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Biotic resistance: exclusion of native rodent consumers releases populations of a weak invader

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Summary

1. Biotic resistance is a commonly invoked hypothesis to explain why most exotic plant species naturalize at low abundance. Although numerous studies have documented negative impacts of native consumers on exotic plant performance, longer-term multi-generation studies are needed to understand how native consumer damage to exotics translates to their population-level suppression over large landscapes.

2. We used rodent exclosures and embedded seed-addition experiments to evaluate the effects of rodent herbivory and granivory on populations of *Tragopogon dubius*, a Eurasian aster that typically occurs at low abundance across North America.

3. Vegetation surveys encompassing 20 000 km^2 of west-central Montana grasslands established that *T. dubius* is regionally well distributed, occurring in 81% of 16 grasslands sampled. However, it consistently occurred at low local abundance, averaging $< 0.5\%$ cover in 1 m^2 plots.

4. In large rodent exclosures, *T. dubius* attained population densities that averaged over five times higher than in paired rodent-access control plots at 11 grassland sites spread over 750 km^2. This pattern was six times stronger in older compared with newer rodent exclosures, indicating enclosed populations were still increasing. Floral herbivory, which reduces or prevents reproduction in this biennial plant, decreased by 99% in rodent exclosures compared with control plots. Additionally, seedling establishment was nearly eight times higher in seed-addition subplots within versus outside of rodent exclosures.

5. *Synthesis*. Our findings illustrate how biotic resistance from granivory and florivory of native generalist rodents can provide an important ecosystem service by strongly limiting the local abundance of a widely distributed exotic weed.

Key-words: biological invasions, biotic resistance, exotic plant, granivory, herbivory, invasion ecology, *Peromyscus maniculatus*, recruitment, *Spermophilus columbianus*, *Tragopogon dubius*

Introduction

Exotic species introductions can result in a broad spectrum of outcomes. At one end of this spectrum, some exotics successfully colonize new locales and ultimately attain high abundance, allowing them to strongly impact recipient systems (Mack *et al.* 2000; Vilá *et al.* 2011). At the other end of the spectrum, where most species lie, exotics either fail to establish or naturalize at low densities (Williamson 1996) and become weak invaders (Ortega & Pearson 2005). Most studies of exotic plant invasions have focused on highly abundant strong, invaders to determine how these species come to dominate native systems. This emphasis is sensible, since these species present the greatest threats to native ecosystems (Mack *et al.* 2000). However, focusing only on highly successful invaders may limit understandings of biological invasions.

One question of general interest concerns why the vast majority of exotic plant species that establish in new ranges fail to attain high local abundance. In cases where abiotic conditions are suitable, the primary obstacle to exotic population growth and spread may be biotic resistance (Elton 1958; Williamson 1996; Mack 1996; Keane & Crawley 2002). Biotic resistance is the idea that native competitors and enemies individually or interactively suppress population abundance of exotics, thereby exerting 'resistance' to invasion. Most work on biotic resistance has focused on the competitive effects of native plant assemblages on invading exotic plants (Levine, Adler & Yelenik 2004). However, an increasing number of

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*Correspondence author. E-mail: dpearson@fs.fed.us studies have shown that native generalist consumers can reduce exotic plant performance by depressing seed production, recruitment, growth or survival (Parker, Burkepile & Hay 2006; Liu, Stiling & Pemberton 2007; Han *et al.* 2008; Hill & Kotanen 2009; Cushman, Lortie & Christian 2011). Yet, few studies have examined the extent to which these reductions in exotic plant performance translate to suppression of exotic abundance (but see Inouye, Byers & Brown 1980; Peart 1989; Brown & Heske 1990; Pierson & Mack 1990; Bossard & Rejmanek 1994). Reductions in exotic plant growth, seed production or survival from native consumers may have minimal effects on plant abundance due to compensatory responses (McNaughton 1983; Crawley 1989; Strauss & Agrawal 1999), which can be particularly strong in exotic plant populations (Garren & Strauss 2009; Swope & Parker 2010; Ortega *et al.* 2012). Although various studies have examined native herbivore impacts on exotic plants using biomass or cover as surrogates for population changes (Parker, Burkepile & Hay 2006), changes in biomass or cover may not reflect suppression of plant abundance, particularly if measured over the short term (McNaughton 1983; Crawley 1989). To better understand the extent to which native generalist consumers actually provide an ecosystem service by imposing biotic resistance, there is a need for long-term, multi-generation studies that examine how frequently native herbivore-driven reductions in the growth, seed production, recruitment or survival of exotics are responsible for suppressing their abundance across landscapes.

We know from work in native-dominated systems that generalist small mammal consumers can have strong effects on native plant recruitment and abundance (Brown & Heske 1990; Ostfeld, Manson & Canham 1997; Howe *et al.* 2006; Maron & Kauffman 2006; Orrock, Witter & Reichman 2008; Bricker, Pearson & Maron 2010; Zwolak *et al.* 2010). Hence, small mammals represent potentially important community filters that may influence invasions. A growing number of studies have shown that small mammal herbivory and granivory can affect the individual performance and even recruitment of exotic plants (e.g. Reader 1993; Vilá & D'Antonio 1998; Lambrinos 2006; MacDougall & Wilson 2007; Nunez, Simberloff & Relva 2008; Pearson, Callaway & Maron 2011). Yet, studies examining population-level responses of exotic plants to native rodent consumers have been mixed (Inouye, Byers & Brown 1980; Peart 1989; Brown & Heske 1990; Pierson & Mack 1990; Bossard & Rejmanek 1994). For example, small mammals substantially reduced recruitment of *Bromus tectorum*, but they did not affect its survivorship and had rather conditional effects on overall population abundance (Pierson & Mack 1990). Thus, consumer impacts on performance did not translate to reduced population abundance. Other studies have shown that small mammal herbivory had no effects on populations of *Cytisus scoparius* and *Anthoxanthum odoratum* (Peart 1989; Bossard & Rejmanek 1994). In contrast, small mammal granivory had rather strong effects on population abundance of *Erodium cicutarium* and *Eragrostis lehmanniana* (Inouye, Byers & Brown 1980; Brown & Heske 1990). These mixed results may partly be attributable to the fact that two of the studies finding negligible effects focused on very strong invaders (*B. tectorum* and *C. scoparius*) that might be expected to resist consumer attack. In contrast, small mammal consumers substantially reduced populations of two of the three less aggressive invaders (*E. cicutarium* and *E. lehmanniana*), suggesting biotic resistance by small mammal consumers may partly explain the lower abundances of some weakly invasive exotics.

Here, we examine the strength of biotic resistance experienced by *Tragopogon dubius*, an exotic forb that generally occurs at low densities in western Montana (Ortega & Pearson 2005). We first quantify the local abundance of this plant in grasslands across west-central Montana, USA, to demonstrate that it commonly occurs at moderate to low densities. We then quantify how the abundance of this plant differs in and out of rodent exclosures (that are up to 9 years old) as a means of documenting longer-term population-level effects of native small mammal consumers. Finally, we use seed-addition experiments and floral herbivory surveys in and out of rodent exclosures to determine the extent to which post-dispersal seed predation by deer mice (*Peromyscus maniculatus*) versus florivory by ground squirrels (*Spermophilus columbianus*) influence recruitment and fecundity of this plant and how these effects translate to densities of this exotic weed over large spatial scales.

Materials and methods

Tragopogon dubius is a biennial native to Eurasia. It is well-established over about 95% of North America, where it generally occurs at low abundance in grasslands, open forest and disturbed habitats (Clements, Upadhyaya & Bos 1999). It is not reported as a noxious or serious problem weed in any US state (http://invader.dbs.umt.edu/). To quantify the local abundance of this weed over a large geographic area, we visually estimated *T. dubius* cover within twenty 1-m^2 plots randomly located within each of 16 natural intermountain grasslands distributed over a 20 000 km^2 area of west-central Montana that encompassed our experimental sites (described later). We estimated per cent cover to the nearest 5% if cover was $\geq$ 5%, to the nearest 1% if cover was < 5%, and plots with < 0.5% cover were assigned 0.1% cover.

Biotic resistance to *T. dubius* was quantified by conducting experiments in grasslands of the Blackfoot Valley, western Montana, USA. These grasslands are dominated by the bunchgrass *Festuca scabrella* or in places by sagebrush *Artemesia tridentata*. Cattle grazing is the primary historic land use, but none of our experimental sites are grazed. The grasslands are predominantly comprised of native species with a few weak invaders, like *T. dubius*, occurring at low densities across the system, and a few strong invaders, like *Centaurea stoebe*, that presently occur in relatively limited patches. Eight years of live trapping indicate that deer mice (*Peromyscus maniculatus*), Columbian ground squirrels (*Spermophilus columbianus*) and montane voles (*Microtus montanus*) are the primary small mammals across Blackfoot Valley grasslands (Maron, Pearson & Fletcher 2010). Of these, deer mice and Columbian ground squirrels are the primary consumers of *T. dubius*. Deer mice readily consume *T. dubius* seed (Pearson, Callaway & Maron 2011) and Columbian ground squirrels eat flower heads. Although ungulates occasionally graze *T. dubius*, our observations indicate Columbian ground squirrels are the primary vertebrate herbivore of this plant in our system. Seed depots placed inside rodent exclosures show virtually no seed loss, suggesting birds and invertebrates are not important seed predators in our system (J.L. Maron and D.E. Pearson, unpublished data).

We determined the effects of rodent consumers on *T. dubius* populations in three ways. First, we quantified the extent of ground squirrel floral herbivory on established plants in and out of rodent exclosures. This, combined with censuses of seeds produced per individual inflorescence and inflorescences per plant, provided an estimate of seed production and pre-dispersal seed loss. Secondly, we conducted seed-addition experiments inside and outside of rodent exclosures to determine how post-dispersal seed predation by deer mice influenced seedling recruitment. Finally, we quantified the density of adult *T. dubius* plants that naturally established through time in rodent exclosures and contrasted this to *T. dubius* densities in nearby rodent exclosure control plots. Differences in *T. dubius* density in and out of rodent exclosures represent an integrative measure of how reducing floral herbivory and post-dispersal seed predation by rodents translates over longer periods to influence plant populations.

We constructed rodent exclosures at four primary and seven ancillary sites distributed over 750 km^2 of grasslands (see Fig. S1). At each site, we established one or more rodent exclosure and paired rodent exclosure control plots that were 10–20 m apart. Rodent exclosures and control plots were 10 × 10 m in all cases except for at five ancillary sites where they were 10 × 15 m. Rodent exclosures were constructed of 0.625 × 0.625 cm wire mesh fencing buried 40 cm deep and extending 60 cm above ground. Fences were topped with 20 cm of solid metal flashing to prevent entry by climbing rodents. Snap traps were maintained within exclosures to ensure they remained secure. At the four primary sites, we constructed two pairs of rodent exclosures and control plots (one pair in 2003 and the other in 2006) within each of three larger 1-ha plots where we had either excluded ungulates alone, all mammalian and avian predators plus ungulates, or allowed access to all animals, that is, controls (Fig. S1) as part of another study (Maron & Pearson 2011). The 1-ha plots were > 100 m apart per site. The seven ancillary sites, each containing a single pair of rodent exclosure and control plots, were established in 2003 (n = 1), 2006 (n = 1) and 2008 (n = 5). Hence, maximum sample size was n = 11.

All rodent exclosure and rodent exclosure control plots were censused for adult *T. dubius* in 2011. Since the ungulate and predator/ungulate exclusion treatments had no impact on the abundance of Columbian ground squirrels or deer mice (Maron, Pearson & Fletcher 2010), the two rodents that consume *T. dubius,* and since those treatments also did not affect herbivory rates on *T. dubius* (see Results), adult *T. dubius* census data for rodent exclosures and controls, respectively, were averaged across the three 1-ha treatment plots and across the two rodent exclosures and rodent exclosure controls to obtain a single *T. dubius* estimate for each of the four primary sites that was comparable to the single estimates obtained from each of the ancillary sites.

In summer 2009, we initiated a seed-addition and disturbance experiment by randomly locating four 0.25 m^2 subplots within each rodent exclosure and its adjacent control at 10 of our 11 sites. At each of the four primary sites, we conducted the experiment in only the control grid of the larger study (i.e. not on ungulate or predator/ungulate exclusion grids) and within only one of the two pairs of rodent exclosure and control plots (Fig. S1). Within each rodent exclosure and control plot, we factorially crossed seed addition with disturbance, randomly assigning each of the four subplots to a unique ± seed addition ± disturbance treatment combination. The vegetation within disturbance subplots was killed in early July 2009 using the broad-spectrum, low-persistence herbicide Roundup®, and plots were subsequently hoed to remove dead plant material in late July. Seed-addition subplots received 50 seeds of *T. dubius*. Seeds were collected locally and added in late August by spreading them evenly over the subplots. As part of a larger seed-addition study, the seed-addition subplots also received seeds of 18 other species of exotic plants. Here, we report only the results for *T. dubius* establishment, the community-level results are reported elsewhere (Maron *et al.* 2012). We replicated this experiment in a new set of subplots at each of the 10 sites in summer 2010. Beginning the spring following seed addition, we censused all seed-addition plots three to four times from May through July and recorded seedling emergence, survival and establishment. We report establishment as the number of seedlings surviving through their first summer to the onset of senescence in late July.

We quantified herbivory at our four primary study sites in 2008 by marking naturally occurring *T. dubius* plants that were beginning to bolt in the spring and returning late summer to evaluate herbivory. We marked all plants inside both rodent exclosures on each 1-ha grid except in a few cases where high plant densities forced us to mark a random subset of plants. Because plant densities on rodent control plots were too low to provide reasonable estimates of herbivory, we located plants outside rodent exclosures by walking 10 1 × 100 m belt transects across each 1-ha grid in which the rodent experiment was embedded (Fig. S1). We returned in late summer after flowering and counted the number of intact flower heads and the number of flower heads that had been eaten per marked plant. This enabled us to determine the percentage of flower heads lost per plant and to estimate the average number of flower heads that a plant could produce in the absence of herbivory.

We analysed data using generalized linear mixed models (PROC GLIMMIX; SAS Institute 2009). Counts of adult plants and seedlings were analysed with a negative binomial distribution, which provided the best fit. We used a binomial distribution to analyse herbivory (flower head eaten or not). Rodent exclosure treatment was a fixed factor in all models, and disturbance and year were also fixed factors in the analysis of seedling establishment as noted below. Site was included as a random effect in all models. Natural seed rain and seed emergence from the soil was minimal as indicated by the fact that virtually no *T. dubius* seedlings established in subplots without seeds added (controls). Therefore, subplots without seeds added were excluded from all analyses. In 2010, no seedlings were counted in the no-disturbance, seed-addition subplots, but this was likely due to failure to detect tiny seedlings that occurred at very low densities among the dense vegetation. The fact that we did see young plants in these subplots in 2011 suggests that we missed them in our 2010 census. Therefore, we excluded the no-disturbance treatment from analysis of 2010 seed-addition data. We were able to overcome this problem in 2011 through greater familiarity with the seedlings and more intensive searches. To account for this asymmetry, we analysed the seedling establishment results first for undisturbed plots only, where we could examine effects of rodent exclusion, year and rodent exclusion by year on seedling establishment. We then analysed 2011 data only, where we examined the effects of rodent exclusion, disturbance and rodent exclusion by disturbance. For these analyses, we used a split-plot design with disturbance or seed addition nested within rodent exclusion treatment. We also examined temporal effects of rodents on *T. dubius* populations by comparing plant densities between rodent exclosures and control plots for old (2003–2006) and new (2008) rodent exclosures. Sites with no adult *T. dubius* plants within either the rodent exclusion or control plots (i.e. plants not established at the site) were excluded from analysis of population densities. We evaluated effects of the ungulate and predator/ungulate exclusion on *T. dubius* herbivory by comparing herbivory rates determined from the belt transects among treatments on the primary sites using a binomial distribution.

Results

Tragopogon dubius was detected within 13 of the 16 grasslands sampled across west-central Montana, where it occurred in > 28% of the 320 1-m^2 plots surveyed. However, it made up, on average, only 0.41% (SD = 0.60) of the total vegetative cover per plot. Rodent exclusion over 3–9 years resulted in a substantial increase in *T. dubius* abundance. Within rodent exclusion plots, naturally occurring adult *T. dubius* plants were > 5 times more abundant compared with paired control plots ($F_{1,10}$ = 16.73, $P < 0.01$; Fig. 1a), and these differences were 5.6 times stronger in old versus new rodent exclosures ($F_{1,7}$ = 10.65, P = 0.01). Herbivory on *T. dubius* adult plants outside of exclosures on control (mean = 56 ± 5% SE) ungulate exclusion (mean = 44 ± 5%) and predator/ungulate exclusion grids (mean = 43 ± 7%) was not significantly different ($F_{2,4}$ = 1.91, P = 0.26). Herbivory rates on adult plants were dramatically lower in rodent exclusion plots compared with controls ($F_{1,5}$ = 15.78, P = 0.01; Fig. 1b). The small amount of herbivory observed within the exclosures appeared to be from ungulates feeding in the rodent exclosures. Post-dispersal seed predation by mice substantially reduced *T. dubius* seedling recruitment in seed-addition experiments. In disturbed treatments, where year and rodent exclusion effects could be contrasted, the number of *T. dubius* seedlings that established was 7.2 times higher in rodent exclusion plots compared to controls ($F_{1,9}$ = 26.46, $P < 0.01$; Fig. 1c), and 2.6 times more seedlings established in 2011 compared to 2010 ($F_{1,18}$ = 8.48, $P < 0.01$). There were no significant interaction between these factors ($F_{1,18}$ = 0.66, P = 0.43). For seed-addition subplots in 2011, rodent exclusion increased seedling establishment by 6.6 times ($F_{1,9}$ = 13.67, $P > 0.01$) and disturbance ($F_{1,318}$ = 15.38, $P > 0.01$) increased seedling establishment 6.2 times (Fig. 1c). Overall, the average number of *T. dubius* seedlings recruiting within exclosures across years and disturbance treatments was 7.6 times higher within rodent exclosures (5.1 ± 1.0) compared to controls (0.67 ± 0.3). There were no significant interactions between treatments ($F_{1,18}$ = 0.56, P = 0.47). In combination, rodent herbivory and seed predation reduced per capita recruitment of *T. dubius* by 76% (Table 1).

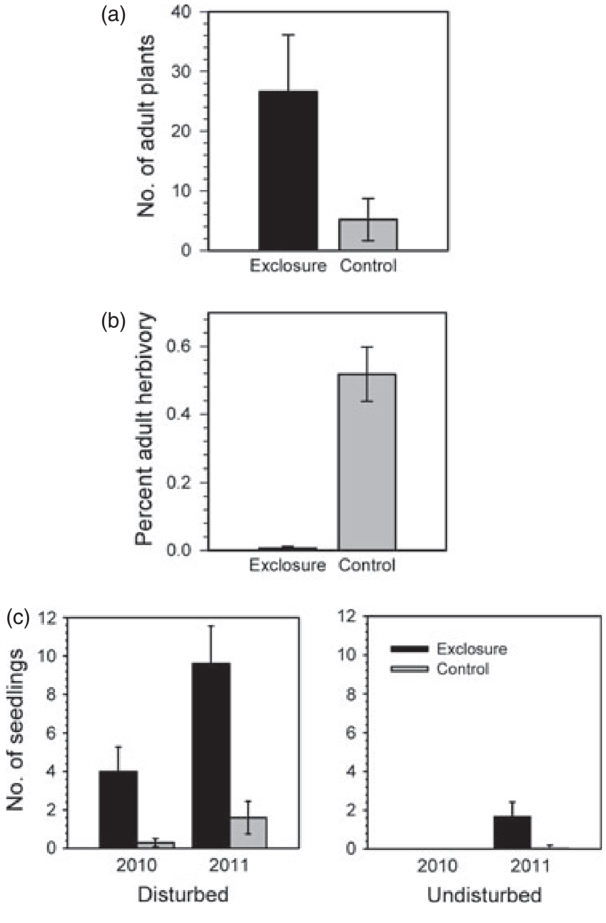

Fig. 1. Effects of rodent exclusion on mean (±SEM): (a) adult *Tragopogon dubius* abundance 100 m^{-2}, (b) the proportion of plants experiencing floral herbivory and (c) seedling establishment in seed-addition subplots in rodent exclosures and rodent exclosure controls.

Discussion

We found that native generalist rodent consumers provided substantial biotic resistance by greatly reducing the abundance of the exotic, *T. dubius*. *T. dubius* is widely distributed across most of North America, as it was across our 16 grassland sites in west-central Montana. However, it typically occurs at low local abundance. For example, local cover of this species across 1-m^2 plots in our surveyed grasslands averaged < 0.5%. Our experiments revealed that this plant experiences high rates of flower destruction and seed consumption by native ground squirrels and deer mice, respectively. Nearly 52% of plants exposed to ground squirrels experienced herbivory, while protected plants went virtually untouched (Fig. 1). Additionally, rodent exclusion that protected seeds

Table 1. Effects of floral herbivory and seed predation on *Tragopogon dubius* recruitment. Floral herbivory estimates were derived from sampling in rodent exclosures and along belt transects where rodents had access to plants. Seed predation effects were estimated from seed-addition experiments in rodent exclosures and rodent exclosure control plots. Values are means with SEs in parentheses

Demographic parameter	Rodent exclosure	Control
Percentage of heads eaten	0.6 (0.6)	51.8 (8.0)
Mean seeds produced per head	74.6 (4.2)	74.6 (4.2)
Mean number of heads per plant	1.73 (0.11)	1.54 (0.15)
Mean number of seeds per plant (calculated from above estimates)	128.3	55.37
Proportion of seeds to seedlings (averaged across disturbance treatment)	0.10 (0.02)	0.01 (0.01)
Mean seedlings per plant	12.83	0.55

from consumption by deer mice resulted in a nearly eightfold increase in seedling establishment. Collectively, heavy florivory and granivory produced a 76% reduction in average *per capita* recruitment, based on independent estimates of the average number of seeds produced per flower head, number of flowers produced per plant, and the proportion of seeds establishing as seedlings from seed addition in and out of rodent exclosures (Table 1). The combined effects of rodent seed predation and herbivory resulted in an overall fivefold increase in adult *T. dubius* populations compared to plants in unprotected plots (Fig. 1). Our population-level results are fairly conservative given that our older rodent exclosures showed population increases that were nearly six times greater than what we observed in newer exclosures, which had only been established for 3 years. Hence, we expect these relative gains in *T. dubius* abundance inside versus outside rodent exclosures will continue to increase over time. We have also observed *T. dubius* attaining extremely high densities in sites such as urban lots with high disturbance and virtually no vertebrate herbivores.

The degree to which exotic plants experience biotic resistance from native generalist consumers will likely depend on their palatability at multiple life stages and their overall life-history strategies. *T. dubius* is a highly palatable plant; its seeds, roots, foliage and flowers are readily eaten by a variety of consumers across North America (Reader 1993; Clements, Upadhyaya & Bos 1999; this study). Because it is a biennial plant that reproduces only by seed, produces large resource-rich flower heads, and relatively few large seeds (Clements, Upadhyaya & Bos 1999), it is both attractive to consumers and also very sensitive to consumer attack at the population level. Consistent with our results, Mittelbach & Gross (1984) showed that rodents aggressively removed *T. dubius* seeds from seed depots in the north-eastern United States, and Reader (1993, 1997) found this species was widely distributed in old fields in eastern Canada but it similarly occurred at low densities and its emergence was strongly limited by rodent seed predation (Reader 1993, 1997). Our study focused on the effects of native herbivores on *T. dubius* in ungrazed grasslands. However, livestock grazing can substantially reduce populations of some exotic invaders (Milchunas, Lauenroth & Chapman 1992). Livestock likely consume *T. dubius* and could contribute to its control through herbivory. However, as we show, *T. dubius* is also very responsive to disturbance, so the net effect of livestock grazing on this species is unclear. Given its high vulnerability to herbivory, *T. dubius*' excellent long-distance dispersal capacity (Clements, Upadhyaya & Bos 1999) may be key to its wide distribution in invaded ranges like North America.

Few studies have examined how plant life-history attributes may render some exotics more or less susceptible to native consumer control (but see Strauss *et al.* 2009 for effects of exotic consumers). Our results suggest that other widespread but weak invaders with traits similar to *T. dubius* may similarly be suppressed in their introduced range. For example, like *T. dubius, Taraxacum officinale* and *Medicago lupulina* are short-lived plants that reproduce only by seed, have relatively large, palatable seeds, and produce palatable foliage (Reader 1992). These species experience high herbivory and granivory (Reader 1992, 1993), and the combination of seed predation and herbivory may be responsible for their low local densities in undisturbed plant communities (Reader & Beisner 1991; Reader 1992, 1997). For example, there is evidence that native floral feeding insects may contribute to control of *Circium vulgare*, a large-seeded exotic biennial (Andersen & Louda 2006). In contrast, species such as *Poa pratensis* and *Hypericum perforatum* produce very small seeds and experience few gains in recruitment when protected from seed predation (Reader 1993; Maron *et al.* 2012). These species also reproduce vegetatively, which buffers them at the population level from negative consumer impacts. As well, *P. pratensis* is highly tolerant to grazing (Del-Val & Crawley 2005). Perhaps as a result, both species commonly reach high local population densities. In general, we might expect that exotic plants that rely only on sexual reproduction, produce relatively few large seeds, have shorter life spans and have limited compensatory responses to herbivory and/or lack physical or chemical defences might be particularly vulnerable to biotic resistance imposed by native consumers (Louda 1995). The effect of life-history traits on susceptibility to native consumers has been elegantly shown for native plants (Louda & Potvin 1995; Louda 1995). The degree to which plants deviate from one or more of these traits should increase their ability to escape or resistance to consumer attack (e.g. MacDougall & Wilson 2007; Eschtruth & Battles 2009; Knight *et al.* 2009). For example, the abundant invader, spotted knapweed (*Centaurea stoebe*) produces relatively large seeds (although smaller than *T. dubius*), which should render it susceptible to seed predation. However, its seeds are avoided by rodents, possibly owing to chemical defences (Pearson, Callaway & Maron 2011). As a result, it escapes biotic resistance from rodent seed predators under conditions where species like *T. dubius* are strongly suppressed (Pearson, Callaway & Maron 2011). Studies that examine consumer effects on multiple exotic plants exhibiting a range of traits could contribute substantially to predicting outcomes of invasions.

Competition is the more commonly studied form of biotic resistance to plant invasions (Levine, Adler & Yelenik 2004). A large body of work indicates that disturbances that reduce plant competition can dramatically improve recruitment and establishment of exotic plants (Mack *et al.* 2000; Paiaro, Mangeaud & Pucheta 2007; Britton-Simmons & Abbott 2008). We similarly found that disturbance strongly increased establishment of *T. dubius*. However, this did not negate the effects of granivory. In fact, in 2011, the overall effect of seed predation and disturbance were fairly comparable (6.6- vs. 6.2-fold increase in seedling recruitment, respectively) and resulted in a strong additive effect which greatly increased seedling recruitment under disturbed conditions when rodents were excluded (Fig. 1). Reader (1993) also found a strong increase in *T. dubius* seedling emergence in response to disturbance in eastern Canada (nearly fourfold), but this effect was completely overshadowed by a 40-fold increase in emergence when seed predators were excluded. A possible explanation for the differing results between studies is that Reader (1993) measured initial seedling emergence while we measured seedling establishment to the end of the growing season. Initial strong effects of seed predation on seedling emergence can diminish through time due to compensatory density dependence as well as density-independent factors such as drought (Edwards & Crawley 1999). However, MacDougall & Wilson (2007) showed that vole seedling herbivory could greatly overshadow effects of disturbance in suppressing recruitment of some weak invaders over time.

While our knowledge regarding population-level responses of exotic plants to native consumers is limited, we know even less about how native competitors and consumers interactively suppress exotics. Many plant traits represent tradeoffs between strategies that confer advantages over competitors versus escape from consumers. For example, larger seed sizes generally favour establishment in the face of plant competition (Turnbull, Rees & Crawley 1999) but also increase plant susceptibility to granivory (Brown & Heske 1990; Reader 1993; Pearson, Callaway & Maron 2011). So how do the relative benefits of such traits relate to biotic resistance and plant recruitment? By examining multiple species with different seed sizes, Reader (1993) showed how the competitive advantages of larger seed sizes can be negated through seed predation. When examining many species representing a large range of seed sizes on these same study sites, we also found that large-seeded species generally recruited better than small-seeded species in the presence of competitors, but were at greater risk of seed predation, while smaller seeded species, especially exotics, responded more strongly to disturbance (Maron *et al.* 2012). These results suggest that the net effect of biotic resistance to plant invasion involves a dynamic interplay between competition and seed predation. As we have shown here for *T. dubius*, Reader (1993) also found that emergence of two species, *M. lupulina* and *Echium vulgare*, was strongly suppressed by both competition and seed predation in an additive manner. Hence, these species might be far more problematic if not for this cumulative biotic resistance effect, and problem populations might be predicted where competition and seed predation are both reduced.

Experimental studies that occur across multiple plant generations are needed to truly quantify the extent to which native consumer-driven reductions in plant fecundity or survival translate to substantive long-term suppression of exotic plant abundance (Maron, Pearson & Fletcher 2010). The current study bolsters a growing body of long-term research addressing effects of native consumers on exotic plants (e.g. Brown & Heske 1990; Detling 1998; Stohlgren *et al.* 1999; Cadenasso, Pickett & Morin 2002; Seabloom *et al.* 2009). Prior long-term studies have shown the full gamut of outcomes from little or no effects of herbivores on exotics (Detling 1998; Stohlgren *et al.* 1999) to herbivore facilitation of exotics (Seabloom *et al.* 2009) to conditional suppression of exotics (Cadenasso, Pickett & Morin 2002). However, most long-term studies involve opportunistic examination of herbivore exclosures initiated for range management purposes, hence the relative roles of the different native and exotic herbivores that are excluded and the specific effects they have on different plant species are not commonly known (Detling 1998; Stohlgren *et al.* 1999; Cadenasso, Pickett & Morin 2002; Seabloom *et al.* 2009).

Since exotic invading plants usually establish nascent populations from seed, seed survival and seedling establishment are particularly important for successful invasions, and pre- and post-dispersal seed predation and seedling herbivory may have strong effects on certain invading plants (Brown & Heske 1990; MacDougall & Wilson 2007; Strauss *et al.* 2009; Pearson, Callaway & Maron 2011; Maron *et al.* 2012). An increasing number of studies show that native granivores readily consume seeds of many exotic plants and in some cases may prefer them over native plant seeds (Inouye, Byers & Brown 1980; Blaney & Kotanen 2001; Vilá & Gimeno 2003; Lambrinos 2006; Shahid, Garneau & McCay 2009; Carrillo-Gavilan, Lalague & Vilá 2010; Alba-Lynn & Henk 2010), and a few studies have shown that such seed predation can impede recruitment of exotics (Reader 1993; Nunez, Simberloff & Relva 2008; Pearson, Callaway & Maron 2011). Reader's (1993) work, although not originally directed at questions about exotic species invasion, was an important first step in illustrating how seed predation by native consumers can suppress recruitment for numerous species of exotic plants. Recent work suggests seedling herbivory could play a similarly important role (MacDougall & Wilson 2007). It may be that cryptic consumers play a larger role in imposing biotic resistance than has been appreciated (MacDougall & Wilson 2007; Strauss *et al.* 2009). However, since population-level compensatory factors can alleviate strong effects that consumers can have on seed availability and even increased seedling recruitment (Garren & Strauss 2009; Swope & Parker 2010; Ortega *et al.* 2012), understanding the full implications of such biotic resistance ultimately requires multi-generation studies that document impacts of consumers on the longer-term abundance of exotics (e.g. Brown & Heske 1990; current study).

Conclusion

The key finding from this study is that high levels of rodent florivory and post-dispersal seed predation can have substantial longer-term impacts on exotic plant abundance over large areas. Our results confirm that native consumers may provide an important ecosystem service by helping to suppress certain exotic plants (Brown & Heske 1990; Cadenasso, Pickett & Morin 2002; Parker, Burkepile & Hay 2006; MacDougall & Wilson 2007). We suggest that the general framework developed by Louda (1995) for understanding how plant traits relate to population-level susceptibility to consumer attack may help predict how consumer biotic resistance influences exotic plant invasions. Understanding why some exotics remain weak invaders, while others obtain high abundance and drive strong ecological impacts remains a key unresolved area within ecology (Vilá *et al.* 2011). Future studies examining how particular traits of exotics relate to their susceptibility to native consumer impacts not just on plant performance but also on invader abundance could greatly improve our ability to predict invasion outcomes. As well, such studies could offer insights for how best to manage for biotic resistance as an ecosystem service.

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References

Alba-Lynn, C. & Henk, S. (2010) Potential for ants and vertebrate predators to shape seed-dispersal dynamics of the invasive thistles *Cirsium arvense* and *Carduus nutans* in their introduced range (North America). *Plant Ecology*, **210**, 291–301.

Andersen, C.P. & Louda, S.M. (2006) Abundance of and floral herviroy on exotic bull thistle versus native tall thistle in western Tallgrass Prairie. (eds J. T. Springer & E.C. Springer). *Prairie Invaders: Proceedings of the 20th North American Prairie Conference*. **20**, 33–50.

Blaney, C.S. & Kotanen, P.M. (2001) Post-dispersal losses to seed predators: an experimental comparison of native and exotic old field plants. *Canadian Journal of Botany*, **79**, 284–92.

Bossard, C.C. & Rejmanek, M. (1994) Herbivory, growth, seed production, and resprouting of an exotic invasive shrub. *Biological Conservation*, **67**, 193–200.

Bricker, M., Pearson, D.E. & Maron, J.L. (2010) Small mammal seed predation reduces forb recruitment and abundance in semi-arid grasslands. *Ecology*, **91**, 85–92.

Britton-Simmons, K.H. & Abbott, K.C. (2008) Short- and long-term effects of disturbance and propagule pressure on a biological invasion. *Journal of Ecology*, **96**, 68–77.

Brown, J.H. & Heske, E.J. (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science*, **250**, 1705–7.

Cadenasso, M.L., Pickett, S.T.A. & Morin, P.J. (2002) Experimental test of the role of mammalian herbivores on old field succession: community structure and seedling survival. *Journal of the Torrey Botanical Society*, **129**, 228–37.

Carrillo-Gavilan, M.A., Lalague, H. & Vilá, M. (2010) Comparing seed removal of 16 pine species differing in invasiveness. *Biological Invasions*, **12**, 2233–42.

Clements, D.R., Upadhyaya, M.K. & Bos, S.J. (1999) The biology of Canadian weed. 110. Tragopogon dubius Scop., Tragopogon pratensis L., and Tragopogon porrifolius L. *Canadian Journal of Plant Science*, **79**, 153–63.

Crawley, M.J. (1989) Insect herbivores and plant population dynamics. *Annual Review of Entomology*, **34**, 531–64.

Cushman, J.H., Lortie, C.J. & Christian, C.E. (2011) Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. *Journal of Ecology*, **99**, 524–31.

Del-Val, E. & Crawley, M.J. (2005) Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight British grassland species *Journal of Ecology*, **93**, 1005–16.

Detling, J.K. (1998) Mammal herbivores: ecosystem-level effects in two grassland national parks. *Wildlife Society Bulletin*, **26**, 438–48.

Edwards, G.R. & Crawley, M.J. (1999) Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia*, **118**, 288–96.

Elton, C. (1958) *The Ecology of Invasions by Animals and Plants*. The University of Chicago Press, Chicago, IL.

Eschtruth, A.K. & Battles, J.J. (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagules pressure in exotic plant invasion. *Ecological Monographs*, **79**, 265–80.

Garren, J.M. & Strauss, S.Y. (2009) Population-level compensation by an invasive thistle thwarts biological control from seed predators. *Ecological Applications*, **19**, 709–21.

Han, X.M., Dendy, S.P., Garrett, K.A., Fang, L. & Smith, M.D. (2008) Comparison of damage to native and exotic tallgrass prairie plants by natural enemies. *Plant Ecology*, **198**, 197–210.

Hill, S.B. & Kotanen, P.M. (2009) Evidence that phylogenetically novel non-indigenous plants experience less herbivory. *Oecologia*, **161**, 581–90.

Howe, H.F., Zorn-Arnold, B., Sullivan, A. & Brown, J.S. (2006) Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology*, **87**, 3007–13.

Inouye, R.S., Byers, G.S. & Brown, J.H. (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology*, **61**, 1344–51.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **4**, 164–70.

Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J. & Kalisz, S. (2009) Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal*, **29**, 110–6.

Lambrinos, J.G. (2006) Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. *Oecologia*, **147**, 327–34.

Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–89.

Liu, H., Stiling, P. & Pemberton, R.W. (2007) Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners *Biological Invasions*, **9**, 773–81.

Louda, S.M. (1995) Effects of seed predation on plant regeneration. *Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia*. (eds. M.T.K. Arroyo, P.H. Zedler & M.D. Fox), pp. 311–344. Springer-Verlag, New York, NY.

Louda, S.M. & Potvin, M.A. (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology*, **76**, 229–45.

MacDougall, A.S. & Wilson, S.D. (2007) Herbivory limits recruitment in an old-field seed addition experiment. *Ecology*, **88**, 1105–11.

Mack, R.N. (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation*, **78**, 101–21.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.

Maron, J.L. & Kauffman, M.J. (2006) Habitat-specific impacts of multiple consumers on plant population dynamics. *Ecology*, **87**, 113–24.

Maron, J.L. & Pearson, D.E. (2011) Vertebrate predators have minimal cascading effects on plant production or seed predation in an intact grassland ecosystem. *Ecology Letters*, **14**, 661–9.

Maron, J.L., Pearson, D.E. & Fletcher, R. Jr (2010) Counter-intuitive effects of large-scale predator removal on a mid-latitude rodent community. *Ecology*, **91**, 3719–28.

Maron, J.L., Pearson, D.E., Potter, T. & Ortega, Y.K. (2012) Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. *Journal of Ecology*, doi: 10.1111/j.1365-2745.2012.02027.x (in press).

McNaughton, S.J. (1983) Compensatory plant growth as a response to herbivory. *Oikos*, **40**, 329–36.

Milchunas, D.G., Lauenroth, W.K. & Chapman, P.L. (1992) Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia*, **92**, 520–31.

Mittelbach, G.G. & Gross, K.L. (1984) Experimental studies of seed predation in old-fields. *Oecologia*, **65**, 7–13.

Nunez, M.A., Simberloff, D. & Relva, M.A. (2008) Seed predation as a barrier to alien conifer invasions. *Biological Invasions*, **10**, 1389–98.

Orrock, J.L., Witter, M.S. & Reichman, O.J. (2008) Apparent competition with an exotic plant reduces native plant establishment. *Ecology*, **89**, 1168–74.

Ortega, Y.K. & Pearson, D.E. (2005) Strong versus weak invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications*, **15**, 651–61.

Ortega, Y.K., Pearson, D.E., Waller, L.P., Sturdevant, N.J. & Maron, J.M. (2012) Population-level compensation impedes biological control of an invasive forb and indirect release of a native grass. *Ecology*, **93**, 783–92.

Ostfeld, R.S., Manson, R.H. & Canham, C.D. (1997) Effects of rodents on survival of tree seeds and seedlings in invading old fields. *Ecology*, **78**, 1531–42.

Paiaro, V., Mangeaud, A. & Pucheta, E. (2007) Alien seedling recruitment in response to altitude and soil disturbance in the mountain grasslands of central Argentina. *Plant Ecology*, **193**, 279–91.

Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459–61.

Pearson, D.E., Callaway, R.M. & Maron, J.L. (2011) Biotic resistance via granivory: establishment by invasive, naturalized and native asters reflects generalist preference. *Ecology*, **92**, 1748–57.

Peart, D.R. (1989) Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonization. *Journal of Ecology*, **77**, 267–89.

Pierson, E.A. & Mack, R.N. (1990) The population biology of *Bromus tectorum* in forests: distinguishing the opportunity for dispersal from environmental restriction. *Oecologia*, **84**, 519–25.

Reader, R.J. (1992) Herbivory, competition, plant mortality and reproduction on a topographic gradient in an abandoned pasture. *Oikos*, **65**, 414–8.

Reader, R.J. (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology*, **81**, 169–75.

Reader, R.J. (1997) Potential effects of granivores on old field succession. *Canadian Journal of Botany*, **75**, 2224–7.

Reader, R.J. & Beisner, B.E. (1991) Species-dependent effects of seed predation and ground cover on seedling emergence of old-field forbs. *American Midland Naturalist*, **126**, 279–86.

SAS Institute (2009). *SAS/STAT User's Guide, Version 9.2*. SAS Institute Inc., Cary, NC.

Seabloom, E.W., Borer, E.T., Martin, B.A. & Orrock, J.L. (2009) Effects of long-term consumer manipultaions on invasion in oak savanna communities. *Ecology*, **90**, 1356–65.

Shahid, A., Garneau, D.E. & McCay, T.S. (2009) Selection of seeds of common native and non-native plants by granivorous rodents in the northeastern United States. *American Midland Naturalist*, **162**, 207–12.

Stohlgren, T.J., Binkley, D., Chong, G.W., Klakhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.

Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*, **14**, 179–85.

Strauss, S.Y., Stanton, M.L., Emery, N.C., Bradley, C.A., Carleton, A., Dittrich-Reed, D.R. *et al.* (2009) Cryptic seedling herbivory by nocturnal introduced generalists impacts survival, performance of native and exotic plants. *Ecology*, **90**, 414–29.

Swope, S.M. & Parker, I.M. (2010) Widespread seed limitation affects plant density but not population trajectory in the invasive plant *Centaurea solstitialis*. *Oecologia*, **164**, 117–28.

Turnbull, L.A., Rees, M. & Crawley, M.J. (1999) Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology*, **87**, 899–912.

Vilá, M. & D'Antonio, C.M. (1998) Fruit choice and seed dispersal of invasive vs. noninvasive *Carpobrotus* (Aizoaceae) in coastal California. *Ecology*, **79**, 1053–60.

Vilá, M. & Gimeno, I. (2003) Seed predation of two alien Opuntia species invading Mediterranean communities. *Plant Ecology*, **167**, 1–8.

Vilá, M., Espinar, J.L., Hedjda, M., Hulme, P.E., Jarošik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–8.

Williamson, M. (1996) *Biological Invasions*. Chapman & Hall. NY.

Zwolak, R., Pearson, D.E., Ortega, Y.K. & Crone, E.E. (2010) Fire and mice: seed predation moderates fire's influence on conifer recruitment. *Ecology*, **91**, 1124–31.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Graphic of experimental design.