

APPARENT COMPETITION WITH AN EXOTIC PLANT REDUCES NATIVE PLANT ESTABLISHMENT

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Abstract. Biological invasions can change ecosystem function, have tremendous economic costs, and impact human health; understanding the forces that cause and maintain biological invasions is thus of immediate importance. A mechanism by which exotic plants might displace native plants is by increasing the pressure of native consumers on native plants, a form of indirect interaction termed “apparent competition.” Using experimental exclosures, seed addition, and monitoring of small mammals in a California grassland, we examined whether exotic *Brassica nigra* increases the pressure of native consumers on a native bunchgrass, *Nassella pulchra*. Experimental plots were weeded to focus entirely on indirect effects via consumers. We demonstrate that *B. nigra* alters the activity of native small-mammal consumers, creating a gradient of consumption that dramatically reduces *N. pulchra* establishment. Previous work has shown that *N. pulchra* is a strong competitor, but that it is heavily seed limited. By demonstrating that consumer pressure is sufficient to curtail establishment, our work provides a mechanism for this seed limitation and suggests that, despite being a good competitor, *N. pulchra* cannot reestablish close to *B. nigra* within its old habitats because exotic-mediated consumption preempts direct competitive exclusion. Moreover, we find that apparent competition has a spatial extent, suggesting that consumers may dictate the rate of invasion and the area available for restoration, and that nonspatial studies of apparent competition may miss important dynamics.

Key words: *apparent competition; biological invasion; Brassica nigra; California (USA) grassland; consumers; granivory; herbivory; Nassella pulchra.*

INTRODUCTION

Biological invasions can imperil the structure, function, and diversity of ecological communities (Mack et al. 2000, Callaway and Maron 2006). Consumers may frequently play an integral role in the spread and impact of invasive plants (Callaway and Maron 2006, Mitchell et al. 2006, Parker et al. 2006). Exotic plants may become successful invaders because they leave behind consumers in their old range, giving exotics an advantage in the introduced range, where native plants remain under the influence of native consumers, i.e., the enemy-release hypothesis (Callaway and Maron 2006, Mitchell et al. 2006). Less appreciated is that the success of exotic plants may also lie in how they alter

interactions between native consumers and native plants. Exotic plants could invade by changing the abundance (Holt 1977) or distribution (Holt and Kotler 1987) of native consumers so that consumers have greater impacts on native plants, an indirect effect termed “apparent competition” (Holt 1977, Holt and Kotler 1987, Noonburg and Byers 2005).

Empirical evidence suggests that apparent competition may be important in plant communities (e.g., Chanton and Bonsall 2000, Caccia et al. 2006). Apparent competition between native and exotic plants may be mediated through exotic consumers (Sessions and Kelly 2002, Rand and Louda 2004), and native consumers may create apparent competition between exotic species (Boyd 1988). Despite these multiple lines of evidence that apparent competition is important, and the substantial effect that native consumers can have on plant communities (e.g., Howe et al. 2006), the role that native consumers might play in apparent competition

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between native and invasive exotic plants remains largely unknown.

In the grasslands of California, nearly 9 million hectares are now dominated by exotic annual plants (Heady 1977, Jackson 1985). Although exotic consumers (i.e., cattle) are often implicated in the dominance of exotic species (Heady 1977), invasion of California grasslands was underway before widespread grazing began (Wagner 1989), and native plants show highly variable signs of recovery, even in patches that have been protected from cattle grazing for decades (Stromberg and Griffin 1996). Rather, several observations suggest that native consumers may play an unappreciated role in promoting the continued dominance of exotic plants. The reestablishment of once-dominant native species is curtailed by seed limitation (Seabloom et al. 2003), which may be driven by consumer pressure: rodents can consume 37–75% of available seeds (Borchert and Jain 1978) and lead to changes in grassland composition (Batzli and Pitelka 1970, Borchert and Jain 1978). Moreover, recent work shows that some native grasses are superior in direct competition with exotic plants (Seabloom et al. 2003), suggesting that the dominance of exotic plants may be maintained through indirect means (e.g., apparent competition).

We examine how the exotic annual plant, *Brassica nigra*, alters the effect of native small-mammal consumers on a native perennial bunchgrass, *Nassella pulchra*, within a grassland in California, USA. *Nassella pulchra* reproduces primarily by seed and may have been a dominant component of southern California grasslands prior to European settlement (Bell and Muller 1973, Heady 1977). Evidence suggests that consumers may have substantial impacts on *Nassella pulchra*: it is seed limited (Hamilton et al. 1999, Seabloom et al. 2003), and removal of *N. pulchra* seeds by consumers can exceed 80% (J. Orrock, unpublished data). *Brassica nigra* contains glucosinolates thought to deter herbivores (Feeny 1977) and small seeds likely to escape granivory (Halligan 1974).

We couple experimental enclosures, seed additions, and monitoring of small-mammal consumers to test two key predictions of invasion maintained via apparent competition. First, if exotic plants provide food resources (Holt 1977) or change consumer foraging behavior (Holt and Kotler 1987), apparent competition predicts an increase in consumer density with proximity to exotic plants (Fig. 1A). Second, the gradient in consumer density predicts a gradient in consumption of native plants, predicting a gradient of native-plant establishment that mirrors patterns of consumer activity (Fig. 1A). Although studies of competition may frequently confound direct competition and apparent competition (Connell 1990), we remove potential competitors from our experimental plots to focus entirely on the role of apparent competition.

MATERIALS AND METHODS

Study area and enclosure design

The study was conducted in a 1-ha portion of Cheeseboro Canyon, part of the Santa Monica Mountains National Recreation Area near Agoura Hills, California, USA. The study area contains characteristic California annual grassland and many stands of *Brassica nigra* (Moyes et al. 2005). Throughout the study area we installed 14 sites at varying distances (0–33 m) from the nearest *B. nigra* patch (sites at 0 m were effectively within a *B. nigra* patch). At each site, a pair of experimental plots was established. Within each 2 × 2 m plot, a central 1 × 1 m area was designated for experimental seed additions.

Three enclosure treatments were used: (1) a complete enclosure that excluded all mammalian consumers, (2) a control enclosure constructed to test for unintended fencing effects that allowed rabbits, squirrels, and small mammals to have access, and (3) an unfenced treatment that allowed all consumers to have access. Disturbance was applied equally to all plots by trenching prior to enclosure installation, regardless of whether a plot was designated for fencing. Complete enclosures consisted of 1.22 m tall hardware cloth (0.8 × 0.8 cm mesh size) projected 20 cm into the soil. The top of the fencing was surrounded with a 15-cm band of aluminum flashing to discourage rodents from climbing over the fence. Control enclosures were identical to complete enclosures, with the exception of four 7 × 7 cm holes cut in the bottom of each side of the fence. Consumers that were not likely to be excluded by our enclosures include pocket gophers, arthropods (e.g., ants, beetles, grasshoppers), and birds. There was no significant difference in the number of *N. pulchra* seedlings emerging ($F_{1,4} = 0.01$, $P = 0.99$) or the number of *N. pulchra* plants ($F_{1,4} = 0.83$, $P = 0.41$) between unfenced treatments and control enclosures, suggesting that the presence of the fence did not influence *N. pulchra* recruitment in any way other than in affecting access of consumers. As such, we combine unfenced treatments and control enclosures in our analysis, treating them as the same treatment, whereby all small vertebrate consumers have access (pooling did not alter the qualitative outcome of our analyses).

Experimental timeline

Enclosure construction.—Plots were tilled to a depth of 20 cm using a mechanical tiller on 18–20 January 2005, and enclosures were installed on 27–28 January 2005. Pairs of enclosures were assigned treatments based on a randomized, incomplete block design (the blocks are incomplete because only 2 of 3 treatments could be assigned to any pair). On 1 February 2005 we broadcast 12.3 cm³ (~500 seeds; M. Witter, unpublished data) of locally collected *N. pulchra* onto the surface of the soil at

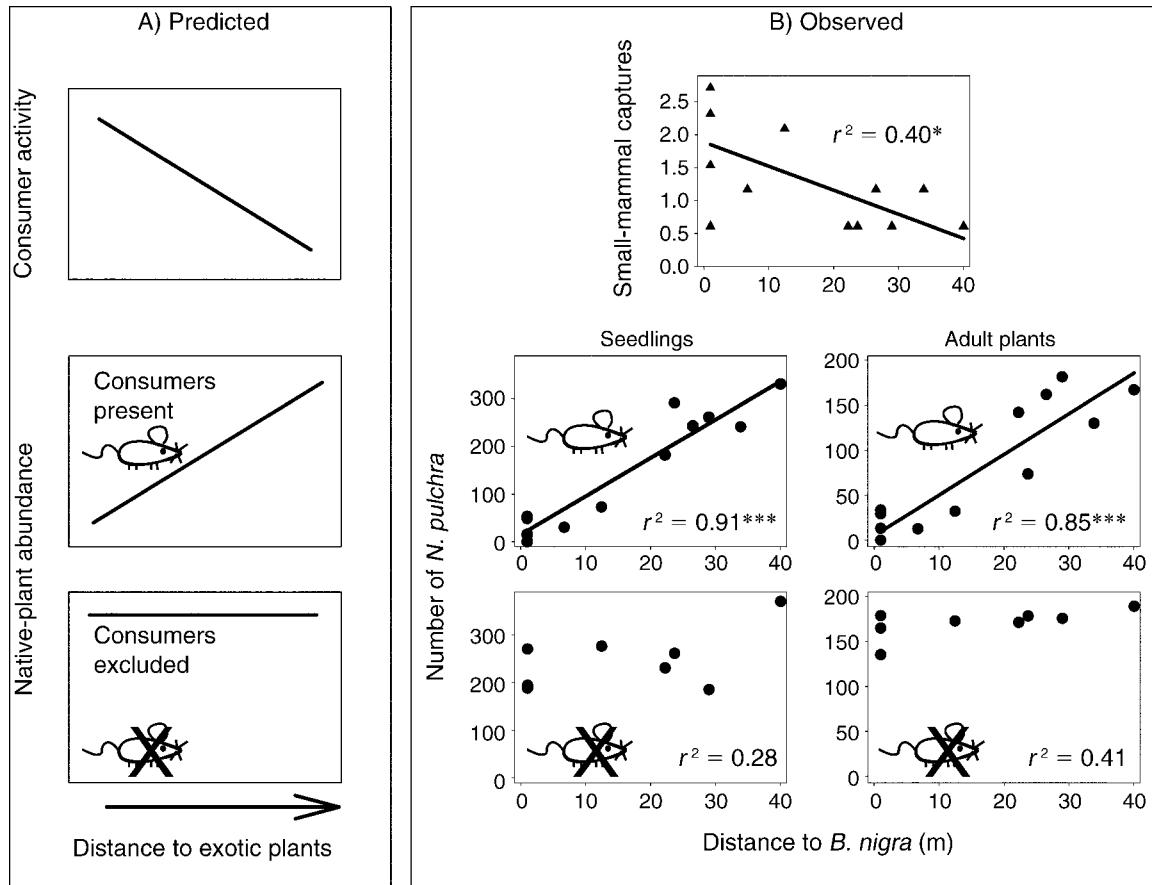


FIG. 1. Predicted and observed small-mammal consumer activity in a California (USA) annual grassland. (A) Predicted changes in small-mammal consumer activity and consumer effect with apparent competition mediated by exotic plants. Consumer activity should increase near invasive plants as these plants change the spatial distribution of foraging (e.g., by changing risk or patch quality) or the local abundance of small-mammal consumers (e.g., by fueling increases in the number of rodents). Changes in consumer distribution are predicted to result in changes in the impact of consumers on native plants. When consumers have access to native plants, a pattern of increasing establishment with distance from exotic plants should arise (the mouse icon indicates that native mice, voles, squirrels, and rabbits can access plants). When consumers are excluded from native plants, there should be no pattern between plant establishment and distance to exotic plants. (B) Observed patterns of consumer activity, measured as the total number of small-mammal captures over the three-day sampling session (transformed as the square root of $[x + 0.5]$), as a function of distance to the exotic annual *Brassica nigra* support predictions. Changes in the number of native *Nassella pulchra* seedlings and adult *N. pulchra* plants are highly dependent on consumer access and distance to *B. nigra*, also consistent with predictions. Best-fit lines by least-squares regression are used to illustrate significant trends.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

each site. This seed density approximates seed production by a mature *N. pulchra* (Hamilton et al. 1999, Seabloom et al. 2003), and is frequently used in restoration efforts (Moyes et al. 2005) and studies of seed limitation (Seabloom et al. 2003). Our experimental enclosure treatments were not confounded by soil or seedbank effects because they were paired, there is very little seedbank in California grasslands (Young et al. 1981), and *N. pulchra* was not present in any of our plots prior to the experiment. The timing of seed placement did not coincide with the schedule of natural seed dispersal for *N. pulchra*, as plants typically shed their seeds in May and June. This timing was chosen to

expand the relevance of our work to ecological restoration, where seeds are generally added during the growing season to promote establishment. As a result, our schedule generates a conservative estimate of the impact of granivores because there is less time before seeds escape granivory via germination.

Data collection.—After seeds were distributed, plots were visited monthly and all seedlings other than *N. pulchra* were removed to eliminate direct competition and focus exclusively on apparent competition. Seedling recruitment was quantified by counting the number of *N. pulchra* seedlings in four 500-cm² areas within each plot, 28–30 March 2005. The number of mature *N.*

pulchra plants alive at the end of the growing season was quantified by counting the number of plants in each plot on 6–14 July 2005. The number of plants was also counted on 13–25 October 2005 to determine survivorship of adult plants after the next growing season had begun.

In April 2005 we quantified the distance of each site to nearby patches of *B. nigra*. A patch of *B. nigra* was defined as a contiguous area that was visually estimated to be $>36 \text{ m}^2$ in size and dominated by *B. nigra* cover (mean proportion of absolute *B. nigra* cover was 0.42 ± 0.04 [mean \pm SE] at 32 locations). However, because most patches of *B. nigra* were well over 100 m^2 , this minimum-size criterion was rarely used. At each site, the distance to the nearest *B. nigra* patch in each cardinal direction was recorded. If any side of a site was located within a *B. nigra* patch, the distance to *B. nigra* was considered to be 0.5 m (the distance of the buffer around our experimental plots). If none of the sides of a site were within or adjacent to *B. nigra*, we averaged the distances to *B. nigra* obtained from all cardinal directions where *B. nigra* was within 100 m of the site (this distance was chosen because it is unlikely that any of the small-mammal consumers examined frequently ranged over a greater distance). For example, if a plot was not adjacent to *B. nigra*, and the nearest *B. nigra* patches in each cardinal direction were 20 m, 10 m, 150 m, and 50 m, the average distance to the nearest patch of *B. nigra* was considered to be 26.7 m (i.e., $[20 + 10 + 50]/3$). Calculating distance to *B. nigra* in this way is strongly correlated with simply measuring the distance to the nearest *B. nigra* patch, regardless of direction ($r^2 = 0.79$, $F_{1,13} = 47.17$, $P < 0.001$). Moreover, this method of averaging has the added benefit of allowing us to include the effect of multiple nearby *B. nigra* patches on a given site. The strong relationship between consumer activity and distance to *B. nigra* patches (see *Results*, below) suggests that our definition of a *B. nigra* patch captured relevant ecological features. In addition to measuring distance to *B. nigra*, vegetation height, and percent cover were recorded for 1 m^2 areas within the nearest *B. nigra* stand and directly adjacent to each pair of exclosures.

We live-trapped small mammalian consumers to examine their abundance and activity by placing six Sherman live traps and four Tomahawk live traps at each site. Use of these different trap types allowed us to sample small rodents (voles and mice) as well as larger consumers (rabbits and squirrels). By placing half of the traps at each site within an exclosure, we were also able to determine whether our designs were successfully excluding consumers. Small-mammal sampling was conducted 17–19 August 2005 to allow us to characterize the size of the rodent population when its impact would presumably be greatest on the survival of *N. pulchra*, because other green vegetation is absent at this time of year. After capture the small mammals were marked

using ear tags and immediately released at the site of capture. We use the total number of captures over this sampling period as an estimate of the relative activity of small vertebrate consumers at each site (Orrock and Danielson 2005).

Statistical analyses

To examine the relationship between distance to *B. nigra* and captures of consumers, we used least-squares regression, after applying a square-root transformation to improve normality of capture data (Quinn and Keough 2002). Fisher's exact test was used to examine patterns of small-mammal captures inside and outside exclosures. We used a mixed-model analysis of covariance (ANCOVA) to examine how consumer exclosure and distance from *B. nigra* affected the number of seedlings and mature *N. pulchra* plants that established. Our model treats each pair of plots as a site and includes site as a random effect in the model, with consumer exclosure as a fixed effect, and distance to *B. nigra* as a covariate (Quinn and Keough 2002). The interaction between exclosure and distance to *B. nigra* was an explicit part of our predictions. Examination of residual plots and normality tests suggested that all analyzed data were normally distributed and homoscedastic.

RESULTS

Native-consumer activity significantly decreased with distance from *Brassica nigra* ($r^2 = 0.40$, $F_{1,12} = 7.89$, $P < 0.02$; Fig. 1B). We captured five species of native mammalian consumer: the western harvest mouse (*Reithrodontomys megalotis*; see Plate 1), pocket mouse (*Chaetodipus californicus*), ground squirrel (*Spermophilus beechyi*), brush rabbit (*Sylvilagus bachmani*), and deer mouse (*Peromyscus maniculatus*). Consumers were found within unfenced treatments and control exclosures with equal frequency (Fisher's exact test, $P = 0.50$), but were never found within complete exclosures (Fisher's exact test, $P = 0.03$), suggesting that our exclosures successfully manipulated consumer access.

Native consumers had strong negative effects on *Nassella pulchra* seedling recruitment (exclosure main effect, $F_{1,12} = 51.36$; $P < 0.001$), as did the distance to *B. nigra* (distance covariate, $F_{1,12} = 49.61$; $P < 0.001$). There was a significant interaction between exclosure and distance ($F_{1,12} = 19.26$; $P < 0.001$). When consumers had access to *N. pulchra*, seedling recruitment was clearly shaped by distance to *B. nigra* (Fig. 1B); when consumers were excluded, seedling recruitment was high regardless of distance to *B. nigra* (Fig. 1B). These effects continued to be important for shaping the number of plants that had established by the end of the growing season, as exclosure ($F_{1,12} = 118.67$; $P < 0.001$) and distance to *B. nigra* ($F_{1,12} = 33.08$; $P < 0.001$) both affected the number of established *N. pulchra* plants, but this pattern was driven by distance-dependent consumer



PLATE 1. A western harvest mouse (*Reithrodontomys megalotis*) travels through an aperture in one of the experimental control exclosures designed to control for unintended fencing effects. Photo credit: Ellen Damschen.

effects on *N. pulchra* plants outside of exclosures (exclosure \times distance interaction; $F_{1,12} = 32.71$; $P < 0.001$; Fig. 1B). The impact of consumers also persisted beyond *N. pulchra* establishment: there was a strong, significant relationship between the number of *N. pulchra* plants at the end of the growing season in June and the number of *N. pulchra* that survived to the beginning of the subsequent growing season in October ($r^2 = 0.63$, $F_{1,26} = 44.46$, $P < 0.001$), despite partial mowing of *B. nigra* as part of Park Service management at the end of the growing season and a fire that swept through the study area on 29 September 2005.

DISCUSSION

We find that exotic plants may curtail the reestablishment of native plants by altering the impact of native consumers (Fig. 1B). Moreover, we show that apparent competition may have a spatial extent: native *Nasella pulchra* near exotic *Brassica nigra* suffered nearly a nine-fold increase in consumer impact, and consumer impact decreased rapidly with distance from *B. nigra* (Fig. 1B). The strong apparent competition we document could affect the conservation and restoration of California grasslands, may create an advancing invasion front unlikely to retreat, and could interact with other mechanisms of biological invasion.

Apparent competition and the grasslands of California

Our work suggests that the invasion of *Brassica nigra* may be facilitated and maintained by increased consumer pressure (Fig. 1B), rather than (or in addition to) allelopathy, as is commonly invoked as an explanation

for the invasive ability of *B. nigra* (Bell and Muller 1973). Although the historical nature of grassland invasion in California precludes examining whether apparent competition was responsible for initial spread of *B. nigra*, our results suggest that apparent competition may contribute to contemporary patterns of *B. nigra* invasion and explain the inability of *N. pulchra* to reestablish in areas it once occupied. Our results further suggest that apparent competition via native consumers can thwart restoration, and may explain why restoration of *N. pulchra* is often unsuccessful despite removal of exotic herbivores (i.e., cattle). Although our findings suggest that apparent competition may be important during the critical establishment phase when *N. pulchra* is generally seed limited, *N. pulchra* is a long-lived perennial. During years when consumer impact is low, *N. pulchra* may be able to establish in areas near *B. nigra*, and subsequently tolerate heavy herbivory after establishment, as suggested by Bartholomew (1970) for perennial grasses near chaparral. However, work at nearby study sites indicates that consumers can affect *N. pulchra* reproduction (Orrock et al., *in press*), suggesting that plants near *B. nigra*, though established, may contribute less to overall *N. pulchra* population dynamics. As such, understanding the dynamics of apparent competition within this system will ultimately require long-term studies to provide parameter estimates to project population growth rates of *N. pulchra* at relevant scales.

The mechanism by which *B. nigra* influences native small-mammal consumers is unlikely to be by providing additional food resources (Noonburg and Byers 2005),

because *B. nigra* seeds and foliage contain chemicals that deter generalist herbivores (Feeny 1977), and its tiny seeds are also likely to escape consumption by small-mammal consumers (Halligan 1974). Rather, *B. nigra* may influence consumers by providing a refuge (Bartholomew 1970, Connell 1990). *Brassica* forms tall, dense stands (Bell and Muller 1973); the mean vegetation height within *B. nigra* stands in this study was >2.5 times greater than the height of vegetation outside of *B. nigra* stands (1.90 ± 0.06 m and 0.75 ± 0.09 m [mean \pm SE], respectively; $F_{1,50} = 116.98$, $P < 0.001$). In support of this mechanism, small-mammal consumer captures were positively related to distance to *B. nigra* (Fig. 1B), and vegetation height declined with distance to *B. nigra* ($r^2 = 0.54$, $F_{1,12} = 14.46$, $P < 0.01$). However, the relationship between distance to *B. nigra* and small-mammal captures is no longer highly significant (partial $r = -0.47$, $t = -1.77$, $P = 0.10$) when partial correlation is used to control for the effect of vegetation height.

*The spatial extent of apparent competition
and the invasion ratchet*

Consumers that seek refuge in one habitat can create gradients of consumption in adjacent habitats that generate dramatic patterns in vegetation (Boyd 1988, Sessions and Kelly 2002), including “halos” near coral reefs (Ogden et al. 1973), bare zones around chaparral (Bartholomew 1970), and increased relative forb abundance near log piles (Chase 1998). Our work suggests that exotic plants may succeed by being a biotic refuge for consumers (Connell 1990), creating a gradient of consumption that curtails establishment of native plants. The spatial extent of apparent competition we have documented suggests that, where apparent competition is important for invasion, the gradient of exotic-mediated consumption may create an invasion that ratchets forward because the native consumers that promote the invasion are likely to follow the advancing invasion front. The invasion ratchet may not move backward because reestablishment of native plants is greatly reduced at the invasion front (Fig. 1B). In systems where invasion has already occurred, like the *B. nigra* system studied here, the spatial extent of apparent competition may dictate the area available for restoration. Our work also illustrates that studies conducted away from the invasion front may miss an important mechanism promoting invasion because of spatial changes in the strength of apparent competition. In this regard, studies that fail to find apparent competition may simply examine dynamics within an inappropriate spatial context.

Although we provide evidence that consumer-mediated apparent competition can help maintain biological invasion by reducing reestablishment of native species, our study has several caveats that highlight important areas for future research. First, longer-term studies over

larger spatial scales are needed to more fully understand whether *B. nigra* alters the small-scale distribution of native consumers, or whether it leads to actual changes in consumer abundance. Second, it remains unclear how often apparent competition is the mechanism by which invasion occurs and whether apparent competition is a general mechanism reducing reestablishment of native plants in invaded areas. Future work along advancing invasion fronts would prove fruitful for examining the former question; to be capable of capturing apparent competition, our work suggests that such studies must be conducted with the spatial extent of apparent competition in mind.

Finally, to focus on apparent competition we eliminated competition by tilling and weeding experimental plots. Studies are needed to assess the degree to which apparent competition and other ecological interactions interact to foster invasion. For example, direct competition can reduce native-plant seed production (Dyer and Rice 1999, Hamilton et al. 1999), and exotic-mediated changes in soil fauna or composition (e.g., allelopathy) can reduce its suitability for native plants (Levine et al. 2006); these processes could interact with apparent competition to increase rates of invasion. Another example that illustrates how apparent competition may interact with other mechanisms of invasion is the finding that exotic plants that become invasive are often larger in their introduced range (Bossdorf et al. 2005). While the coincidence between size and invasiveness may be due to enemy release (Callaway and Maron 2006, Mitchell et al. 2006) or the evolution of increased competitive ability (EICA; Bossdorf et al. 2005, Callaway and Maron 2006), our work suggests another mechanism that is not mutually exclusive: size may be related to invasiveness because plant size may provide the means through which exotic plants become invasive plants by providing a refuge for native consumers.

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