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Multiple drivers of apparent competition reduce re-establishment of a native plant in invaded habitats

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Although rarely examined, apparent competition, whereby exotic plants increase consumer pressure on native plants, could play a significant role in affecting native plant establishment in invaded habitats. Moreover, although terrestrial consumer communities often contain many consumer species, little is known about which consumers may generate apparent competition, and whether the strength or mechanism of apparent competition differs among different members of the consumer community. Using consumer-specific experimental exclosures and seed additions in the invaded grasslands of California, we demonstrate that multiple mechanisms of apparent competition are capable of limiting the re-establishment of the native grass *Nassella pulchra* in the absence of direct competition with exotic plants. The effect of small mammalian consumers (mice and voles) and larger consumers (e.g. rabbits, squirrels, deer) decreased with distance to the exotic forb *Brassica nigra*, which varied from 0–33 meters from focal *N. pulchra*. The effect of larger consumers also depended upon characteristics of the plant community directly adjacent (i.e. approx. 1 m) from focal *N. pulchra*. The effect of large consumers also increased with the richness of the exotic plant community and the degree to which the exotic plant community was dominated by exotic grasses as opposed to exotic forbs. Our finding that apparent competition can be driven by different mechanisms, that the importance of each mechanism depends upon which consumers have access, and that each mechanism has a different spatial extent, suggests that the composition of both the consumer community and the exotic plant community may shape the spatial dynamics of reestablishment, the potential for restoration, and the need for conservation.

A growing body of evidence suggests that indirect effects may be important in determining the dynamics of biological invasions and in shaping the success of conservation and restoration programs for native species (Noonburg and Byers 2005, Borer et al. 2007, Didham et al. 2007). Apparent competition is one such indirect effect (reviewed by Connell 1990, Chaneton and Bonsall 2000); in the context of invasive plants, apparent competition occurs when invasive plants increase consumer pressure on native plants by changing the foraging behavior of native consumers (Holt and Kotler 1987), changing the abundance of native consumers (Holt 1977), or both. The importance of apparent competition in the dynamics of native and exotic species has been supported by several recent studies (Rand and Louda 2004, Malmstrom et al. 2005, Noonburg and Byers 2005, Borer et al. 2007, Meiners 2007, Orrock et al. 2008, Pearson and Callaway 2008). While these studies clearly indicate the potential importance of apparent competition, many studies focus on limited suites of consumer species or are incapable of separating the effect of particular consumers, e.g. studies that examine either all mammalian consumers or no mammalian consumers (Orrock et al. 2008).

Examining consumer-specific patterns of apparent competition is important because many plants are attacked by a variety of consumers, and consumers may or may not have compensatory effects on plant communities (Reichman 1979, Orrock et al. 2003, Howe et al. 2006). Moreover, consumer foraging may lead to indirect effects on neighboring plants (McNaughton 1978, Palmer et al. 2003, Baraza et al. 2006), and consumers may forage over different spatial scales (Palmer et al. 2003, Baraza et al. 2006). Apparent competition could also arise via different mechanisms through different suites of consumers. For example, one invasive species might promote apparent competition by changing consumer density, and another invasive species could create apparent competition by changing consumer foraging behavior (i.e. short-term apparent competition; Holt and Kotler 1987). As a result, whether or not apparent competition occurs, the mechanisms that create apparent competition, as well as the strength and spatial extent of apparent competition, may depend largely upon the composition of the local consumer community, how consumers interact, and how exotic plants affect particular consumers. We coupled consumer-specific exclosures and seed additions to examine the role of consumer-mediated apparent competition in the grasslands of California.

California grasslands are an excellent system for examining how apparent competition via different consumer guilds