## **Comment on "Opposing Effects of Native and Exotic Herbivores on Plant Invasions"**

Anthony Ricciardi\* and Jessica M. Ward

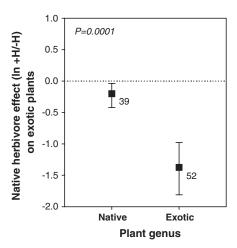
Parker *et al.* (Reports, 10 March 2006, p. 1459) showed that native herbivores suppress exotic plants more than native plants. Further analysis reveals that the effect of native herbivores is reduced on exotic plant species that are closely related to native species in the invaded region. Exotic plants may share traits with native congeners that confer similar resistance to resident herbivores.

hrough a meta-analysis of published experimental data, Parker et al. (1) demonstrated that native herbivores typically reduce the survival and abundance of introduced exotic plants, but tend to have weak positive effects on co-occurring native plants. Parker et al. concluded that plants are particularly susceptible to generalist herbivores that they have not been selected to resist. Here, we expand their analysis by considering the phylogenetic relationship of the exotic and native plants. Given that genetic divergence decreases as taxonomic relatedness increases, evolutionary logic suggests that species of the same genus are more likely to be functionally similar (2, 3). Indeed, congeneric plants do tend to have similar herbivore defenses (4, 5). Therefore, exotic plants that share a genus with native plants in the invaded range might be similarly susceptible to native herbivores, whereas those that belong to a novel genus would likely have differential susceptibility-potentially affecting their ability to persist and spread in their new environment.

We tested this hypothesis using the data set of native herbivore impacts on exotic plants, compiled by Parker et al. (1). For each experiment in the data set, we determined whether a native plant of the same genus as the exotic plant was historically present in the region in which the experiment was performed, by consulting native species lists provided by the Flora Europaea database (6) and the U.S. Native Plant Information Network of the Lady Bird Johnson Wildflower Center (7). We then performed an unweighted, fixed-effects model meta-analysis using Meta-Win 2.1 (8), following the same procedure as Parker et al. We generated 95% bias-corrected bootstrap confidence intervals and tested for significant differences between herbivore effects on native and exotic genera using a randomized resampling technique for meta-analysis with 9999 iterations (9). Our

analysis revealed that the negative effects of native herbivores are more pronounced on introduced plants belonging to exotic genera (Fig. 1). The mean  $\log_{e^{-}}$  transformed effect on exotic genera exceeded that on native genera by a factor of 5.8. We obtained similar results using a mixed-effects model.

More than 83% of the data set we used were measurements of plant survival. Because Parker *et al.* found that vertebrate herbivores exerted a greater negative effect than invertebrate herbivores on exotic plant survival, we considered that our results might be biased by differences in the proportions of vertebrate herbivores in studies involving native and exotic plant genera, respectively. However, when we ran replicate



**Fig. 1.** Effects of native herbivores on exotic plant abundance and survival in 18 experimental studies reported by Parker *et al.* (1). Effects are weakest on plants belonging to native genera, i.e., those that share a genus with a native species in the invaded region. Symbols show means  $\pm$  95% confidence intervals, which were calculated by using a bias-corrected bootstrapping technique with 9999 randomized iterations (9). Numbers to the right of the symbols are the number of experiments contributing to the mean. *P* value indicates difference in effects on exotic (unshared) versus native (shared) genera.

meta-analyses on the exclusive effects of vertebrate and invertebrate herbivores, respectively, the same result was obtained as for the combined data set.

This finding supports the view that variation in an invader's success and impact is, at least in part, explained by the invaded community's previous experience with functionally similar species (10). Factors proposed to explain the variation in the success of exotic species include the number of introduced propagules (e.g., seeds, eggs, and individuals), reproductive capacity, environmental tolerance limits, previous disturbance in the recipient community, and release from natural enemies (11-13). To date, few studies have examined invasion success as a function of the phylogenetic relationship between the introduced species and members of the recipient assemblage. Darwin hypothesized that introduced plants are more successful in colonizing areas that do not contain native species of the same genus because they would compete with their close relatives and encounter herbivores that could more easily exploit them (14, 15). Our study rejects this hypothesis and suggests that exotic plants are preadapted to conditions of herbivory experienced by congeneric native species. This provides further support for the view that generalist herbivores should have greater effects on exotic species with which they have not shared any evolutionary experience. Our results, together with those of Parker et al., demonstrate the inadequacy of "enemy release" models that simply relate the success of an invader to the absence of its natural predators in the invaded region (13).

## References and Notes

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Redpath Museum, McGill University, Montreal, Quebec H3A 2K6, Canada.

<sup>\*</sup>To whom correspondence should be addressed. E-mail: tony.ricciardi@mcgill.ca