $P = 0.001$; fecundity: $F_{9,\,147} = 2.08$, $P = 0.035$; day of first flowering: $F_{9,\,166} = 2.66$, $P = 0.007$).

In the German garden, plants from introduced populations were larger (Fig. 1d; Tukey posthoc test: $P < 0.001$) and produced more seeds (Fig. 1e; Tukey posthoc test: $P = 0.006$) than those from native populations. In contrast, in the Montana garden, plants from native populations produced slightly more seeds on average than those from introduced populations, although these differences were not statistically significant (Fig. 1e; Tukey posthoc test: $P = 0.24$). In contrast to plant size and fecundity, the day of first flowering showed a very different pattern both within and between gardens (Fig 1c, f). Plants from both ranges flowered earlier in the German garden and on average, native populations flowered earlier than introduced populations in both gardens (Fig. 1f; Table 3).

Nutrient addition experiment

Populations from both ranges responded positively to nutrient additions, with plants in the high nutrient treatment attaining significantly larger size in the first year and higher fecundity in the second year (Fig 2a, 2b; Table 4). In all treatments, populations from the introduced range were, on average, larger or produced more seeds. However, the strength of this plastic response was not higher for introduced populations as indicated by the non-significant interaction between nutrient treatment and range of origin (Table 4). Day of first flowering did not change between nutrient treatments, but occurred marginally significantly earlier in native populations (Fig. 2c; Table 4). We observed significant variation among populations for day of first flowering and plant size, but not for fecundity (Table 4).

Although we expected that individuals in the low nutrient treatment might not reach the threshold flowering size, the majority of plants that survived to their second year flowered (97%). Vegetative size was a strong predictor of the probability of flowering ($\chi^2_1 = 52.67$, $P < 0.001$), but we found no significant difference in median threshold flowering size between plants from native and introduced populations in the pot experiment (range: $\chi^2_1 = 2.65$, $P = 0.10$; range × size: $\chi^2_1 = 0.95$, $P = 0.33$). We were unable to detect differences in threshold flowering size in the main common garden experiments, because all plants either flowered in their second year or did not survive.

DISCUSSION

Our study demonstrates the importance of using more than one environment to examine evolutionary changes in invasive plants. The substantial differences in size and fecundity between plants grown in the Montana and German common gardens (Figs. 1d, e) demonstrate that *C. officinale* from both native and introduced populations can respond dramatically to different growing conditions. The fact that introduced populations of *C. officinale* were larger and more fecund, but only in experiments in the native range (Germany), highlights the potential pitfalls of interpreting data collected in only one common environment. Had we conducted experiments only in Germany, we might have concluded that introduced populations had evolved to be larger, and used that as a possible explanation for the success of this invasive plant. However, this was not true in the common garden in the introduced range (Montana), where we observed no significant differences between continent of origin for plant size or fecundity and in fact, plants from populations from the native range were slightly more fecund. Taken together, our contrasting results across gardens do not support the EICA hypothesis, as we found no consistent evidence that introduced populations were significantly larger or more fecund than native populations. However, our results dramatically illustrate that the genetically based differences between native and introduced populations that the EICA hypothesis predicts (Blossey and Nötzold 1995) may not be revealed unless experiments are conducted in more than one location. Additionally, while plasticity may be an important contributor to exotic plant success, its role cannot be determined without growing plants in multiple gardens or habitats.

Even with multiple gardens, a challenge in testing the EICA hypothesis is that common gardens are often assumed to be representative of conditions in the range in which they are located. Yet, no one site can adequately represent conditions across either the entire native or introduced range. In our case, although the gardens represented differences in climate between the Rocky Mountains and Europe, edaphic conditions did not necessarily reflect differences between ranges. For example, plants growing in the German garden were much larger than those occurring in natural populations in either the native or introduced range (J. Williams, unpublished data). Although we found that soil nitrogen content was higher in the Montana garden, we measured the total pool size of N rather than plant-available nitrogen. In Germany, higher nutrient availability at the garden site and a milder growing season, with less extreme summer and winter temperatures and higher summer rainfall, likely explain the absolute size differences between gardens. Differences in size and fecundity were less pronounced in the nutrient addition experiment, with both increasing only slightly between the medium and high fertilizer treatments (Figs. 2a, 2b). These results suggest that factors other than nutrients, potentially size of pots, limited growth and seed production.

Phenotypic plasticity across gardens for size and fecundity was generally higher among introduced populations compared to native populations. Although one might interpret these results as evidence for the evolution of increased plasticity within the introduced range, a more likely explanation may be that founder effects played a strong role in creating the differences we observed. We base this interpretation on three lines of evidence. First, we found no genetically-based phenotypic differentiation in plasticity of size and fecundity among introduced populations and yet significant among population variation in plasticity for size and fecundity among native populations. Second, given the wide variety of habitats where introduced populations occur, in the absence of founder effects it is unlikely that all introduced populations would evolve in a unidirectional way to produce relatively low among-population variation in plasticity. Finally, recent genetic analysis involving more populations than used in our common garden experiments indicate that both allelic diversity and average heterozygosity are lower among individuals from introduced populations compared to native populations (J. Williams, unpublished data). This suggests that introduced populations represent only a subset of diversity found within the native range. It may be that founding genotypes in the native range originated from a portion of Europe where plasticity is particularly high.

The fact that we found substantial plasticity in size and fecundity raises the question of whether such plasticity is adaptive. One possibility is that the large differences in plasticity for traits strongly associated with fitness (fecundity and size) reflects much lower levels of plasticity in underlying physiological traits that directly influence fitness. If physiological traits are more canalized, it could result in reductions in fitness in sites where the environment differs from optimal, since physiological traits would lack the ability to plastically compensate for suboptimal conditions. In a similar reciprocal common garden study involving the invasive plant, *Hypericum perforatum*, Maron et al. (2007) found significantly greater plasticity in size and fecundity than in physiological traits such as water use efficiency and leaf nitrogen.

Unlike our results for size and fecundity, plasticity in date of first flowering showed a very different pattern. Plants from both ranges flowered earlier when growing in Germany than in Montana (Fig. 1f). However, no plasticity in date of first flowering was observed for plants from either range grown at different nutrient levels within the same garden (Fig. 2c). These contrasting results suggest that climatic conditions and the length of the growing season are more important in controlling when plants flower than nutrient availability. Other studies have found similar patterns for date of first flowering in common gardens at different latitudes (Clausen et al. 1940; Griffith and Watson 2006; Jonas and Geber 1999; Lacey 1988). Similar to the fitness related traits we measured, only populations from the native range displayed a significant amount of variation among populations (Fig. 1c). This narrow range of variation and lack of differentiation in introduced compared to native populations offers further support for the presence of a founder effect in introduced populations of *C. officinale*.

Life history theory predicts that threshold flowering size should increase when the probability of pre-reproductive mortality decreases (Roff 1992; Wesselingh et al. 1997), as might be the case with introduced plants that escape their specialist enemies. However, we found no evidence that an evolutionary change in threshold flowering size has occurred in *C. offinicale*. In the nutrient experiment, the vast majority of plants attained threshold size in their first year and were able to flower in the second. In addition, even if plants in the introduced range in North America wait to attain a larger size before flowering, we might not detect this in a common environment with high levels of resources. Instead, when growing conditions are favorable, as in our experiment, plants appear to be able to acquire enough resources to surpass a minimum threshold size.

In conclusion, we found no consistent advantage in size or fecundity of *C. officinale* for introduced populations across gardens, thus offering no support for the EICA hypothesis. However, we did find plasticity for size, fecundity and date of first flowering, with plants able to respond to more favorable environments. This ability to take advantage of favorable growing conditions has long been attributed to weedy species, particularly those that occur in disturbed habitats (Baker 1965). For phenotypic plasticity to explain the increased success of *C. officinale* where it is introduced, we would need to observe higher levels of plasticity in introduced populations for traits that confer a fitness advantage (Richards et al. 2006). Our measurements of average population level plasticity do not fully address the possibility of adaptive plasticity. Rather, our results point to the potential for founder effects to be important among introduced populations. This hypothesis is supported by the lack of differentiation among introduced populations and the narrower range of variation in traits among introduced versus native populations, together with recently analyzed genetic data (J. Williams unpublished data). Future studies of the role of evolution in invasive plants could benefit by explicit consideration of the role of genetic by environmental interactions in affecting the results of common garden experiments.

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Table 1. Conditions in common gardens: Germany garden in Bad Lauchstädt, Saxony-Anhalt, and Montana garden in Missoula, Montana. Bad Lauchstädt climate data from UFZ Department of Soil Physics working group "C/N Dynamics" and Missoula climate data from U.S. National Weather Service, Missoula station; long-term averages reported for both gardens. Soil properties are reported with one standard error of the mean. Significant differences in soil properties between gardens denoted as ** for $P < 0.001$ and * for marginal significance, $0.05 < P < 0.10$.

	Germany garden	Montana garden
Mean annual rainfall (mm)	484	351
Mean January high temperature (°C)	4.0	-0.7
Mean January low temperature (°C)	-0.6	-8.8
Mean July high temperature (°C)	23.9	28.7
Mean July low temperature (°C)	13.8	19.4
Percent soil nitrogen	0.18 ± 0.01	0.35 ± 0.02**
Percent soil carbon	2.46 ± 0.30	4.10 ± 0.23**
Soil carbon/nitrogen ratio	13.58 ± 0.85	11.66 ± 0.06*
Soil pH (measured in water)	7.56 ± 0.06	6.81 ± 0.04**

Table 2. Source populations of *Cynoglossum officinale* seeds used in common gardens.

Continent	State/Country	Collection site	Latitude and longitude
North America	Wyoming	Afton	42°43’N; 110°58’W
North America	Montana	Boulder River	45°39’N; 110°06’W
North America	Montana	Livingston	45°43’N; 110°28’W
North America	Washington	Clarkston	46°25’N; 117°03’W
North America	Idaho	Dworshak Resevoir	46°42’N; 116°17’W
North America	Montana	Ninemile Prairie	46°57’N; 113°32’W
North America	Montana	Lavalle Creek	46°58’N; 114°04’W
North America	Montana	Tamarack Creek	47°21’N; 115°03’W
North America	British Columbia	Fenwick Road	49°33’N; 115°32’W
North America	Alberta	Pincher Creek	49°44’N; 114°02’W
Europe	Hungary	Cobex	46°28’N; 020°25’E
Europe	Hungary	Korduskut	46°30’N; 020°40’E
Europe	Germany	Aseleben	51°28’N; 011°41’E
Europe	Germany	Salziger See	51°29’N; 011°44’E
Europe	Germany	Lettewitz	51°34’N; 011°50’E
Europe	Germany	Hohenerxleben 1	51°51’N; 011°38’E
Europe	Germany	Hohenerxleben 2	51°50’N; 011°37’E
Europe	Netherlands	Bierlap	52°08’N; 004°21’E
Europe	Netherlands	Meijendel Dunes	52°09’N; 004°20’E
Europe	Germany	Neustrelitz	54°22’N; 013°05’E

Table 3. Results from ANOVA testing for plasticity of plant volume, fecundity and date of first flowering between common gardens in Germany and Montana.

	F	df	*P*
Plant volume			
Garden	1271.96	1, 18.8	**<0.001**
Range of origin	26.46	1, 20.2	**< 0.001**
Range × Garden	5.96	1, 18.8	**0.025**
Population (Range)	0.36	18, 18.0	0.98
Population (Range) × Garden	2.53	18, 279	**< 0.001**
Fecundity (total seed production)			.
Garden	609.85	1, 19.0	**<0.001**
Range of origin	0.76	1, 20.8	0.39
Range × Garden	7.70	1, 19.0	**0.012**
Population (Range)	0.38	18, 18.0	0.98
Population (Range) × Garden	1.79	18, 271	**0.026**
Date of first flowering (Julian day)			
Garden	146.83	1, 19.0	**<0.001**
Range of origin	3.90	1, 18.1	0.064
Range × Garden	0.02	1, 19.0	0.89
Population (Range)	6.81	18, 18.0	**<0.001**
Population (Range) × Garden	1.86	18, 271	**0.019**

Table 4. Results from an ANOVA testing for plasticity in plant volume, fecundity and date of first flowering from nutrient addition (pot) experiment.

	F	df	*P*
Plant volume			
Range of origin	17.67	1, 18.0	**<0.001**
Nutrient level	162.97	2, 36.2	**<0.001**
Range × Nutrient level	0.35	2, 36.2	0.70
Population (Range)	3.62	18, 36.1	**<0.001**
Population (Range) × Nutrient	0.58	36, 296	0.98
Fecundity (total seed production)			
Range of origin	5.23	1, 18.4	**0.034**
Nutrient level	41.68	2, 32.8	**<0.001**
Range × Nutrient level	1.43	2, 32.8	0.25
Population (Range)	1.27	18, 37.1	0.26
Population (Range) × Nutrient	0.95	36, 237	0.56
Date of first flowering (Julian day)			
Range of origin	3.74	1, 18.1	0.069
Nutrient level	0.71	2, 37.7	0.50
Range × Nutrient level	0.33	2, 37.7	0.72
Population (Range)	18.54	18, 36.6	**<0.001**
Population (Range) × Nutrient	1.09	36, 252	0.34

FIGURE LEGENDS

Figure 1. Norms of reaction for plant volume (a, d), fecundity (b, e), and day of first flowering (c, f). Both plant volume and fecundity are natural log transformed. Panels a-c show plasticity across gardens, with each line representing mean trait values for individuals from different native (solid lines) and introduced (dashed lines) populations. Panels d-f show averages of population means for each range (native or introduced), with error bars representing one standard error of the mean; when error bars are not visible, they are obscured by the points.

Figure 2. Norms of reaction for plant volume (a), fecundity (b) and day of first flowering (c) from the nutrient experiment. Both plant volume and fecundity are natural log transformed. Panels show averages (± 1 SEM) of population means for each range (native or introduced) at low, medium or high nutrient levels.

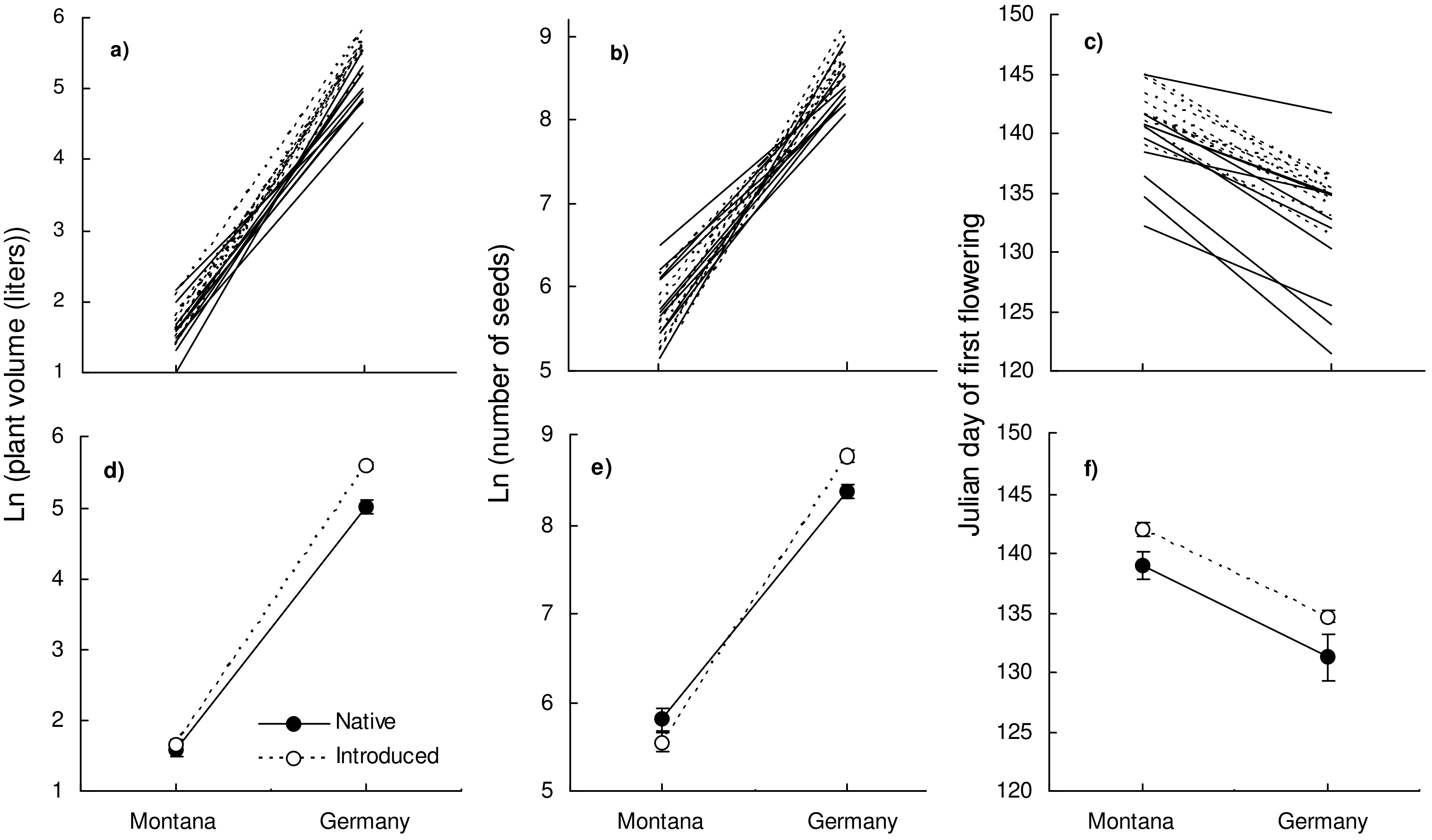
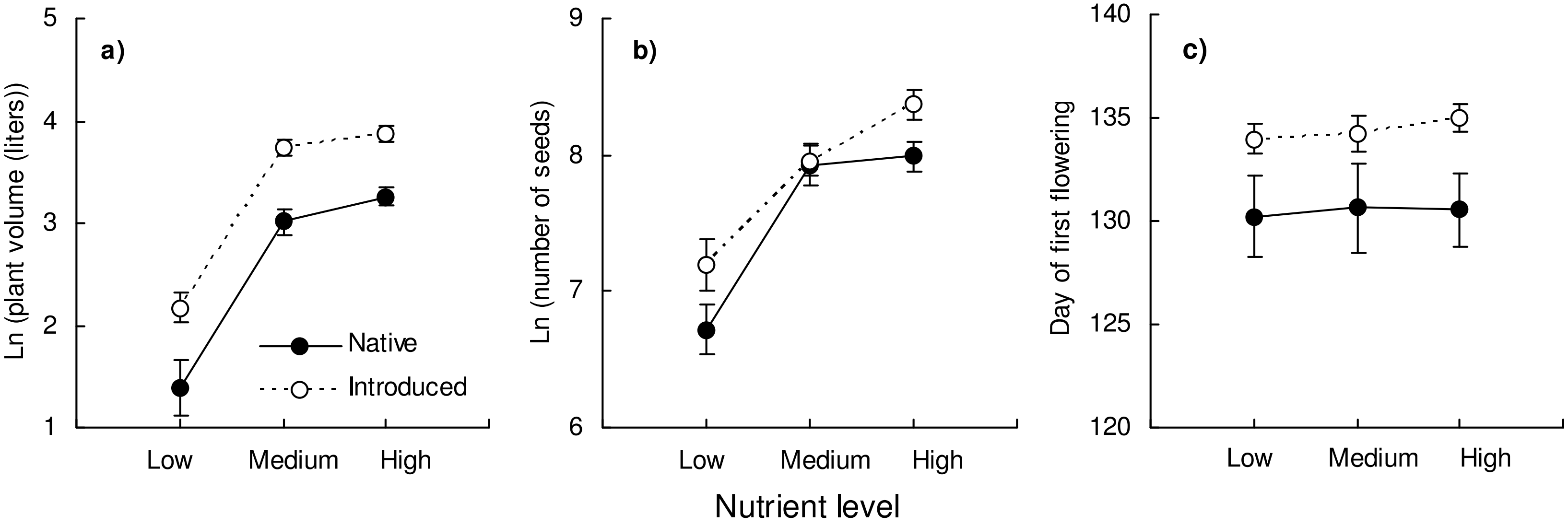

a)
b)
c)
d)
e)
f)
Ln (plant volume (liters))
Ln (number of seeds)
Julian day of first flowering
1
2
3
4
5
6
5
6
7
8
9
120
125
130
135
140
145
150
Native
Introduced
Montana
Germany
Montana
Germany
Montana
Germany

Figure 1



a)
b)
c)
Ln (plant volume (liters))
5
4
3
2
1
Native
Introduced
Ln (number of seeds)
9
8
7
6
Day of first flowering
140
135
130
125
120
Low
Medium
High
Low
Medium
High
Low
Medium
High
Nutrient level

Figure 2

CHAPTER 2

FLOWERING LIFE HISTORY STRATEGIES DIFFER BETWEEN THE NATIVE AND INTRODUCED RANGES OF A MONOCARPIC EXOTIC PLANT

ABSTRACT

Life history theory makes several key predictions regarding flowering strategies in plants. Two such predictions concern optimal flowering size and whether semelparity or iteroparity is favored. I tested these life history predictions and explored how they might differ in the native and introduced ranges of the exotic biennial *Cynoglossum officinale*. I first compared demographic vital rates that underlie when each strategy should be optimal. I then used these vital rates to parameterize integral projection models to calculate population growth rate (λ) as a surrogate 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 much more common than in the native range. The observed and predicted strategy for size at flowering were similar in the native range. However, in the introduced range even though plants flowered at a larger size, the observed size was not as large as the predicted optimum. Iteroparity conferred higher fitness in both ranges, suggesting that severe constraints, potentially specialist herbivores, prevent this strategy from becoming more common in the native range. These results suggest an alternative way that escape from natural enemies may lead to exotic plant success and rapid evolution in the introduced range: changing life history strategy rather than a reallocation from defense to growth.

INTRODUCTION

A long standing puzzle for life history theory has been how both semelparity and iteroparity are maintained in nature. Cole's research highlighted this problem (Cole 1954). Cole asked how there could be so many more perennials than annuals, given that a population of annual plants could achieve the same population growth rate as a population of perennials by simply producing one more seed per year than perennials (Cole 1954; Roff 1992). The apparent paradox was resolved by Charnov and Schaffer (1973), who demonstrated that if juvenile survival is much lower than adult survival, annuals must produce many more seeds than perennials to achieve the same population growth rate. Variation in survival also affects the timing of when an individual, either semelparous or iteroparous, 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 when the optimal time to begin reproducing is (Hart 1977; Klinkhamer et al. 1997; Metcalf et al. 2003; Roff 1992), but empirical tests are still needed.

The flowering strategies of monocarpic plants can provide useful tests of life history theory for a number of reasons. First, although reproduction is fatal in monocarpic plants, individuals can live for two 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 both by the benefits of growing another year, that is having more energy to devote to reproduction, versus the cost of potentially dying before reproduction (Metcalf et al. 2003; Rose et al. 2005). Theory predicts that plants can maximize their lifetime fitness at any range of flowering sizes depending on the specific demographic rates of the individuals involved. Second, individuals of some species that are classified as monocarpic may not actually be monocarpic and can vary the number of times they flower (Hart 1977; Metcalf et al. 2003). A few studies have documented heritable variation both for when to flower and the number of times to flower, as well as significant genetic variance for plasticity (Johnson 2007; Wesselingh et al. 1997). 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 when environmental circumstances lead to differences between juvenile and adult survival, the optimal number of times to flower, (i.e. whether to be annual, biennial or perennial) should change (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). Johnson (2007) found that *Oenothera biennis* switched from annual to biennial across sites that varied in resource availability, with the biennial strategy favored in moderate productivity environments where juvenile survivorship was lower. In variable environments, species with short-lived or nonexistent seedbanks may be able to buffer against fluctuations by spreading seed production across more than one year. In addition to intraspecific variation across habitats or regions, individuals may also vary in 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 others. Such variation within populations is particularly apparent in observed variation in threshold flowering size (Sletvold and Grindeland 2007; Wesselingh et al. 1997).

Species introductions provide excellent opportunities for testing life-history theory because selection pressures can change dramatically between a species' 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 (Jakobs et al. 2004; Memmott et al. 2000; Mitchell and Power 2003; Torchin et al. 2003; Wolfe 2002). Release from enemy pressure may lead to changes in both individual growth and survival, although this is less well documented (but see DeWalt et al. 2004; Reinhart et al. 2003). 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 can tip the optimal strategy from semelparity to iteroparity (Klinkhamer et al. 1997). Second, increased survival due to enemy escape could increase the optimal size at flowering within introduced populations. If there are no genetic constraints, selection might favor a shift from semelparity and flowering at a relatively small size in a plant's native range, where it is subject to mortality from specialist enemies, to iteroparity and flowering at a larger size where plants escape from enemies through introduction (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 demography to examine underlying vital rates and to explore how changes in these vital rates might influence particular life-history solutions (Metcalf and Pavard 2007). By quantifying variation in vital rates, one can make predictions about which life history strategy should be favored under different ecological circumstances. Further, vital rates can be used to parameterize population models, which can yield an estimate of the population growth rate (λ). Since λ is also a surrogate for individual fitness (van Tienderen 2000), one can explore what particular life-history attributes might maximize λ given underlying vital rates (Metcalf et al. 2003; Rees and Rose 2002; Rose et al. 2005).

Here I compare the demography of the exotic biennial houndstongue, *Cynoglossum officinale* L. (Boraginaceae), in its native and introduced ranges. I explore how variation in vital rates across ranges influences the optimal flowering strategies, and then ask how observed life history strategies differ from what may be optimal. 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; Hyatt and Araki 2006; Paynter et al. 2003). Several features make *C. officinale* an interesting system to explore these issues. First, although *C. officinale* is considered a monocarpic biennial, 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 be intense (Prins et al. 1992). 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). Preliminary measurements suggest much more variation in the extent of iteroparity and very different vital rates in the introduced range. Because of this, it is of interest to know whether a shift towards increased iteroparity is favored in the introduced range.

I address the following specific 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 and (3) Do observed flowering strategies match these predictions?

METHODS

Study system

Houndstongue, *Cynoglossum officinale* L. (Boraginaceae), 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-19th century as a feed contaminant and is now present across the U.S. and southern Canada, where it is particularly common in forest clearcuts and overgrazed rangelands (Upadhyaya et al. 1988). It is classified as a noxious weed in six western states, where it occurs at high density (Upadhyaya et al. 1988).

Cynoglossum officinale is a self-compatible, facultatively biennial forb (de Jong et al. 1990) that forms a rosette of basal leaves in its first year after germinating in the early spring, overwinters as a rosette and taproot, and then bolts and flowers in the summer of its second or later year, depending on plant size and environmental conditions (Figure 1). Whether or not plants flower at the end of 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 at the end of the summer 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 prior to 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 (see illustration of iteroparous adults in Figure 1).

A specialist root-boring weevil, *Mogulones cruciger*, that is present only in the native range, preferentially attacks large rosettes and flowering plants, and can reduce seed set (Prins et al. 1992). Adult *M. cruciger* lay their eggs in late fall and during 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, pers. comm.).

Demographic monitoring

From 2004-2007 I monitored the fate of marked *C. officinale* individuals within three populations located in the center of both the native and introduced ranges (Appendix 1). I selected study populations that grew at similar moderate densities and occurred in broadly representative habitats. By studying populations that grew at comparable densities, I minimized the chances that demographic rates would be skewed by large differences in the strength of density dependence across ranges. I also chose sites within the native and introduced range to minimize climatic differences. 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 U.S. than might other populations in central Europe (see Appendix 2 for climate data). Two populations grew in open grassland, and one occurred in an open *Robinia* woodland, with an understory dominated by *Bromus sterilis*. In the introduced range, study populations were within 120 km of Missoula, Montana, USA. Two of the populations occurred in mostly native prairie, dominated by native perennial bunch grasses, with low densities of other introduced species. The third population grew in a former clearcut that was also dominated by native grasses and forbs.

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 in the native range, where densities were lower to include enough individuals. New seedlings were marked in the spring (April in Germany, May in Montana) and uniquely tagged the following summer, when they were one-year olds. In summer, the size of all plants was recorded by counting the number of leaves and measuring length of the longest leaf. At this time (early July in Germany, late July in Montana), plants have set seed, and the number of seeds produced was estimated by counting the number of inflorescences. I counted seeds on a subset of flowering plants to estimate the relationship between inflorescences and seed production.

To more closely examine the transition from seed to seedling, as well as the longevity of seeds in the seedbank, I initiated a seed addition experiment at all six sites in late summer 2004. Details of this experiment are reported elsewhere (J. Williams, Dissertation, Chapter 3). Briefly, I added 80 seeds from locally collected sources to 25 × 25 cm plots in both 2004 and 2005, with six replicates in the first cohort and eight in the second. Germination and the fate of seedlings was followed through summer 2007 in plots with seeds added, as well as those with no seed additions.

Life history monitoring

To document the proportion of *C. officinale* flowering more than once, I used belt transects (50 m × 2 m) that sampled at least 50 plants in 11 populations in the native range and 9 populations in the introduced range (see Appendix 1 for population locations). I expanded the number of sites beyond the 3 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. After plants have set seed it is easy to determine whether a plant will survive to flower again by the presence of basal rosette leaves. From these data, I calculated the proportion of iteroparous plants in populations in each range.

To investigate 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 inflorescences in the year the plants were marked, and followed their fate and reproductive output in the next year (2006 and 2007). Since iteroparity is extremely rare in the native range, I was unable to follow plants there.

Data Analysis

I compared the mean proportion of iteroparous plants in each population between ranges using a t-test that assumed unequal variance. I compared total lifetime fecundity of semelparous and successful iteroparous plants in the introduced range using an analysis of variance that controlled for year and site.

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, fecundity, the size of new adults (one-year olds), and the probabilities of establishment and seedling survival. Size was measured as (number of leaves)*(length of longest leaf), and then log transformed. This composite variable was highly correlated with biomass ($R^2 = 0.96$, $F_{2,97} = 1172.6$, $P < 0.0001$) and easy to measure in the field. To compare vital rates between ranges, range (native or introduced) was treated as a fixed effect and population nested within range as a random effect; significant differences between ranges then indicated that vital rates differed between the regions where the field sites were located. I also included year as a random effect to examine differences in environmental stochasticity, as well as interactions between size, year, and range. Best fit models were selected using Akaike's information criteria (AIC). 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. Analyses were done in SAS, using the MIXED procedure for growth, fecundity, size of new adults, and probabilities of seedling establishment and survival, and the GLIMMIX procedure for the probability of adult survival and the probability of flowering (SAS 9.1, SAS

Institute 2003). The model for survival did not converge when population(range) was included as a random effect, so results are reported with this as a fixed effect.

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, size and number of inflorescences were log transformed and probabilities were arc-sin square root transformed to meet assumptions of equal variance.

Model structure

I used integral projection models (IPMs) to calculate population growth rate (λ) as a surrogate for individual fitness life history strategies at each site, both for a range of flowering sizes and for comparing semelparity versus iteroparity. IPMs are similar to size-based demographic matrix models, but they use continuous relationships between size and vital rates, rather than dividing up the population into discrete size classes (Easterling et al. 2000; Ellner and Rees 2006). They have been used to examine the optimal threshold flowering size in semelparous plants (Metcalf et al. 2003; Rees and Rose 2002; Rose et al. 2005), because unlike in traditional matrix models, the size at flowering is allowed to vary, thus they are particularly well suited to examine life history differences in *C. officinale*.

Here I extend the approach of Rees et al. (2006) to incorporate four discrete stages into the integral projection model framework: three discrete early-life stages, for seeds on adults and in the soil, and seedlings, as well as one class for iteroparous plants (Figure 1). A separate class for seedlings was necessary, because seedling size was not a good predictor of survival or growth (J. Williams, unpublished data), so these plants could not be lumped together with adults. Further, completion of the biennial life cycle (in two years) in the field was extremely rare in the native range and never observed in the introduced range.

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

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

where $n(y, t+1)$ = number of individuals of size y in time $t+1$, $s(x)$ is the survival of individuals of size x, p_f 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 $t+1$. 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 one-year olds and $R(t)$ is the number of recruits at time t.

New seedlings (recruits, described by $R(t)$) can come either from seeds in the seedbank or from seeds produced in the previous year by adults:

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

where $R(t+1)$ = number of recruits (i.e. seedlings) in time $t+1$, p_{eS} and p_{eSB} are the probabilities of seeds establishing from current seeds and seeds in the seedbank, respectively and $S(t)$ and $B(t)$ are the number of seeds on adult plants and in the seedbank, respectively.

Seeds exist in the model in one of two states. They can either be from the current year's seed production, on the dead stalks of adult plants, or in the soil, from the previous year. Current seeds on adult plants can be described by:

$$S(t+1) = \int_{\Omega} p_{eS} f(x) n(x,t) dx \tag{3}$$

The fecundity function is the same as in a typical IPM, where $f(x)=s(x)p_f(x)f_n(x)$, such that the number of seeds produced by an individual of size x ($f(x)$) is equal to the probability of survival ($s(x)$) * probability of flowering $p_f(x)$* size specific fecundity $f_n(x)$ (Ellner and Rees 2006).

If seeds do not germinate in the first year, they can remain in the seedbank until the following year.

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

For *C. officinale*, most seeds germinate the year after they are produced, and a smaller proportion in the second year, but the probability of surviving in the seedbank for multiple years is zero in some populations and very close to zero in others (J. Williams, unpublished data), so the model does not allow for seedbank persistence.

The fecundity equation can be modified to incorporate iteroparous plants. Flowering in all plants is initiated in late summer, when vegetative meristems of those plants that have reaches a minimum threshold size change to flowering meristems(de Jong et al. 1998). Iteroparous plants retain at least one vegetative meristem at this time. The fecundity equation can be modified to include their contribution:

$$f(x) = s(x)p_{\mathrm{f}}(x)[(1 - p_{itero})f_{\mathrm{n}}(x) + p_{itero}f_{itero}(x)] \tag{5}$$

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. They contribute seeds in the following year (average fecundity of f_{itero2}), if they survive to reproduce again (s_{itero}). Following what is observed in the field, where the probability of flowering three times is extremely low, the model allows plants to flower only twice.

I used parameter estimates from the best-fit models for survival, growth, probability of flowering, fecundity, and size of one-year old plants. I first used estimates from models for each site and each year to create 12 different matrices, one for each site in each of the three yearly transitions (2004-05, 2005-06, 2006-07). I then incorporated temporal stochasticity into the models by using average parameter estimates and standard errors derived from the random year effects in the models.

To estimate the probability of seedlings becoming one-year olds in the next year, I used data from marked plants in the demography transects at each site. I calculated survival in each 1 m^2 plot, and then took the average across all plots at each site for each yearly transition. The estimates for the probability of establishment from either seeds on adult plants or in the soil came from the seed addition experiment. 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 on adults that become seedlings (2004-05, 2005-06). To estimate the proportion of seeds germinating from the soil seedbank, 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/number of seeds that did not germinate in 2005). This estimate of p_{eSB} (the probability of establishment from the soil) includes both survival of seeds in the soil from the probability of germinating and surviving as a seedling. In both ranges, seedlings that established three years after seeds were added were extremely rare (fewer than 1%), so the simplifying assumption that seeds cannot remain in the soil seedbank for more than one year is reasonable.

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 λ and vital rate sensitivities and elasticities (Caswell 2001; Easterling et al. 2000; Ellner and Rees 2006; Morris and Doak 2002). 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.

To estimate the predicted flowering size in each range based on current demographic rates, I used an optimality approach similar to the *r*-model previously applied to *C. officinale* (Wesselingh et al. 1997). I calculated λ for a range of median threshold sizes (the size at which more than 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. For each simulation, I calculated relative fitness by scaling λ as a percentage of the maximum for that run of the model. I averaged across all site × year combinations in each range (9 total) to calculate the average optimum for the native and introduced ranges. I could then compare the observed median threshold size to the size which maximized λ.

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 calculated an average matrix for each site, and then compared λ for a population of individuals where the probability of iteroparity was either 0 or 1. Here, I use λ as a surrogate for individual fitness (van Tienderen 2000). In the native range, where iteroparity is extremely rare, I used values from the introduced range for the survival of an iteroparous plant to the second year and fecundity in the second year. Second, I included temporal stochasticity by drawing parameters that varied among years from a distribution with the mean the same as that used in the deterministic simulation. For continuous vital rates, the standard deviations came from the random year effect in the mixed models (Appendix 3); for categorical transitions, I calculated the appropriate beta distribution from the actual values. I started the stochastic simulations using the stable stage distribution vector from the deterministic analysis. In each year, a matrix was generated through a random draw of the vital rates that varied in time, multiplied by the vector from the previous year to calculate a new population size and log growth rate, and then the vector was rescaled to 1 (Morris and Doak 2002). After 5000 iterations, stochastic λ was calculated by taking the mean of the log growth rate from each iteration. Again, I compared the absolute and proportional difference in λ at each site where the probability of iteroparity was either 0 or 1. All matrix simulations and analyses were done using Matlab (Release 14, Mathworks, Inc. 2004).

RESULTS

Differences between ranges in vital rates

Adult survival, average size and growth rate were all higher in populations in the introduced range compared to the native range (Figures 2A, 2B, Table 1, statistical results for all vital rate comparisons in Appendix 4), although these results were marginally significant. Fecundity, as measured by the number of inflorescences produced, did not differ between ranges (Figure 1C, Table 1). Both seedling survival and the size of new adults (one-year-olds) entering the population did not differ significantly between ranges (Figures 2D, 2E, Table 1), but the probability of seedling establishment was higher in the native range (Figure 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 (Appendix 4).

Differences between ranges in threshold flowering size

In the native range, optimality models demonstrated that relative fitness was 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 larger (Figure 3A). In the introduced range, the largest sizes always conferred the highest relative fitness (Figure 3B). 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 (Figure 3C). In the introduced range, plants flowered, on average, when they were bigger than those in the native range, but not at a size as large as the optimum.

Differences between ranges in the degree of semelparity vs. iteroparity

Although a few individuals in the native range occasionally flower more than once, in general, the vast majority of plants are semelparous (Figure 4). In contrast, despite substantial site-to-site variation in the introduced range (the percentage of iteroparous plants ranged from 2 – 45%), the proportion of iteroparous plants was significantly higher in the introduced versus native range (Figure 4; $t_{18} = 3.51$, $P = 0.008$).

If individuals flowered twice, their total lifetime fecundity was higher than that of semelparous plants (Figure 5A; $F_{1, 210} = 28.53$, $P < 0.001$). 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 and had lower lifetime fecundity than semelparous plants (Figure 5A). Thus the fecundity advantage of iteroparity depends on the probability a plant survives to flower in the second year once it has committed to this strategy. To examine where this tipping point might be, I calculated relative fitness as seed production in the first year plus seed production in the second year multiplied by the probability of surviving. This is illustrated for a range of survival probabilities in Figure 5B, in comparison to the semelparous strategy, where relative fitness does not depend on survival. The iteroparous strategy will lead to higher relative fitness when the probability of survival to the second year is 0.53. This is within the range of survival probabilities observed over 2005 – 2007. Total fecundity of iteroparous plants did not differ among sites or years (year: $F_{1, 90} = 2.54$, $P = 0.11$, site: $F_{2, 210} = 2.50$, $P = 0.085$).

Iteroparous plants had higher fitness in comparison to strictly semelparous plants as measured by λ for simulations run in both the native and introduced ranges (Figure

5C). The advantage was higher in a stochastic environment than in the deterministic environment in both ranges, but particularly so in the native range (Figure 5C).

DISCUSSION

Most research on invasive plants occurs where they are introduced, but greater insight into their success can be gained by comparisons between the novel and native ranges (Hierro et al. 2005). Examining differences in demography is a useful place to begin making comparisons, because differences in vital rates can provide clues as to where in a plant's life history release from regulatory factors may occur, thereby enabling the plant to grow at higher densities in the introduced than native range. I found increases in adult survival and individual growth rates in *C. officinale* between its native range in central Europe and its introduced range in intermountain western North America (Table 1). These differences lead to interesting consequences for how flowering life history strategies may change between ranges.

The differences I observed in the size at which plants flower 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 close to the optimal predicted strategy (Figure 3A). In contrast, in the introduced range, where survival was higher, both observed and predicted median threshold sizes were higher than in the native range (Figures 3B, C). These results concur with a study in the native range of *C. officinale*, which found that plants flowered at larger sizes at sites where survival and relative growth rates were higher (Wesselingh et al. 1997). These authors attributed some of the differences in size at flowering and the underlying vital rates to the presence of *Mogulones cruciger*, a specialist root-boring weevil, which did not occur at field sites in Britain (Wesselingh et al. 1997). 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 provided strong selection pressure for a smaller optimal flowering size. The absence of *M. cruciger* in the United States, along with several other specialist herbivores that feed on *C. officinale*, likely contributes to the differences in size at flowering between ranges. Threshold flowering size can be affected by both genetic and environmental contributions (Wesselingh et al. 1997), so whether the shifts in life-history I observed are evolved responses to differential selection pressures across ranges is unclear. However, my results suggest that *C. officinale* may be rapidly evolving changes in life-history in the introduced range in response to reduced specialist enemy pressure.

The absence of *M. cruciger* in the introduced range may also contribute to the shift from almost exclusive semelparity in native populations to some introduced populations exhibiting high frequencies of iteroparity (Figure 4). This life history shift matches the predictions of Klinkhamer et al.'s (1997) theoretical model: that semelparity should be favored when the probability of adult survival is low. The observed higher survival of young plants in the native range compared to the introduced also fits theoretical predictions that semelparity is favored when juvenile survival is high compared to adult survival. This is the first time this life history shift has been explicitly documented in an invasive plant, although authors have speculated that such a shift might occur (Müller-Schärer and Steinger 2004). However, I found that in both ranges, a population of iteroparous individuals would have higher lifetime fitness than a population of semelparous individuals, as measured by λ. This advantage of iteroparity in the native range, where it is rare, suggests severe constraints on this strategy. One such constraint could be that attack by specialist herbivores greatly increases the probability of mortality as plants age. Thus, even if a plant that flowered once were to save energy in a side rosette for a second bout of reproduction in the following year, the probability of that plant surviving given the presence of *M. cruciger* might be extremely low.

Variation in the frequency of iteroparity among introduced populations suggests that escape from specialist herbivores is not the only factor affecting the shift in life history, and that abiotic factors may be important as well. 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 U.S. In contrast, where it is native in central Europe, summer rain is common. This difference in mid-summer moisture may explain the differential survival of early life stages in the introduced range, compared to late life stages, which are less affected by summer drought. 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. The iteroparous strategy confers higher lifetime fecundity only when plants survive, and the observed survival rates were very close to the point at which the advantage occurs (Figure 5B). If some populations have higher background levels of survival to the second year, we 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 (Sletvold and Grindeland 2007). Indeed, the optimality models support this prediction, but I found no variation in the 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 one-year old adults also varied among years; most sites had at least one year where recruitment was very close to zero due to very low survivorship to summer following spring germination. It is this variation in the success of early life stages across years that may contribute to the advantage iteroparity confers as a bet-hedging strategy. I found that iteroparity increases fitness more in a variable environment than in a constant environment (Figure 5C). For a plant such as *C. officinale*, with a short-lived seedbank, spreading the risk of poor recruitment across multiple years is advantageous.

The effects of insects on plant populations, particularly in regard to the escape from natural enemies for exotic species, are typically examined as direct effects of herbivore consumption on plant size or fecundity, with inferred consequences for population growth (DeWalt et al. 2004; Maron and Vilà 2001). The life history shifts in *C. officinale*, to a larger threshold flowering size and increased frequency of iteroparity in the introduced range, provide an example of another mechanism by which herbivores may influence population dynamics via their influence on life history strategy. 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 escaping 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 for genetic shifts to have occurred since the initial introduction.

Finally, much attention on invasive species has focused on the sometimes observed larger sizes of organisms in recipient communities compared to where they are native (Crawley 1987; Grosholz and Ruiz 2003; Thébaud and Simberloff 2001). 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 non-flowering *C. officinale* in the introduced range were, on average, larger than those in native populations. Additionally, in broader scale surveys across both ranges, introduced populations had flowering plants that produced more inflorescences than populations in the native range (J. Williams, unpublished data). These results differ from previous common garden studies, where *C. officinale* from introduced populations were larger and more fecund only in one environment, but the opposite was true in a second common garden in a different environment (Williams et al. In press). 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* is larger, on average, in the introduced versus native range because it flowers at a larger size in North America compared to Europe. This larger size at flowering, in-turn, leads to greater seed production in North American 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 in both the success of introduced plants and more generally, of plant population dynamics.

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Table 1. Differences in vital rates between the native and introduced ranges of *C. officinale*. Plus (+) indicates the range where the vital rate is higher, minus (-) lower, and equals (=), where they are indistinguishable. See Appendix D for results of statistical tests.

Vital Rate	Introduced	Native
Survival	+	–
Size (growth intercept)	+	–
Growth rate	+	–
Fecundity	=	=
Size of 1 year old adults	=	=
Probability of seedling survival	=	=
Probability of seedling establishment (from seeds on adult plants)	–	+
Probability of seedling establishment (from seeds in the soil)	=	=

FIGURE LEGENDS

Figure 1. Life cycle diagram of *Cynoglossum officinale*. In the native range, the transition marked “A” occurs at extremely low probability.

Figure 2. Relationships between size and (A) probability of survival, (B) growth, (C) fecundity and (D) size distribution of one-year old adults. Lines show best fit model predictions for the native and introduced ranges of *C. officinale*. (E) and (F) depict differences in seedling survival and establishment, respectively, between ranges. Displayed functions (A-D) and values (E-F) were used to parameterize integral projection models for each range.

Figure 3. Relationship between threshold size and relative fitness in the native (A) and introduced ranges (B). Dark lines show average relationship, and dotted lines show yearly estimates for each site (three years × 3 sites in each range). Arrows show observed average median threshold size in each range. Observed probability of flowering in each range (C), median threshold size occurs when the probability of flowering in 0.5.

Figure 4. Proportion of plants flowering twice in each range (see Appendix B for population locations).

Figure 5. (A) Fecundity (number of inflorescences) of semelparous and iteroparous plants; solid bars show fecundity in the first year and dashed bar in the second year. (B) Relationship between the probability of plants surviving to flower in their second year mean relative fitness. Fecundity of semelparous plants, which does not depend on survival shown for comparison. (C) Effects of iteroparity on fitness, as measured by population growth rate (λ) for populations of exclusively semelparous or iteroparous plants (mean ± 1 SE for three populations in each range).

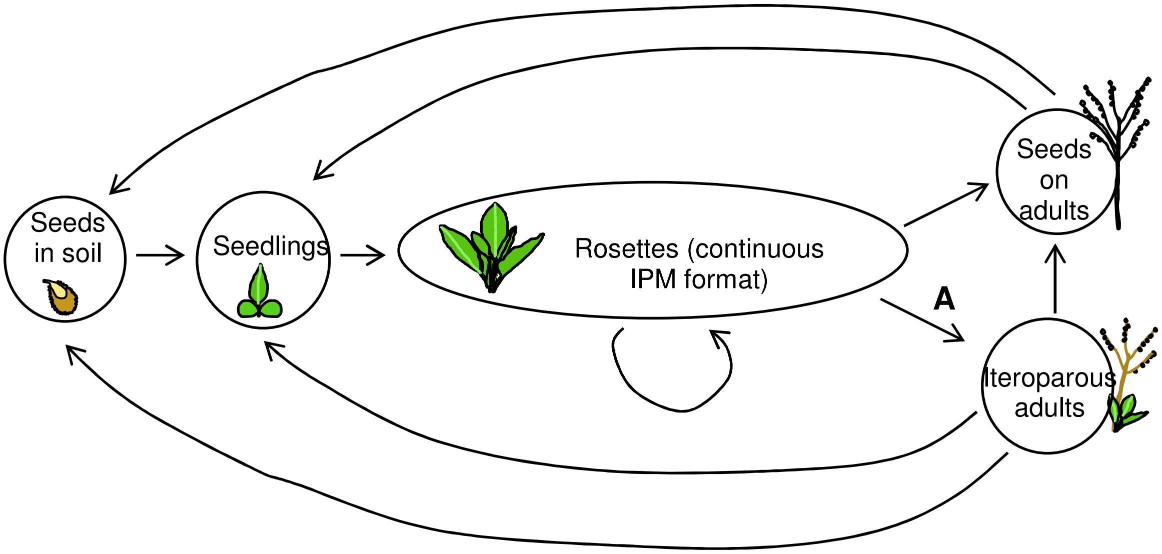

Seeds in soil
Seedlings
Rosettes (continuous IPM format)
Seeds on adults
A
Iteroparous adults

Figure 1

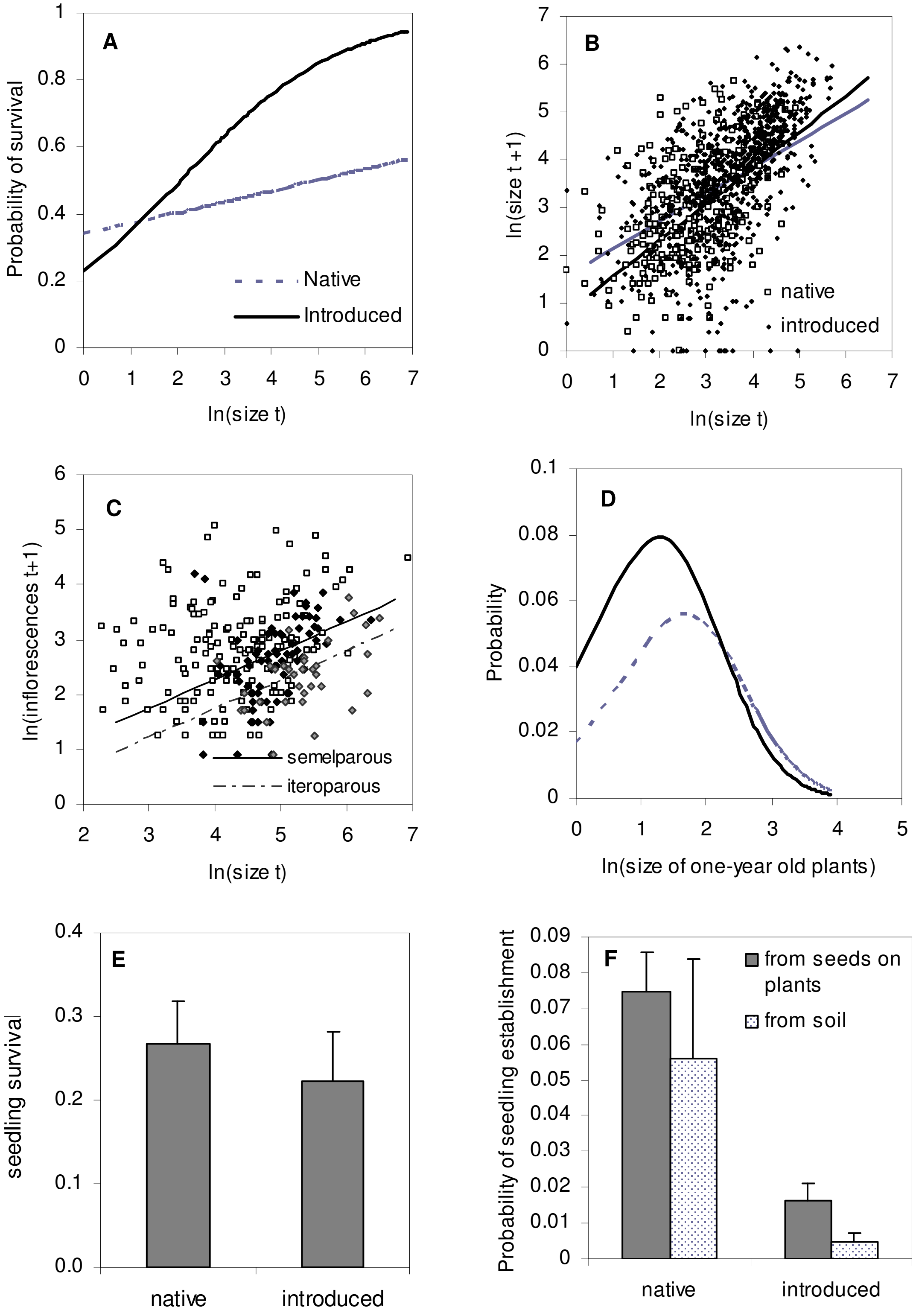

A
Probability of survival
0
0.2
0.4
0.6
0.8
1
Native
Introduced
ln(size t)
0 1 2 3 4 5 6 7
B
ln(size t +1)
0 1 2 3 4 5 6 7
native
introduced
ln(size t)
0 1 2 3 4 5 6 7
C
ln(inflorescences t+1)
0 1 2 3 4 5 6
semelparous
iteroparous
ln(size t)
2 3 4 5 6 7
D
Probability
0 0.02 0.04 0.06 0.08 0.1
ln(size of one-year old plants)
0 1 2 3 4 5
E
seedling survival
0.0 0.1 0.2 0.3 0.4
native
introduced
F
Probability of seedling establishment
0 0.01 0.02 0.03 0.04 0.05 0.06 0.07 0.08 0.09
from seeds on plants
from soil
native
introduced

Figure 2

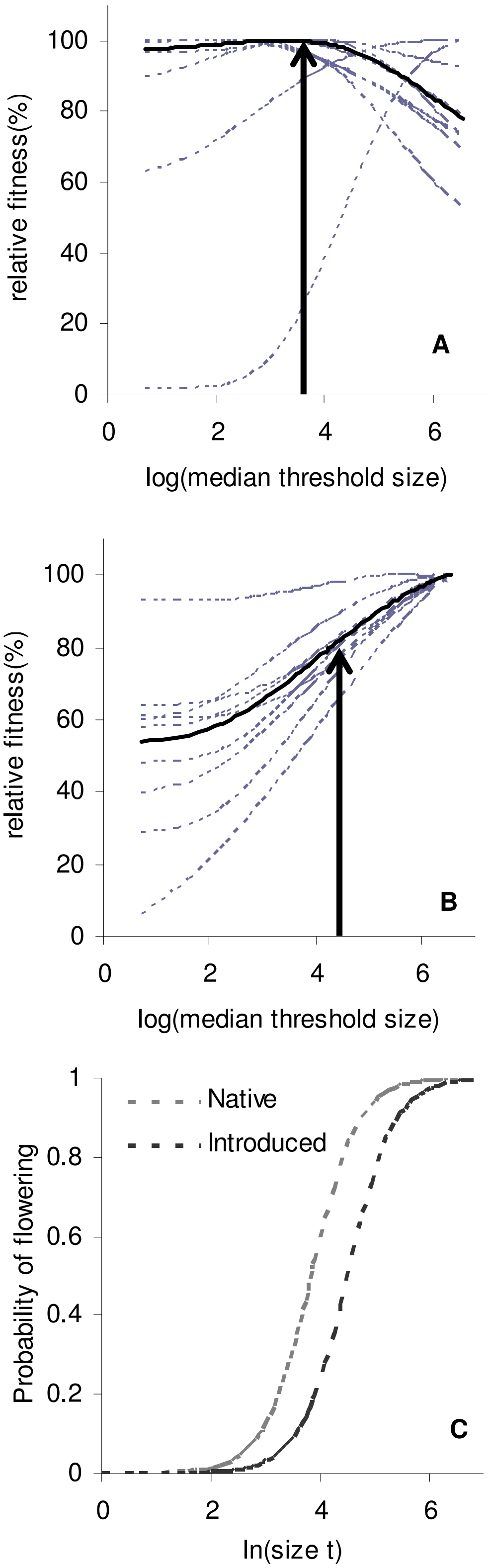

relative fitness(%)
100
80
60
40
20
0
0
2
4
6
log(median threshold size)
A
relative fitness(%)
100
80
60
40
20
0
0
2
4
6
log(median threshold size)
B
Probability of flowering
1
0.8
0.6
0.4
0.2
0
0
2
4
6
ln(size t)
Native
Introduced
C

Figure 3

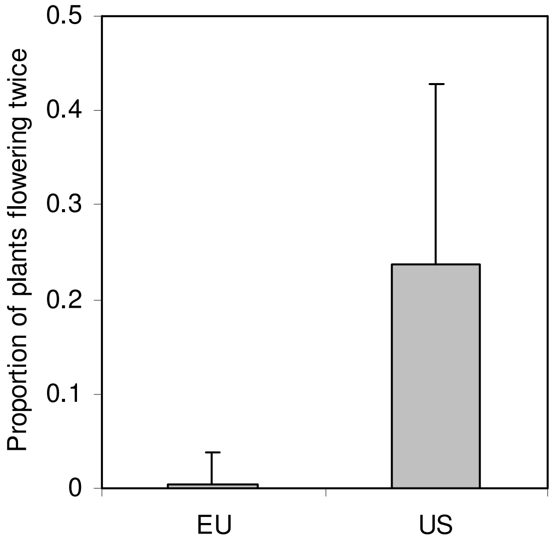


Figure 4

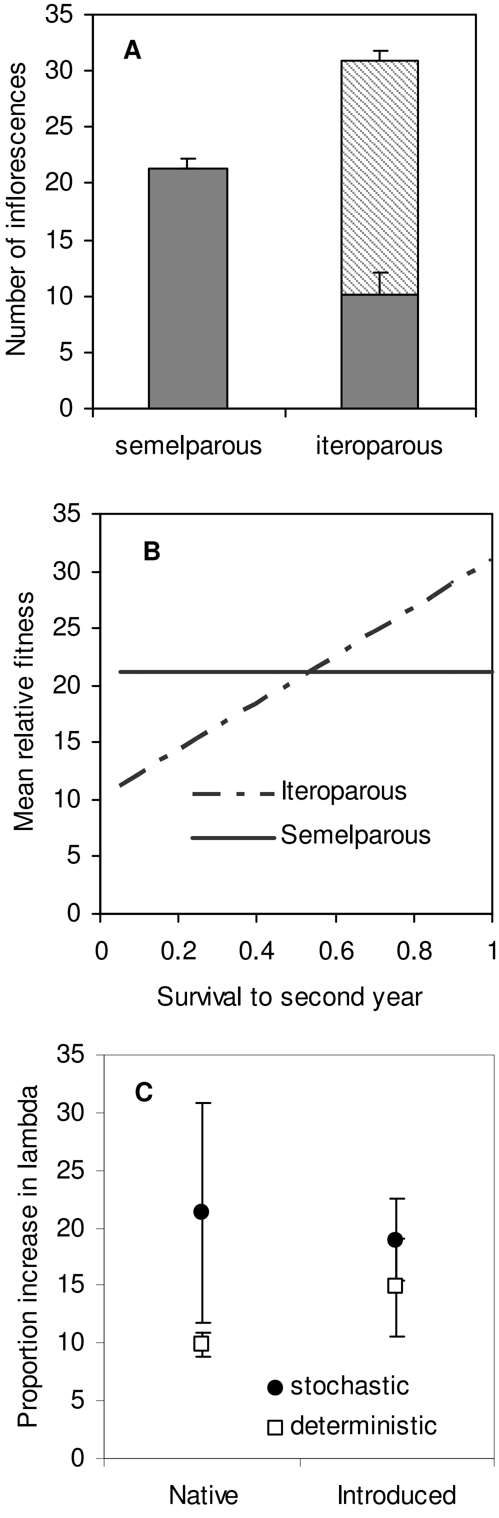
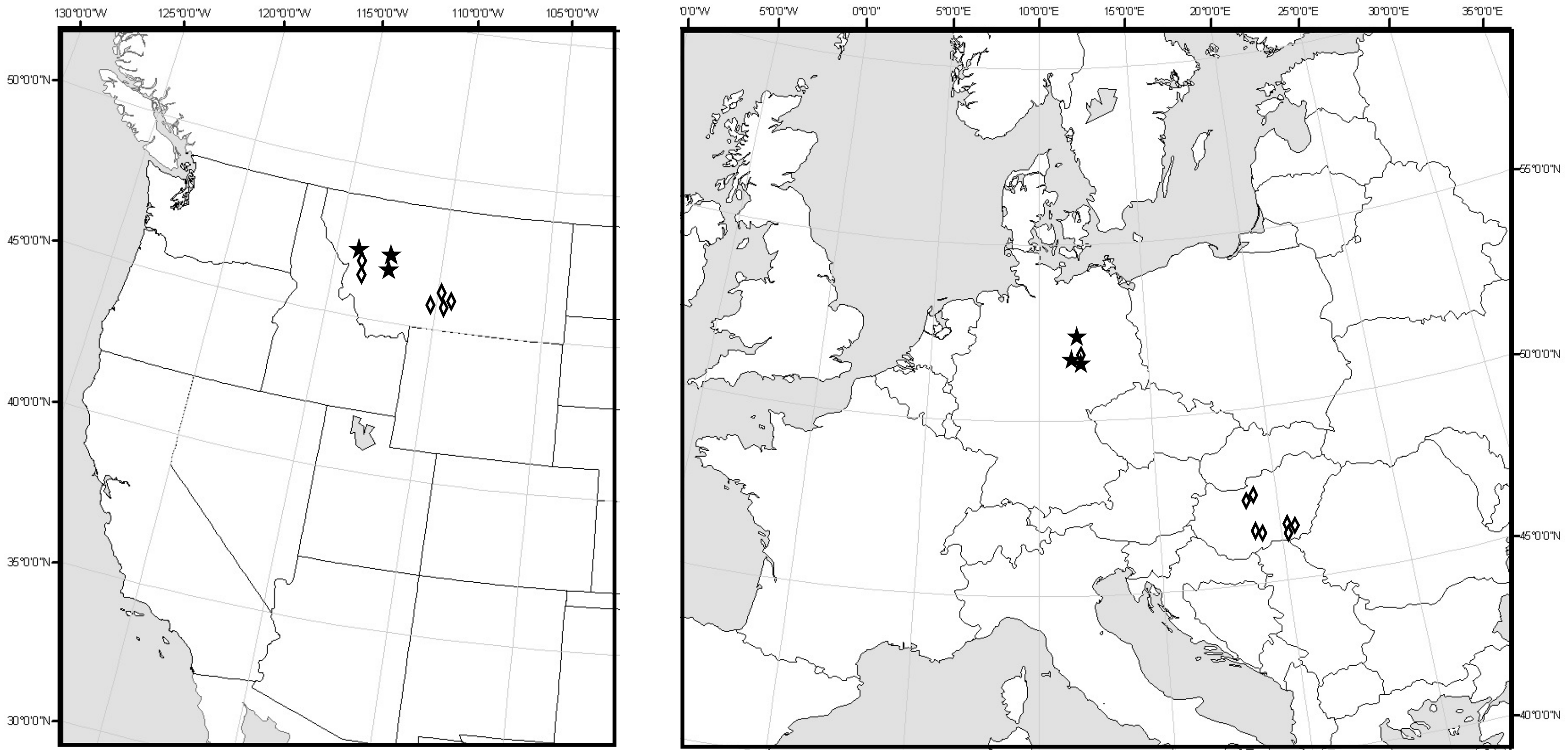

A
Number of inflorescences
0
5
10
15
20
25
30
35
semelparous
iteroparous
B
Mean relative fitness
0
5
10
15
20
25
30
35
Iteroparous
Semelparous
0
0.2
0.4
0.6
0.8
1
Survival to second year
C
Proportion increase in lambda
0
5
10
15
20
25
30
35
● stochastic
□ deterministic
Native
Introduced

Figure 5

Appendix A. Maps depicting approximate locations of populations sampled in the native and introduced ranges of *C. officinale.* Stars indicate locations of focal study populations, open diamonds indicate locations of other survey populations.



Appendix B. Differences in climate between field sites in the native range (near Bad Lauchstädt, Saxony-Anhalt, Germany) and the introduced range (near Missoula, Montana, USA). Germany climate data come from UFZ Department of Soil Physics working group "C/N Dynamics" in Bad Lauchstädt and Missoula climate data from U.S. National Weather Service, Missoula station; long-term averages reported for both gardens.

	Germany	Montana
Mean annual rainfall (mm)	484	351
Mean January high temperature (°C)	4.0	-0.7
Mean January low temperature (°C)	-0.6	-8.8
Mean July high temperature (°C)	23.9	28.7
Mean July low temperature (°C)	13.8	19.4

Appendix C. Model structures and functional forms for error distributions.

Vital rate	Model	Stochasticity
Survival	$s(x) = \dfrac{\exp(b_0 + b_1 \log(x))}{1 + \exp(b_0 + b_1 \log(x))}$	b_0 Normal b_1 Normal
Probability of flowering	$p_f(x) = \dfrac{\exp(b_0 + b_1 \log(x))}{1 + \exp(b_0 + b_1 \log(x))}$	None
Growth	$\log(x_{t+1}) = a_0 + a_1 \log(x_t)$	b_0 Normal b_1 None
Fecundity	$\log(S_{t+1}) = a_0 + a_1 \log(x_t)$	None
Size distribution for 1 year olds	$\ln[R]$	Normal

Appendix D. Comparison of vital rate values between the native and introduced ranges. Range refers to the native and introduced ranges (populations in Germany and Montana, respectively).

	χ^2 or F	df	P
Survival			
size	91.98	1, 2571	< 0.001
range	5.11	1, 2571	0.024
size × range	38.04	1, 2571	< 0.001
year		2	< 0.05
Growth			
size	332.91	1, 1059	<0.001
range	4.61	1, 10.3	0.0565
size × range	11.05	1, 1057	<0.001
site(range)	30.5	4	<0.001
year	92.1	2	<0.001
Fecundity			
size	62.39	1, 264	< 0.001
range	1.35	1, 4.13	0.31
life history (semelparous or iteroparous)	11.60	1, 264	< 0.001
site(range)	30.4	4	<0.001
Probability of flowering			
size	209.61	1, 1370	< 0.001
range	5.35	1, 4	0.082
site(range)		4	< 0.05

Size of 1-year-old adults			
range	0.39	1, 4.05	0.58
site(range)	369.4	4	<0.001
year	55.8	2	<0.001
year × *site(range)*	12.2	8	0.14
Probability of seedling survival			
range	0.28	1, 3.78	0.62
site(range)	10.1	4	0.039
year	25.6	2	<0.001
year × site(range)	24.0	8	0.002
Probability of seedling establishment (from seeds on plants)			
range	14.06	1, 4	0.02
site(range)	4.1	4	0.39
Probability of seedling establishment (from seeds in the soil)			
range	3.82	1, 3.98	0.12
site(range)	18.5	4	0.001
year	18.2	1	<0.001
year × range	28.1	4	<0.001

Note: Random factors (listed in *italic* font) were tested using likelihood ratio tests (χ^2 statistic), except for the models for adult survival and probability of flowering, where AIC was used to select the best model. Fixed factors in mixed models were tested using Type III F tests with numerator and denominator degrees of freedom as listed in the "df" column.

CHAPTER 3

DOES HERBIVORE ESCAPE OR DISTURBANCE EXPLAIN EXOTIC PLANT SUCCESS? A BIOGEOGRAPHICAL TEST

ABSTRACT

A central question in ecology concerns how some exotic plants that occur at low densities in their native range are able to attain much higher densities where they are introduced. This question has remained unresolved in part due to a lack of experiments that simultaneously assess factors that affect the demography and population growth or abundance of plants both where they are native and introduced. We tested two prominent hypotheses for exotic plant success: escape from specialist insect herbivores and disturbance. Within three introduced populations in Montana and three native populations in Germany, we experimentally manipulated insect herbivore pressure and created small scale disturbances to determine how these factors affect the performance of houndstongue (*Cynoglossum officinale*), a widespread, biennial exotic in western North America. Herbivores reduced plant size and fecundity in the native range, but had little effect on plant performance in the introduced range, where they were consumed only by generalists. Small-scale experimental disturbances enhanced seedling recruitment in both ranges but subsequent seedling survival was more positively affected by disturbance in the introduced range than in the native range. We used these experimental results, along with demographic data from each population to parameterize population models to assess how enemy escape and disturbance might differentially influence *C. officinale* in North America versus Europe. Model output suggests that escape from specialist insects, through its positive effects on fecundity, only slightly increases the growth rate (λ) of introduced populations. In contrast, the greater differential response to disturbance in the introduced versus native range had much greater positive effects on λ than did enemy escape. These modeling results suggest that the differences in response to small disturbances by *C. officinale* may contribute to higher abundance in the introduced range compared to at home.

INTRODUCTION

Human mediated transport of organisms across continents has drastically increased over the past two hundred years, leading to unprecedented rates of biological invasion (Levine and D'Antonio 2003). A subset of introduced species is particularly problematic, because they occur at dramatically greater abundance where introduced compared to where they are native. Plants that grow at very high density where introduced have great potential to fundamentally alter the systems they invade, changing ecosystem function and drastically reducing the abundance of native organisms (D'Antonio and Vitousek 1992, Schmitz et al. 1997, Walker and Steffen 1997, Mack et al. 2000). Yet, how some invaders attain such high densities in their introduced ranges, given that they that occur at lower densities in their native range, remains an unresolved problem in ecology. Although many non-mutually exclusive hypotheses have been proposed to explain exotic plant success, few have received rigorous experimental tests (Shea and Chesson 2002).

One of the oldest and most prominent explanations for exotic success is the enemy escape hypothesis. This hypothesis posits that release from specialist herbivores or pathogens drives the increase in abundance of an exotic species in its new range (Elton 1958, Keane and Crawley 2002). While broadly cited, evidence supporting the enemy escape hypothesis remains mostly anecdotal (but see Reinhart et al. 2003, DeWalt et al. 2004). While increasing evidence indicates that exotic plants have reduced herbivore or pathogen loads (Memmott et al. 2000, Wolfe 2002, Mitchell and Power 2003, Torchin et al. 2003, Jakobs et al. 2004, Vila et al. 2005), and thus less damage compared to where they are native (Reinhart et al. 2003, DeWalt et al. 2004),whether this difference in damage explains the sometimes dramatic increases in plant abundance across ranges remains unclear (Maron and Vilà 2001). Two conditions must be met for the enemy escape hypothesis to explain the differential success of exotic plants: first, plant population abundance must be limited by enemies in the native range; second, lower rates of attack or damage in recipient communities must translate to higher population growth or abundance (Jongejans et al. 2006).

A second prominent explanation for invader success is disturbance (Baker 1974, Hobbs 1989, Hobbs and Huenneke 1992, Williamson 1996, Davis et al. 2000, Mack et al.

2000), although this is rarely tested (but see Parker 2001, Kellogg and Bridgham 2004, Hierro et al. 2006, Britton-Simmons and Abbott 2008). Disturbances are thought to facilitate invasion by opening safe sites for colonization and increasing resource availability, which ruderal invaders exploit more quickly than most native plants (Hobbs and Huenneke 1992, Seabloom et al. 2003). Yet, in their native range, exotic plants also encounter disturbance. Thus, for disturbance to truly explain their success, disturbances either need to be more frequent in recipient communities and/or introduced plants need to respond more favorably to disturbance than in the native range.

This highlights an important issue in invasion biology, which is that understanding the differential success of exotic species in their native and novel habitats requires a biogeographical approach. Such an approach demands that parallel experiments exploring the effects of various factors on plant demography and population growth be conducted in both ranges (Hierro et al. 2005). Most research that has addressed the question of success of exotic plants, however, has focused solely on the effects of particular factors on exotic plant performance in recipient communities. Two notable exceptions are DeWalt et al.'s (2004) study, which demonstrated that in some habitats, herbivory on seedlings decreased the survival of an exotic shrub more in its native range than in its introduced range. Second, Hierro et al.'s (2006) study demonstrated that disturbance had a greater effect on the biomass and fecundity of an annual forb in the introduced than native range. Beyond these studies, we know of no work that has examined the relative importance of multiple factors in influencing exotic plant success in both ranges.

A particular challenge to understanding exotic plant success is that some life stages are more readily measured than others, and differences in performance of these life stages may or may not translate to enhanced population growth or abundance. One way to accomplish this is to combine experimental results and plant demographic data in population models to forecast the effects of particular processes on plant population growth. Even for native plants, common biotic interactions such as herbivory have well documented negative effects at the individual level, but an understanding of how these interactions influence plant abundance is still limited (Ehrlen 1995, Louda and Potvin 1995, Kelly and Dyer 2002, Maron and Crone 2006, Kolb et al. 2007). Conversely, demographic studies of plants are common (Harper 1977, Silvertown et al. 1993, Franco and Silvertown 2004), but are infrequently integrated with experimental studies on the effects of biotic interactions or abiotic factors.

Here we report results from parallel manipulative experiments conducted in the native and introduced ranges to simultaneously test the roles of natural enemy escape and small-scale disturbances in explaining the success of houndstongue (*Cynoglossum officinale*), a widely distributed exotic plant. In the same populations in which experiments were conducted, we quantified the demography of *C. officinale* and then used these data to parameterize integral projection population models. This enabled us to forecast how herbivory or disturbance might differentially influence *C. officinale* population growth in both ranges. We also performed larger scale surveys across portions of the native and introduced range, to quantify the difference in population abundance of *C. officinale* at home and abroad. These combined approaches enabled us to determine: 1) the magnitude of difference in *C. officinale* population abundance between Europe and North America, 2) whether the intensity of insect herbivory varies between ranges, and how herbivore pressure in each range influences plant survival and reproduction. 3) whether the frequency of small-scale disturbances and the effect of experimentally-induced disturbances on plant recruitment and subsequent performance differ between ranges, and 4) the cumulative influences of these interacting factors on projected population growth of *C. officinale* in both ranges.

METHODS

Study system

Houndstongue, *Cynoglossum officinale* L. (Boraginaceae), 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-19th century as a feed contaminant and is now present across the U.S. 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 western states, where it occurs at high density and is toxic to livestock (Upadhyaya et al. 1988).

Cynoglossum officinale is a self-compatible, facultatively biennial forb (de Jong et al. 1990) that forms a rosette of basal leaves in its first year after germinating in the early spring, overwinters as a rosette and taproot, and then bolts and flowers in the summer of its second or later year, depending on plant size and environmental conditions (see life cycle diagram in Figure 1). Each flower produces fruits at the end of the summer 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). Seeds require cold stratification to break dormancy (van Breemen 1984).

Small-scale disturbances are known to enhance recruitment of *C. officinale* in the native range (de Jong and Klinkhamer 1988). A specialist root-boring weevil, *Mogulones cruciger*, that is present only in the native range, preferentially attacks large rosettes and flowering plants, and can reduce seed set (Prins et al. 1992, Schwarzlaender 1997). Houndstongue is also attacked by a specialist stem-boring weevil and two leaf-feeding flea beetles, *Longitarsus* spp (Schwarzlaender 2000, M. Schwarzlaender, pers. comm.).

We selected three study populations from the center of each range that occurred in broadly representative habitats, where climatic differences were minimized (map of locations in Appendix 1). In the native range, we 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 U.S. than might other populations in central Europe (J. Williams, Dissertation Chapter 2). Two populations grew in open grassland, and one occurred in an open *Robinia* forest, with an understory dominated by *Bromus sterilis.* In the introduced range, study populations were within 150 km of Missoula, Montana, USA. Two of the populations occurred in mostly native prairie, dominated by native perennial bunch grasses, with low densities of other introduced species. The third population grew in a former clear-cut but that was also dominated by native grasses and forbs. We chose populations in both ranges that were not at the maximum density, so that population dynamics would not be driven by density dependence.

To quantify differences in abundance across ranges at an additional 10 sites in the native range (across 700 km in Hungary and Germany) and 7 sites in the introduced range (across 500 km in Montana), we measured plant density (Appendix 1). All sites occurred in similar habitat to the sites we used for the experiments and intensive demographic monitoring. In two 1 × 10 m transects located in the densest part of each population, we counted the number of vegetative and flowering plants, and then calculated the average density of adult plants. Since these surveys were conducted opportunistically throughout the growing season, we did not include seedlings in the analysis.

Small-scale disturbances

We documented the amount of disturbance at each of the three primary study sites in each range using two 50 × 1 m transects. We recorded the size and location of each disturbance, defined as bare or turned over soil, and then calculated the proportion of disturbed ground.

Since disturbance had previously been shown to affect the success of early life stages (de Jong and Klinkhamer 1988), we examined the relative impacts of small-scale disturbances on recruitment and subsequent seedling establishment in both the native and introduced ranges. In 2004, we established 4 - 25 × 25 cm plots in each of 6 experimental blocks at each of the three primary sites in Germany and Montana. Half of the plots were cleared by clipping all vegetation and then disturbing the top 5 cm of soil with a small rake and hoe to simulate natural disturbances. In the native range, these natural disturbances are caused by rabbits (*Oryctolagus cuniculus*), moles (*Talpa europa*) and wild boar (*Sus scropha*); in the introduced range, they are caused by ground squirrels (*Spermophilus* spp.), gophers (*Thomomys* spp.) and cattle. We added seeds collected from the same site to plots at the end of the summer, when plants typically disperse their seeds. We added 0 or 80 seeds to each plot in 2004; this density was chosen to reflect the natural density of seeds that would drop under a parent plant (*C. officinale* produced heavy seeds that are not wind dispersed). We repeated these experiments in summer 2005 within 8 newly established experimental blocks at each site. Plots within a site were separated by 1 m, and blocks by 20 – 100 m. We followed germination of seeds in disturbed and control plots beginning in 2005, during the spring and summer, and monitored survival and new recruitment of both cohorts through 2007.

Small-scale disturbances may change not only the biotic environment by eliminating competition, but they may also affect abiotic conditions, which in turn could affect plant performance. To determine whether experimental disturbances increased nutrient availability, we buried mixed-bed ion exchange resin capsules (Unibest Inc., Bozeman, Montana, USA) at a depth of 5 cm in early spring 2005 to disturbed and undisturbed plots in each of the 6 blocks at each site, where no *C. officinale* seeds were added. At the end of the growing season in 2005 we excavated the resin capsules, put them on ice and immediately returned them to the laboratory. Subsequently, we extracted NO_3^- and NH_4^+ by bathing each capsule in three sequential 30-minute rinses of 2 M KCl (10 mL per rinse). Capsules were gently shaken on a shaker table during each rinse, after which KCl extracts were decanted to create a total extract volume of 30 mL. Extracts were then analyzed for NH_4^+ and NO_3^- on an Autoanalyzer III (Bran Luebbe, Chicago, IL) at the University of Montana Soils Laboratory.

Escape from specialist herbivores

We initiated herbivore exclusion experiments at two sites each in Montana and Germany in April 2004. At each site, we planted 85-100 *C. officinale* seedlings (germinated in greenhouses from seed collected at each site in 2003); transplants were necessary due to low abundance of plants in the native range in 2004. To ensure a large enough sample size and to take year-to-year environmental variation into account, we added a new cohort of 40-50 haphazardly selected naturally occurring rosettes in spring 2005 at the same two sites in the native range and at all three sites in the introduced range. One site in the native range was located on a nature preserve, where it was not permitted to spray insecticide, so we were unable to include plants at this site.

Half of the plants were treated with insecticide as a soil drench every 3 weeks to exclude herbivorous insects. Each plant received 1.8 mg of imidacloprid in 30 mL of water, at a rate of 1800 g/ha (in Germany, Provado 5 WG, Bayer AG, Leverkusen, Germany; in Montana, Advanced Garden Tree & Shrub Insect Control, Bayer Advanced LLC, Birmingham, AL). Imidacloprid is a systemic insecticide designed to exclude sucking insects. To facilitate uptake of the insecticide in dry soils, plants treated with insecticide received an additional 70 mL of water for a total of 100 mL; control plants (no insecticide) also received 100 mL of water. In addition to the soil drench, insecticide (or water as a control) was sprayed on the leaves beginning in 2005, when higher leaf feeding rates were observed. The insecticide did not reduce or stimulate growth or survival, as compared to only water, in a preliminary experiment in the greenhouse, where plants were grown in 1 L pots and insecticide was applied every 3 weeks, as in the field ($F_{1,38} = 2.31$, $P = 0.13$).

We followed growth and survival of the plants at bimonthly intervals during the 2004 – 2006 growing seasons. Plant size was assessed by counting the number of leaves and measuring the length of the longest leaf; the product of these two measurements is highly correlated with plant biomass ($R^2 = 0.96$, $F_{2,97} = 1172.6$, $P < 0.0001$). We also visually estimated leaf damage at each census by classifying damage on a scale of 1 – 5: 1 = 0%, 2 = < 10%, 3 = 11-25%, 4 = 26-50%, 5 = > 50%. We measured fecundity on all plants that flowered in 2005 and 2006, by counting the number of seeds produced by each plant, and dissected tap roots of flowering plants to look for evidence of weevil herbivory

Statistical analyses

We compared plant density between ranges, as measured by the average number of adult plants per m^2, using a t-test. The proportion of disturbed ground at each of the three sites in each range was compared using an analysis of variance, with range and site nested within range as fixed factors in the model. Differences in total plant-available nitrogen sorbed to ion-exchange resin capsules ($NO_3^- + NH_4^+$) were assessed using an ANOVA (Proc GLM, SAS, Type III sums of squares) with range, site(range), disturbance and range × disturbance as model factors. Tukey posthoc tests were used to compare differences between groups.

In the disturbance experiment, total first year recruitment, cumulative recruitment over two years, seedling survival to one-year old adults and final plant establishment in disturbed and undisturbed plots were analyzed using ANOVA. Range, disturbance treatment, year (of experiment initiation), range × disturbance, year × disturbance, and site nested within range were fixed factors in all models. Site, nested within continent was treated as a fixed effect in these analyses for two reasons. First, one assumption of the experimental design was that the effects of disturbance differed between ranges, but not between sites within a range. Second, to appropriately test the interaction between range × disturbance when site(range) is random, models would need to include a site(range) × disturbance as a random factor and with low replication at the site level, these models would not converge. Although the experiment was designed as a randomized complete block design, models did not converge when block(site(cont)) was included.

We quantified leaf herbivory, measured on a categorical scale from 1 – 5. We compared this index between the control and insecticide treatments using a non-parametric Kruskal Wallis test, because these categorical data were not normally distributed. Effects of the insecticide treatment on plant size and fecundity were analyzed separately for each continent due to unequal sample sizes and variances with an ANOVA, with site, insecticide treatment and year as factors.

Total nitrogen, numbers of seedlings, plant size and fecundity were log-transformed and seedling survival was arcsine square-root transformed to meet assumptions of equal variance.

Demographic monitoring

At each of the three primary sites in each range, we followed the demographic fate of all individuals in two 1 × 10 m transects that included at least 100 plants. These transects were lengthened in the native range where densities were lower to include enough individuals. New seedlings were marked in the spring (April in Germany, May in Montana) and uniquely tagged the following summer, when they were one-year olds. In summer, the size of all plants was recorded by counting the number of leaves and measuring length of the longest leaf. At this time (early July in Germany, late July in Montana), plants have set seed, and the number of seeds produced was estimated by counting the number of inflorescences. We counted seeds on a subset of flowering plants to estimate the relationship between inflorescences and seed production. To more closely examine the transition from seed to seedling, as well as the longevity of seeds in the seedbank, we used results from the disturbance experiment.

Population model

We used integral projection models (IPMs) to calculate the population growth rate (λ) under different scenarios of disturbance and herbivory. IPMs are similar to size-based demographic matrix models, but they use continuous relationships between size and vital rates, rather than dividing up the population into discrete size classes (Easterling et al. 2000, Ellner and Rees 2006).

Here we extend the approach of Rees et al. (2006) to incorporate four discrete stages into the integral projection model framework: three discrete early-life stages, for seeds on adults and in the soil, and seedlings, as well as one class for iteroparous plants (Figure 1). A separate class for seedlings was necessary, because seedling size was not a good predictor of survival or growth (J. Williams, unpublished data), so these plants could not be lumped together with adults. Further, completion of the biennial life cycle (in two years) in the field was extremely rare in the native range and never observed in the introduced range.

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

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

where $n(y, t+1)$ = number of individuals of size *y* in time *t* +1, $s(x)$ is the survival of individuals of size *x*, p_{f} is the probability of plants of size *x* flowering, and $g(y, x)$ is the size an individual of size *x* will be in *t* +1. The second term is the new adults entering the population, where p_{SR} is the probability of a seedling becoming an adult, $f_{\mathrm{r}}(y)$ is the size distribution of one-year olds and $R(t)$ is the number of recruits at time *t*.

New seedlings (recruits, described by $R(t)$) can come either from seeds in the seedbank or from seeds produced in the previous year by adults:

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

where $R(t+1)$ = number of recruits (i.e. seedlings) in time *t* +1, p_{eS} and p_{eSB} are the probabilities of seeds establishing from current seeds and seeds in the seedbank, respectively and $S(t)$ and $B(t)$ are the number of seeds on adult plants and in the seedbank, respectively.

Seeds exist in the model in one of two states. They can either be from the current year's seed production, on the dead stalks of adult plants, or in the soil, from the previous year. Current seeds on adult plants can be described by:

$$S(t+1) = \int_{\Omega} p_{eS} f(x) n(x,t) dx \tag{3}$$

The fecundity function is the similar to a typical IPM, where

$$f(x) = s(x)p_{\mathrm{f}}(x)[(1 - p_{itero})f_{\mathrm{n}}(x) + p_{itero}f_{itero}(x)] \tag{4}$$

such that the number of seeds produced by an individual of size x ($f(x)$) is equal to the probability of survival ($s(x)$) * probability of flowering $p_{\mathrm{f}}(x)$* size specific fecundity $f_{\mathrm{n}}(x)$ (Ellner and Rees 2006). In the introduced range, flowering twice can be common and this function allows for that with the inclusion of p_{itero}, the probability that a flowering plant will be iteroparous and $f_{itero}(x)$, the size-specific fecundity of an iteroparous plant in the first year it flowers. Iteroparous plants can remain alive with a probability of $s(x)p_{\mathrm{f}}(x)$ p_{itero}. They contribute seeds in the following year (average fecundity of f_{itero2}), if they survive to reproduce again (s_{itero}).

If seeds do not germinate in the first year, they can remain in the seedbank until the following year.

$$B(t+1) = (1 - p_{eS})S(t) \tag{5}$$

For *C. officinale*, most seeds germinate the year after they are produced, and a smaller proportion in the second year, but the probability of surviving in the seedbank for multiple years is zero in some populations and very close to zero in others in both ranges (J. Williams, unpublished data), so the model does not allow for seedbank persistence.

We used data from demographic monitoring plots at each site to estimate all parameters in these models, except for seedling establishment and seedling survival (p_{SR}), which came from the disturbance experiment. The best-fit statistical models for survival, growth, probability of flowering, fecundity, and size of one-year old plants are described in detail in Williams (2008, Dissertation Chapter 2). We used estimates from models for each site and each year to create 12 different matrices, one for each site in each of the three yearly transitions (2004-05, 2005-06, 2006-07).

The estimates for the probability of establishment from either seeds on adult plants (p_{eS}) or in the soil (p_{eSB}) came from the disturbance experiment. In each plot, we 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 on adults that become seedlings (2004-05, 2005-06). To estimate the proportion of seeds germinating from the soil, we calculated the proportion of seeds that germinated and survive 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/number of seeds that did not germinate in 2005). This estimate of p_{eSB} includes both survival of seeds in the soil from the probability of germinating and surviving as a seedling. To estimate the probability of seedlings becoming one-year olds in the next year (p_{SR}), we used data from disturbed and undisturbed plots in the disturbance experiment. We calculated average seedling survival at each site in disturbed and undisturbed plots for 2005-06 and 2006-07, and used the average of the two years for 2004-05. These values were comparable with seedling survival in the demographic monitoring plots (J. Williams, unpublished data).

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 λ and vital rate sensitivities and elasticities (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.

For each of the following disturbance scenarios, we calculated deterministic λ for each site in each year with: (1) no disturbance, (2) mean disturbance, and (3) maximum disturbance. For the mean disturbance scenario, we used parameter values from experimentally disturbed plots in each site and each year for seedling survival (p_{SR}) and probabilities of establishment from seeds on plants and in the soil (p_{eS} and p_{eSB}). For the maximum disturbance scenario, we used the highest yearly average at each site for all 3 transitions. The maximum disturbance scenario was included to explore how disturbance could affect λ under the best case scenario that we observed. At each of these levels of disturbance, we calculated λ for background levels of herbivory and for a scenario when insects were excluded. For the insect exclusion scenario, we increased fecundity in the native range by the amount observed in the experiment. Here we report average λ for each range, across 3 sites and 3 yearly transitions, with 95% confidence limits, calculated from the *t*-distribution for n = 9.

To more carefully examine which vital rates contributed to the observed differences in λ, we used a Life Table Response Experiment (LTRE, Caswell 2001). This approach decomposes differences in λ between treatments into contributions by each vital rate. For the LTRE, we compared λ in the average disturbance scenario when insects were excluded (treatment) to a control scenario, where there was no disturbance and natural levels of herbivory. We calculated contributions of each vital rate (*i*) with parameter value (p_i) as follows (Caswell 2001):

$$\Delta\lambda \approx \sum_{all\ p_i} \Delta p_i \left(\frac{\partial \lambda}{\partial p_i} \right) \Bigg|_{p_{i\ midpoint}}, \qquad (6)$$

where Δλ is the difference between λ's and Δp_i is the difference in parameter values of a vital rate in the treatment (disturbance, no insects) and the control (no disturbance, insects). Thus, the contribution of each vital rate is the difference between the vital rate in the treatment and control scenarios multiplied by the sensitivity of the vital rate. Only four vital rates were affected in these scenarios: p_{SR}, p_{eS}, p_{eSB} and $f_n(x)$. Sensitivities for each vital rate were calculated from a midpoint matrix, half-way between the control and the treatment (Caswell 2001). We calculated sensitivities by using manual perturbations of 0.01 and 0.05 on each vital rate independently and examining the absolute effect on λ. Since both perturbations gave the same results, we used those from perturbations of 0.01. We also calculated sensitivities and elasticities (proportional effect on λ) for the disturbance scenario to assess the relative importance of vital rates between regions. All matrix simulations and analyses were done using Matlab (Release 14, Mathworks, Inc. 2004).

RESULTS

Plant abundance

Cynoglossum officinale occurred, on average, at 3.5 times the density in introduced populations compared to native populations at locations sampled across both ranges (mean number of adult plants/m^2 ± SE: native: 2.71 ± 0.34, introduced: 10.89 ± 1.74; $t_{21} = -5.63$, $P < 0.001$).

Effects of small-scale disturbances on early life stages

The amount of ground covered by natural small-scale disturbances did not differ between study sites in the native and introduced ranges ($F_{1,12} = 1.23$, $P = 0.29$). On average, approximately 12% of the area at each site was disturbed (mean percentage of disturbed ground ± SE: native: 12.3 ± 3.7, introduced: 11.0 ± 3.0).

Disturbance enhanced recruitment in both the native and introduced ranges; twice as many seedlings recruited into experimentally disturbed plots in the year following the disturbance treatment (Figure 3A; $F_{1,156} = 5.67$, $P = 0.018$). This effect of disturbance on seedling recruitment was stronger in the introduced range than the native range, with marginal significance (range: $F_{1,156} = 0.00024$, $P = 0.99$; range × disturbance: $F_{1,156} = 3.51$, $P = 0.063$). The effect of disturbance was also stronger for the cohort of seeds planted in 2004, for which total recruitment was higher (year: $F_{1,156} = 28.93$, $P < 0.001$; year × disturbance: $F_{1,156} = 5.66$, $P = 0.019$). Finally, seedling recruitment differed among sites within each range (site(cont): $F_{4,156} = 6.54$, $P < 0.001$).

Within the disturbance experiment, artificially disturbed plots filled in more quickly with species other than *C. officinale* in the native range than in the introduced range (Figure 2A). By the end of the first growing season, disturbed plots in the native range had only slightly more bare space than undisturbed plots, and this difference was negligible by the spring of the next year.

The effects of disturbance on plant-available soil nitrogen varied by range (Figure 2B; range × disturbance $F_{1,61} = 11.63$, $P = 0.001$). In the introduced range, disturbance significantly increased the amount of available N (Tukey post hoc test $P < 0.034$), but there was no difference between disturbed and undisturbed plots in the native range ($P = 0.18$). Across ranges, the amount of available N was similar in disturbed plots ($P = 0.98$), but undisturbed plots had higher available N than disturbed plots in the native range ($P < 0.001$).

The effects of disturbance were still apparent at the end of the first growing season (for each cohort: July 2005 and 2006). In July, disturbed plots continued to have more *C. officinale* seedlings than undisturbed plots (Figure 3B; $F_{1,156} = 48.7$, $P < 0.001$), but this difference was accentuated in the introduced range (range × disturbance: $F_{1,156} = 3.76$, $P = 0.05$), where there were fewer overall seedlings than in the native range (range: $F_{1,156} = 49.0$, $P < 0.001$).

Disturbance had a much larger positive effect on the survival of seedlings to one-year old adults in the introduced range, where very few seedlings survived in undisturbed plots, compared to the native range, where there was little difference in survival (Figure 2B; range × disturbance: $F_{1,102} = 10.86$, $P = 0.001$). Survival did not depend on year ($F_{1,102} = 1.16$, $P = 0.28$) or density of seedlings in the previous year ($F_{1,102} = 0.50$, $P = 0.48$).

Some seedlings emerged in plots the second year following disturbance (May 2006 and 2007), when the effects of the disturbance were no longer as apparent (particularly in the native range; Figure 2A). Total cumulative germination across two years was higher in disturbed than in undisturbed plots, and this difference was somewhat greater in the introduced range (mean ± SE cumulative number of seedlings in the introduced range: disturbed 33.4 ± 2.8 vs. undisturbed 17.9 ± 2.2; and native range: disturbed 21.9 ± 1.9 vs. undisturbed 14.3 ± 1.6). In both ranges, we very rarely observed seedling emergence in either the third year following the initial disturbance or in plots where no seeds were added, indicating that *C. officinale* does not have a persistent seed bank.

Effects of insect herbivory on plant performance

Plants in the native range suffered leaf damage by specialist flea beetles (*Longitarsus* spp). In both ranges, plants were attacked by generalists such as grasshoppers and various Lepidopteron larvae as well as by snails in the native range (J. Williams, personal observation). The magnitude of leaf damage by specialist and generalist consumers was not significantly different between ranges (Mann-Whitney U =

5101, $\chi^2_1 = 1.45$, $P = 0.23$). Leaf damage was significantly reduced by insecticide treatment (Figure 4A; native range: Mann-Whitney U = 4167, $\chi^2_1 = 17.41$, $P < 0.001$; introduced range: Mann-Whitney U = 105110, $\chi^2_1 = 21.21$, $P < 0.001$). In the native range, more than 80% of plants in the control treatment had specialist root-boring weevil larvae (*Mogulones cruciger*) in their tap roots (Figure 4B). The weevils are not present in the U.S.

Insect herbivory significantly reduced plant size in the native range, but not in the introduced range (native range: $F_{1,88} = 9.50$, $P = 0.003$; introduced range: $F_{1,169} = 0.81$, $P = 0.37$). Insect exclusion resulted in a 35% increase in seed production in the native range, but had no effects on fecundity in the introduced range (Figure 4C, native range: $F_{1,117} = 4.54$, $P = 0.015$; introduced range: $F_{1,29} = 0.101$, $P = 0.75$). Although experimental plants in the native range produced more seeds than those in the introduced range, this does not reflect differences in average fecundity of plants between ranges; in the demography plots at these sites, average fecundity did not differ between ranges (J. Williams, unpublished data). Insect exclusion had no effect on plant survival in either range, although plants in both treatments suffered mortality (average mortality of natural rosettes in the native range: insecticide 0.47 vs. no insecticide 0.31, $\chi^2 = 2.29$, P = 0.13; and introduced range: insecticide 0.38 vs. no insecticide 0.45, $\chi^2 = 0.46$, P = 0.50).

Model results: translating effects of insects and disturbance on performance to effects on λ

In the introduced range, disturbance had large positive effects on λ whereas in the native range disturbance slightly reduced forecasted λ (Figure 5A). When the maximum average parameter values for disturbed plots were used in simulations, λ increased in both ranges, and this was the only scenario in which confidence limits for λ overlapped 1 in the introduced range (Figure 5A). An increase in fecundity simulating release from insect herbivores in the native range resulted in an increase in λ in all disturbance scenarios (mean $\Delta\lambda \pm$ SE: 0.054 ± 0.005). If specialist herbivores from the native range were brought to the introduced range and affected demographic rates in the same way (reducing fecundity by 30%), they would slightly decrease λ (mean $\Delta\lambda \pm$ SE: 0.034 ± 0.003)

Demographic rates of early life stages (seedling survival, and probabilities of establishment) had the highest sensitivities in both ranges (Figure 6). The absolute values of these rates are low, so the pattern of elasticities, where the effect of proportional changes in demographic rates was examined, is different. In the introduced range, adult survival and growth have by far the highest elasticities (Figure 6B). In contrast, in the native range, early life stages such seedling survival and average size of one-year olds, have similar elasticity values to adult survival and growth, indicating a greater influence of these early life stages on population dynamics compared to the introduced range (Figure 6A).

The LTRE results showed that seedling survival was the most important factor contributing to increased λ in the disturbance scenario in the introduced range (Figure 5B). These results also pointed to the importance of establishment from the previous year's seeds in the introduced range. In the native range, the LTRE results indicated that seedling establishment contributed to increased λ in the disturbance scenario, but the negative contribution from lower seedling survival in disturbed plots cancelled out the disturbance advantage (Figure 5B). Finally, the LTRE results indicated that the effects of the release from insects on fecundity in the native range had approximately the same effect on λ as disturbance had on recruitment.

DISCUSSION

Our results point to disturbance as being an important factor contributing to the greater success of *C. officinale* in the introduced versus native range. Recruitment in both ranges was enhanced by disturbance, as was previously shown at the western edge of the native range, in the Netherlands (de Jong and Klinkhamer 1988). However, small-scale disturbances had much larger effects on recruitment, seedling survival, and ultimately, population growth rate, in the introduced range than in the native range (Figures 3, 5A). In the native range, estimates of population growth were only elevated under a maximum disturbance scenario, when the positive influence on recruitment outweighed the slight negative effect on seedling survival. In contrast, in the introduced range, the increases in λ in both the disturbance and maximum disturbance scenarios were driven by much higher seedling survival and establishment in disturbed plots. Only one other study has similarly demonstrated a strong biogeographical pattern between ranges in the impacts of disturbance, for the annual exotic invader *Centaurea stolstitialis* (Hierro et al. 2006). In general, the relative importance of disturbance in native and introduced ranges is poorly understood (Hierro et al. 2006).

That small disturbances benefit a ruderal plant is not surprising (Sletvold and Rydgren 2007). Disturbance in the introduced range has long been known to facilitate invasion (Hobbs and Huenneke 1992, Williamson 1996, Mack et al. 2000, Lockwood et al. 2007). What is more surprising is that disturbances differentially affected both performance and population growth in the introduced versus the native range. This is especially important since we did not find differences in the amount of disturbed ground between the three primary study sites in each range (although the limited number of populations sampled in each range necessarily limits our scope of inference). There is an important caveat to our results, however. We used λ as a metric to assess how the impacts of disturbance at one life stage (seedling recruitment and survival) affect the population when all life stages are considered. This is a very useful approach, in that it enables one to translate impacts on individuals at a particular life stage to the growth or decline of an entire population and to compare the relative importance of more than one factor. However, since the rate at which a population is growing or declining does not necessarily reflect the absolute number of individuals at the current time, our approach is only one step towards fully explaining difference in *C. officinale* abundance between ranges.

Although it is tempting to interpret our data as implying that disturbance increases recruitment more in the introduced range compared to the native range, a more biologically reasonable interpretation may be that λ is more depressed when there are no small disturbances in the introduced range. The reason for this is that in Europe, disturbed patches quickly fill in with both *C. officinale* as well as seedlings of other plant species (Figure 2A). In contrast, in the introduced range, colonization by native plants in these dry grasslands is slower, so *C. officinale* faces competition only in undisturbed plots. Thus it may be the slow colonization of disturbed patches in the introduced range by native plants that allows *C. officinale* to attain higher abundance there. Its poor performance in undisturbed plots in the introduced range compared to the native range suggests strong competition with its novel plant competitors, compared to those with which it has a longer evolutionary history.

A second mechanism may contribute to the differences in the effect of small-scale disturbances on recruitment and survival between ranges: the opposite response of plant-available soil nitrogen to artificial disturbances between ranges. In the native range, disturbance resulted in a decrease in soil nitrogen whereas in the introduced range disturbance increased soil N (Figure 2B). These differences might have been due to differences between ranges in the timing of rainfall, and how this affects N immobilization by microbes or N leaching. If nitrogen is limiting to plant growth, then disturbed plots would be more favorable than undisturbed in the introduced range, but not in the native range.

The other mechanism we examined for explaining the increased success of *C. officinale* is escape from natural enemies. The enemy escape hypothesis has been the most broadly cited explanation for success of invasive species (Keane and Crawley 2002), but complete tests of it that examine impacts of enemies in both ranges and their consequences for population growth are virtually non-existent. In the native range of *C. officinale*, insects negatively impact plant performance, both by reducing size and fecundity (Figure 4). This damage was caused mainly by specialists, which are absent in the U.S. The attack rate of plants by the specialist root-boring *M. cruciger* at the two study sites where we carried out this experiment was similar to that observed across 11 additional sites in the native range (J. Williams, unpublished data). The observed 35% increase in fecundity when insects were excluded was remarkably similar to results from a previous study on *C. officinale* in sand dune habitats in the Netherlands (Prins et al. 1992). These reductions in plant performance appear to limit population growth rate, albeit slightly.

In the introduced range, where herbivores did not affect plant performance (Figure 4C), has *C. officinale* benefited from escape from its enemies? The release from specialist insects may have contributed slightly to increased population success, but is unlikely to drive the entire pattern if the main effect of specialist insects is to reduce fecundity. This is because fecundity has a much smaller effect on population growth rate (lower sensitivity) than other vital rates (Figure 6). This illustrates an important fact:

estimates of the impacts of herbivores on plant performance between regions do not in themselves fully test the enemy escape hypothesis. This is because enhanced performance of a particular vital rate, such as fecundity, as a result of enemy escape does not necessarily lead to large effects on population growth.

Our approach to understanding the factors responsible for exotic plant success is comprehensive. The strengths of combining field experiments with population modeling are that this approach permits the most appropriate tests of competing hypotheses for the mechanisms of plant invasion. In other words, one can simultaneously test the relative importance of alternative causal factors in affecting the population growth of a plant at home and abroad. Yet our work also illustrates several challenges and limitations of this biogeographic approach. One challenge involves choosing experimental populations for study. For logistical reasons we could only examine three populations on each continent. This necessarily reduces the statistical power with which to detect differences in vital rates across continents, and it is obviously a small sample from which to generalize. Since we deliberately chose populations in both Europe and North America where conditions (plant density, climate, etc.) were as similar as possible, we treated these sites as a fixed factor in our analyses. This means one must be cautious in extrapolating our results, since the scope of inference of this study is limited to the habitats and climate where we have studied this species.

A second challenge in performing parallel demographic studies across continents is that there can be considerable spatial variation in demography within a range, and in our case, substantial year-to-year variation in vital rates. For example, in the introduced range, several years had lower precipitation than normal, while in the native range, the variation was high, with some years hotter and drier and other years cooler than wetter than average. Since such weather extremes influence vital rates, this temporal and spatial variability potentially obscures differences in demography between continents that might become clear with a longer term study at a larger number of sites.

Finally, the sometimes large variation in recruitment and survival between years that we observed can lead to large population fluctuations. For example, at one study site in the native range, the number of adult plants varied by an order of magnitude across five years, and no adult plants were alive during the final year of the study (J. Williams, unpublished data). This pattern has been observed in *C. officinale* in the native range in both Hungary (S. Toepfer, personal communication) and the Netherlands (de Jong and Klinkhamer 1988, van der Meijden et al. 1992), and is typical of biennials that may go locally extinct and then recolonize from the seedbank or by dispersal of new seeds. Whether these population fluctuations are driven by weather or by buildup of the specialist insect *M. cruciger* is unknown (de Jong and Klinkhamer 1988, van der Meijden et al. 1992). Whatever the cause of these fluctuations, they may both move a population off its stable stage distribution and keep a population from attaining asymptotic growth. For these reasons it is necessary to interpret absolute values of λ with caution. However, even with population fluctuations, the relative importance of disturbance and insect herbivory was the same across years and sites, leading us the same conclusion whether or not the long term predictions were for a population to grow or shrink.

Despite these considerations, our study provides a rigorous test of the relative importance of factors that may be responsible for exotic plant success. These results can then be applied control *C. officinale* populations in the introduced range. The sensitivity analysis suggests that reducing adult survival, which has a high proportional effect on λ (high elasticity, Figure 6B), has the potential to lead to reduced population size. If biocontrol agents such as *M. cruciger* were to be effective, they would need to have much larger effects on both performance and population growth in the introduced range than was observed in the native range during this study. Weed management programs also have the potential to locally eradicate small populations when they remove plants by pulling or with herbicide, if future dispersal can be prevented, due the short life of the seedbank in *C. officinale*, with the vast majority of seeds germinating within two years of being produced. Future studies on exotic plants that examine mechanisms for success in both ranges have great potential for elucidating the causes of increased success, and may be especially useful for improving eradication programs in the introduced range.

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FIGURE LEGENDS

Figure 1. Life cycle diagram of *Cynoglossum officinale*. Labeled transitions are affected by insect herbivory or disturbance as follows: A. Probability of seedling establishment seeds on adult plants (p_{eS}). B. Contribution to seeds in soil ($1 - p_{eS}$). C. Probability of establishment fro seeds in the soil (p_{eSB}). D. Probability of seedling survival (p_{SR}). E. Fecundity (equation 5), insects affect $p_f(x)$. F. Probability of iteroparity and contributions to seeds and seedlings occurs only in the introduced range (Williams 2008, Dissertation Chapter 2).

Figure 2. Mean (± SEM) (A) % cover of bare ground and (B) plant-available soil nitrogen in experimentally disturbed (open symbols) and undisturbed (closed symbols) plots in the introduced and native range. Plots were artificially disturbed at the end of the 2004 growing season, when bare space in disturbed plots was 100%. N=3 sites in each range.

Figure 3. Mean (+ SEM) (A) number of seedlings recruited in the year following disturbance and seed addition, (B) final seedling establishment and (C) survival of established seedlings to one-year old plants in disturbed and undisturbed plots.

Figure 4. (A) Mean (+ SEM) effect of herbivores on leaf damage and (B) total percentage of native plants attacked by specialist root boring weevils in experiment. Leaf damage was visually assessed on a categorical scale as follows: 1 = 0%, 2 = < 10%, 3 = 11-25%, 4 = 26-50%, 5 = > 50%. (C) Mean (+ SEM) fecundity of plants.

Figure 5. (A) Effects of disturbance on estimated deterministic population growth rate (λ) of *C. officinale* under ambient herbivory conditions. Error bars indicate 95% confidence limits that represent variation across sites and years. (B) Life Table Response Experiment (LTRE) contribution of each vital rate to $\Delta\lambda$ when insects are excluded (disturbance – no disturbance).

Figure 6. Elasticity and sensitivity values for model parameters, perturbing values by 1%, in the (A) native range and (B) introduced range. Demographic rate abbreviations: seedling surv, seedling survival to one-year old adults; prob est seeds and pro best soil, probabilities of seedling establishment from seeds produced in previous year or in the soil seedbank; adult survival, size-specific adult survival; growth, size-specific adult growth; ave 1yr old size, average size of one year-old adult plants; flowering size, median threshold flowering size; fecundity, seed production.

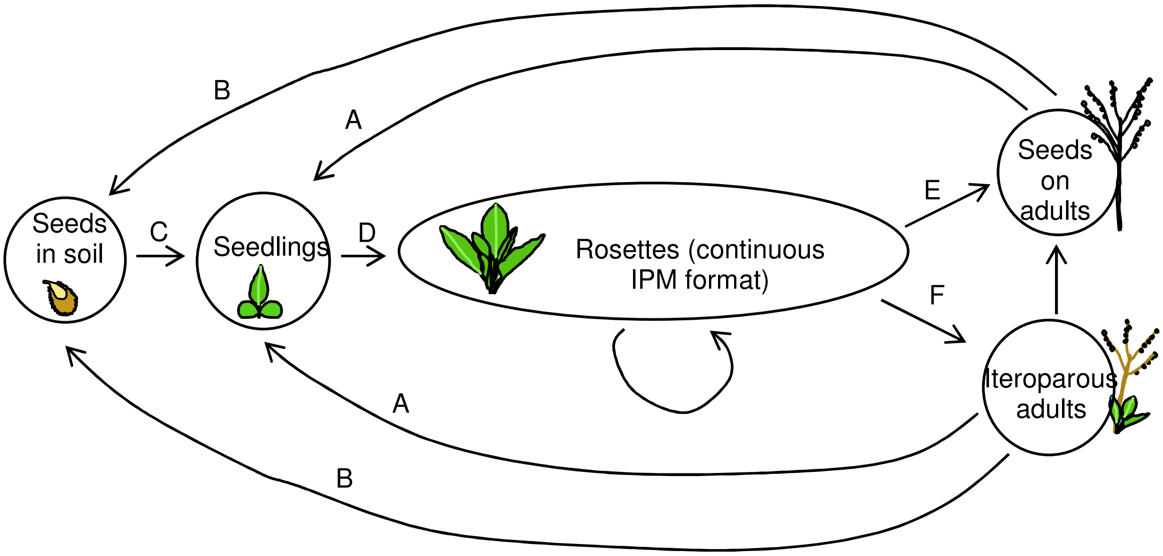

B
A
Seeds in soil
C
Seedlings
D
Rosettes (continuous IPM format)
E
F
Seeds on adults
Iteroparous adults
A
B

Figure 1

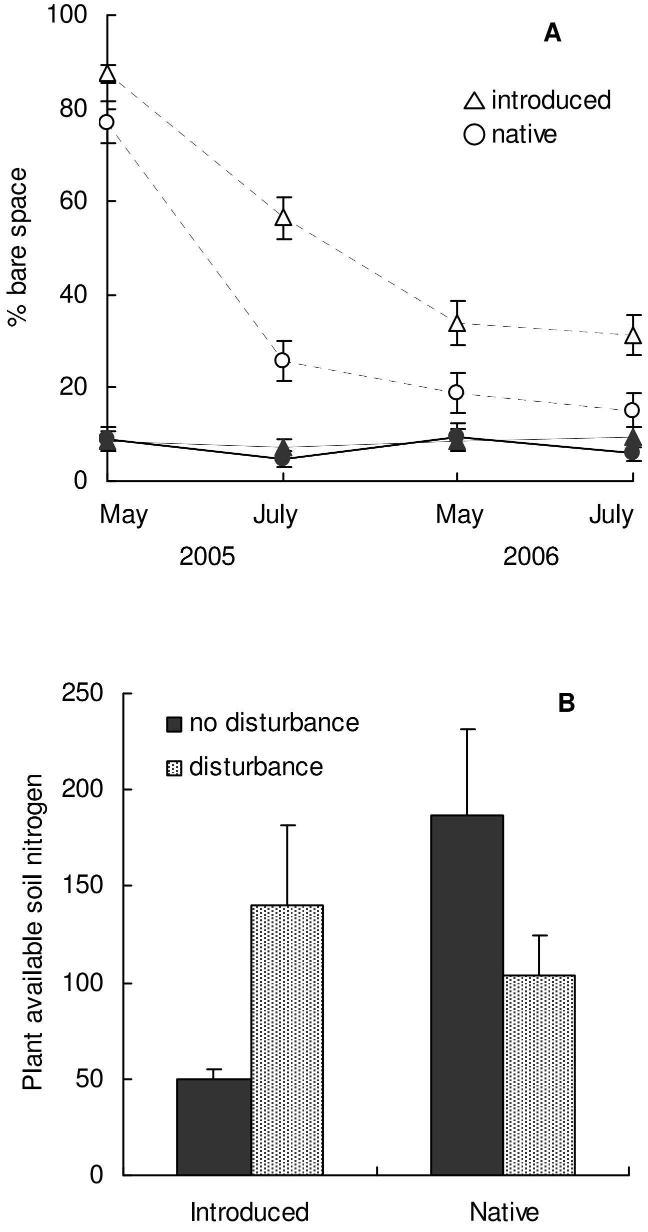

100
80
60
40
20
0
% bare space
A
△ introduced
○ native
May
July
May
July
2005
2006
250
200
150
100
50
0
Plant available soil nitrogen
B
■ no disturbance
▨ disturbance
Introduced
Native

Figure 2

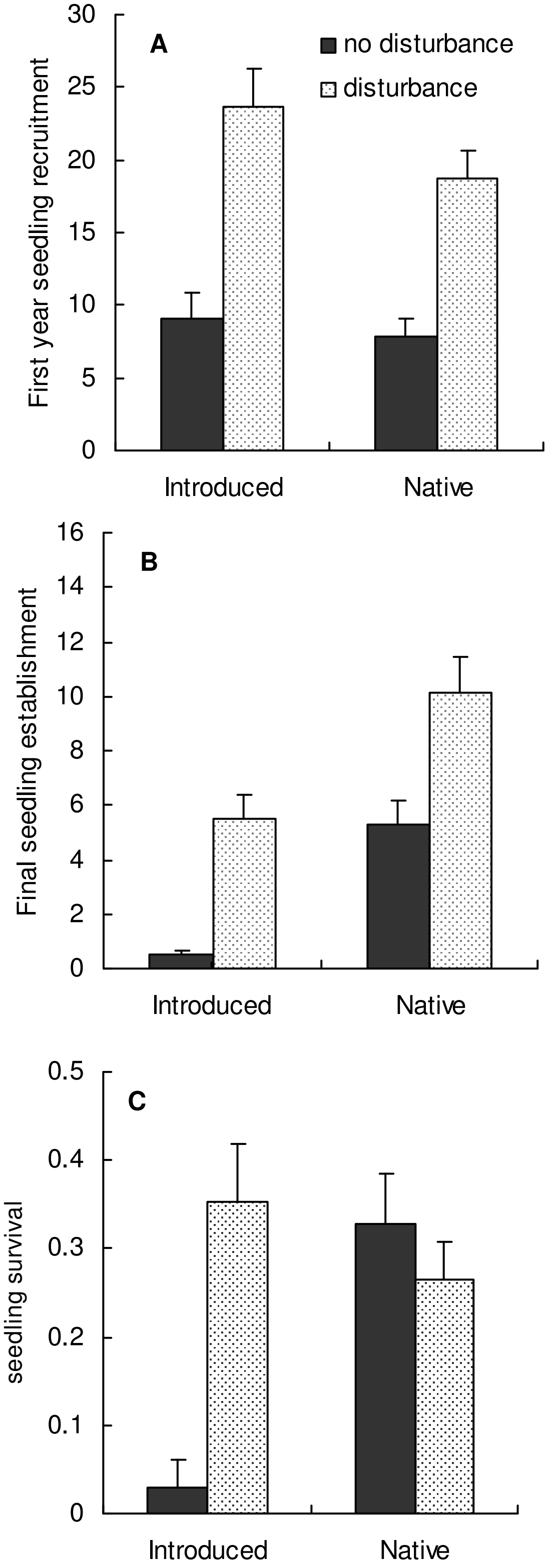

A
no disturbance
disturbance
First year seedling recruitment
30
25
20
15
10
5
0
Introduced
Native
B
Final seedling establishment
16
14
12
10
8
6
4
2
0
Introduced
Native
C
seedling survival
0.5
0.4
0.3
0.2
0.1
0
Introduced
Native

Figure 3

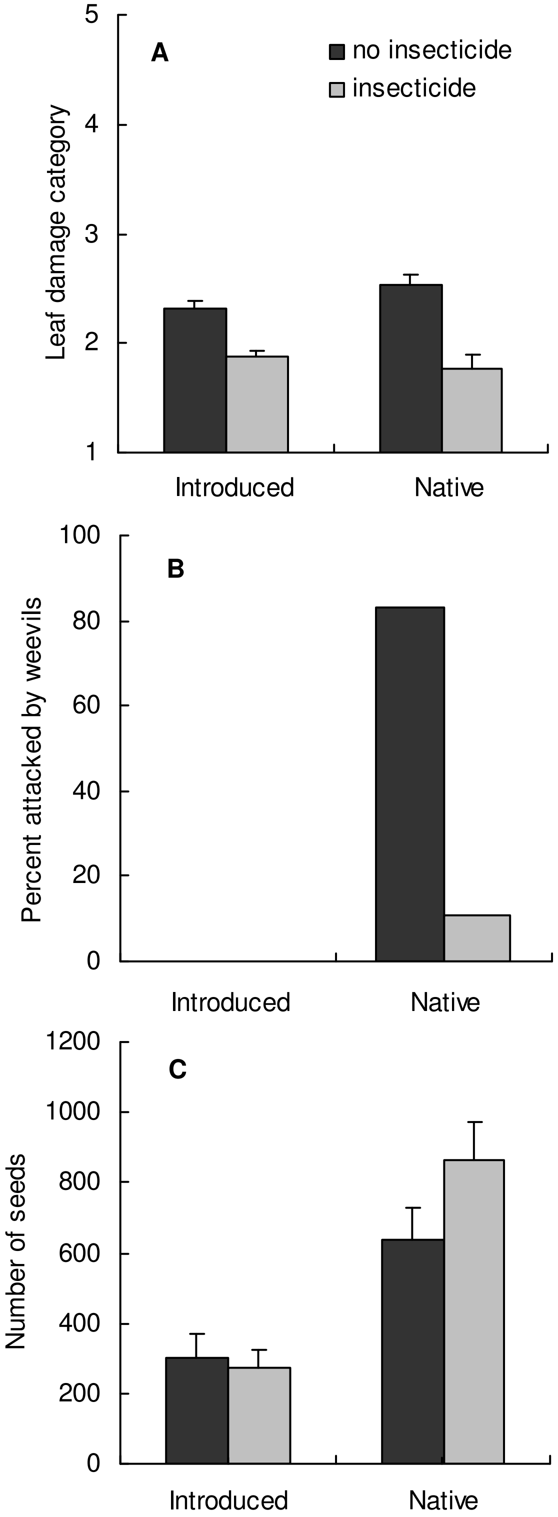
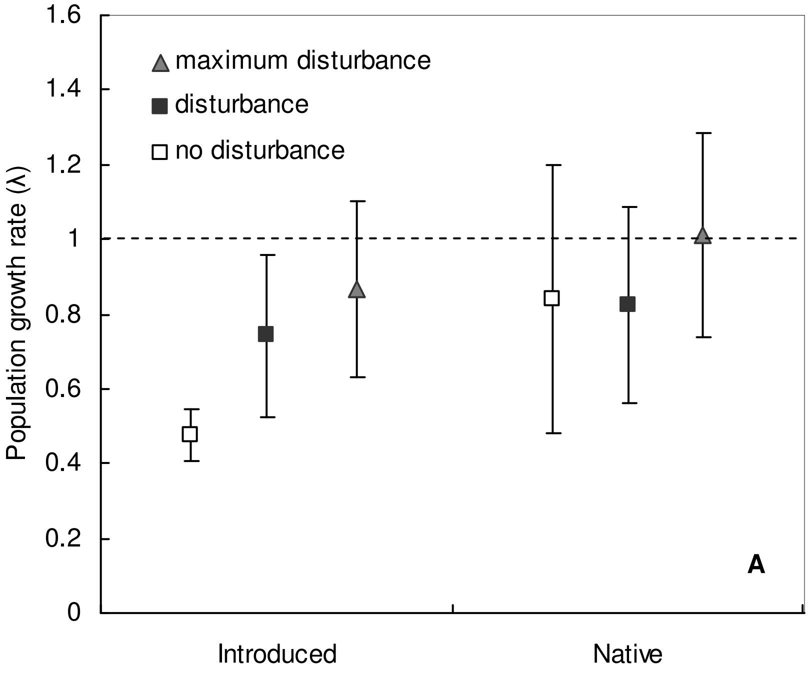
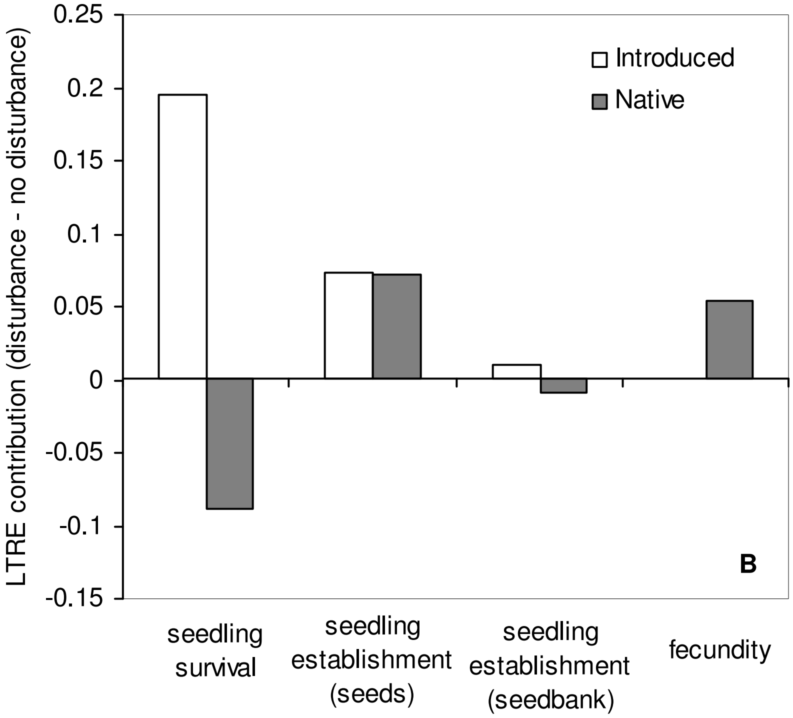

5
4
3
2
1
A
■ no insecticide
▨ insecticide
Leaf damage category
Introduced
Native
100
80
60
40
20
0
B
Percent attacked by weevils
Introduced
Native
1200
1000
800
600
400
200
0
C
Number of seeds
Introduced
Native

Figure 4



1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Population growth rate (λ)
maximum disturbance
disturbance
no disturbance
A
Introduced
Native



0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
LTRE contribution (disturbance - no disturbance)
Introduced
Native
B
seedling survival
seedling establishment (seeds)
seedling establishment (seedbank)
fecundity

Figure 5

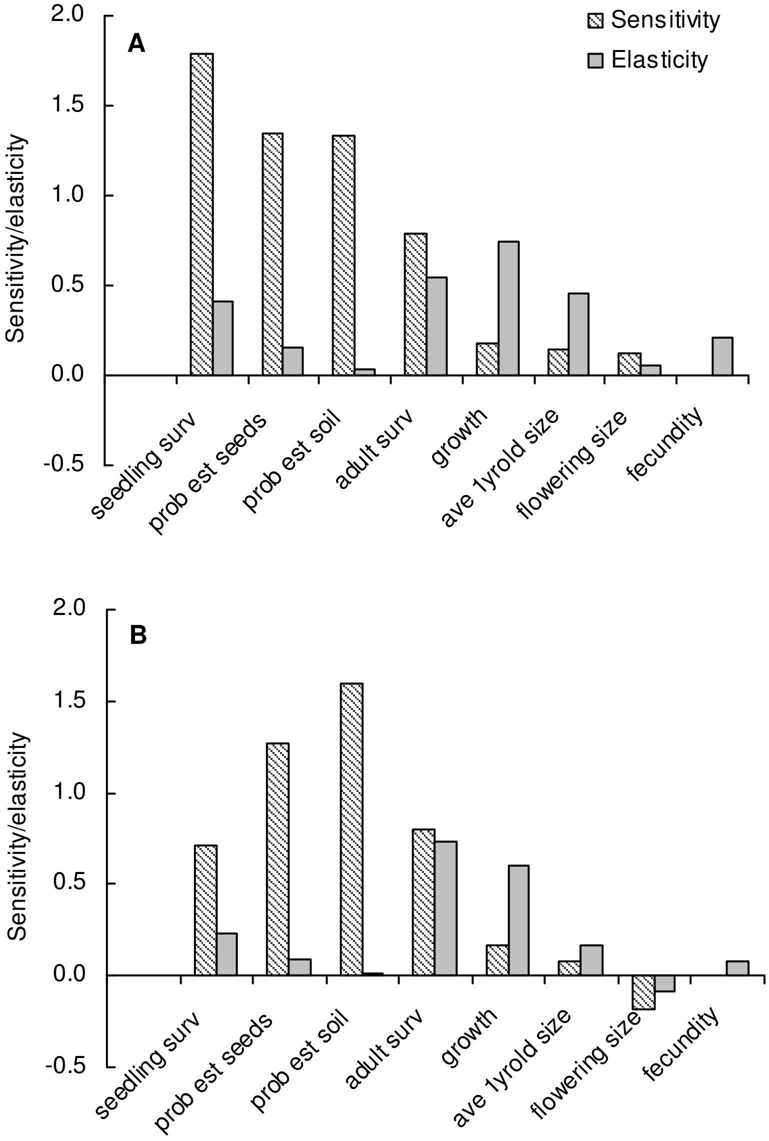

A
B
Sensitivity
Elasticity
Sensitivity/elasticity
2.0
1.5
1.0
0.5
0.0
-0.5
seedling surv
prob est seeds
prob est soil
adult surv
growth
ave 1yrold size
flowering size
fecundity

Figure 6

Appendix A. Maps depicting approximate locations of populations sampled in the native and introduced ranges of *C. officinale*. Stars indicate locations of focal study populations, open diamonds indicate locations of other survey populations.