



## 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 enclosures 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, Chanton 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 enclosures 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

affects the re-establishment of native plants. Pre-invasion grasslands are thought to have been dominated by native bunchgrasses like *Nassella pulchra* (Heady 1977); the majority of the 7–9 million ha in this ecosystem are now dominated primarily by exotic annual grasses and forbs of Mediterranean origin (Jackson 1985). Although many factors may have contributed to the invasion of this system, including grazing, alteration of fire regimes, use of land for agriculture, and direct seeding (Heady 1977, Jackson 1985, Stromberg and Griffin 1996), several characteristics of this system may set the stage for apparent competition. Consumers are often ubiquitous (Lidicker 1989, Schiffman 2007) and can have large effects on plant populations and communities (Batzli and Pitelka 1970, Borchert and Jain 1978, Rice 1987, Lidicker 1989, Reichman and Seabloom 2002, Schiffman 2007, Orrock et al. 2008, 2009), although most studies focus on the effect of one or a few consumer species within the larger suite of consumers, and studies often focus on exotic grazers (reviewed in Lidicker 1989, Schiffman 2007). Perennial native grasses are frequently seed-limited (Hamilton et al. 1999, Seabloom et al. 2003, Orrock et al. 2009), and evidence suggests that consumers may limit plant recruitment (Orrock et al. 2009) and long-term abundance in the community (Seabloom et al. 2009). In contrast, the abundance of exotic annual plants (97% cover in the experimental area) and their continued domination of California grasslands suggests that consumers do not have appreciable negative effects on their dynamics (Bell and Muller 1973). On the contrary, analysis of long-term enclosure studies suggests that consumers may have positive effects on exotic plants, as exotic plant abundance increases in the presence of consumer pressure (Seabloom et al. 2009). Exotic annuals produce prodigious quantities of seeds and foliage that may elevate densities of native consumers, e.g. mean litter size of California voles *Microtus californicus* is significantly greater in habitats dominated by exotic annual plants (Krohne 1980). One exotic annual forb that can dominate grasslands, *Brassica nigra* (Bell and Muller 1973), may alter consumer foraging behavior, increasing consumer pressure on native *N. pulchra* (Orrock et al. 2008). However, perennial native grasses can be strong competitors compared to exotic annual grasses (Seabloom et al. 2003), suggesting that established native grasses are capable of resisting invasion by exotic plants, and indirect interactions mediated by consumers (e.g. apparent competition) might be a mechanism that maintains the dominance of invaders.

We experimentally manipulated consumer access to areas seeded with the native perennial grass, *Nassella pulchra*, to directly examine whether apparent competition affected re-establishment and whether the strength of apparent competition differed depending upon the suites of consumers with access. *Nassella pulchra* is thought to have once been a dominant component of California grasslands (Heady 1977) and is commonly the focus of restoration efforts (Seabloom et al. 2003, Moyes et al. 2005, Orrock et al. 2009). Our experiment was designed to focus only on the indirect effect of apparent competition (i.e. plots were weeded to eliminate direct competitive interactions among plants) and was conducted with restoration of native plants in mind. As such, we introduced native plants to invaded communities rather than manipulating exotic

plants within communities of native plants. This approach allowed us to examine how suites of consumers might mediate apparent competition without the potentially confounding effects of competitive interactions among plants and without intentionally introducing invasive exotic plants.

## Methods

The study was conducted in Cheeseboro Canyon, part of the Santa Monica Mountains National Recreation Area near Agoura Hills, California. The study area is characteristic California annual grassland dominated by a mix of exotic annual grasses and forbs (Moyes et al. 2005). Within the study area, we installed eight sets of experimental enclosures; the location of each set of enclosures was random with respect to the distance to *B. nigra* or the nature of the surrounding exotic plant community. Each set of enclosures was a rectangular area with four smaller  $5 \times 2$  m areas. Each of these smaller areas received one of four different enclosure treatments: 1) exclusion of all non-volant vertebrate consumers; 2) small-mammal access treatments that excluded rabbits, squirrels, and deer; 3) small- and medium-sized consumer access treatments that allowed small mammals, rabbits and squirrels access but excluded deer; 4) an unfenced treatment that allowed all consumers to have access. Plots were tilled on 18–20 January 2005, and enclosures were installed on 27–28 January 2005. Enclosures for the exclusion of all non-volant vertebrate consumers consisted of 1.22 m tall hardware cloth ( $0.8 \times 0.8$  cm mesh size) buried 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. Small-mammal access treatments were open to rodent consumers and constructed of poultry wire with  $2.5 \times 2.5$  cm holes and without a band of aluminum flashing at the top. Small- and medium-sized consumer access treatments were identical to small treatments, but had  $20 \times 20$  cm holes cut into the fence at uniform intervals. All-consumer access treatments were not fenced. To control for the disturbance created by fence installation, each enclosure area was trenched prior to enclosure installation, regardless of enclosure treatment. Our experimental enclosure treatments are not confounded by soil or seedbank effects because all four enclosure treatments were present in each block and randomly assigned; moreover, there is very little long-term seedbank in California grasslands (Young et al. 1981), and *N. pulchra* was not present in any of our plots prior to the experiment.

Small-mammal consumers found at our study site included deer mice *Peromyscus maniculatus*, harvest mice *Reithrodontomys megalotis*, pocket mice *Chaetodipus californicus* and meadow voles *Microtus californicus*. Medium-sized consumers at our site included ground squirrels *Spermophilus beecheyi* and brush rabbits *Sylvilagus bachmani*. Large consumers at our study site were mule deer *Odocoileus hemionus*. Live-trapping of small-mammal consumers in and around enclosures confirmed the presence of these consumers and demonstrated that enclosures were highly effective in manipulating their access; although a single deer mouse was captured in a single no-consumer access

enclosure, an average of 5 times more consumers were captured outside of no-consumer enclosures (Orrock et al. 2009). Our enclosures did not manipulate access by arthropod or avian consumers.

Within each enclosure type, one of three square  $1 \times 1$  m plots was used for this study. The other two plots in each enclosure were used for a separate study of mycorrhizae and *N. pulchra*, and a study examining the role of seed density and consumers reported elsewhere (Orrock et al. 2009). On 1 February 2005, all plots were seeded by broadcasting seeds of locally-collected *Nassella pulchra* onto the surface of the tilled soil at 500 seeds per  $m^2$ , a common seeding density for restoration (Moyes et al. 2005) as well as seed-limitation experiments (Seabloom et al. 2003). The timing of seed placement in our study 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 make our work more relevant to restoration efforts, which generally add seeds during the growing season to promote establishment. As a result, our schedule generates a conservative estimate of the impact of granivores, because seeds would typically be vulnerable to consumers for a longer period prior to germination.

At each experimental site, the surrounding plant community was characterized in April 2005 by visually estimating the percent cover of all plants within a  $1 \times 1$  m area on each of the four sides of the site, for a total of four measures per site. In addition, the distance to the nearest patch of *B. nigra* was also determined because *B. nigra* forms tall, dense stands in California grasslands (Bell and Muller 1973) that have been shown to previously affect consumer impact on native plants (Orrock et al. 2008). A patch of *B. nigra* was defined as a contiguous area that was visually estimated to be  $> 36 m^2$  in size and dominated by *B. nigra* cover (mean proportion of *B. nigra* cover was  $0.42 \pm 0.04$  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 within 100 m in each cardinal direction was recorded and averaged; see Orrock et al. (2008) for more details. Calculating distance to *B. nigra* in this way is strongly correlated with simply measuring the distance to the nearest *B. nigra* patch (linear regression,  $r^2 = 0.96$ ,  $F_{1,6} = 133.57$ ,  $p < 0.001$ ), and has the added benefit of capturing the effect of multiple nearby *B. nigra* patches on a given site.

The number of mature *N. pulchra* plants alive in each plot was counted between 16 June – 6 July 2005, corresponding to the end of the growing season. Plots were re-visited at the beginning of the next growing season (October 2005) and in a subsequent year (August 2006) to verify that our summer estimate of *N. pulchra* abundance was strongly correlated with the number of *N. pulchra* that survive to the end of the next growing season.

We focus on three aspects of the exotic plant community to characterize the components potentially driving apparent competition: the richness of exotic plants, the total proportion of the exotic plant community composed of exotic forbs, and the proportion of the exotic plant community composed of exotic grasses. To reduce collinearity and dimensionality, these variables were subjected to factor analysis and two resulting principal components were

retained. Because it has been shown to be important in previous work in the study area (Orrock et al. 2008), we also include the distance to the nearest patch of *Brassica nigra* to the study plot as an independent variable.

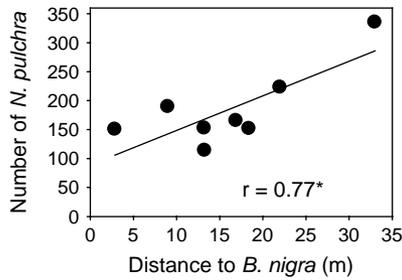
We compare overall enclosure effects using a mixed-model analysis of variance with enclosure treatment as a fixed effect and site as a random effect. For each suite of consumers, we used multiple linear regression with stepwise selection (Quinn and Keough 2002) to construct the best model to explain *N. pulchra* recruitment, using the distance to the nearest *B. nigra* patch and factors describing the plant community adjacent to experimental plots as independent variables. Additional selection approaches (e.g. backwards elimination, model building using information-theoretic approaches) yielded identical final models. The largest condition index for either of the multiple regression models was 4.7, well below the value of 30 suggestive of collinearity (Quinn and Keough 2002), and examination of residual plots suggested that data were normally distributed with homogeneous variance.

## Results

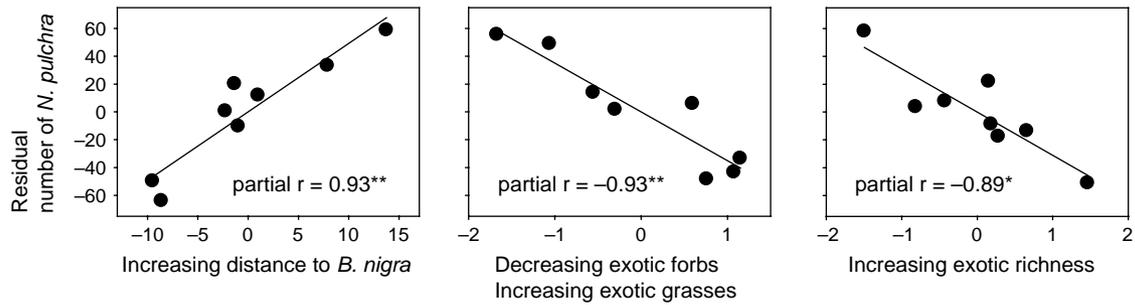
The communities surrounding enclosure plots seeded with *Nassella pulchra* were almost entirely composed of exotic plants: percent cover of exotic plants adjacent to experimental plots ranged from 91.8% to 100% (mean of  $97.1 \pm 1.1\%$  SE), with the number of native species adjacent to plots ranging from 0 to 2. A total of 11 exotic species was found in the study, with the majority of percent cover (over 94%) dominated by the exotic annual grasses *Bromus diandrus* ( $38.0 \pm 8.3\%$ ), *Hordeum murinum* ( $3.1 \pm 3.1\%$ ), *Avena fatua* ( $2.6 \pm 1.4\%$ ), and the exotic annual forbs *Melilotus officianalis* ( $16.8 \pm 8.1\%$ ), *Medicago polymorpha* ( $15.5 \pm 5.7\%$ ), *Erodium cicutarium* ( $8.0 \pm 2.3\%$ ), *Brassica nigra* ( $7.6 \pm 2.7\%$ ) and *Malva parviflora* ( $2.8 \pm 0.7\%$ ). Factor analysis produced two principal components; the first principal component explained 68.1% of the variation in the original data and described increasing cover of exotic grasses (Pearson correlation,  $r = 0.99$ ,  $n = 8$ ,  $p < 0.001$ ) and decreasing cover of exotic forbs ( $r = -0.99$ ,  $n = 8$ ,  $p < 0.001$ ). In addition to these metrics, this principal component described portions of the surrounding plant community not included in the factor analysis, such as increasing richness of native plants ( $r = 0.76$ ,  $n = 8$ ,  $p < 0.03$ ), decreasing evenness of the entire plant community ( $r = -0.84$ ,  $n = 8$ ,  $p < 0.01$ ), and changes in the proportional cover of *Bromus diandrus* ( $r = 0.85$ ,  $n = 8$ ,  $p < 0.01$ ). The second principal component explained 31.8% of the variation in the original data and described increases in the richness of the exotic plant community ( $r = 0.96$ ,  $n = 8$ ,  $p < 0.001$ ). The second principal component also captured changes in the plant community that were not part of the factor analysis, describing richness of both exotic forbs ( $r = 0.87$ ,  $n = 8$ ,  $p < 0.01$ ), the richness of the entire plant community (i.e. both native and exotic;  $r = 0.77$ ,  $n = 8$ ,  $p < 0.03$ ), and the proportional cover of *Melilotus officianalis* ( $r = -0.81$ ,  $n = 8$ ,  $p < 0.01$ ) and *Medicago polymorpha* ( $r = 0.73$ ,  $n = 8$ ,  $p < 0.05$ ).

Consumer enclosures had a significant effect on *N. pulchra* recruitment ( $F_{3,21} = 10.10$ ,  $p < 0.001$ ). When

### A. Access by mice and voles



### B. Access by mice, voles, squirrels, and rabbits



### C. Access by all mammalian consumers

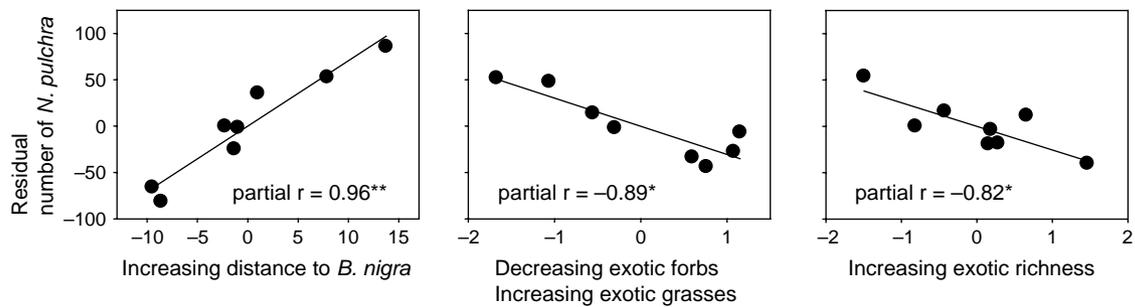


Figure 1. Consumer-mediated apparent competition was a function of the consumer guild with access as well as the characteristics of the local exotic plant community and the presence of exotic plants at a distance. *Nassella pulchra* abundance was not related to any factors when all consumers were excluded (all  $p > 0.20$ ), and *N. pulchra* recruitment was uniformly high. (A) when only mice and voles had access to *N. pulchra*, recruitment of *N. pulchra* depended only on the distance to the exotic forb *Brassica nigra*. (B) when mice, voles, squirrels and rabbits had access, recruitment of *N. pulchra* was lower when local plant communities were dominated by exotic grasses and lower when the richness of exotic plants was high. (C) similarly, when all consumers had access (mice, voles, squirrels, rabbits and deer), the recruitment of *N. pulchra* was greater with increasing distance from *B. nigra*, increasing prevalence of exotic forbs, decreasing prevalence of exotic grasses, and decreasing richness of the adjacent exotic plant community. Note that, where multiple independent variables exist in a model (panels B and C), residual values are used for the y-axis (i.e. panel A represents a simple plot of raw data, whereas panels B and C are partial regression plots). Significance values of are indicated by asterisks (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ).

no consumers had access to experimental plots, characteristics of the exotic plant community and distance to *B. nigra* did not explain patterns of *N. pulchra* recruitment (linear regression, all  $p > 0.20$ ), and average recruitment was uniformly high ( $217.75 \pm 25.49$  plants). Access by only mice and voles did not significantly reduce *N. pulchra* recruitment ( $184.88 \pm 25.49$  plants) compared to plots with no consumer access (linear contrast  $F_{1,21} = 1.26$ ,  $p = 0.27$ ). Access by squirrels, rabbits, voles, and mice ( $78.25 \pm 25.49$  plants), and access by all mammalian consumers ( $103.81 \pm 25.49$  plants) had significant negative effects on *N. pulchra* recruitment compared to plots with no consumer access (linear contrasts, both  $F_{1,21} > 15.09$ ,  $p < 0.001$ ) as well as compared to plots where only mice and voles had access

(linear contrasts, both  $F_{1,21} > 7.61$ ,  $p < 0.012$ ). There was no significant difference in *N. pulchra* recruitment in plots open to all consumers and plots open to squirrels, rabbits, voles and mice (linear contrast,  $F_{1,21} = 0.76$ ,  $p = 0.39$ ).

These average trends indicate the potential for significant consumer impact, but also demonstrate that consumer effects were highly variable: recruitment of *N. pulchra* in enclosures open to any of the consumer guilds ranged from 6–335 plants. This variation in consumer impact was largely explained by distance to *B. nigra* and characteristics of the exotic plant community (Fig. 1). When enclosures allowed small mammals (mice and voles) to access *N. pulchra* plants, the distance to *B. nigra* became a significant predictor of consumer impact on plant

recruitment (model  $R^2=0.62$ ;  $F_{1,6}=9.71$ ,  $p=0.02$ ; Fig. 1A). When small mammals, squirrels, and rabbits were allowed access to *N. pulchra* plants, consumer impact was greater when *B. nigra* was closer, consumer impact was lower when the adjacent plant community was composed largely of exotic grasses compared to exotic forbs, and greater when the adjacent plant community contained many invasive plant species and these species were not equitably distributed (model  $R^2=0.97$ ;  $F_{3,4}=36.75$ ,  $p=0.002$ ; Fig. 1B). When small mammals, squirrels, rabbits, and deer were allowed access to *N. pulchra*, all three independent variables remained significant (model  $R^2=0.97$ ;  $F_{3,4}=37.86$ ,  $p=0.002$ ; Fig. 1C).

The effect of consumers persisted until the beginning of the next growing season, as the number of *N. pulchra* in all 32 experimental exclosures was a significant predictor of the number of *N. pulchra* that were alive at the start of the next growing season in October 2005 ( $r^2=0.80$ ;  $F_{1,30}=122.22$ ,  $p<0.001$ ). A subsequent survey in the next year demonstrated that these effects continued to persist through the end of the next growing season: the percent cover of *N. pulchra* in August 2006 was significantly related to the number of adult plants in summer 2005 ( $r^2=0.33$ ;  $F_{1,30}=14.87$ ,  $p<0.001$ ).

## Discussion

We show that consumer-mediated effects may constrain the re-establishment of native *N. pulchra* (Fig. 1). Our work adds several additional insights to recent studies that document the importance of apparent competition in the context of invasions (Borer et al. 2007, Meiners 2007, Orrock et al. 2008, Pearson and Callaway 2008). First, the degree to which apparent competition affects establishment of native *N. pulchra* depends on which consumers are acting on local plants (Fig. 1). Second, the mechanism responsible for generating apparent competition (i.e. distance to *B. nigra*, composition of the exotic plant community) also depends upon which consumers have access to *N. pulchra* (Fig. 1). Third, these indirect effects of consumers are generated by exotic plants at two different spatial scales, as consumer impacts are affected by the characteristics of the exotic plant community directly adjacent to *N. pulchra*, as well as by plants (*B. nigra*) that are many meters away.

The importance of local community characteristics and distance to *B. nigra* suggest that several forms of apparent competition may occur in California grasslands and the importance of different forms of apparent competition may vary among consumer types. Small-mammal consumers may experience elevated densities due to increased reproduction when eating diets rich in exotic plants (Krohne 1980), which could create classical apparent competition due to changes in consumer population sizes (Holt 1977). However, the effect of small-mammal consumers was only related to proximity to *B. nigra*, which is unlikely to provide a substantial food source (Bell and Muller 1973, Feeny 1977). Therefore, if this form of apparent competition is occurring, it seems most likely to be mediated through larger consumers whose effects depended on the abundance of exotic grasses (Fig. 1) that may form a substantial food

resource (Fitch 1948, Fitch and Bentley 1949, Chapman 1974).

When consumers are mobile herbivores that select among native and exotic plants, short-term apparent competition may occur (Holt and Kotler 1987) if local plant communities that are increasingly dominated by exotic plants act to attract consumers due to the production of increased amounts of food resources or by having more palatable tissues, i.e. the increased consumer impact on *N. pulchra* in plots with rich exotic plant communities dominated by grasses may be one of the “perils of having tasty neighbors” (Palmer et al. 2003). Larger consumers such as ground squirrels (Fitch 1948) and rabbits (Chapman 1974) are known to feed heavily on exotic grasses common in our study area. Small-mammal consumers may forage heavily on exotic plant seeds and foliage, but will also consume insects and other items (Fitch and Bentley 1949, Batzli and Pitelka 1971, Meserve 1976, Lidicker 1989). The greater mobility of larger consumers (e.g. squirrels, rabbits and deer) may allow them to be more selective of the composition of the areas where they forage for food, and thus explain why characteristics of the exotic plant community were important when squirrels, rabbits, and deer were allowed access, but not when small mammals alone had access (Fig. 1).

Both classical apparent competition and short-term apparent competition require that the per-capita effect of consumers in limiting *N. pulchra* is greater than consumer effects on exotic annual grasses. Exotic annual grasses may be largely buffered from these consumer impacts because they produce prodigious quantities of seed (Marshall and Jain 1967, Young et al. 1981). The asymmetrical effect of consumers on exotic and native plants is further supported by long-term consumer manipulations, as exotic plants increase in abundance when consumers have access and decrease when consumers are excluded (Seabloom et al. 2009).

Refuge-mediated apparent competition, when exotic plants provide native consumers with shelter from their predators or a preferred microclimate for resting between foraging bouts (Connell 1990, Chanton and Bonsall 2000, Orrock et al. unpubl.), may also be acting to affect *N. pulchra*. For example, *Brassica nigra* is a tall exotic forb that forms dense stands. If native consumers restrict their foraging to be near *B. nigra* because it provides a refuge, as is suggested by a different experiment in this study area (Orrock et al. 2008), the presence of *B. nigra* nearby may increase consumer pressure on *N. pulchra* (Connell 1990, Chanton and Bonsall 2000, Orrock et al. unpubl.). Consumers seeking refuge near *B. nigra* are likely to have little negative effect on *B. nigra* because it produces small seeds that are likely to be of low importance to rodent granivores, and *B. nigra* tissues also contain secondary defense compounds (Feeny 1977). This hypothesis is supported by previous research (Bell and Muller 1973) as well field observations that seed removal of *N. pulchra* by vertebrates was greater than seed removal of *B. nigra* (Orrock et al. unpubl.). Although refuge-mediated apparent competition is capable of limiting re-establishment of *N. pulchra*, it may also affect recruitment of exotic grasses, as Bell and Muller (1973) observed greater rates of seed removal for one exotic grass inside stands of *B. nigra*.

However, given the disparity between native and exotic grass seed production, it is likely that any effects of *B. nigra* on seeds of exotic annual grasses are less than its effect on seeds of native perennial grasses. More generally, refuge-mediated apparent competition may be important in affecting community structure and pattern in other systems (Orrock et al. unpubl.), e.g. the “bare zone” between grassland and chaparral vegetation (Bartholomew 1970).

Our results illustrate that the average effect of small-mammal consumers does not significantly reduce *N. pulchra* recruitment compared to treatments that exclude all consumers, while allowing medium-sized mammals and all mammals access leads to significant reductions in average *N. pulchra* recruitment. Although consumers may have different effects on average, our results (Fig. 1) suggest that these average effects can be misleading because proximity to *B. nigra* and the characteristics of the exotic plant community can generate substantial spatial heterogeneity in consumer limitation of *N. pulchra*. For example, although rodents do not lead to a significant reduction in recruitment of *N. pulchra* when exclosures at all distances from *B. nigra* are used, there are highly significant effects of rodents when the four exclosures located nearest *B. nigra* (mean distance  $9.59 \pm 3.64$  m) are examined (linear contrast comparing exclosures with no consumer access to rodent-access exclosures,  $F_{1,9} = 16.35$ ,  $p < 0.01$ ). When apparent competition generates spatial variation in consumer foraging, average rates of consumption can obscure important consumer impacts.

In addition to emphasizing the general importance of considering consumers in planning restoration and conservation (Howe et al. 2002, MacDougall and Wilson 2007), our work suggests that conservation and restoration efforts must accommodate the potential for interactions between consumers and exotic plants. Established *Nassella* stands have been found to be long-lived and persistent without active management in the absence of fire, grazing, and tilling for agriculture (Stromberg and Griffin 1996). As such, consumer-mediated apparent competition will likely be most important for determining expansion of existing patches of remnant *N. pulchra* and the restoration of grasslands that have been overtaken by exotics, as these are situations where seed limitation is likely to drive dynamics, a process that might be exacerbated by reduced seed output as a result of consumers (Orrock et al. 2009). Our findings suggest that reduction of nearby exotic plants (e.g. via mowing or tilling) may be effective for reducing consumer pressure and facilitating the establishment of new *N. pulchra* stands or the expansion of remnant stands of *N. pulchra*. Indeed, a strong test of the importance of refuge-mediated apparent competition would be to couple mowing of nearby *B. nigra* with consumer exclosures and *N. pulchra* seed addition. Importantly, despite the increase in local consumer pressure caused by apparent competition, increasing the amount of *N. pulchra* seeds added to restoration plots leads to increases in recruitment and *N. pulchra* adults (Orrock et al. 2009).

Although overcoming the indirect effect of exotic plants on native restoration may be accomplished by providing initial populations of native plants that are large enough to

establish despite considerable consumer pressure (Orrock et al. 2009), we stress that additional studies are needed to fully characterize the suite of direct and indirect effects that limit the establishment and spread of *N. pulchra*. For example, competitive relationships between *N. pulchra* and exotic plants may differ depending upon geographic location (reviewed by Corbin et al. 2007). Direct competition may also contribute to consumer effects on *N. pulchra* by further reducing seed production by *N. pulchra* (Dyer and Rice 1999, Hamilton et al. 1999). As such, although high-density seed additions may increase *N. pulchra* establishment, it remains unclear whether established *N. pulchra* plants can produce seeds in densities great enough to expand into an exotic-dominated habitat. Exotic herbivores (cattle) were not present at our study site, and their effects may compound those observed here. Cattle effects may be especially important for future studies because cattle may increase the susceptibility of native grasses to the Barley Yellow Dwarf virus (Malmstrom et al. 2005), thus promoting pathogen-mediated apparent competition (Borer et al. 2007), i.e. apparent competition via multiple pathways may be important in understanding biological invasions, and facilitation among invaders (i.e. invasional meltdown; Simberloff and Von Holle 1999) may occur via consumer-mediated indirect effects such as apparent competition.

Our work illustrates how apparent competition may reduce the reestablishment of a native plant in invaded habitats, demonstrates that the strength and type of apparent competition may be consumer-specific, and suggests that apparent competition may occur at different spatial scales. Taken together, these findings suggest that changes in consumer communities may lead to changes in the strength and extent of apparent competition, with potential implications for restoration, conservation, and invasion. For example, shifts in consumer communities caused by habitat fragmentation (Bolger et al. 1997) may alter the opportunities for invasion by plants that rely upon consumer-mediated indirect effects to persist. Although indirect effects alone were sufficient to lower re-establishment of *N. pulchra* (Fig. 1), a critical question is the degree to which consumer-mediated apparent competition is common mechanism of invasion, which types of apparent competition are most important, and the relative importance of such indirect effects compared to other mechanisms (e.g. direct competition). It is likely that multiple factors contribute to invasions (Mack et al. 2000), that the importance of particular mechanisms can change during an invasion (Dietz and Edwards 2006), and that important interactions can occur via direct or indirect means (Noonburg and Byers 2005, Didham et al. 2007, Pearson and Callaway 2008). Future research that examines the joint effects of indirect and direct effects, especially as they pertain to positive interactions among exotics that facilitate and maintain invasions, i.e. invasional meltdown, should be a priority.

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