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Variable effects of large mammal herbivory on three non-native versus three native woody plants

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Abstract

(1) The enemy release hypothesis posits that introduced species leave behind co-evolved pathogens and predators, thereby gaining an advantage over native competitors. On the other hand, introduced plants may encounter biotic resistance from local generalist herbivores such as large mammals.
(2) We conducted a replicated, manipulative field experiment to compare the effects of large-mammal herbivory on growth and survival of three native and three invasive woody species over 2 years. Non-native *Acer platanoides*, *Frangula alnus* P. Mill. (=*Rhamnus frangula* L.) and *Elaeagnus umbellata* were each paired with a likely native competitor of similar life form and shade tolerance. Seedlings were planted with and without large-mammal exclosures, in open and understory environments.
(3) In the open, *E. umbellata* grew taller than its paired native only when exposed to herbivory, but *F. alnus* grew taller than its paired native only within exclosures. The effects of exclosure on growth rate did not differ between *A. platanoides* and its native congener. In the understory, exposure to browsing reduced height growth rate overall in native species, but not in invasive species.
(4) Browsing increased understory mortality only in the native shrub *Viburnum dentatum*, and did not affect mortality in the open. Within exclosures, there was a general trade-off between open growth and understory survival, but outside of exclosures, *E. umbellata* exhibited both greater open growth and greater understory survival than its native competitor.
(5) Although large-mammal herbivory did not consistently favor non-natives, lack of browsing impact played an important facilitating role for *E. umbellata* in particular.

Keywords: Invasive species; Enemy release hypothesis; Biotic resistance; Herbivory; Exclosure; Trade-offs

1. Introduction

Invasive plants often grow more vigorously or densely in their introduced range than in their indigenous range (Keane and Crawley, 2002; Hinz and Schwarzlaender, 2004; Bossdorf et al., 2005). A long-standing and oft-cited explanation for this trend is the enemy release hypothesis, which posits that introduced species leave behind their co-evolved herbivores, parasites or pathogens (Darwin, 1859; Elton, 1958; Maron and Vilà, 2001; Colautti et al., 2004). The enemy release hypothesis is supported by an accumulating body of research indicating that invasive plant species generally experience reduced herbivore loads and attack rates in their introduced ranges, compared with their indigenous ranges (Wolfe, 2002; Colautti et al., 2004; Hinz and Schwarzlaender, 2004; Bossdorf et al., 2005; Vilà et al., 2005).

On the other hand, although introduced species may escape their historical enemies, they may also encounter new potential adversaries in their introduced range. Another long-standing principle of invasion ecology, the biotic resistance hypothesis, predicts that the spread of alien species into new habitats may be limited by interactions with resident species (Elton, 1958; Levine et al., 2004). Both enemy release and biotic resistance may influence the invasive success of a given species. Across a large sample of European plant species naturalized to North America, the reported 'noxiousness' of an invader was

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positively correlated with the loss of pathogens from its home range, but negatively correlated with the accumulation of new pathogens from its introduced range (Mitchell and Power, 2003).

In particular, although introduced plant species may leave behind co-evolved specialist enemies, they may still be vulnerable to generalist enemies in their new habitats (Memmot et al., 2000; Maron and Vilà, 2001; Keane and Crawley, 2002; Hinz and Schwarzlaender, 2004; Levine et al., 2004). Such generalists include small vertebrate seed predators and large vertebrate grazers, as well as generalist arthropods. Although large mammal herbivory can exert strong effects on community composition (Waller and Alverson, 1997; Keane and Crawley, 2002), few quantitative studies have assessed the relative impact of such herbivory on invasive exotics and their native competitors (Maron and Vilà, 2001; Keane and Crawley, 2002; Levine et al., 2004). Moreover, most exclosure experiments assessing the impact of mammal herbivory on exotics have tended to focus on herbaceous rather than woody species (Levine et al., 2004). One study of a woody invader found that exposure to native mammal herbivory had a more negative effect on the growth of the native vine *Lonicera sempervirens* than on its invasive congener *L. japonica*, in part due to compensatory growth by the invader (Schierenbeck et al., 1994). In light of widespread concern about the impact of record high deer populations on tree regeneration in forest systems (Waller and Alverson, 1997), additional research is needed into the effects of large-mammal browsing on native versus non-native woody forest species.

We conducted a manipulative field experiment comparing the effects of mammal browsing on growth and survival of three native and three non-native, invasive woody species in western Massachusetts, to determine the role of local generalists in facilitating or inhibiting the spread of these invaders. We planted seedlings of each species, with and without exclosures, in replicated plots within both open and understory environments. We focused on the seedling and sapling stages of growth because it is during this period that mammal browsing is most likely to exert a controlling influence on establishment. In selecting species for our study, we chose non-native woody invaders of varying life form and shade tolerance, and paired each with a native of similar life form and shade tolerance. We, thus, compare each individual invader with a likely local competitor and take into account differences due to ecological type.

Our exclosures were designed to limit access by mammal browsers such as white-tailed deer (*Odocoileus virginianus*) and porcupine (*Erethizon dorsatum*), both seen frequently at the study site. Because the herbivores excluded by our treatment were generalists, we expected that exposure to browsing would reduce the growth or survival of both non-native and native species to some degree. The enemy release hypothesis predicts that this effect should be greater in natives than in non-natives, however, with the result that non-native invaders should have a greater advantage over their local competitors in the presence of local herbivores. An opposite result (invaders have a lesser advantage in the presence of herbivores) would suggest that biotic resistance is important for these species.

Rates of herbivory and the capacity for compensatory growth may vary considerably between open and understory conditions, as well as among plant types. We compared the effects of herbivory on growth and survival of native and invasive non-native species in both open and understory conditions. While competitive success in open environments may be predicted by height growth, survival may be a more important indicator of success in the understory (Kobe et al., 1995). Among woody species, growth rate in open environments is often negatively correlated with survival in understory conditions (Kitajima, 1994; Kobe et al., 1995; Walters and Reich, 1999; Sanford et al., 2003). We predicted that herbivory would reduce both growth and survival more for natives than for invaders, such that invaders would exhibit both greater understory survival and greater open growth than natives when exposed to browse.

2. Methods

2.1. Study species

We selected three pairs of native and non-native woody species, representing a spectrum of life form and shade-tolerance classes. The native shrub *Cornus amomum* (silky dogwood) and the invasive shrub *Elaeagnus umbellata* (autumn olive) are both classified as shade-intolerant and are found primarily at forest edges, while the native shrub *Viburnum dentatum* (arrowwood) and the non-native *Frangula alnus* P. Mill. (=*Rhamnus frangula* L.) (glossy buckthorn) are both classified as shade-tolerant and may be found in forest understories (Gleason and Cronquist, 1991; Weatherbee et al., 1999). The native tree *Acer saccharum* (sugar maple) and its non-native congener *Acer platanoides* (Norway maple) are both highly shade-tolerant (Gleason and Cronquist, 1991; Weatherbee et al., 1999; Meiners, 2005). Each of the non-native species chosen has been identified as an invasive threat in the eastern United States (US Forest Service, 1998; Swearingen et al., 2002) and may be found growing in close proximity to its paired native species in fields or forests near our study area.

2.2. Study site and experimental design

In June and July 2000, we planted seedlings of each species in eight replicate blocks within Mount Toby Demonstration Forest, an upland hemlock-hardwoods forest in Sunderland, MA (42.502°N, 72.517°E). Each replicate block consisted of one open and one understory plot, each 8 m × 20 m, with a surrounding 5-m treatment buffer. Understory plots were located in 14-year-old closed-canopy stands dominated by *Betula* species and *Prunus pensylvanica*. Open plots were created for this study by chain-sawing and removing trees from adjacent sections of these stands. Twenty rows of seedlings, each containing all six species, were planted in each of the eight open and understory plots. *F. alnus* seedlings were transplanted from local Massachusetts populations; all other species were purchased bare-root from nurseries. Native and non-native species of similar life form and shade tolerance were of similar