Opposing Effects of Native and Exotic Herbivores on Plant Invasions

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Exotic species are widely assumed to thrive because they lack natural enemies in their new ranges. However, a meta-analysis of 63 manipulative field studies including more than 100 exotic plant species revealed that native herbivores suppressed exotic plants, whereas exotic herbivores facilitated both the abundance and species richness of exotic plants. Both outcomes suggest that plants are especially susceptible to novel, generalist herbivores that they have not been selected to resist. Thus, native herbivores provide biotic resistance to plant invasions, but the widespread replacement of native with exotic herbivores eliminates this ecosystem service, facilitates plant invasions, and triggers an invasional "meltdown."

Invasive exotic species threaten native biodiversity (*1*), alter ecosystem structure and function (*2*), and annually cost up to $120 billion in the United States alone (*3*). Determining the ecological traits and interactions that affect invasion success are therefore critical for predicting, preventing, and mitigating the negative effects of biological invasions. The leading hypothesis for why some exotic species become superabundant in their new ranges is the enemy release hypothesis, proposing that exotic species thrive because they lack coevolved enemies in their new ranges (*4*–*9*). However, introduced ranges contain evolutionarily novel enemies that exotic invaders may not be adapted to deter (*10*, *11*), and the biotic resistance hypothesis suggests that resistance by native enemies in the new range will limit the establishment or spread of most invaders (*4*–*6*). Regardless of the mechanisms involved, invasions by exotic species are increasingly common, and it has been hypothesized that positive feedbacks among this increasing number of exotic species can facilitate additional invasions and lead to an invasional "meltdown" (*12*). Such meltdowns might be exacerbated by humans introducing exotic species into, and harvesting native species from, native ecosystems, potentially both lowering the capacity for biotic resistance and increasing the potential for positive feedbacks among exotic species.

Exotic plants are often assumed to gain enemy release because herbivores will selectively attack native over exotic plants (*7*). However, this may be more applicable for specialist enemies that require host-specific feeding cues than for generalist consumers that view most plants as foods unless deterred by plant defenses. The distinction between generalist and specialist herbivores is especially critical because generalists often have larger impacts on plant community structure than specialists do (*13*, *14*); they commonly consume exotic plants in preference to native plants in laboratory feeding assays (*15*); and their effects on plant invasions have been historically overlooked (*7*). Rarely, however, have experimental exclusions of generalist herbivores been used to test whether these herbivores alter the abundance of exotic plants in natural communities. Instead, most tests of enemy release and biotic resistance have focused on correlative response variables that may not translate into demographic impacts (e.g., the number of native enemy species attacking an exotic species rather than the damage inflicted) (*8*, *9*), or on a few "model" species (*16*, *17*) that may not be typical of exotic species in general.

We tested the effects of herbivores on exotic plant invasions using meta-analysis to examine 63 published studies that experimentally excluded herbivores and monitored the success of more than 100 exotic plant species. Most (n = 35) of the studies we found monitored herbivore effects on entire plant communities rather than on plant invasions per se and thus avoided potential bias due to focusing on particular species. For these studies, we evaluated how herbivores affected the relative abundance of exotic plants (the fraction of the total plant community that was non-native) and the absolute abundance (e.g., plant biomass and cover) and species richness of both native and exotic plants (*18*). An additional 28 studies monitored herbivore effects only on specific species of exotic plants. These studies were used to assess native herbivore impacts on the establishment of exotic plants and to broaden our analysis by examining an additional 29 exotic plant species not included in the community-wide investigations. We did not include studies reporting enemy diversity or leaf damage alone because these indirect estimates may not translate to impacts on plant demography (*19*). Studies were drawn from a range of biomes (grasslands, scrublands, forests, deserts, freshwater and saltwater marshes, and lake bottoms) and herbivores (native bison, elk, deer, antelope, waterfowl, wallabies, rabbits, rodents, land crabs, fishes, mollusks, and insects; and exotic cattle, horses, deer, sheep, goats, rabbits, rodents, fishes, mollusks, and insects) (*18*).

In studies assessing herbivore effects on entire plant communities, native and exotic herbivores had opposing effects on the relative abundance of exotic plants. Native herbivores strongly suppressed, whereas exotic herbivores strongly enhanced, the relative abundance of exotic plants (Fig. 1). Native herbivores decreased the relative abundance of exotic plants by 28% (log response ratios correspond to a decrease in the relative abundance of exotic plants from 36.6 ± 5.5% in the exclusion treatments to 26.5 ± 5.2% in the grazed communities; mean ± SE), consistent with the biotic resistance hypothesis. In contrast, exotic herbivores increased the relative abundance of exotic plants by 65% (from 24.3 ± 3.8% in the exclusion treatments to 40.2 ± 4.9% in the grazed communities), consistent with the invasional meltdown hypothesis. Overall, the relative abundance of exotic plants was 52% higher in communities grazed by exotic herbivores (40.2 ± 4.9%) than in communities grazed by native herbivores (26.5 ± 5.2%).

An assessment of absolute, as opposed to relative, abundance also demonstrated that native and exotic herbivores had strongly opposing effects on native versus exotic plants. Native herbivores suppressed the abundance of exotic plants, whereas exotic herbivores suppressed the abundance of native plants (Fig. 2, A and B). Grazing by exotic herbivores also

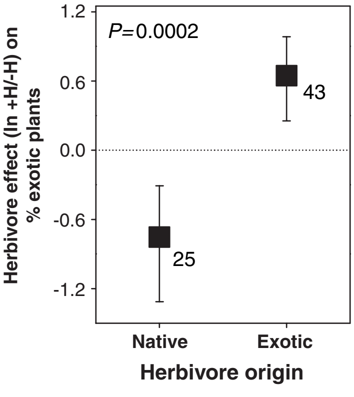

Fig. 1. Effects of native and exotic herbivores on the relative abundance (% of total plant cover or biomass) of exotic plants from 35 studies involving 68 experiments. Negative numbers indicate a decrease, and positive numbers an increase, in the relative abundance of exotic plants in the presence versus absence of herbivores. Numbers to the right of symbols are the number of experiments contributing to the mean. Points show means ± bias-corrected 95% confidence intervals. Effects are significant when the 95% confidence interval does not cross zero; P value tests difference in effects of native versus exotic herbivores.

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increased the species richness of exotic plants (Fig. 2D), whereas native herbivores had no detectable effect on the species richness of either native or exotic plants (Fig. 2C). Thus, native herbivores limited the abundance of exotic plants but not the likelihood of colonization by new species. In contrast, exotic herbivores promoted exotic plant dominance and richness by disproportionately reducing the abundance of native species. Although these results could be confounded if experiments on native versus exotic herbivores differed systematically in variables such as productivity, grazing rate, etc., that could affect herbivore impact (*20*, *21*), we found no evidence of such bias (*18*). Moreover, the general patterns we found were not driven by any one, common herbivore type; if we removed the studies with herbivores that were common and that had strong impacts (e.g., cattle, waterfowl), these general patterns persisted and remained significant (*18*).

Most previous assessments of release from herbivores have focused on effects of native invertebrate herbivory on exotic plant size or growth (*6*, *7*). In contrast, our analyses of native herbivores focused primarily on the impacts of vertebrates (24 of 25 experiments). We hypothesized that vertebrate herbivores would have larger effects than invertebrates by virtue of their larger size, enhanced mobility, broader diets, and propensity to kill plants rather than suppress plant growth (*13*, *22*). To test this hypothesis, we analyzed the impacts of native vertebrate and invertebrate herbivores on survivorship of exotic plant species. Native vertebrate herbivores had a three- to fivefold larger impact on exotic plant survival than did native invertebrate herbivores (*18*). This suggests that studies focused on native invertebrate herbivores alone may find small effects on plant invasions (*7*, *11*) because smaller and more specialized invertebrate herbivores have relatively modest impacts on plant survival.

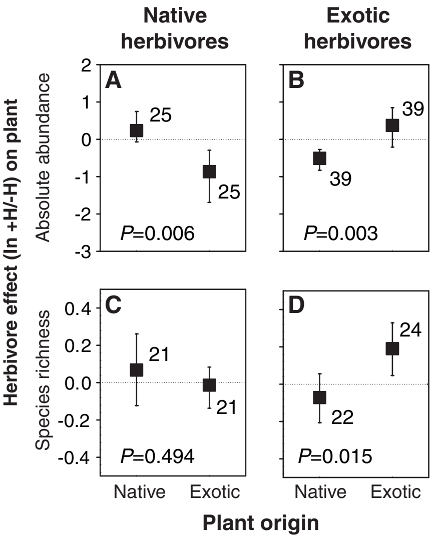

Fig. 2. Effects of native (left) and exotic herbivores (right) on the absolute abundance (**A** and **B**) and the species richness (**C** and **D**) of native and exotic plants. *P* values test differences between herbivore effects on native and exotic plants for each contrast. Other analyses as in Fig. 1.

Most exotic plants are noninvasive residents of their new communities (*23*), and the mean patterns shown in Figs. 1 and 2 could hide important biotic signals if noninvasive exotic plants were strongly suppressed by native herbivores but invasive exotic plants were not. Such a pattern could mean that the enemy release hypothesis would be valid for the small subset of species that become aggressive invaders. We thus asked whether herbivores had weaker impacts on plants that were more widely listed as invasive throughout the United States (*8*). However, neither native nor exotic herbivores had weaker effects on plants that were broadly considered invasive across the United States (Fig. 3). This pattern also held when we categorized plants as invasive even if they were listed as noxious by only a single U.S. state or natural resource agency (*18*). Thus, whether noxiousness was considered a continuous or categorical variable, and whether we considered agricultural or natural area invaders, noxious exotic plants were no less affected by herbivores than were noninvasive exotic plants.

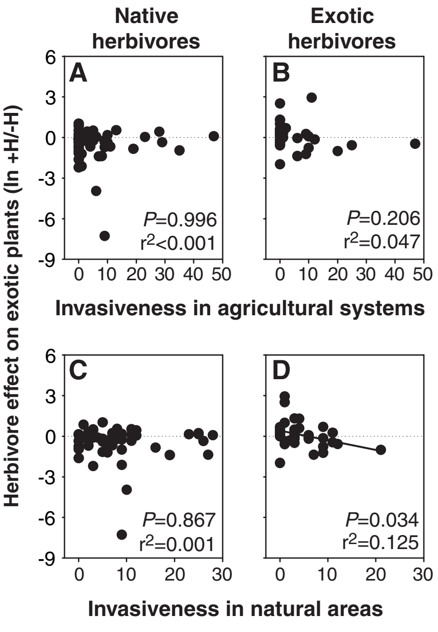

Fig. 3. Mean effects of native herbivores (**A** and **C**) and exotic herbivores (**B** and **D**) on exotic plant species as a function of the number of states or natural resource agencies within the United States listing each species as noxious in agricultural (A and B) or natural areas (C and D), respectively. Statistical analysis was by linear least-squares regression.

Historically, exotic species were thought to thrive by escaping their coevolved, specialist enemies (*4*, *5*), and little attention was paid to the consequences of gaining evolutionarily novel, generalist enemies in their new ranges. Evolutionary logic, however, suggests that exotic plants may be less adapted than native plants for repelling native herbivores (*10*). In fact, native, generalist herbivores preferentially attack exotic over native plants in the laboratory (*15*) and they suppress the abundance of exotic plants in the field (Figs. 1 and 2A). Similarly, exotic herbivores are novel enemies to native plants, and exotic herbivores selectively suppress the abundance of native plants in the field (Fig. 2B). The evolutionary logic for exotic herbivores suppressing native but not exotic plants makes sense only if many of the exotic plants are from the same home range and thus potentially adapted to the exotic herbivore. This was the case for our data set. Of the 41 exotic plant species for which native ranges were known, 88% originated from the same region of the same continent as the exotic herbivores used in that study (*18*). Thus, by negatively affecting evolutionarily naïve, native plants, exotic herbivores promoted the relative abundance and species richness of coadapted exotic plants from the same native range.

In recent centuries, weeds of European descent have left a global legacy of European ecological imperialism (*24*). Despite ample opportunity, comparatively fewer New World species have managed to invade the Old World (*24*, *25*). For more than a century, naturalists have been mystified by the "invisible barrier…preventing passage Eastward though allowing it Westward" and by "this total want of reciprocity in migration" (*24*, p. 166). Our analyses suggest that anthropogenic alteration of herbivore communities has facilitated exotic plant invasions. When Europeans initially colonized North and South America, Australia, and New Zealand, they largely extirpated native bison, elk, kangaroos, prairie dogs, moas, and tortoises and replaced them with introduced cattle, pigs, horses, sheep, goats, rabbits, and other exotic herbivores from Eurasia (*12*, *24*, *26*). Thus, a source of biotic resistance to plant invasions (native herbivores, Figs. 1 and 2A) was replaced with species that promote further invasions (exotic herbivores, Figs. 1 and 2, B and D). Consequently, exotic generalist herbivores decimated naïve, New World plants and paved the way for invasions of Old World plants that were adapted to these herbivores (*25*, *27*). Thus, exotic plants may thrive not by escaping their native enemies, but by following them. These findings have considerable implications for ecosystem conservation, suggesting that eradication of exotic herbivores and restoration of native generalist herbivores could mitigate exotic plant invasions and avoid problems associated with introductions of nonnative herbivores for biocontrol (*28*).

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Supporting Online Material
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A Major Ecosystem Shift in the Northern Bering Sea

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Until recently, northern Bering Sea ecosystems were characterized by extensive seasonal sea ice cover, high water column and sediment carbon production, and tight pelagic-benthic coupling of organic production. Here, we show that these ecosystems are shifting away from these characteristics. Changes in biological communities are contemporaneous with shifts in regional atmospheric and hydrographic forcing. In the past decade, geographic displacement of marine mammal population distributions has coincided with a reduction of benthic prey populations, an increase in pelagic fish, a reduction in sea ice, and an increase in air and ocean temperatures. These changes now observed on the shallow shelf of the northern Bering Sea should be expected to affect a much broader portion of the Pacific-influenced sector of the Arctic Ocean.

The northern Bering Sea, despite its seasonal ice cover (Fig. 1A), supports some of the highest benthic faunal biomass densities in the world's oceans (*1*, *2*). Over most of the Bering Sea shelf, zooplankton grazing and microbial processing in the water column have a small impact on pelagic retention, and therefore a large fraction of usable carbon settles to the benthos (*3*). However, in the southern (subarctic) region of the Bering Sea, the resulting benthic biomass is largely consumed by upper trophic level demersal fish and epifaunal invertebrates, whose northern distribution is limited by the presence of near-freezing bottom temperatures (*4*, *5*). The location of this temperature-determined subarctic-Arctic boundary is thus the primary agent determining ecosystem variability. In the absence of demersal fish and predatory invertebrates, benthic-feeding seabirds and marine mammals become the primary consumers in the northern (Arctic) region of the Bering Sea (*6*, *7*).

A change from arctic to subarctic conditions is under way in the northern Bering Sea, with an attendant northward shift of the pelagic-dominated marine ecosystem that was previously limited to the southeastern Bering Sea (*8*). The ice-dominated, shallow ecosystem favoring benthic communities and bottom-feeding sea ducks, such as spectacled eiders (*Somatera fuscgeri*), and marine mammals, including walrus (*Odobenus rosmarus*) and gray whales (*Eschrichtius robustus*), is being replaced by one dominated more by pelagic fish. Such shifts clearly affect both subsistence harvests and commercial fisheries. Yupik hunters of St. Lawrence Island, for example, have observed an increase in warm winds in winter and the replacement of stable pan and pack ice with brash and thin ice, changes that affect their ability to

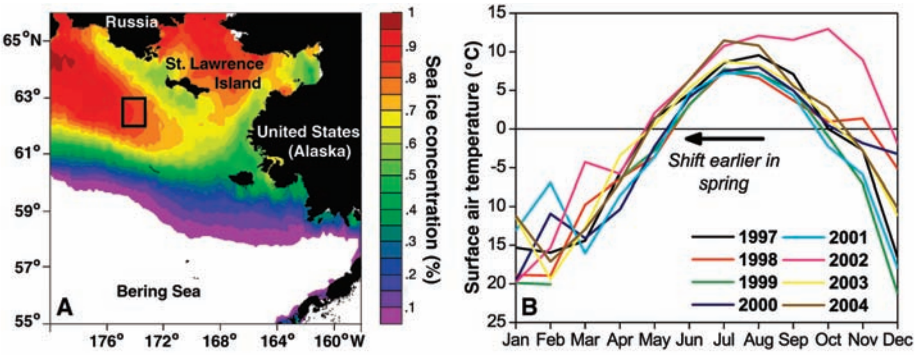

Fig. 1. (**A**) Location map (box indicates location of time-series biological sites) and average April sea ice concentration (1 corresponds to 100%, and 0.1 corresponds to 10%) in the northern Bering Sea from 2000 to 2004. Ice concentrations are based on microwave satellite instruments, Defense Meteorological Satellites Program SSM/I (*12*, *16*). (**B**) Monthly averaged surface air temperature measured at Savoonga (63.68°N, 170.5°W) on St. Lawrence Island over the years 1997 to 2004. Note the interannual variability in the timing of melt onset (~3 weeks) based on date air temperature rises above 0°C (*13*).

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