ORIGINAL PAPER

Rodent seed predation as a biotic filter influencing exotic plant abundance and distribution

D. E. Pearson · J. L. Hierro · M. Chiuffo · D. Villarreal

Abstract Biotic resistance is commonly invoked to explain why many exotic plants fail to thrive in introduced ranges, but the role of seed predation as an invasion filter is understudied. Abiotic conditions may also influence plant populations and can interact with consumers to determine plant distributions, but how these factors jointly influence invasions is poorly understood. In central Argentina's Caldenal savannas, we experimentally examined how seed predation and water availability influenced recruitment/establishment of nine exotic plant invaders over 2 years. We then explored how seed predation patterns related to invasion patterns. Excluding rodent seed predators dramatically increased seedling recruitment for eight of nine exotic species (by 100–300 % in most cases) and increased young/adult plant abundance for four species in one or both years. Adding water to ameliorate drought tended to increase seedling numbers for most species, but these trends were not significant. Vegetation surveys revealed that exotic plant richness was 50 % lower in matrix habitat compared with disturbed roadsides and that cover of the two most aggressive invaders, which were both strongly suppressed by seed predation, was 75–80 % lower in matrix than roadside habitats. Seed offerings indicated seed removal by rodents was 11 times greater in intact matrix habitat compared with roadsides. Rodent seed predation represents a significant source of biotic resistance to plant invasions. Ubiquitous disturbances such as road construction can disrupt this filter. The widely recognized role that disturbance plays in facilitating invasions, which is largely attributed solely to reduced plant competition, may also arise from disruption of top–down controls.

Keywords Biotic resistance · Road disturbance · Plant recruitment · Seed predation · Water addition

D. E. Pearson (✉)
Rocky Mountain Research Station, U.S.D.A. Forest Service, Missoula, MT 59801, USA
e-mail: dpearson@fs.fed.us

D. E. Pearson
Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

J. L. Hierro · M. Chiuffo
INCITAP (CONICET-UNLPam), Av. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina

J. L. Hierro · D. Villarreal
Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Av. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina

Introduction

Most exotic plants that successfully traverse the world's oceans to reach new *terra firma* fail to establish or thrive in their new ranges (Williamson and Fitter 1996; Mack 1996). Hence, an important question for both understanding invasions and for

better managing natural defenses against invaders is, "What factors limit the establishment and proliferation of exotic species?" The primary hypothesis proposed to explain why many invaders may fail to thrive in recipient communities is the biotic resistance hypothesis (Elton 1958; Mitchell and Power 2003; Parker et al. 2006). This hypothesis states that invading species may encounter varying degrees of resistance from biotic interactions such as competition, predation, and parasitism, which can impede their ability to establish and proliferate (Elton 1958). Studies of biotic resistance to plant invasions have historically focused on competitive interactions (Levine et al. 2004). Although consumer effects are increasingly recognized as a potentially important source of biotic resistance to plant invasions (Parker et al. 2006), the bulk of this work has focused on consumers acting as herbivores. Yet, some of the best documented cases of consumer effects on native plant populations and communities derive from studies illustrating the importance of seed predators in limiting plant recruitment (Louda 1982, 1983; Brown and Heske 1990; Maron and Kauffman 2006). For terrestrial plants, invaders generally arrive as seeds which must survive, germinate, and establish nascent plant populations. Additionally, seeds are often the primary mechanism allowing invasions to progress beyond the initial bulkhead. Hence, seed survival and seedling establishment are critical stages for successful colonization and expansion of invading plant populations.

Post-dispersal seed predation by rodents can substantially impact native plant recruitment (Reader 1993; Ostfeld et al. 1997; Edwards and Crawley 1999; Orrock et al. 2008; Pearson and Callaway 2008; Zwolak et al. 2010), and a few studies show that reduced recruitment from post-dispersal seed predation can affect adult plant population density (Maron and Kauffman 2006), plant community structure (Brown and Heske 1990), and plant distributions (Bartholomew 1970; Louda 1983). However, only a handful of studies have examined the effects of rodent seed predation on exotic plant invasions. These studies indicate that rodents can affect recruitment and establishment of exotics, particularly for larger-seeded species (Reader 1993; Nuñez et al. 2008; Pearson et al. 2011, 2012; Maron et al. 2012). Such rodent seed-predation can contribute to long-term and widespread reductions of exotic plant populations (Pearson et al. 2012), which can have community-level ramifications

as shown by long-term rodent exclusion studies in the southwestern US where exotics were among the species showing strongest population increases in response to rodent exclusion (Brown and Heske 1990; Allington et al. 2013). These studies suggest that rodents may present a significant source of biotic resistance via seed predation that could help to determine exotic plant abundance and distributions within invaded ranges and that seed size may be one important factor influencing this filter (Brown and Heske 1990; Reader 1993; Nuñez et al. 2008; Pearson et al. 2011, 2012; Maron et al. 2012). However, the general importance of this filter in affecting plant invasions across systems is unknown, and we know virtually nothing about how this filter may vary temporally or spatially as a function of abiotic drivers such as disturbance and precipitation.

One aspect of invasion resistance implicitly not addressed in the biotic resistance hypothesis is abiotic resistance. It is generally accepted that certain environmental conditions strictly preclude many prospective invaders (e.g., tropical species cannot invade arctic tundra due to physiological constraints), though this question is rarely formally tested (Mack 1996). Yet many invaders undoubtedly become established in environments where conditions may fluctuate temporally from optimal to hostile. Such situations may serve as conditional controls over invader abundance rather than outright barriers, and they may also influence biotic resistance. Ultimately, the interaction between biotic and abiotic factors may determine the distribution and local abundance of plants by controlling natural enemy abundance or affecting plant life history transitions in ways that influence natural enemy efficacy (Louda 1983; Louda and Rodman 1996; DeWalt et al. 2004; Shea et al. 2005; Maron and Crone 2006). Recent studies show that temporally variable abiotic conditions such as fluctuating water inputs may be as important as biotic factors in affecting exotic plant population dynamics (Carrillo-Gavilán et al. 2012; Ortega et al. 2012; Allington et al. 2013). Because seed predation affects seedling emergence and establishment, stages when plants are particularly sensitive to water limitation, it is likely that seed predation may interact with precipitation inputs such that the effects of seed predation are important in wet years when they carry forward to later plant stages, but seed predation effects may be overwhelmed by abiotic constraints when

precipitation is low and most seedlings that survive predation die from abiotic stress. The role of abiotic conditions and the interaction of biotic and abiotic processes in affecting plant invasions is a potentially important but underdeveloped area of research.

Here we experimentally examine the independent and interactive effects of; (1) post-dispersal seed predation by rodents; and (2) water addition for ameliorating drought conditions on recruitment and establishment of nine exotic plant species in the Caldenal savanna of central Argentina. We also examine how spatial variation in seed predation rates relates to local patterns of exotic plant abundance to assess whether observed impacts of seed predation on recruitment might help explain spatial patterns of exotic plant abundance.

Materials and methods

Study system

We located our study in Parque Luro Provincial Reserve, a 7,500-ha provincial park 30 km south of Santa Rosa, in La Pampa Province, central Argentina (36°56′4.29″S, 64°13′51.64″W). Mean annual temperature is 15.4 °C (1941–1990). Mean annual precipitation is 634 mm (1911–2010 for Santa Rosa, 30 km S to Parque Luro, Vergara, UNLPam, *unpublished data*) and occurs mostly during the spring–summer (October–March). Mean precipitation during the 2-year study was 375 mm in 2009 and 705 mm in 2010. The park lies within the Caldenal vegetation type, a forest/savanna habitat dominated by the tree *Prosopis caldenia* (Cano 1980). We selected the park because it contains largely intact native vegetation communities, but has extensive patches of plant invasion, particularly along roads, fire breaks, and other heavily disturbed areas. There is no domestic grazing or hunting in the park. Large herbivores present include *Sus scrofa*, *Cervus elaphus*, and *Rhea americana*. We focused on open grassland–savanna habitat where understory vegetation was dominated primarily by native grasses such as *Nassella tenuissima*, *Piptochaetium naposteanse*, and *Poa ligularis*, with *Solanum* spp. and *Baccharis* spp. among the more common native forbs.

We examined the following nine exotic species because they represent a range of invasiveness: *Carduus thoermerii*, *Centaurea solstitialis*, *Chenopodium album*, *Diplotaxis tenuifolia*, *Hypochaeris radicata*, *Rumex crispus*, *Salsola kali*, *Taraxacum officinale*, and *Tragopogon dubius*. Recent surveys (Pearson et al. unpubl data) indicate that these species represent 15 % of 62 of the exotics in the area and range from highly invasive weeds that occur commonly and at high local density across the region (e.g., *D. tenuifolia*, *C. solstitialis*, *C. album*) to more naturalized species that occur uncommonly and at low local abundance (e.g., *H. radicata*, *T. officinale, R. crispus*). The study species disperse seeds mid-late summer, emerge in the fall, and flower in late spring-early summer (Troiani and Steibel 2008). Exceptions in this phenological pattern are *C. album* and *S. kali,* which disperse seeds in the fall, emerge in late winter-early spring, and flower in late summer. Although two species, *C. solstitialis* and *C. album* are known to produce seeds with delayed germination (Hierro et al. 2009; Estanga-Mollica unpubl data), a large proportion of the seeds produced annually by these and the other species used in our study readily germinate upon watering under optimal greenhouse conditions (Chiuffo unpubl data).

Small mammal species that have been documented in the general area and are known to consume seeds as part or most of their diet include *Akodon azarae*, *Calomys musculinus*, *Calomys laucha*, *Eligmodontia typus*, *Graomys griseoflavus*, *Microcavia australis*, *Oryzomys flavescens*, and *Thylamys pusillus* (Ellis et al. 1998; Giannoni et al. 2005). Some of these small mammals are also insectivorous and herbivorous. Granivorous birds and invertebrates are also present in the system, but this study targeted small mammals (we addressed invertebrates in another study). Rodent populations tend to peak from December to March (Mills et al. 1992).

Rodent exclusion and water addition experiments

We evaluated effects of rodents on exotic plant recruitment by adding seeds of focal species to cages that either allowed or precluded rodent access. Cages were constructed of 0.5 cm by 0.5 cm wire mesh that was 40 cm × 40 cm wide and 20 cm deep with tops that opened and closed to access the contents. Cages were placed in the ground by digging a 10 cm deep hole, inserting the cage, and refilling it 10 cm with the excavated soil. Thus, soils were disturbed and free of

established plants prior to seed addition. Cages were randomly assigned to rodent access (open) or no access (closed) in each pair. Open cages had two 10 cm wide × 7 cm high holes cut into each side just above the ground surface to allow rodent entry, while closed cages were left intact. Both treatments precluded entry by birds in this system, but ants and small invertebrates had full access to both treatments. Cages were set out in three replicate pairs (one open and one closed cage in each pair) at each of 10 locations. Paired cages were placed 0.5 m apart, and pairs were spaced 30–60 m apart at each site. Minimum distance between sites was 1 km. Cage locations were placed ≥2 m from exotic plants; sites were usually tens of meters from exotic plants.

Seeds were collected from wild plants around the study area as they became mature for each species. Fifty seeds per species were added to each cage in January 2009. The exceptions were the two later fruiting species, *C. album* and *S. kali*, which were added in April and May, respectively. In all cases, only seeds that looked healthy and filled with an embryo were used in the experiments. Seeds were spread evenly across cage floors with a 3 cm-wide boundary from cage walls and patted down so they were set into the soil surface but plainly visible. Sites were visited approximately every 2 weeks from March until early November 2009, and the total number of live seedlings per species in each cage was counted on each visit. On the last visit, the number of young/adult and flowering plants was counted.

Water inputs can be highly variable in this system and an important limiting factor for plant recruitment (Hierro et al. 2009). To examine how water inputs affected exotic plant recruitment, we repeated the above experiment in 2010 except that we added a fourth pair of cages to each site and randomly assigned two of each of the cage pairs to a water treatment (either ambient conditions or water addition). Ambient water treatments experienced natural drought (Fig. 1). Water addition treatments received water as needed to ensure mean monthly precipitation inputs (Fig. 1, based on the 95 years average 1911–2006 for Santa Rosa et al. *unpublished data*). These plots received a maximum of 1–2 L of water per cage per application to ensure water was absorbed in the soil and did not run off. Watering began 29 April when precipitation first fell below normal and continued as needed (when precipitation fell below normal) until 30 November,
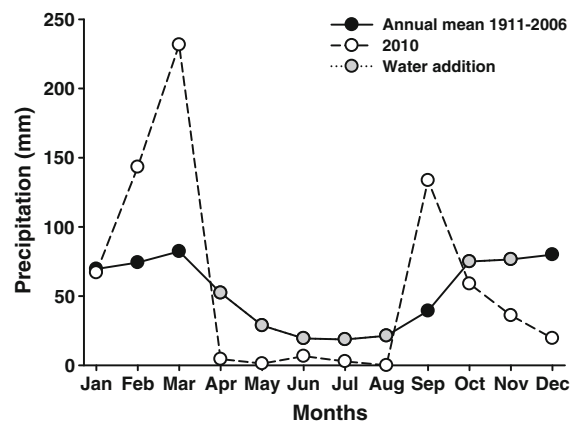

Fig. 1 Monthly mean annual precipitation, 2010 precipitation, and 2010 water addition levels for the study area and experimental plots in Parque Luro, central Argentina. Annual mean precipitation shows up as *grey filled circles* where water addition levels overlap

which is the end of the growing season for most of the species. Seed addition occurred in 2010 in early February. Plots were visited monthly February–December to count seedlings (early periods) and young/adult plants (later periods), because the 2009 surveys indicated monthly visits were sufficient to quantify emergence. Data were collected as two phases: emergence (period when the seedlings first emerged with cotyledons to first leaves) and establishment at the end of the season (surviving young/mature/flowering plants). The timing for each species differed based on phenology. Herbivory was also quantified by classifying plants as showed signs of feeding or not, but this was minimal and so is not reported. All exotics used were already established in the region, and only seeds from these naturalized populations were used. At the end of the experiment each year, all plants were destroyed before seed set. Sites were monitored into 2013 to ensure no exotic plants established from the experiment.

Vegetation patterns

Vegetation patterns in the park suggested that exotic plant abundance was dramatically higher in disturbed areas, particularly along roadsides. To quantify this effect, vegetation was surveyed when plants were at peak biomass at the end of the growing season in November and December, 2007 in roadside disturbance zones and within the Caldenal savanna (Chiuffo

2009). Vegetation was sampled along 14.5 m wide belt transects that extended from within the disturbance zone created by the road-cut to 100 m into the matrix habitat (defined as the predominant grassland–savanna habitat that was dissected by the roads), perpendicular to the road. Sampling was conducted at five locations along each transect, two of which were in the road-cut (0 m, which is the road edge, and five meters from the road edge, which was always several meters from the matrix habitat) and three of which were within the matrix habitat (25, 50, and 100 m from the road edge). At each sampling location, five 0.25 m^2 quadrats were placed at 3 m intervals parallel to the road. All species were identified in each plot and percent cover was estimated for each plant species in each quadrat. Three such transects were stratified across the park.

Seed predation patterns

To determine whether large disturbances like road construction disrupted rodent seed predation, we compared rodent seed removal between undisturbed Caldenal savanna (matrix habitat) and recently graded roadsides from February to April 2010. We focused on roads that had been graded within the past year to examine conditions associated with initial plant establishment following disturbance. We set out *Phalaris canariensis* seeds (a non-native, highly palatable, pet-food seed) on the surface of clean sand in 14-cm dia. Petri trays (80 seeds per tray). Trays were set out in pairs, with one tray placed 20 m from the road edge into the matrix habitat and the other tray placed within the road disturbance zone between the roadbed and the matrix vegetation (usually ≥5 m from the matrix edge). Each tray was covered with a 40 cm × 40 cm square of 0.5 cm × 0.5 cm wire mesh placed over the tray in an arc that peaked 10 cm above the ground to prevent birds from accessing the trays (ground foraging birds in the area are predominantly doves and larger). Ten such pairs were set out at each of ten sampling sites located along roadways across the park with 100 m between each sample pair within a site and 1 km between each sampling site. Trays were set out for 4–5 days sessions (three to four transect pairs at a time), after which remaining seeds were collected and counted. Ants occasionally were able to access the dishes, but ant seed removal was distinguishable from rodent seed

removal by the absence of husked seeds, tracks, and feces left by rodents, and the presence of ant tracks and dead ants trapped in the trays. Stations accessed by ants were excluded from analyses (11 of 100 pairs).

Statistical analyses

Exotic plant recruitment (number of live seedlings per plot) was examined using MANOVA (PROC GLM SAS version 9.3; SAS Institute 2009). The model for the 2009 data included rodent treatment (access or no access) as a fixed factor and site as a random factor, while the model for 2010 data also included water treatment (ambient drought vs water addition) and its interaction with rodent treatment as fixed effects. Cage pairing was incorporated as a blocking factor. Average emergence (February–May) was used as the response because some seedlings died and new ones emerged across sampling periods. Hence, this variable represents the average effect of rodents on seedling recruitment. We used similar models to examine rodent exclusion effects on the number of mature or flowering plants counted at the end of the growing season during the final sampling period each year. In this analysis, we ignored the 2010 watering treatment (it was not significant), but examined between year effects by treating rodent exclusion, year, and year by rodent exclusion as fixed factors. Four species (nearly half) had sufficient abundance at the end of the season for this analysis. We transformed the seedling and mature plant abundance data using natural log transformations to meet assumptions of multivariate normality. We used linear regression to examine the relationship between seed mass and rodent effect on recruitment (average number of seedlings emerging) in 2009. We compared the number of seeds removed from trays in matrix and roadside habitats using a generalized linear mixed model (PROC GLIMMIX) fitted to a negative binomial distribution, with habitat (matrix vs roadside) as the fixed factor, station pairing as a blocking factor, and site as a random factor. We used similar models to examine exotic species richness and cover treating habitat (matrix = all plots within the matrix versus roadside = all plots in the disturbance zone) as the fixed factor, and site and replicates within site and strata as random factors. The negative binomial distribution was used for the species richness data and the beta distribution was used for the percent cover data.
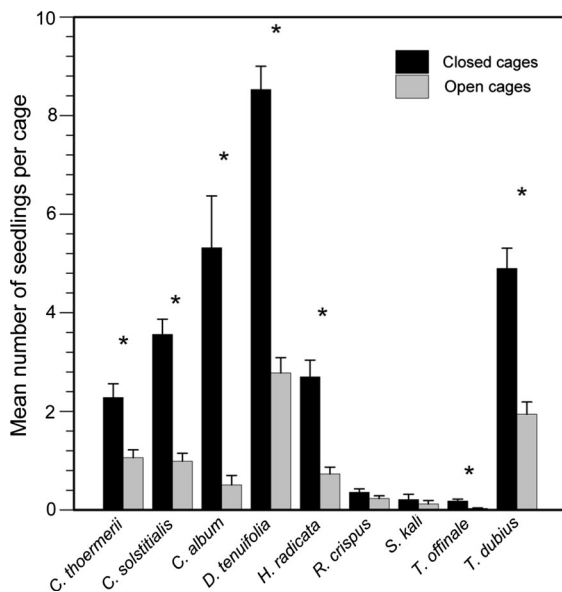
Fig. 2 Effects of rodent exclusion on seedling recruitment for nine exotic plants in 2009 in Caldenal savannas of central Argentina (mean ± SE). Open cages allow rodent access while closed cages preclude rodents. *Asterisks* indicate significant differences between pairings at $P = 0.05$

Results

Emergence of all but one exotic species increased substantially (doubled or more) in one or both years when seeds were protected from rodent seed predation (Figs. 2, 3). In 2009, the overall MANOVA for rodent effect was highly significant ($F_{9,50} = 5.98$, $P < 0.001$), with seedling emergence increasing substantially for seven of the nine species when rodents were excluded (Table 1). In 2010, the overall MANOVA for rodent effect was also highly significant ($F_{9,68} = 5.90$, $P < 0.001$), but the water treatment was not significant ($F_{9,68} = 0.51$, $P = 0.86$) and there was no significant interaction between rodent exclusion and water addition ($F_{9,68} = 0.51$, $P = 0.866$). In 2010, six of the nine species showed significant increases in emergence in response to rodent exclusion and a seventh species, *C. thoermerii*, showed a marginally significant increase (Table 2). However, none of the individual species showed a significant increase in emergence in response to water treatments or interactions between water treatments and rodent exclusion (Table 2). Seed size (Table 1) was not significantly correlated with the effect of seed predation on seedling emergence ($F = 0.44$; $P = 0.529$;

$r^2 = 0.059$), i.e. the difference in emergence between seed predator-exclusion and seed predator-access cages.

Rodent effects on seedling recruitment carried through to affect abundance of mature and flowering plants by the end of the season, though results varied by year for some species (Fig. 4). Rodent exclusion significantly increased abundance of mature and flowering plants of the annual *C. solstitialis* ($F_{1,136} = 4.57$, $P = 0.034$) with greater abundance in 2009 than in 2010 ($F_{1,136} = 110.73$, $P < 0.001$), and no significant year by rodent exclusion interaction ($F_{1,136} = 2.05$, $P = 0.155$). End-of-season abundance of the perennial *D. tenuifolia* was higher in rodent exclusion cages ($F_{1,136} = 17.11$, $P < 0.001$), higher in 2009 than in 2010 ($F_{1,136} = 42.40$, $P < 0.001$), and the rodent effect was much stronger in 2009 than in 2010 ($F_{1,136} = 12.59$, $P < 0.001$). Final abundance of the annual *S. kali* was not significantly higher in rodent exclusion cages overall ($F_{1,136} = 0.99$, $P = 0.322$), nor did its abundance differ between years ($F_{1,136} = 0.23$, $P = 0.631$), but rodent exclusion significantly increased plant abundance in 2010 compared to 2009 ($F_{1,136} = 10.62$, $P = 0.001$). Final abundance of mature/flowering *T. dubius* was significantly greater in rodent exclusion cages compared with control cages ($F_{1,136} = 8.77$, $P = 0.004$) but this effect was driven mostly by stronger effects in 2010 ($F_{1,136} = 3.34$, $P = 0.070$). *T. dubius* abundance did not differ between years ($F_{1,136} = 1.87$, $P = 0.174$).

Exotic species richness was significantly higher along roadsides than within matrix habitat ($F_{1,11} = 10.09$, $P = 0.009$; Fig. 5b). Mean percent cover was significantly higher in roadside than matrix habitats for *D. tenuifolia* ($F_{1,11} = 8.99$, $P = 0.012$; Fig. 5c) and *C. solstitialis* ($F_{1,11} = 17.12$, $P = 0.002$; Fig 5d), the two most invasive study species and the only two which were common enough in both vegetation types to compare between habitats. The number of seeds removed from seed offering trays was about 11 times lower along the roadsides compared to within the matrix habitat ($F_{1,160} = 21.86$, $P < 0.001$; Fig. 5a).

Discussion

Although biotic resistance is commonly invoked to explain why most exotics fail to establish or thrive in invaded systems, the role that native generalist seed

Fig. 3 Effects of rodent exclusion and water addition (to ameliorate drought) on seedling recruitment for nine exotic plants in 2010 in Caldenal savannas of central Argentina (mean ± SE). Asterisks indicate significant differences between pairings for the rodent treatment at $P = 0.05$. No water treatment effects or interactions were significant. Note that the scale for *T. dubius* differs from the others due to very high recruitment for this species
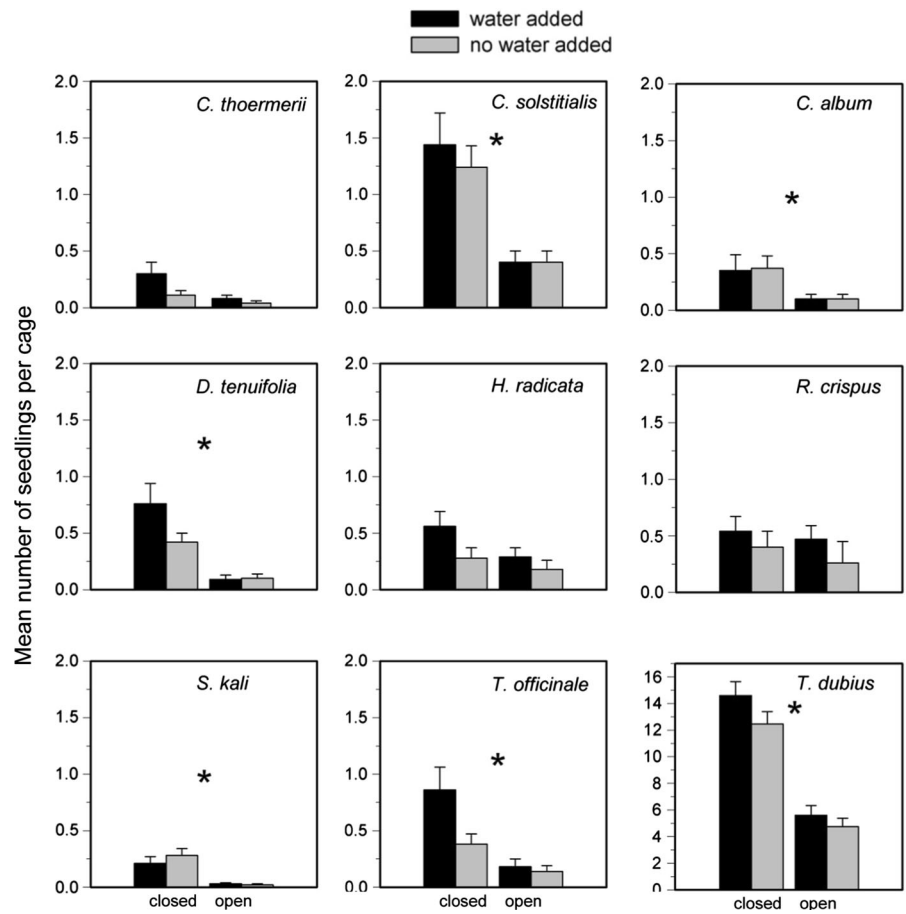
predators play in suppressing exotic plants is poorly understood. We found that rodents represent a substantial source of biotic resistance to exotic plants in Caldenal savannas of central Argentina. Precluding rodent access to seeds dramatically increased recruitment of eight of nine exotic species that we examined in one or both years of the study. The effects of rodents in suppressing recruitment resulted in substantial reductions in final abundance of young and adult flowering plants for nearly half of the species studied. We also found that rodent seed predation pressure differed substantially in relation to large-scale disturbances; seed predation was 11 times lower along roadsides compared with adjacent undisturbed matrix habitat. Invader success followed a reciprocal pattern of abundance, with higher overall invader richness in the roadsides and greater abundance of two of the most aggressive invaders along disturbed roadsides as compared with adjacent matrix habitats. Although this pattern of invader success undoubtedly reflects

differences in plant competition between disturbed roadsides and matrix habitat (e.g., Hierro et al. 2011), our results suggest that rodent seed predation may contribute substantially to these patterns as well. Contrary to our expectation, water inputs did not significantly influence exotic plant recruitment or the strength of rodent seed predation effects for any of the species we examined.

Numerous studies have quantified removal of exotic seeds by granivores in a variety of systems (Blaney and Kotanen 2001; Vilá and Gimeno 2003; Shahid et al. 2009; Alba-Lynn and Henk 2010; Carrillo-Gavilán et al. 2010, 2012), but few have examined how seed predation relates to recruitment and establishment of exotic plants (Pierson and Mack 1990; Reader 1993; Nuñez et al. 2008; Pearson et al. 2011, 2012; Maron et al. 2012). Making the link between seed predation and its effects on plant establishment is crucial to understanding how this filter might affect plant community composition given

Table 1 Rodent exclusion effects on seedling emergence in 2009 based on MANOVA for nine exotic plant species

Species	Life-history strategy	Seed mass	Effect size	F	P
C. album	A	0.0005	146	5.51	**0.022**
C. solstitialis	A	0.0017	174	49.75	**<0.001**
C. thoermerii	B	0.0037	80	8.36	**0.005**
D. tenuifolia	P	0.0002	221	27.95	**<0.001**
H. radicata	P	0.0006	263	29.43	**<0.001**
R. crispus	P	0.0014	59	2.28	0.137
S. kali	A	0.0012	11	0.12	0.735
T. dubius	A/B	0.0090	133	15.94	**<0.001**
T. officinale	P	0.0003	133	4.13	**0.047**

Seed masses (g) and life history strategy (A = annual, B = biennial, P = perennial) are also given along with the percent increase in emergence in the absence of small mammals (effect size). In all cases df = 1,58

Bold values indicate the p-values that are significant at P < 0.05 level

Table 2 Effects of rodent exclusion, water addition, and the interaction between rodent exclusion and water addition on seedling emergence in 2010 based on MANOVA results for nine exotic plant species

Species	Treatment	F	P
C. album	Rodent	4.53	**0.037**
	Water	0.04	0.835
	Interaction	0.06	0.808
C. solstitialis	Rodent	7.64	**0.007**
	Water	0.08	0.783
	Interaction	0.00	0.96
C. thoermerii	Rodent	3.01	0.087
	Water	1.21	0.274
	Interaction	0.35	0.557
D. tenuifolia	Rodent	9.35	**0.003**
	Water	0.61	0.438
	Interaction	0.57	0.451
H. radicata	Rodent	1.67	0.200
	Water	2.45	0.122
	Interaction	0.26	0.608
R. crispus	Rodent	0.44	0.511
	Water	1.11	0.296
	Interaction	0.50	0.481
S. kali	Rodent	12.10	**<0.001**
	Water	0.37	0.544
	Interaction	0.58	0.450
T. dubius	Rodent	32.77	**<0.001**
	Water	0.70	0.404
	Interaction	0.01	0.924
T. officinale	Rodent	5.38	**0.023**
	Water	0.93	0.337
	Interaction	0.38	0.539

In all cases df = 1,78

Bold values indicate the p-values that are significant at P < 0.05 level

that seed predation may not lead to impacts on recruitment if plants are safe-site rather than seed limited (Eriksson and Ehrlen 1992). We found strong effects of rodent seed predation on exotic plant recruitment, with 89 % (8 of 9) of the species we examined being suppressed in one or both years, generally by 100–300 % or more. A growing number of studies have now shown rodent seed predation impacts on recruitment for a range of exotic tree and herbaceous plant species in a variety of systems (Reader 1993; Nuñez et al. 2008; Pearson et al. 2011; Maron et al. 2012), but how seed predation impacts translate to adult plant populations is rarely explored (Brown and Heske 1990; Pierson and Mack 1990; Pearson et al. 2012; Allington et al. 2013). Maron and Simms (2001) showed that even small effects of seed predation on recruitment can result in large effects on plant populations over time. We found that seed predation impacts on plant recruitment carried through to substantially reduce abundance of mature cohorts and flowering adults for four of our nine species in one or both years, including three of the top ten invaders in this system. We saw similar trends for other species, but data were insufficient to test these effects. Collectively, these studies suggest that rodent seed predation is an important biotic filter to invasion. Recent work suggests that this filter may help explain which invaders become abundant and which do not as

a function of selective seed predation (Pearson et al. 2011, 2012). However, in our system the affected species ranged from the strongest to weakest invaders, suggesting that rodent seed predation did not qualitatively determine which invaders thrived and which did poorly, but rather quantitatively reduced recruitment of virtually all species to a half or a third of their invasive potential.

Numerous studies of rodent seed predation have shown that seed selection is largely a function of seed size, with rodents tending to select for larger seeds (Mittelbach and Gross 1984; Brown and Heske 1990;
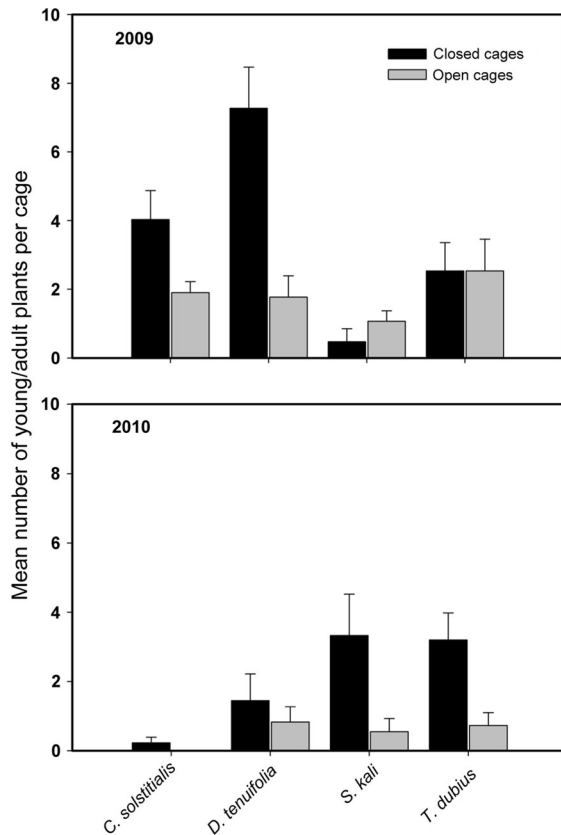
Fig. 4 Effects of rodent exclusion on abundance of young/adult and flowering plants (mean ± SE) by the end of the growing seasons in 2009 and 2010 for the four species with sufficient final abundance to statistically test for rodent effects

Reader 1993; Edwards and Crawley 1999; Pearson and Callaway 2008; Nuñez et al. 2008; Zwolak et al. 2010; Pearson et al. 2011; Maron et al. 2012; Connolly et al. unpublished data, but see Carrillo-Gavilán et al. 2010). A few studies have linked such selection to differential plant recruitment, showing that rodents more strongly suppress larger seeded plants (Reader 1993; Pearson and Callaway 2008; Pearson et al. 2011; Maron et al. 2012; Connolly et al. unpublished data). In our system, we found no relationship between rodent impacts on recruitment and seed size, but most of our species had relatively large seeds exceeding the minimum size threshold (0.0005 g) that others have observed for rodent impacts on plant recruitment (Maron et al. 2012). Nonetheless, we observed significant reductions in recruitment of two species (*D. tenuifolia* and *T. officinale*) which fell below this threshold, indicating that this threshold did not apply in our system. Size of rodent granivores is correlated

with seed-size selection (Brown and Lieberman 1973). Hence, the rich rodent seed predator guild of the Caldenal, which is comprised of numerous large and small seed predators [ranging from around 235 g for adult *M. australis* down to 13 g adults in *C. laucha* (Yahnke et al. 2001)], may obscure seed predation-seed size relationships through compensatory effects when compared with temperate systems where seed predator communities may be dominated by one or few species (Reader 1993; Maron et al. 2012). While seed size may influence rodent seed predation at the species level, in more species rich granivore communities, seed size may not clearly predict impacts on plant recruitment.

Seedling emergence and plant recruitment can vary substantially due to a variety of factors (e.g., Smith et al. 2000). Rodent population density can also vary greatly over time, and rodent abundance directly correlates with intensity of rodent seed predation and can interact with other factors affecting plant populations (Pearson and Fletcher 2008; Pearson and Callaway 2008; Zwolak et al. 2010; Allington et al. 2013). We saw substantially lower seedling recruitment in 2010 versus 2009 (in all treatments) despite higher early precipitation in 2010 and our attempts to ameliorate drought during this year. Although we saw weak trends toward increased recruitment for most of the species we examined when we ameliorated drought, particularly in the absence of rodents, these effects were not significant. However, our water addition experiment was only conducted for 1 year and, although most of the growing season had below average precipitation, there were large precipitation events at the beginning of the growing season which resulted in above average rainfall for the year that may have undermined our watering treatment. The lack of evidence for drought effects suggests that other unmeasured processes such as pathogens or invertebrate seed predators may have driven differences in recruitment between years. In this semiarid environment pathogens may have relatively lower impacts on seeds, but little is known about this. Our work on invertebrate seed predation in this system indicates that ants have very strong effects on these same species (unpublished data). Pathogens, ants, and other factors affecting seedling emergence would have equal access to both rodent cage treatments and so would not confound our results, but they could overshadow effects of rodents by reducing the
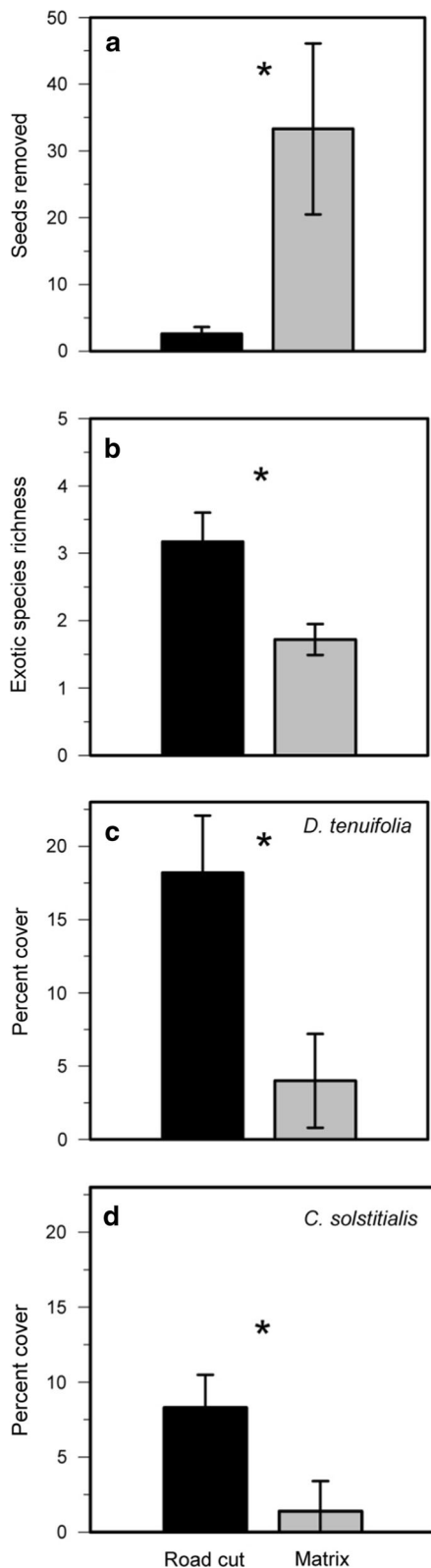
numbers of seedlings recruiting within cages, particularly if they acted in a density dependent manner to have stronger effects in control cages. Despite these substantial differences in seedling emergence between years, rodents had strong effects on recruitment of most species in both years.

Foraging pressure by insects and rodents can create cryptic distribution limits for native plants that are sometimes mistakenly attributed to plant competition or abiotic constraints (Louda 1982; Louda and Rodman 1996; Orrock et al. 2006; Ferreira et al. 2011). A few studies have shown that spatial differences in foraging pressure from native herbivores may also limit distributions of some exotic plants (Lambrinos 2006; Cushman et al. 2011; Eckberg et al. 2012). Our seed predation assays showed that seed predation pressure by rodents was 11 times higher in matrix habitat versus roadsides, potentially contributing to the pattern of higher exotic plant richness along roadsides compared to matrix habitat. Additionally, two of the more widespread and aggressive invaders in this system, *D. tenuifolia* and *C. solstitialis*, species which experienced very strong release from rodent seed predators, were significantly more abundant along roadsides relative to the matrix habitat. The common pattern of exotic plant invasions correlating with disturbances is generally attributed entirely to increased resource availability associated with reduced plant competition (e.g., Davis et al. 2000). Undoubtedly, competition plays a substantial role in the patterns we observed (Hierro et al. 2011). However, our results show that rodent seed predation can substantially reduce recruitment of numerous exotic species (see also Reader 1993; Pearson et al. 2011; Maron et al. 2012), and that such predation pressure can be greatly reduced in recent large-scale disturbances such as road-cuts where exotics commonly thrive and establish source populations for spreading into matrix habitat (e.g., Gelbard and Belnap 2003).

This study demonstrates that seed predation by native generalist rodents can strongly suppress recruitment of a variety of exotic plants, strongly enough to

affect densities of mature and flowering plants, a result rarely documented. It also shows that seed predation pressure can be dramatically reduced in large-scale disturbances and may contribute to the greater abundance of exotics commonly observed in disturbed habitats. Rodent seed predation appears to be an important general source of resistance to plant invasions (Reader 1993; Brown and Heske 1990; Pierson and Mack 1990; Pearson et al. 2011, 2012; Maron et al. 2012; Connolly et al. unpublished data). Prior studies suggest that seed size is an important trait for determining which exotic species may be affected by seed predation (Reader 1993; Pearson et al. 2011; Maron et al. 2012). Our results suggest that predicting seed predation impacts may become more complex as seed predator community richness increases. While rodents appear to be the primary seed predators in some systems (Maron et al. 2012; Connolly et al. unpublished data), ants and birds are important seed predators in others (Mares and Rosenzweig 1978; Inouye et al. 1980; Kelt et al. 1984), and different seed predator guilds can have very different effects on plant recruitment. For example, while rodents tend to select for larger-seeded species, ants may tend to select for smaller-seeded species (Inouye et al. 1980; Ferreira et al. 2011). Hence, the net effect of biotic resistance on invasion will vary as a function of the specific seed predator or guild and their cumulative effects on native versus exotic plant recruitment. Developing a more complete understanding of how seed predation affects plant recruitment and plant community structure will advance our understanding of community ecology and facilitate management for improved biotic resistance.

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 Ecol 210:291–301

Allington GRH et al (2013) Niche opportunities and invasion dynamics in a desert annual community. Ecol Lett 16:158–166

Bartholomew B (1970) Bare zones between California shrub and grassland communities: the role of animals. Science 170:1210–1212

Blaney CS, Kotanen PM (2001) Post-dispersal losses to seed predators: an experimental comparison of native and exotic old field plants. Can J Bot 79:284–292

Brown JH, Heske EJ (1990) Control of a desert–grassland transition by a keystone rodent guild. Science 250:1705–1707

Brown JH, Lieberman GA (1973) Resource utilization and coexistence of see-eating desert rodents in sand dune habitats. Ecology 54:788–797

Cano E (1980) Inventario integrado de los recursos naturales de la provincia de La Pampa. INTA-UNLPam, Buenos Aires, Argentina (In Spanish)

Carrillo-Gavilán MA et al (2010) Comparing seed removal of 16 pine species differing in invasiveness. Biol Invasions 12:2233–2242

Carrillo-Gavilán MA et al (2012) Establishment constraints of an alien and a native conifer in different habitats. Biol Invasions 14:1279–1289

Chiuffo M (2009) Efecto de las picadas y caminos en la invasion de especies herbaceas en la reserva provincial Parque Luro. Undergraduate's Thesis, Universidad Nacional de La Pampa, Santa Rosa, Argentina

Cushman JH et al (2011) Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. J Ecol 99:524–531

Davis MA et al (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

DeWalt SJ et al (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub Clidemia hirta. Ecol 85:471–483

Eckberg JO et al (2012) Insect herbivory and propagules pressure influence *Cirsium vulgare* invasiveness across the landscape. Ecology 93:1787–1794

Edwards GR, Crawley MJ (1999) Rodent seed predation and seedling recruitment in mesic grassland. Oecologia 118:288–296

Ellis BA et al (1998) Dietary habits of the common rodents in an agroecosystem in Argentina. J Mammal 79:1203–1220

Elton C (1958) The ecology of invasions by animals and plants. The University of Chicago Press, Chicago

Eriksson O, Ehrlen J (1992) Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360–364

Ferreira AV et al (2011) Seed predators limit plant recruitment in Neotropical savannas. Oikos 120:1013–1022

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv Biol 17:420–432

Giannoni SM et al (2005) Main food categories in diets of sigmodontine rodents in the Monte (Argentina). Mast Neotrop 12:181–187

Hierro JL et al (2009) Germination responses of an invasive species in native and non-native ranges. Oikos 118:529–538

Hierro JL et al (2011) Resistance to Centaurea solstitiatis invasion from annual and perennial grasses in California and Argentina. Biol Invasions 13:2249–2259

Inouye RS et al (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. Ecology 61:1344–1351

Kelt DA et al (1984) Seed predation by birds and small mammals in semiarid Chile. Oikos 104:133–141

Lambrinos JG (2006) Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. Oecologia 147:327–334

Levine JM et al (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989

Louda SM (1982) Variation in plant recruitment over a gradient in relation to insect seed predation. Ecol Monogr 52:25–41

Louda SM (1983) Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Aseraceae), along a climatic gradient. Ecology 64:511–521

Louda SM, Rodman JE (1996) Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, Bittercress). J Ecol 84:229–237

Mack RN (1996) Biotic barriers to plant naturalization. In: Moran VC, Hoffmann JH (eds) Proceedings of the IX international symposium on biological control of weeds. University of Cape Town Stellenbosch, South Africa, pp 39–46

Mares MA, Rosenzweig ML (1978) Granivory and North and South American deserts: rodents, birds, and ants. Ecology 59:235–241

Maron JL, Crone EC (2006) Herbivory: effects on plant abundance, distribution, and population growth. Proc R Soc B 273:2575–2584

Maron JL, Kauffman MJ (2006) Habitat-specific impacts of multiple consumers on plant population dynamics. Ecology 87:113–124

Maron JL, Simms EL (2001) Rodent-limited establishment of bush lupine: field experiments on the cumulative effect of granivory. J Ecol 89:578–588

Maron JL et al (2012) Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. J Ecol 100:1492–1500

Mills JN et al (1992) Reproductive characteristics of rodent assemblages in cultivated regions of central Argentina. J Mammal 73:515–526

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627

Mittelbach GG, Gross KL (1984) Experimental studies of seed predation in old-fields. Oecologia 65:7–13

Nuñez MA et al (2008) Seed predation as a barrier to alien conifer invasions. Biol Invasions 10:1389–1398

Orrock JL et al (2006) See predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. J Ecol 94:838–845

Orrock JL et al (2008) Apparent competition with an exotic plant reduces native plant establishment. Ecology 89:1168–1174

Ortega YK et al (2012) Population-level compensation impedes biological control of an invasive forb and indirect release of a native grass. Ecology 93:783–792

Ostfeld RS et al (1997) Effects of rodents on survival of tree seeds and seedlings in invading old fields. Ecology 78:1531–1542

Parker JD et al (2006) Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461

Pearson DE, Callaway RM (2008) Weed biocontrol insects reduce native plant recruitment through second-order apparent competition. Ecol Appl 18:1489–1500

Pearson DE, Fletcher RJ Jr (2008) Mitigating exotic impacts: restoring native deer mouse populations elevated by an exotic food subsidy. Ecol Appl 18:321–334

Pearson DE et al (2011) Biotic resistance via granivory: establishment by invasive, naturalized and native asters reflects generalist preference. Ecology 92:1748–1757

Pearson DE et al (2012) Biotic resistance: exclusion of native rodent consumers releases populations of a weak invader. J Ecol 100:1383–1390

Pierson EA, Mack RN (1990) The population biology of *Bromus tectorum* in forests: distinguishing the opportunity for dispersal from environmental restriction. Oecologia 84:519–525

Reader RJ (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. J Ecol 81:169–175

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

Shahid A et al (2009) Selection of seeds of common native and non-native plants by granivorous rodents in the northeastern United States. Am Mid Nat 162:207–212

Shea K et al (2005) Context-dependent biological control of an invasive thistle. Ecol 86:3174–3181

Smith SE et al (2000) Geographic variation in predictive seedling emergence in a perennial desert grass. J Ecol 88:139–149

Troiani H, Steibel P (2008) Reconocimiento de malezas: Región subhúmeda y semiárida pampeana. Universidad Nacional de La Pampa, Colegio de Ingenieros Agrónomos de La Pampa, Santa Rosa (In Spanish)

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

Williamson MH, Fitter A (1996) The characters of successful invaders. Biol Conserv 78:163–170

Yahnke CJ et al (2001) Patterns of infection with Laguna Negra virus in wild populations of *Calomys laucha* in the central Paraguayan Chaco. Am J Trop Med Hyg 65:768–776

Zwolak R et al (2010) Fire and mice: seed predation moderates fire's influence on conifer recruitment. Ecology 91:1124–1131