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**Herbivores and the success of exotic plants: A phylogenetically controlled experiment**

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**ABSTRACT**

In a field experiment with 30 locally occurring old-field plant species grown in a common garden, we found that non-native plants suffer levels of attack (leaf herbivory) equal to or greater than levels suffered by congeneric native plants. This phylogenetically controlled analysis is in striking contrast with recent findings from surveys of exotic organisms, and suggests that even if ‘enemy release’ does accompany the invasion process, this may not be an important mechanism of invasion, especially for plants with close relatives in the recipient flora.

Key words: Congeneric pairs, exotics and aliens, herbivory, invasive species, plant invasions, plant-insect interactions
Introduction

The accidental or intentional introduction of non-native organisms continues to threaten natural and agricultural ecosystems worldwide (Mack et al. 2000; Pimentel 2002). Recent studies have demonstrated that exotic plant species have smaller pathogen and herbivore communities in their introduced range than in their region of origin (Fenner & Lee 2001; Wolfe 2002; Mitchell & Power 2003). This reduced parasite biota potentially gives exotic plants an advantage in comparison with native plants, as predicted by the classic “enemy release” hypothesis for the success of introduced organisms (Keane & Crawley 2002; Wolfe 2002; Mitchell & Power 2003; Torchin et al. 2003). Lacking from most previous studies, however, are direct experimental comparisons of impacts on native versus exotic organisms in a common habitat (Schierenbeck et al. 1994). This comparison is critical because 1) a lower diversity of enemies does not necessarily translate to less damage (Maron & Vilà 2001), 2) the local processes that control populations of native and exotic plants could be masked in continent-wide surveys, and 3) measuring native and exotic plants in a common environment ensures that any observed differences are not the product of unmeasured environmental or faunal variation between native and foreign sites.

Old-field habitats of eastern North America are dominated by a mixture of native and exotic herbaceous plant species. To test for the impacts of folivorous insects on native versus exotic plants, we conducted a field experiment with 30 taxonomically paired old-field plant species in a common garden. Using congeneric pairs factors out a large component of interspecific variation, leaving behind species that are similar except for their native/exotic status.

Materials and Methods
We collected seeds from 30 old-field plant species occurring at or near our field site, The University of Toronto's Koffler Scientific Reserve at Jokers Hill: 44° 03' N, 79° 29' W, near Newmarket in southern Ontario, Canada (Table 1). These 30 species formed 14 congeneric pairs and 1 confamilial pair, in which one species from each pair was a native, and one an exotic of Eurasian origin. All of the exotic plant species we used likely have been in the region for less than 200 years. Seeds from each species were germinated in a greenhouse in the spring of 2002 and planted to a plowed field in a completely randomized design (n≈15 plants for each of the 30 species). Plants were spaced 1 meter apart and the plot was not weeded or irrigated.

Late in the growing season we conducted a survey of percent leaf damage by naturally occurring insect herbivores. Percent leaf damage was estimated on September 24, 2002 by destructively harvesting 10 random leaves, while looking away, from each of our 390 surviving plants and by visually scoring each leaf for percent damage to the nearest 10%. Percent damage of each plant was then estimated as the mean percent of leaf area missing due to herbivory.

We also conducted a laboratory bioassay of resistance to a generalist lepidopteran (Spodoptera exigua Noctuidae). S. exigua is a widely employed generalist herbivore known to feed on plants in well over 20 families. This test examines whether there are differences between the native and exotic plants, irrespective of their fauna of enemies; these differences may have evolved since invasion or may simply reflect the longer evolutionary history of the plants. To assay resistance, we cut a single leaf off of each of our field plants and placed it in a 90mm petri dish lined with moist filter paper in a cooler. Petri dishes were brought back to a non-air conditioned lab and one S. exigua neonate was introduced to each dish. Petri dishes were sealed with parafilm and the larvae were allowed to feed for 5 days at ambient temperature. After this
assay period, we assayed mortality of the herbivore and growth of the survivors. Growth was assayed by weighing frozen wet mass of larvae to the microgram.

We employed fixed-factor factorial ANOVAs for the analyses; we used arcsine square root transformed values for the percent leaf damage. Effects on larval mortality in the bioassay were assessed with a paired t-test on arcsine square root transformed percent larval death on each plant species, by taxonomic pair.

Results and Discussion

Contrary to the predictions of the enemy release hypothesis, our census of leaf damage revealed that there were greater levels of herbivory by naturally occurring herbivores on exotic plants than on natives (Figure 1, 7.5% compared to 5.3% herbivory, $F_{1,360}=7.391$, $P = 0.007$). Herbivore damage varied significantly among genera ($F_{14,360}=25.073$, $P < 0.001$), supporting our decision to pair congenerics for the analysis. Although overall levels of herbivory were low, and pairs did significantly vary in the relative level of herbivory on native vs. exotics (interaction term: $F_{14,360}=2.027$, $P = 0.015$), the pattern of greater herbivory on exotics was found in 11 of the 15 taxonomic pairs. At minimum, our finding soundly rejects the hypothesis that exotics generally have lower levels of herbivory (Figure 1). It is unclear whether the higher levels of damage on our exotic plants was a product of higher diversity of herbivores compared to natives; the correlation between herbivore diversity and damage is an issue requiring further study.

Plant abundance was not a clear explanatory variable for the patterns of herbivory we observed; all species in our study are considered common to very common in the region (Abundances ranked by the Ontario Natural Heritage Information Centre, http://www.mnr.gov.on.ca/MNR/nhic/nhic.cfm). Similarly, invasiveness did not strongly correlate
with variation in herbivore damage (Invasiveness ranked by Ontario Society for Ecological Restoration (OSER), http://www.serontario.org/publica.htm). For example, OSER ranks both *Campanula rapunculoides* and *Bromus inermis* as Category 4, exotic species that do not pose a serious threat. Yet, in comparison with their native congener, alien *Campanula* had nearly 12 times more damage, while alien *Bromus* has a slightly lower level of damage (Figure 1).

In our bioassay of resistance with a single generalist herbivore, neither larval mass of the survivors ($F_{1,87}=1.280, P = 0.269$) nor larval mortality ($t=1.189, df=14, P=0.254$) were affected by native vs. exotic origin. This result indicates that exotic species are no more resistant to herbivores than native congeners, although the mortality data tended to be lower on exotics, consistent with patterns of leaf damage (percent mortality of *S. exigua* ± s.e.m. on native plants was 78 ± 5 versus 64 ± 7 on exotic plants). This similarity between natives and exotics is likely a consequence of the chemical and physical similarity between congeners, and may not apply to exotics that are more phylogenetically distant from the native flora. Such ‘phylogenetically isolated’ species may be more likely to escape enemies in new regions (Darwin 1859; Rejmánek 1999; Duncan & Williams 2002), perhaps contributing to the evidence of predator escape produced by broad but phylogenetically uncontrolled surveys (e.g., Mitchell & Power 2003). One limitation of using congeneric pairs is that inference is limited to highly similar species, potentially biasing results against finding the patterns evident in phylogenetically broader studies. However, even congeneric plants often differ in invasiveness: Mack *et al.* (2000) indicate that “guilt by [taxonomic] association has proven imprecise at predicting invasive potential”. Thus, we contend that the benefits of phylogenetic control outweigh the costs, since significant variation in invasiveness remains even after unwanted noise been reduced by phylogenetic correction.
Had we examined enemies other than invertebrate folivores, it is possible we might have found different results. For example, Mitchell and Power (Mitchell & Power 2003) considered foliar pathogens and viruses, Wolfe (Wolfe 2002) assayed several herbivore and pathogen guilds, and Fenner and Lee (Fenner & Lee 2001) focused on insect seed predators. Blaney and Kotanen (Blaney & Kotanen 2001) obtained results similar to ours, however, in an experiment designed to assess the impacts of fungal seed pathogens on native and exotic congeners, including most of the pairs included in our experiment. This study found that fungi caused significant losses of seeds in wet meadows, but that these losses did not differ between native and exotic plant species. Finally, Maron and Vilà (2001) documented numerous cases of attack by native enemies on exotic plants, suggesting that even successful escape from some enemies may not translate to less damage or better performance in the novel environment. Ultimately, the net impact on plant fitness (summing across plant resistance and tolerance to attack) will determine the role of enemies in the success of exotic plants (Strauss & Agrawal 1999).

Our report challenges the enemy release hypothesis, as exotic flowering plants appear to be experiencing greater levels of attack across a broad range of families, compared to their native counterparts. Although knowing the identity and origin of the herbivores responsible will be critical for conclusions about the causes of the patterns we observed, the finding that exotic plants are less able to escape herbivory than congeneric natives indicates that native plants may be better adapted to the local herbivore fauna than non-natives (Shea & Chesson 2002), as asserted by the “new association” principal of biological control (Hokkanen & Pimentel 1989).

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References


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Table 1. Species employed in the experiment. Presence of wild plants at our study site is indicated by an “x” under JH; “?” indicates possible occurrence; all other plants occur in southern Ontario. Native or alien origin follows Morton & Venn (1990) and nomenclature follows Gleason & Cronquist (1991). LH = Life History from Newmaster et al. (1998): “A” = Annual, “B” = Biennial, “P” = Perennial. The numbers in parentheses refer to the taxonomic pair shown in Figure 1. Under the numbers in parentheses and family name, we provide the results from an individual t-test on that pair alone; see Figure 1 for the mean differences in herbivory.

<table>
<thead>
<tr>
<th>Plant family</th>
<th>Species</th>
<th>Origin</th>
<th>JH</th>
<th>LH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asclepidaceae</td>
<td>Asclepias syriaca</td>
<td>Native</td>
<td>x</td>
<td>P</td>
</tr>
</tbody>
</table>
|                   | Cynanchum rossicum     | Alien  | x  | P  | t=3.1, df=26, P<0.01
| Asteraceae       | Lactuca canadensis     | Native | x  | B  |
|                   | Lactuca serriola       | Alien  | x  | BA |
|                   | Senecio pauperculus    | Native | P  |
|                   | Senecio vulgaris       | Alien  | x  | A  | t=1.1, df=16, P=0.29
| (2) Asteraceae   | Artemisia campestris   | Native | B  | t=3.0, df=21, P<0.01
|                   | Artemisia biennis      | Alien  | x  | B  |
| Asteraceae       | Lepidium densiflorum   | Native | x  | A  | t=0.7, df=28, P=0.47
|                   | Lepidium campestre     | Alien  | x  | AB |
| (3) Asteraceae   | Campanula rotundifolia| Native | x  | P  | t=4.6, df=19, P<0.01
|                   | Campanula rapunculoides| Alien  | x  | P  |
| Cerastium arvense| Native                 | ?      | P  | t=1.7, df=31, P=0.09
| Campanulaceae    | Cerastium fontanum     | Alien  | x  | P  |
| (4) Caryophyllaceae| Silene antirrhina    | Native | x  | B  | t=1.5, df=29, P=0.14
|                   | Silene vulgaris        | Alien  | x  | P  |
| (5) Brassicaceae | Lepidium campestre     | Alien  | x  | AB |
| (6) Caryophyllaceae| Chenopodium simplex   | Native | x  | A  | t=0.9, df=18, P=0.37
|                   | Chenopodium album      | Alien  | x  | A  |
| (7) Caryophyllaceae| Plantago rugelii      | Native | x  | AP |
|                   | Plantago major         | Alien  | x  | AP |
| (8) Poaceae      | Bromus kalmii          | Native | P  | t=0.2, df=25, P=0.91
|                   | Bromus inermis         | Alien  | x  | P  |
| (9) Rosaceae     | Elymus trachycalus     | Native | P  | t=1.8, df=29, P=0.08
|                   | Elymus repens          | Alien  | x  | P  |
| (10) Rosaceae    | Geum aleppicum         | Native | x  | P  | t=1.7, df=24, P=0.11
|                   | Geum urbanum           | Alien  | x  | P  |
| (11) Rosaceae    | Potentilla arguta      | Native | x  | P  | t=1.3, df=15, P=0.22
|                   | Potentilla recta       | Alien  | x  | P  |
| (12) Rubiaceae   | Galium boreale         | Native | x  | P  | t=3.0, df=25, P<0.01
|                   | Galium verum           | Alien  | x  | P  |

Figure 1. Effects of plant origin on herbivory by naturally occurring insects in a common garden plot (Koffler Scientific Reserve at Jokers Hill, University of Toronto). The top panel summarizes effects across all species (raw mean ± s.e.m.), while the bottom panel shows the means for each of the 15 taxonomic pairs. The taxonomic identity of each pair in the bottom panel is given by the number and corresponds to Table 1.