# Why Alien Invaders Succeed: Support for the Escape-from-Enemy Hypothesis

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ABSTRACT: Successful biological invaders often exhibit enhanced performance following introduction to a new region. The traditional explanation for this phenomenon is that natural enemies (e.g., competitors, pathogens, and predators) present in the native range are absent from the introduced range. The purpose of this study was to test the escape-from-enemy hypothesis using the perennial plant *Silene latifolia* as a model system. This European native was introduced to North America in the 1800s and subsequently spread to a large part of the continent. It is now considered a problematic weed of disturbed habitats and agricultural fields in the United States and Canada. Surveys of 86 populations in the United States and Europe revealed greater levels of attack by generalist enemies (aphids, snails, floral herbivores) in Europe compared with North America. Two specialists (seed predator, anther smut fungus) that had dramatic effects on plant fitness in Europe were either absent or in very low frequency in North America. Overall, plants were 17 times more likely to be damaged in Europe than in North America. Thus, *S. latifolia*'s successful North American invasion can, at least in part, be explained by escape from specialist enemies and lower levels of damage following introduction.

*Keywords:* aliens, herbivory, invasion, *Silene latifolia*, *Hadena*, *Microbotryum*.

Although biological invasions represent a leading threat to biodiversity (Crawley 1987; Ruesink et al. 1995; Kareiva 1996; Rejmánek and Richardson 1996; Williamson 1996; Rahel 2000; Mack 2001) and are economically costly (Cox 1999), the attributes responsible for the spread of invasive species are poorly understood (Kolar and Lodge 2001). Introduction represents a rather dramatic event in a species' history, and both ecological and genetic elements of its biology may be affected (Novak and Mack 1993; Ross et al. 1993; Eckert et al. 1996; Barrett 2000; Callaway and Aschehoug 2000). Furthermore, a variety of new interactions are likely to arise in the adventive range that may have direct and/or indirect effects on both the invader and members of the local community (Parker 1997; Schoener and Spiller 1999; Blaney and Kotanen 2001).

An often reported observation in the literature is that invasive organisms exhibit enhanced individual growth and vigor in the adventive range following introduction (Baker 1965; Noble 1989; Blossey 1993; but see Thébaud and Simberloff 2001). The most commonly invoked explanation for this phenomenon is that natural enemies (e.g., competitors, predators, and pathogens) that are present in the native range do not follow the migrating species and are thus absent from the introduced range (Lawton and Brown 1986; Crawley 1987; Blossey and Notzold 1995). Despite its appeal as the reason for invasion success, researchers have rarely sampled both parts of a species' range to quantify levels of damage with the goal of evaluating the escape-from-enemy hypothesis (Memmott et al. 2000). This is surprising given the potential insights to be gained from such comparisons.

*Silene latifolia* (Caryophyllaceae; hereafter referred to as *Silene*) is a dioecious, short-lived perennial that grows in disturbed areas such as along roadsides and the margins of agricultural fields (Baker 1947*a*). The species is native to Europe and is thought to have been accidentally introduced to northeast North America following the spread of agriculture in the early to mid-1800s (Baker 1947*a*; Godwin 1975; Prentice 1979). Since its introduction, *Silene* has subsequently expanded its range to include a large portion of North America. *Silene* is considered an invasive species in the United States and Canada and is listed as a noxious weed of farmlands and pastures (McNeill 1977). This is in stark contrast to Europe, where the plant is valued for its scented, night-blooming flowers and is even available for purchase from seed catalog companies. Thus, it is of interest to determine what factors may have contributed to its successful invasion of North America. The purpose of this study was to quantitatively test the escape-from-enemy hypothesis using the herbaceous plant *S. la-*

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*tifolia* as a model system. If the escape-from-enemy hypothesis is correct, I predicted that the level of enemy attack on *Silene* would be greater in the native part of its distribution (Europe) compared with the introduced range (North America). *Silene* is a particularly appropriate organism with which to evaluate the validity of the escape-from-enemies hypthothesis since it is attacked by a variety of predators and pathogens.

## Material and Methods

To test the escape-from-enemy hypothesis, I sampled 50 populations in Europe and 36 populations in North America in June–August 2001. The North American populations were sampled in Illinois, Iowa, Maryland, Michigan, Minnesota, North Carolina, Ohio, Pennsylvania, Tennessee, and Virginia. European populations were sampled in Great Britain, Denmark, France, Holland, Italy, Poland, and Spain. Populations were located by driving along rural roads and highways. A population was considered all plants within an area that was separated from any other population by at least 3 km. Because most populations were not excessively large (mean ± SE: 66.1 ± 33.5 individuals; range 1–1,000), I was able to sample all individuals within each. In large populations (500–1,000), I sampled about 50% of the individuals by examining all plants encountered along transect(s) through the population.

I recorded four measures of enemy attack in each *Silene* population. (1) Phloem-feeding aphids: these insects typically occured in large congregations on stems throughout the plant. (2) Floral herbivory: damage (e.g., torn petals, holes in the corolla, eaten reproductive organs) was recorded on open flowers before floral senescence. (3) Fungal disease: infections by the anther smut fungus *Microbotryum violaceum* (hereafter *Microbotryum*) result in sexual sterility in male and female *Silene* plants (Baker 1947*b*). The disease is evident by the presence of dark gray fungal spores produced by modified anthers. The spores are subsequently transmitted by pollinators (Altizer et al. 1998), and although plants may eventually recover from infection, the disease usually becomes systemic (Alexander 1987; Alexander and Antonovics 1988). (4) Fruit and seed predation: *Silene* fruits are attacked by a specialist predator (*Hadena rivularis*, Noctuidae; hereafter *Hadena*) that feeds exclusively on *Silene*. This insect has a rather interesting life history, since adult females serve as major pollinators of *Silene* (Brantjes 1976). After pollination, females oviposit eggs on the flowers, and the larvae subsequently eat flowers and developing fruits (Jennersten 1983). I haphazardly collected 25–50 fruits from each population (one per plant) to yield an estimate of the fraction of fruit that was damaged. In addition, I counted the number of seeds in a subsample of fruit to quantify the impact of fruit predation on seed production.

All statistical analyses were conducted using JMP 3.1.5 (SAS Institute). Student's *t*-test was used to compare levels of damage (percent of individuals damaged) between European and North American populations. Values for the percent of individuals attacked were calculated by averaging the attack rate (number of plants attacked/total number of plants in the population) over all populations within Europe or North America. These values were arcsine–square root transformed before analysis. Contingency table analysis (*G*-test) was used to compare the fraction of populations in the two ranges that was attacked by natural enemies. Linear regression was used to examine the relationship between population size and the number of enemies present.

## Results

*Silene* was attacked by a variety of organisms, and the magnitude of damage was significantly greater in the native European range at both the population and individual level. About 60% of North American populations contained no enemies, and plants completely escaped damage. In contrast, 84% of European populations had damage from at least one type of enemy. Furthermore, 50% of populations in Europe experienced damage from two to three different types of organisms.

Aphids were observed in 31% of European populations, while in North America these insects were seen only in a single *Silene* Michigan population (fig. 1). Overall, 12% (range 0%–75%) of European individuals were infected with aphids compared with <1% (range 0%–5%) in North

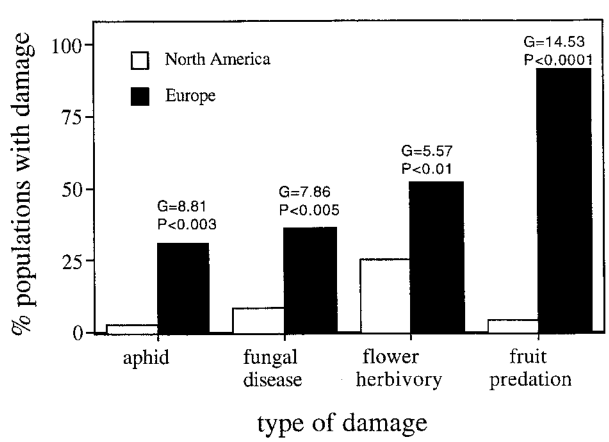


**Figure 1:** Incidence of damage inflicted by different natural enemies on *Silene latifolia* in North America and Europe. The statistics on top of bars are from *G*-tests.

America (fig. 2). The aphids caused plants to bear shriveled stems and produce wilting flowers. Flowers in both geographic ranges were frequently the target of herbivores. More than 50% of European populations received some damage to floral parts compared with 25% of North American populations (fig. 1). At the individual level, 15% (range 0%–67%) of European *Silene* plants suffered some damage to flowers compared with 2% (range 0%–10%) of North American flowers (fig. 2).

In addition to generalist enemies such as the floral herbivores and aphids discussed above, *Silene* was also attacked by two specialists. More than one-third (36%) of European populations were infected with the fungus *Microbotryum* compared with 8% of North American populations (fig. 1). *Microbotryum* was also more geographically widespread in Europe than in North America. This fungus was found in all the countries I sampled in Europe, but in North America, *Microbotryum* was seen only in Virginia. Overall, about 7% (range 0%–56%) of plants were infected in Europe compared with <1% (range 0%–20%) in North America (fig. 2).

The specialist fruit predator *Hadena* was devastating in Europe but was not present in North American *Silene* populations. I found *Hadena* in more than 90% of European populations (fig. 1), where it was responsible for the destruction of almost 25% of all *Silene* fruit produced (fig. 2). The level of fruit predation was so great that there were some European populations in which no seed was found (L. M. Wolfe, personal observation). *Hadena* had a strong effect on seed production, since uneaten *Silene* fruit produced significantly more seeds than fruit that had been attacked (mean ± SE: 350 ± 41 vs. 53 ± 25; *t*-test, $t = 6.14$, $P < .0001$). However, it should be noted that the seed number for attacked fruit is likely an overestimate, since

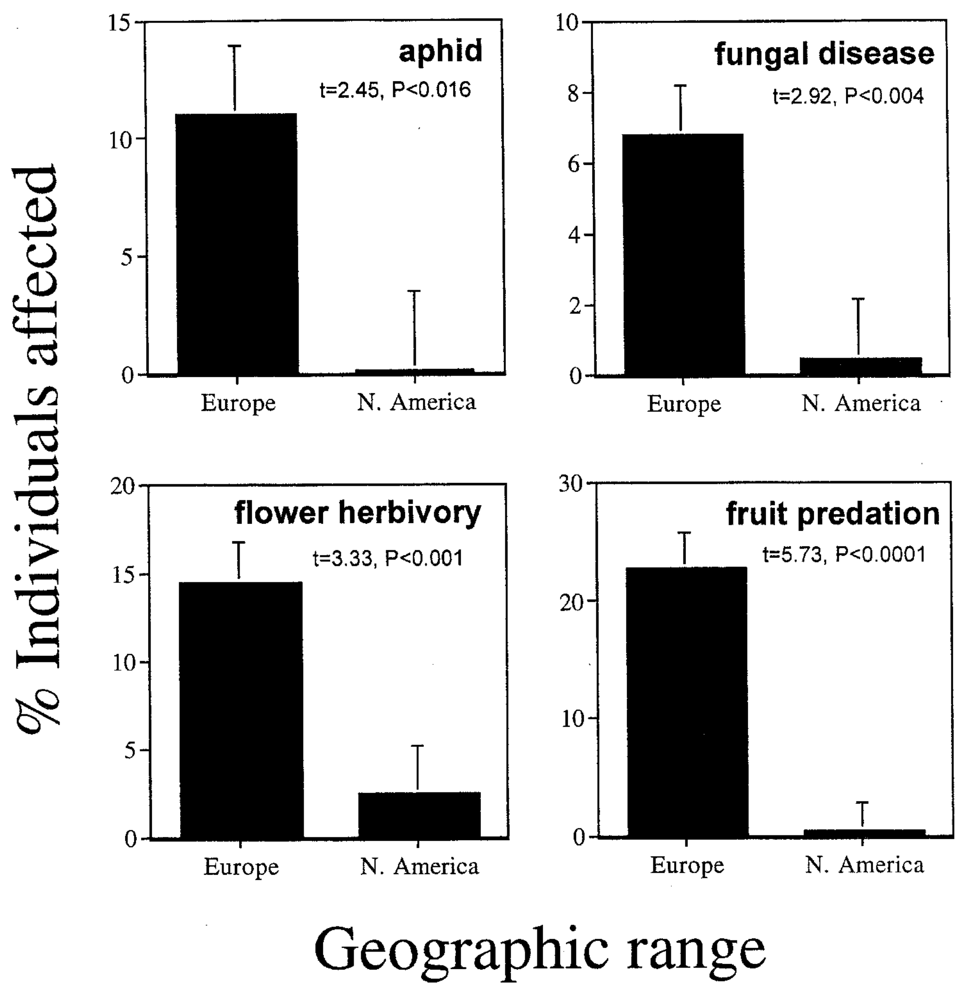


**Figure 2:** Percentage (mean ± SE) of *Silene latifolia* individuals damaged by different enemies in European and North American populations

this does not take into account fruits that were completely destroyed during predation.

Populations in both Europe and North America varied in size (range 1 to ~1,000), yet there was no significant difference in the number of plants per population in the two regions (mean ± SE: North America 45.8 ± 25.7, Europe 58.6 ± 22.0; $t = 0.375$, $P = .708$). Of interest, population size did influence the pattern of enemy attack in Europe: there was a significant positive relationship between population size and the number of different types of enemies present (fig. 3). However, there was no relationship between population size and enemy diversity in North American *Silene* populations.

### Discussion

A major goal of research on biological invasions has been to understand why some plant and animal species become notorious invaders while others remain benign (Crawley 1987; Simberloff 1995; Kareiva 1996; Rejmánek and Richardson 1996; Blackburn and Duncan 2001; Chittka and Schurkens 2001; Kolar and Lodge 2001; Grotkopp et al. 2002). The escape-from-enemy hypothesis posits that decreased regulation by natural enemies results in increased abundance and distribution following introduction. If one takes into account all sources of damage, a *Silene* individual chosen at random is about 17 times more likely to be attacked in its native Europe than in North America. It is worth pointing out that the levels of damage reported in this article are likely underestimates owing to the fact that I focused on damage to reproductive structures. For example, snails were observed grazing on leaves and stems in 50% of the populations in Spain and southern France but were never seen on North American *Silene.* Not only is the probability of damage greater in Europe, but also plants in that region were attacked by a greater variety of enemies. In the more southern European populations, it was not uncommon to find single individuals that were simultaneously being attacked by aphids, floral herbivores, *Microbotryum*, and *Hadena.* These enemies all have different impacts on the host plant. For example, sterilization by *Microbotryum*, consumption of reproductive organs (stamens and pistils) by floral herbivores, and seed predation by *Hadena* larvae will clearly have a direct negative effect on fitness. Alternatively, herbivory on corollas may indirectly affect reproductive success if damaged flowers are less attractive to pollinators (Krupnick and Weis 1999). Taken together, these organisms combine in either an additive or a multiplicative fashion, resulting in a higher quality of life for *Silene* in the introduced North American range.

It is likely that enemy species vary in their ability to control host populations depending on the degree of specialization of the relationship (Keane and Crawley 2002). Previously published theoretical work has considered how generalist and specialist predators differ in their ability to control prey populations (e.g., Murdoch 1994), and I believe we can apply this to extend our understanding of invasive species. We might imagine generalists to be relatively difficult to escape, since their ecological role can be filled by species already present in the introduced range (Blaney and Kotanen 2001). In contrast, specialist enemies are likely to be the product of generations of interactions with the host and possibly even of coevolution (Berenbaum et al. 1986). Thus, if a host does manage to leave a specialist enemy behind, it is unlikely to encounter another following introduction. The majority of *Silene* individuals damaged in Europe were attacked by two specialists. Of these, one is not present in North America (*Hadena*), and the other is very rare (*Microbotryum*).

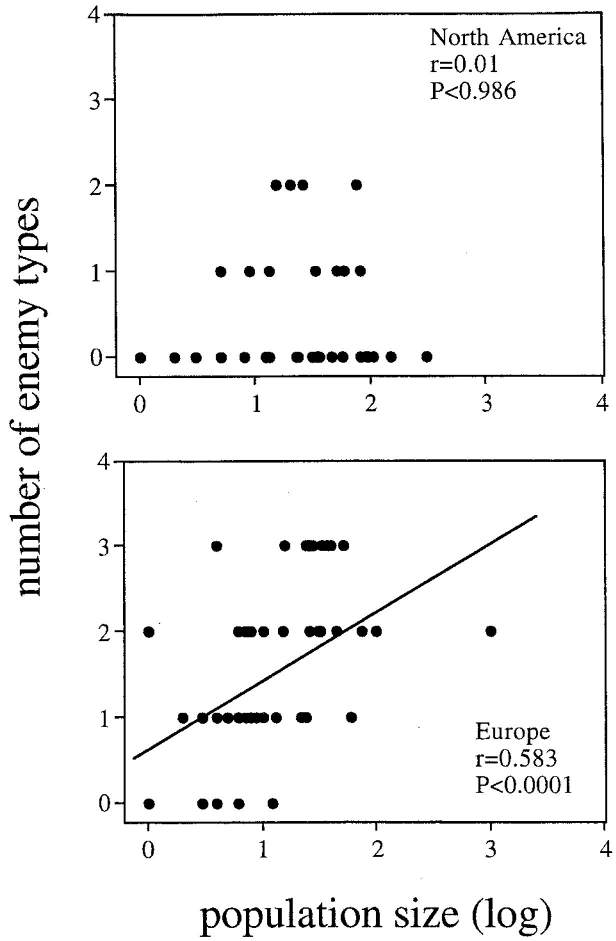


**Figure 3:** Relationship between the size of North American and European *Silene latifolia* populations and the number of different enemy types present.

Clearly, the human-mediated transport of *Silene* approximately 200 yr ago from Europe to North America allowed the plant to completely escape *Hadena*. Even though individual *Silene* plants in North America produce large fruit crops (L. M. Wolfe, personal observation), no other seed predator has apparently filled the niche vacated by *Hadena*. Alternatively, even though the specialist fungus *Microbotryum* did manage to cross the Atlantic Ocean, it remains severely restricted geographically and seems to infect *Silene* only in Virginia (this study; J. Antonovics, personal communication). It is not known what factors are responsible for the apparent inability of the fungus to spread within the introduced range.

The patterns revealed from surveys of natural populations in this study are consistent with the notion that *Silene*'s relatively rapid spread across the North American continent in 200 yr was due to reduced interactions with two specialists. These two organisms directly affect fitness and result in lower per capita reproductive success in Europe compared with North America. Thus, this study offers strong support for the escape-from-enemy hypothesis. However, even though the suite of natural enemies impacts individual fitness, it is not known to what degree this translates into population-level consequences. It would be necessary to determine the factors that limit recruitment (e.g., microsite availability) before being able to conclude that these enemies actually regulate population growth in *Silene*. Even though the average number of individuals per population did not differ between the two regions, population size appears to play a site-dependent role in the dynamics of enemy abundance. The positive relationship between population size and enemy diversity within Europe demonstrates that plants in larger populations must contend with greater numbers of predator and pathogen species. In contrast, the low overall attack rate in North America is not related to population size, indicating that *Silene*'s enemy biology differs dramatically between the native and introduced ranges.

The escape-from-enemy hypothesis is ecological in nature because it evaluates the role of interspecific interactions. In addition, it is possible that other factors play a key role in successful invasions. For example, it is likely that evolutionary forces are also involved in determining the outcome of an introduction (Sakai et al. 2001). Introductions will almost certainly result in a decrease in genetic diversity because of genetic drift resulting from bottlenecks (Novak and Mack 1993; Ross et al. 1993; Amsellem et al. 2000; Tsutsui et al. 2000). Such a reduction has been found to have profound consequences on breeding patterns in plants (Eckert et al. 1996) and social behavior in animals (Ross et al. 1996). It is not unreasonable to expect that the western spread of *Silene* through North America resulted in a series of drift events such that subsequently founded populations became increasingly genetically depauperate. Furthermore, an increase in additive genetic variance resulting from bottlenecks (Goodnight 1988) may allow for rapid response to natural selection by invaders (Carroll and Dingle 1996). Given the relaxation of predation pressure in North America, natural selection may have favored the reallocation of resources to phenotypic traits that favor "weedy" growth (Blossey and Nötzold 1995; but see Willis et al. 1999). The interactive effect of evolution by drift, and natural selection resulting from varying degrees of specialization in host-enemy interactions, may help explain successful invasions.

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