REPORT

Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*

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Abstract

One of the influential hypotheses invoked to explain why species become invasive following introduction is that release from natural enemies favours a shift in investment from defence to traits enhancing growth and reproduction. *Silene latifolia* was introduced from Europe (EU) to North America (NA) *c.* 200 years ago where it experiences lower damage by natural enemies. A common garden experiment in EU using seeds from 20 EU and 20 NA populations revealed (1) genetically-based differences in life history between plants from EU and NA; plants from NA have evolved a weedy phenotype that flowers earlier, and has a two- to threefold higher reproductive potential; (2) higher susceptibility of NA plants to fungal infection, fruit predation, and aphid infestation. These results suggest that the invasive NA phenotype has evolved at the expense of defensive abilities. Despite this increased susceptibility to enemies, NA populations still outperformed EU populations in this common garden.

INTRODUCTION

Despite the fact that biological invasions represent one of the greatest threats to biodiversity, we still know relatively little about their underlying causes (Cox 1999; Pimentel *et al.* 2000; Simons 2003). Why does a species that is a benign entity in its native ecosystem become invasive following its movement to a new location? The traditional explanation in the literature argues that enhanced performance is a plastic response to a release from damage by enemies normally present in the native range (Crawley 1987). Indeed, there have been a number of recently published studies that have found support for the escape-from-enemies hypothesis both with respect to above-ground (Wolfe 2002; Mitchell & Power 2003; Torchin *et al.* 2003) and below-ground (Reinhart *et al.* 2003) natural enemies. Yet, reduced interactions with pathogens, herbivores and predators is a phenomenon that is ecological in nature and may also have evolutionary consequences. While mechanical and/or chemical defensive characters may be adaptive in the presence of enemies, they become unnecessary and costly when these enemies are absent. As a result, selection should favour reduced investment into defence, and saved resources may

be reallocated to contribute to enhanced growth and reproduction (Blossey & Nötzold 1995). Clearly, the challenge to understanding invasions rests in determining the relative contributions of ecological and genetically-based evolutionary forces (Sakai *et al.* 2001; Lee 2002).

The most direct way to determine if invasiveness is the result of phenotypic plasticity or genetics is to grow native and introduced specimens in a common garden. Under such controlled conditions, any differences that arise in phenotypic traits between material from the two ranges are considered to be genetically-based. In contrast, if native and introduced individuals do not differ when grown together, it may be concluded that there has not been evolutionary change since introduction.

A small number of studies have used the common garden approach to explore the basis of biological invasions and these have found equivocal results. Willis *et al.* (2000) found no differences in four plant species sampled from their introduced and native ranges. On the other hand, introduced *Sapium sebiferum* attained greater size after 14 years of growth compared with native material (Siemann & Rogers 2001). Similarly, Leger & Rice (2003) reported that introduced California poppies

outperformed native conspecifics under relatively benign non-competitive conditions. Results from greenhouse and field common garden experiments with *Silene latifolia* also demonstrate that genetic change can play an important role in invasions. Blair & Wolfe (2004) reported that *S. latifolia* from the introduced North American (NA) range exhibit a weedier phenotype with greater germination rates, enhanced growth rates and reproductive output than plants from native Europe (EU).

What makes the *S. latifolia* example of post-introduction evolution particularly interesting is that the species' interactions with enemies have been well documented. A recent investigation of *c.* 100 populations across its native and introduced ranges clearly demonstrated that with its introduction to NA, *S. latifolia* has successfully escaped a number of generalist and specialist enemies (Wolfe 2002). In addition, common garden experiments revealed that NA plants invest less into trichomes on the calyx that are presumed to have a defensive function (Blair & Wolfe 2004). These patterns suggest evolution via natural selection and support the untested hypothesis that reduced enemy attack favoured decreased investment to defence, which ultimately resulted in selection for traits associated with invasion success.

Yet, the conclusions derived from a common garden experiment are likely to be geography-dependent. For example, if a species that experiences different enemy regimes in its native and introduced ranges, the location of the experiment can profoundly influence the outcome. The most relevant way to test if phenotypic shifts in defensive characters are costly is to examine their performance in the native range. In other words, it is necessary to observe the performance and fate of native and introduced plants with enemies present. If in fact investment to defence is costly and natural selection has favoured a reduction in defence in the introduced range, then we would expect introduced plants to be particularly susceptible to enemies. Thus, when grown in a common garden in the native range, we predict that introduced plants will suffer disproportionately relative to native genotypes.

The main goal of this study was to examine the performance of NA and EU *S. latifolia* when grown in the presence of enemies from its native range. This was achieved by conducting a common garden experiment in EU. Specifically, we addressed the following two questions. (1) Are the differences in morphological and life history traits between plants from the two continents exhibited under experimental conditions in NA maintained when plants are grown in EU? (2) Do we find that less defended NA *S. latifolia* suffer disproportionally relative to EU plants when faced with natural enemies? This is one of first attempts to contrast the performance of native and introduced populations for a species in which the level of enemy damage in both ranges is known.

MATERIALS AND METHODS

Study species

Silene latifolia Poiret (*S. alba* Krause; *Melandrium album* Garcke) (Caryophyllaceae) is a dioecious, short-lived perennial that was accidentally introduced to NA from EU in the mid-1800s (Baker 1947). The species has become a problematic weed of cultivated fields in southern Canada and the northern USA (USDA-ARS 1965; McNeil 1977). Damage by a suite of natural enemies can be particularly severe in EU and almost non-existent in NA populations (Wolfe 2002). Specialist enemies include the lepidopteran fruit predator *Hadena bicruris* Hufn. (Noctuidae), the anther-smut fungus *Microbotryum violaceum* (Pers.:Pers.) Deml & Oberw. (*Ustilago violacea* [Pers.] Fuckel) (Ustilaginales) and the aphid *Brachycaudus lychnidis* (Linnaeus 1758) (Aphididae). *Hadena bicruris* oviposits on the ovary of flowers on female plants (Brantjes 1976). First instar caterpillars chew a hole in the ovary wall and develop inside the fruit, devouring all the seeds (primary predation). Fourth or fifth instar caterpillars emerge from the empty capsule and migrate to other fruits that they chew open and consume from the top (secondary predation) (Biere *et al.* 2002). *Microbotryum violaceum* is a systemic plant pathogen that sterilizes its Caryophyllaceous host plants (Thrall *et al.* 1993). It produces spores in the anthers of both male and female hosts; the latter undergo a morphological sex reversal upon infection. Spores are florally transmitted by pollinating insects. *Brachycaudus populi* infests flower stalks of bolting and flowering plants; it is a holocyclic, Eurasian species specialized on *S. latifolia*. While these organisms are widespread throughout EU (Wolfe 2002), the fruit predator and aphid are absent from NA and the sterilizing fungus is apparently geographically restricted to *S. latifolia* populations in the Appalachian Mountains.

Experimental set-up

The experiment was conducted in a sandy experimental plot (21 × 1.5 m) in the common garden at The Netherlands Institute of Ecology (NIOO) in Heteren, NL. Seeds used in the experiment were collected between 1999 and 2001 from 20 European and 20 NA populations (10 plants per population). The sampling spanned the majority of *S. latifolia*'s distribution in the two continents (see Blair & Wolfe 2004 for details). Seeds from different maternal plants in the same population were mixed, and *c.* 20 seeds per population were germinated in an unheated greenhouse on 11 April 2002. Due to insufficient germination and/or flowering of plants, only 17 of the 20 EU populations could be included in the study. A total of 419 seedlings [2–15 per population (average = 11.3)] were transplanted to the plot on 14 May when the majority had reached the six-leaf stage. Individuals were planted in five rows of 84 plants at

inter-plant distances of 25 cm in a completely randomized design. Plants were regularly watered and received no additional fertilizer. The plot was weeded throughout the season to maintain a non-competitive environment. The experimental garden has a *c.* 10 years history of the presence of *S. latifolia* plots and plants are frequently attacked by *H. bicruris*, *M. violaceum* and *B. lychnidis*. Two natural source populations of *S. latifolia*, where these natural enemies are present, occur within a 5 km radius of the experimental garden.

Life-history traits and enemy attack

From 14 June when the first plants started to flower, until 11 October when flowering had ceased, plants were censused weekly to assess life-history traits and levels of enemy attack. For each plant we recorded survival, onset of flowering (number of days between transplantation and first flower production), sex, number of inflorescences, and the total number of flowers produced. Total flower number was estimated from weekly counts of both the number of open flowers and the number of pedicels per plant. For each flower on female plants we recorded whether it had produced a fruit. Over-winter survival of plants was scored in the summer of 2003.

Infection by *M. violaceum* was documented by examining flowers for the presence of the characteristic dark fungal spores. Plants did not produce diseased flowers until 5–14 weeks after they had initiated flowering. Infection was scored qualitatively (plants infected or not) and quantitatively (number of diseased flowers produced). Predation by *H. bicruris* was documented by examining each mature fruit for small entrance holes and frass, leaving a red stain on the interior of the capsule (primary predation), or a large entrance hole without stain, often with part of the capsule teeth removed (secondary predation) (Biere & Honders 1996). The proportion of primary and secondary damaged fruit was calculated for each individual female plant.

Infestation of flower stalks by *B. lychnidis* was observed between mid-June and early-August. The proportion of infested plants peaked around July 19 (66.4%) and had sharply decreased by August 2 (4.0%). For plants that were bolting and/or flowering between 14 June and 2 August, an average score was calculated based on weekly counts of the maximum number of aphids per stalk, scored on the basis of a logarithmic scale: 0, 0 − 5; 1, 5 − 25; 2, 25 − 125.

Data were analysed with generalized linear models, for male and female plants separately, using SAS 8.0 procedure GENMOD (SAS Institute, Cary, NC, USA). Effects (mean deviances) of Continent (EU vs. NA) were tested over effects of Populations (nested within Continent). Survival and the presence of *M. violaceum* were analysed as binomially distributed variables with a logit link function. Other variables were analysed as normally distributed variables with an identity link function after appropriate transformation. Onset of flowering and the numbers of inflorescences, flowers and fruits were all ln-transformed; fruit set and the proportion of damaged fruits per plant were arcsine square-root transformed prior to analysis.

RESULTS

Life history

Survival of plants within the season was high (96.2%) and did not differ between plants from the two continents ($F[1,38] = 0.13$, $P = 0.72$). Overall, NA plants significantly outperformed those from EU in terms of reproduction (Table 1). A larger proportion of NA plants (86.0%) initiated reproduction than EU plants (68.9%) ($F[1,38] = 10.50$, $P = 0.003$). For both males and females, the NA plants started flowering almost 2 weeks earlier and produced $1.5 − 3$ times more inflorescences and flowers than EU plants (Table 1). As fruit set did not differ between NA and EU plants, females from NA also produced three times as many fruits as females from EU (Table 1). Most of the reproductive traits also showed significant variation among populations within the continents (Table 1).

Over-winter survival was overall low (18.3 %) and did not significantly differ between EU (19.1%) and NA plants (17.8%) ($F[1,38] = 0.11$, $P = 0.747$). The number of surviving plants that had not initiated flowering in 2002 but flowered in 2003 was negligible (nine individuals, 10.5%).

Susceptibility to enemy attack

Both fungal infection, fruit predation and aphid infestation were significantly higher for plants from NA than for plants from EU (Table 1), although production of uninfected flowers and undamaged fruits was still higher for plants from NA (Table 1).

Overall, 16% of female and 40% of male plants became infected by *M. violaceum* (Fig. 1). The difference between the sexes was highly significant (effect of sex on % infection in a GLM with sex, continent and population, $F[1,284] = 28.27$, $P < 0.001$). The proportion of infected plants was more than three times higher for NA plants than for EU plants (Fig. 1, Table 1). Differences in infection rates were also significant at the population level (Table 1). While only half of the EU populations had any infected plants, 90% of the NA populations had at least a single infected individual, but differed in the proportion of individuals that became infected (Fig. 1; Table 1). Fungal infection was related to plant size. Generally, the probability of infection was

Table 1 Mean values (±1 SE) for traits related to fecundity and damage by natural enemies for male and female *S. latifolia* plants from 17 European and 20 North American populations, grown in a common garden in Europe

	Europe (SE)	North America (SE)	F[continent]	F[population]
Fecundity				
Females (*n* = 176)				
Onset of reproduction (days)	70.82 (2.64)	58.09 (1.58)	8.93**	2.48***
Number of inflorescences	2.08 (0.18)	3.48 (0.17)	16.04***	2.17**
Total number of flowers	8.46 (0.89)	24.43 (1.99)	27.85***	2.13**
Number of healthy flowers	7.54 (0.73)	21.15 (1.49)	35.89***	1.50
Fruit set (%)	67.12 (3.85)	74.37 (1.37)	0.58	1.00
Total number of fruits	5.31 (0.58)	15.99 (1.23)	35.27***	1.56*
Number of undamaged fruits	4.46 (0.47)	12.41 (0.97)	26.37***	1.51
Males (*n* = 142)				
Onset of reproduction (days)	68.46 (2.46)	56.30 (1.49)	10.45**	2.52***
Number of inflorescences	2.18 (0.19)	3.22 (0.19)	9.07**	2.02**
Total number of flowers	97.95 (14.74)	153.20 (12.79)	7.35*	2.13**
Number of healthy flowers	93.85 (12.90)	143.61 (12.00)	6.69*	2.50***
Damage by natural enemies				
Females (*n* = 176)				
Fungal infection (% of plants)	4.91 (2.79)	19.13 (3.68)	5.31*	2.39***
Aphid infestation (average score)	0.41 (0.08)	0.91 (0.06)	11.35**	3.35***
Total fruit predation (%)	12.82 (2.69)	20.64 (1.71)	12.12**	0.94
Primary fruit predation (%)	7.40 (1.67)	11.38 (1.06)	10.54**	0.99
Secondary fruit predation (%)	5.41 (2.00)	9.26 (1.13)	8.09**	0.87
Males (*n* = 142)				
Fungal infection (% of plants)	16.36 (5.03)	54.02 (5.37)	10.70**	2.11**
Aphid infestation (average score)	0.71 (0.08)	0.88 (0.06)	1.39	2.92***

F-values and significance of differences among continents (Europe vs. North America) and populations within continents were obtained from generalized linear models (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).
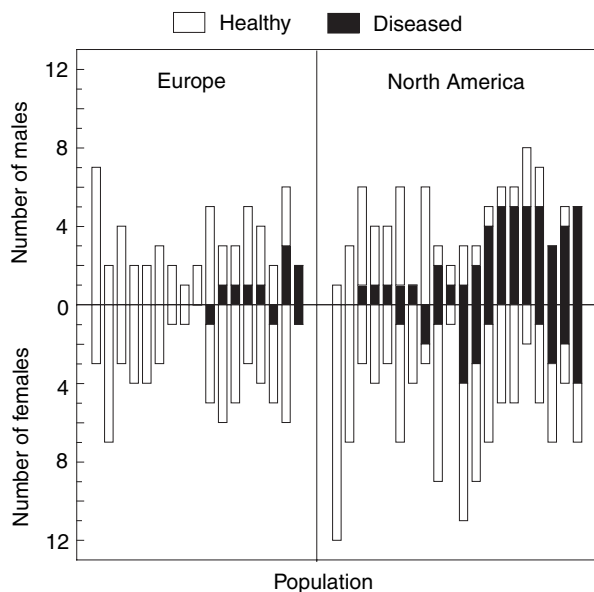

Figure 1 Number of male (top) and female (bottom) *Silene latifolia* plants from native European (left) and introduced North American populations (right) that became infected by the anther smut fungus *Microbotryum violaceum* (black parts of bars) or remained healthy (white parts of bars), when grown in a common garden in Europe.

positively correlated with the number of flowers on a plant (Fig. 2a). Since NA plants on average produced more flowers than EU plants, differences in infection rates could thus simply reflect differences in flower number. Therefore, analyses of differences in infection rate between NA and EU plants were repeated with the number of (uninfected) flowers as a covariate. For male plants, the effect of the covariate was indeed highly significant ($F[1,103] = 28.60$, $P < 0.001$). However, the effect of continent (EU vs. NA) was still significant ($F[1,35] = 8.06$, $P = 0.008$) indicating that for any given plant size (number of flowers) NA plants were still more susceptible to fungal infection than EU plants (Fig. 2a). For female plants, the covariate was also highly significant ($F[1,139] = 19.79$, $P < 0.001$), but effects of continent disappeared ($F[1,34] = 0.53$, $P = 0.47$), indicating that the higher susceptibility of NA plants could be simply attributed to their higher flower production.

Fruit predation was also significantly higher for NA plants (21%) than for EU plants (13%) (Table 1). This was due both to a higher rate of primary predation, probably reflecting a higher rate of successful ovipositions, and to a higher rate of secondary predation (Table 1). Fruit predation rates increased with plant size (number of fruits) (Fig. 2b),
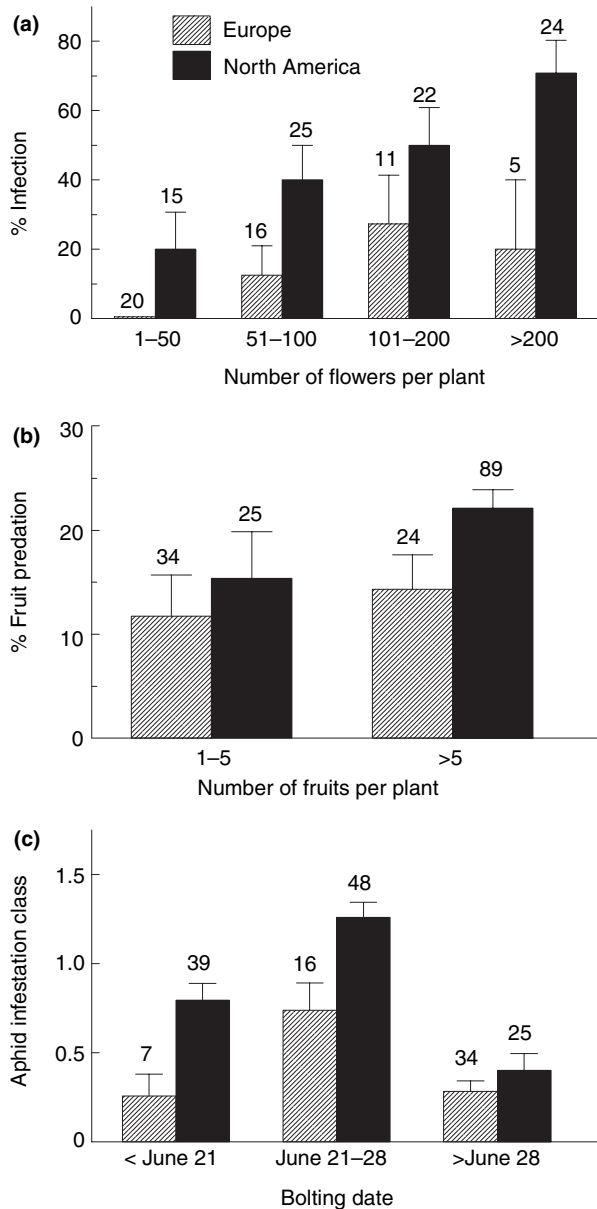
Figure 2 Susceptibility (+1 SE) of *Silene latifolia* plants from native European (hatched bars) and introduced North American populations (black bars) to enemies from the native range when grown in a common garden in Europe. (a) Infection of male plants by the anther smut fungus *Microbotryum violaceum*; (b) fruit predation of female plants by the noctuid *Hadena bicruris*; (c) infestation of female plants by the aphid *Brachycaudus lychnidis*. Numbers on top of bars are sample sizes. Flower number and phenology differ between plants from the two continents and affect susceptibility, hence separate bars for flower number and phenology classes are presented.

hence the higher predation rates of fruits on NA plants could potentially reflect a difference in plant size. However, when fruit number was included in the analysis as a covariate ($F[1,137] = 26.62$, $P < 0.001$), fruit predation was significantly higher in NA plants as well ($F[1,32] = 4.50$, $P = 0.042$), indicating that for a given plant size, NA plants are still more susceptible to fruit predation.

Average levels of aphid infestation were significantly higher for female plants from NA than for female plants from EU (Table 1). Infestation levels were affected by flowering phenology. They were relatively low for both early-bolting and late-bolting plants and high for plants with intermediate phenology (Fig. 2c). Including these bolting classes as a covariate in the analyses indeed revealed a significant effect of bolting time ($F[2,132] = 45.36$, $P < 0.001$), but differences in infestation levels between NA and EU females were still significant ($F[1,33] = 6.99$, $P = 0.013$). In contrast to female plants, male plants did not differ in susceptibility to aphid infestation (Table 1).

DISCUSSION

Our study reveals two major findings. First, we corroborate the existence of strong genetically-based differences in life-history traits between *S. latifolia* populations from the native EU range and from the introduced NA range as reported in Blair & Wolfe (2004). Plants from the introduced range are larger and have higher reproductive potential. These differences might contribute to their invasiveness in the novel habitat. Second, we observed a significantly higher susceptibility of plants from NA populations to natural enemies from the native range, compared with plants from EU populations.

The differences in life-history between plants from the two continents that we observed in the common garden in EU are in close agreement with the results from a corresponding common garden experiment that was carried out simultaneously in NA, using seed material from the same source populations (Blair & Wolfe 2004). When grown in a common garden in Virginia, plants from NA populations appeared to have a more 'weedy' phenotype than plants from EU populations. They germinated faster, produced over 20% more vegetative biomass, were more likely to flower in the first year, had an earlier onset of flowering, and had a twofold higher flower production. The fact that we find a similar pattern (i.e. a higher reproductive potential of plants from NA populations) when plants are grown in EU is significant. It indicates that this pattern does not result from a home-site advantage or local adaptation. Rather, the superior growth and reproductive performance of NA plants appears to be due to a genetically-based difference between populations from the two ranges that is expressed in both continents.

Both findings, the enhanced growth and reproductive potential and the enhanced susceptibility to natural enemies in the introduced range, are consistent with one of the

influential hypotheses regarding the invasiveness of organisms in novel environments, the Evolution of Increased Competitive Ability hypothesis (EICA; Blossey & Nötzold 1995). The basic idea is that release from natural enemies in the novel environment allows introduced species to shift investment from traits involved in defence to traits that are important attributes of invasiveness. Although NA and EU *S. latifolia* do not differ in competitive ability (Blair & Wolfe 2004), release of *S. latifolia* from natural enemies in its introduced range is well documented. In line with the general finding of enemy release both for introduced animals (Torchin *et al.* 2003) and plants (Mitchell & Power 2003, but see Agrawal & Kotanen 2003), a survey of 50 NA and 50 EU *S. latifolia* populations revealed that NA populations experience on average 17-fold lower levels of damage from natural enemies than EU populations (Wolfe 2002). The evolutionary shift of *S. latifolia* plants towards larger, earlier flowering plants with a high reproductive potential in the introduced range is consistent with a scenario of natural selection for increased reproductive potential in the absence of natural enemies. However, at this point we cannot rule out a possible role of other evolutionary forces such as genetic drift or hybridization (Ellstrand & Schierenbeck 2000).

If the difference in life-history between NA and EU populations is indeed due to an evolutionary shift in allocation from defence to growth and reproduction, we expect NA populations to show increased susceptibility to native natural enemies, provided that defences against these enemies are costly. Indeed, we observed strongly increased susceptibility to fungal infection by *M. violaceum*, fruit predation by *H. bicruris* and aphid infestation by *B. lychnidis* in NA *S. latifolia*. Part of the higher susceptibility was a direct consequence of the altered life-history of these plants. Early flowering and high fruit production enhanced overall susceptibility to fungal infection and fruit predation, respectively, irrespective of where plants originated from. Likewise, intermediate phenology enhanced overall susceptibility to aphid infestation. Since a larger proportion of plants from NA populations fell into these 'risk categories', they had an overall increased susceptibility to natural enemies.

Interestingly, when we corrected for differences in size or phenology, plants from NA populations were still more susceptible to these natural enemies. This suggests that their higher susceptibility does not just reflect a higher contact rate with natural enemies, but is at least partly due to differences in resistance that are independent of the observed differences in life-history. Costs of resistance to herbivores and pathogens are a general phenomenon (Strauss *et al.* 2002). For male *S. latifolia*, fitness costs of biochemical resistance to *M. violaceum* have been well documented (Biere & Antonovics 1996). Release from *M. violaceum* might thus increase resources available for reproduction. Interestingly, biochemical resistance in male *S. latifolia* appears to be genetically correlated with later onset of flowering (Biere & Antonovics 1996). Release from *M. violaceum* and a concomitant reduction in biochemical defence might thus release the genetic constraint on onset of flowering. Lower resistance of NA *S. latifolia* to fruit predation by *H. bicruris* could partly be related to altered fruit characteristics. Blair & Wolfe (2004) found that plants from NA populations had 19% less trichomes on the calyx and that fruits of plants from NA have a significantly thinner fruit wall. Both shifts could contribute to increased fruit predation. Capitate trichomes on the inner calyx surface of *S. latifolia* are hypothesized to play a role in flower discrimination by specialized pollinators and seed predators (Bopp 1999) and may affect primary predation rates, whereas fruit wall thickness might affect both primary and secondary predation rates since these require creation of entrance holes through the fruit wall. However, it should be noted that even if these traits indeed contribute to lower fruit predation, we do not know whether the observed differences in these traits evolved as a response to reduced natural enemy encounters in the introduced range or to other selection pressures in the novel environment.

Studies investigating differences in susceptibility between plants from native and introduced ranges are scarce and have produced equivocal results. Chinese tallow trees (*S. sebiferum*) introduced into NA (Siemann & Rogers 2003) and smooth cordgrass populations (*Spartina alterniflora*) introduced in ranges with a low incidence of a specialist grasshopper common to the native habitat (Daehler & Strong 1997; Garcia-Rossi *et al.* 2003) show reduced resistance to their natural enemies, but this does not appear to be the case for tolerance to herbivory in *Solidago canadensis* introduced into EU (Van Kleunen & Schmid 2003). Clearly, more studies are required before we can arrive at any generalization.

An important result of our study is that, despite the higher susceptibility of NA plants to the native EU enemies and their higher attack rates by these enemies when transplanted into EU, these plants still outperformed their EU counterparts in the presence of these natural enemies. In other words, they did not only have a higher reproductive potential, but also a higher realized reproduction (undamaged flower and fruit production). This indicates that the benefits of increased reproductive potential were not outweighed by the increased susceptibility to natural enemies in the original environment. This raises the question why EU populations have not evolved a similarly high reproductive capacity and overall 'weedy phenotype' in their native environment. There are at least two possible explanations for this. First, although the organisms we studied are the three main aboveground enemies that we encounter in natural systems, exposure to natural enemies in the common garden may not have been sufficiently representative of

biotic stress in natural populations. As a corollary of this idea, temporal variation in the form of year-to-year fluctuations in enemy attack may favour the maintenance of resistance to enemies in EU populations, even though this may be costly in years with lower densities of enemies. Second, the distribution of habitat types in which *S. latifolia* occurs in N. America and EU is not necessarily the same. *S. latifolia* is a species from ruderal habitats. The weedy phenotype of NA populations may be less able to persist in successional stages with a slightly less open vegetation. This can only be tested by growing populations from NA and EU in natural habitats in the two continents.

With the growing awareness of the devastating impacts of biological invasions, it is critical that we understand the forces that cause a species to behave differently after its introduction to a novel environment. Only relatively recently have biologists begun to consider the contribution that short-term rapid evolution can make to invasion success. The results of this study, as well as that of Blair & Wolfe (2004), clearly demonstrate that there has been genetically-based changes in *S. latifolia* and that the direction of these changes are consistent with natural selection resulting from altered interactions with enemies.

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