

LETTER

Vertebrate predators have minimal cascading effects on plant production or seed predation in an intact grassland ecosystem

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Abstract

The strength of trophic cascades in terrestrial habitats has been the subject of considerable interest and debate. We conducted an 8-year experiment to determine how exclusion of vertebrate predators, ungulates alone (to control for ungulate exclusion from predator exclusion plots) or none of these animals influenced how strongly a three-species assemblage of rodent consumers affected plant productivity. We also examined whether predator exclusion influenced the magnitude of post-dispersal seed predation by mice. Both ungulates and rodents had strong direct effects on graminoid biomass. However, rodent impacts on plant biomass did not differ across plots with or without predators and/or ungulates. Deer mice removed more seeds from seed depots on predator exclusion plots, suggesting trait-mediated indirect effects of predators, but this short-term behavioural response did not translate into longer-term impacts on seed survival. These results suggest that vertebrate predators do not fundamentally influence primary production or seed survival in our system.

Keywords

Giving up density, herbivory, indirect effects, predators, seed predation, small mammals, trait-mediated indirect effects, trophic cascade.

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INTRODUCTION

In terrestrial habitats, studies have shown that single small predators such as spiders (Gomez & Zamora 1994; Beckerman *et al.* 1997; Schmitz 2006), beetles (Letourneau *et al.* 2004), ants (Dyer & Letourneau 1999), lizards (Spiller & Schoener 1994) or guilds of birds (reviewed by Mooney 2007) can have cascading indirect effects on focal plants. In cases where these indirect effects influence dominant plants, such effects can also influence plant diversity and ecosystem level processes at small scales (Schmitz 2006). While this research has added tremendously to our appreciation of the roles that predators play in terrestrial food webs, two important questions remain unanswered. First, to what extent do the damage cascades revealed in small scale experiments involving single predator–prey treatments translate to more reticulate food webs that harbour diverse predator and consumer guilds? That is, in more complex systems, does one see substantial long-term impacts of groups of predators on plant community production akin to what has been found in some aquatic systems (e.g., Carpenter & Kitchell 1993)? Second, do results from studies that have primarily focused on invertebrate predators and their prey (Borer *et al.* 2005) generalise to larger spatial and temporal scales and to systems with larger-bodied and wider-ranging vertebrate predators and consumers?

Most of what we know about the cascading indirect effects of larger vertebrate predators on terrestrial vegetation has come from ‘natural experiments’. These have examined the consequences of fortuitous additions or removals of predators, often to islands (McLaren & Peterson 1994; Fukami *et al.* 2006; Maron *et al.* 2006; Terborgh *et al.* 2006; Beschta & Ripple 2009). One well known example of this type of research comes from Yellowstone National Park, where scientists have asserted that wolf reintroduction has resulted in greatly increased recruitment of Aspen and Willow due to reduced herbivory by elk in

sites where wolf predation risk is high (Ripple *et al.* 2001; Ripple & Beschta 2007). However, recent research has challenged these findings (Kauffman *et al.* 2010), and thus even in this well-studied system, it is presently unclear how strongly wolves have indirectly affected deciduous tree recruitment. Experiments can help decipher causation from correlation, but such experiments have rarely been conducted at large spatial scales over longer time frames for food webs with vertebrate predators and consumers (Sinclair *et al.* 2000; Meserve *et al.* 2003).

For the last 8 years, we have excluded all mammalian and avian predators and ungulates (deer and elk), ungulates alone or none of these animals from 1-ha plots in a grassland ecosystem in western Montana. Our goal was to examine how a diverse predator community influences plant dynamics via effects on an assemblage of small mammals consisting of deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*) and Columbian ground squirrels (*Spermophilus columbianus*). To determine the effects of these consumers on vegetation, we embedded smaller 100 m² rodent exclusion subplots within each large 1-ha treatment plot.

The simplicity of this rodent consumer assemblage is advantageous for understanding the routes through which predators may indirectly influence plant community dynamics (Fig. 1). Montane voles and Columbian ground squirrels are primarily herbivores that can potentially suppress graminoid biomass. By contrast, deer mice consume mostly seeds (and insects) and any impacts they have on vegetation are likely to occur via reduction in recruitment of larger-seeded species (Pearson & Callaway 2008; Bricker *et al.* 2010). To date, our experiment has shown that montane vole abundance is strongly influenced by predators whereas ground squirrel abundance is not (Maron *et al.* 2010). Thus any indirect effects of predators on plant biomass in our system would occur by predators suppressing vole abundance (a density-mediated pathway), or by predators changing vole and/or ground squirrel behaviour (a trait-mediated pathway)

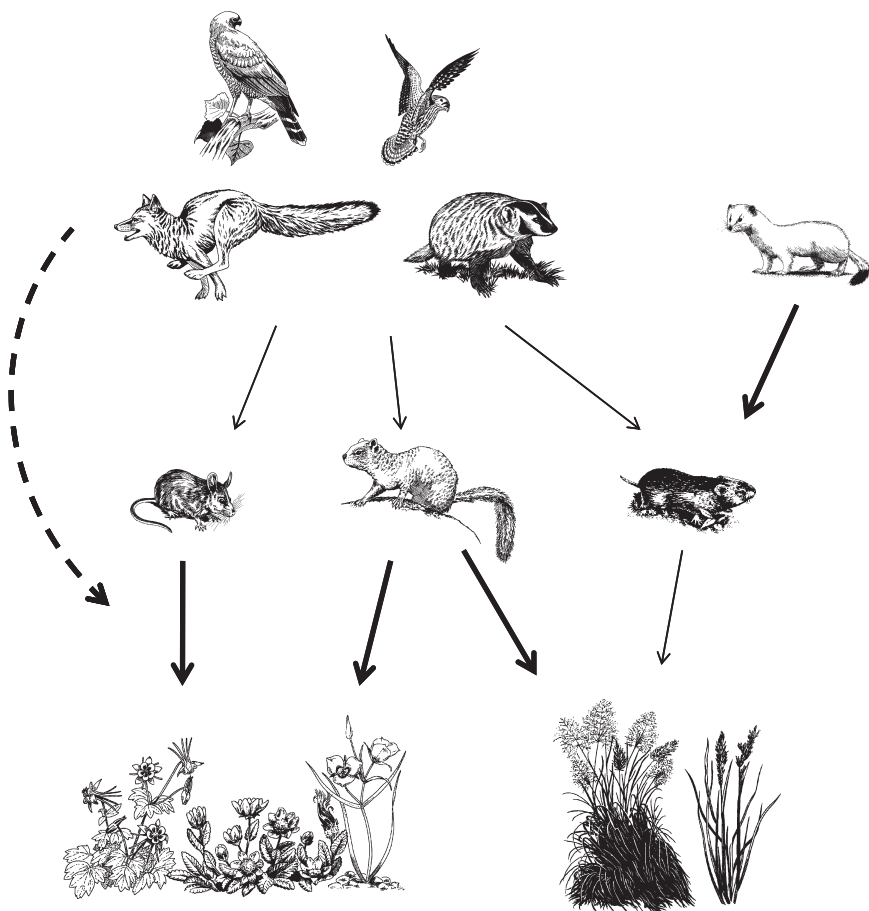


Figure 1 Depiction of food web linkages and interaction strengths in the upper Blackfoot Valley, Western Montana. Of all avian and mammalian predators, only weasels show strong predation effects and only on vole abundance (based on Maron *et al.* 2010). For the three abundant small mammals (mice, ground squirrels and voles; from left to right), mice have strong effects on forbs through seed predation, ground squirrels have strong effects on forbs through flower predation and on grasses through reductions in biomass from herbivory and voles have weak effects on vegetation. The dotted arrow indicates the strong trait-mediated indirect effect that predators have on mouse seed foraging behaviour. Arrows indicate the direction of interactions, with heavier arrows indicating stronger interactions. The illustrations in this figure are copyrighted by Zackery Zdinak (1999–2003).

in ways that influence how strongly they impact plants. Such trait-mediated effects can be quite powerful and can propagate to the base of food webs (Werner & Peacor 2003; Schmitz *et al.* 2004; Peckarsky *et al.* 2008). Regardless of route, if indirect effects of predators are strong, then voles and ground squirrels should have greater suppressive effects on plant production on plots closed to predators compared with those with predator access. Furthermore, the difference in plant production between rodent exclusion and control subplots should be greater for those nested in predator exclusion plots compared with those in plots open to predators (Fig. 2).

The abundance of the third small mammal in our system, deer mice, is also unaffected by predator exclusion (Maron *et al.* 2010). Thus, any indirect effect that is propagated through deer mice must occur via a trait-mediated effect. Predators could alter deer mouse foraging behaviour in ways that influence the intensity or spatial distribution of post-dispersal seed predation, which could then affect plant recruitment. Predator impacts on granivore foraging behaviour have most commonly been assessed by determining how the giving up density (GUD) for seeds changes across environments that vary in predation risk (Brown 1988; Brown *et al.* 1988; Kotler *et al.* 1991, 2004). We assayed how predator and/or ungulate exclusion influenced deer mouse foraging at seed depots placed across our large 1-ha treatment plots. Determining whether predator exclusion at this scale influences the intensity and spatial aspects of rodent foraging behaviour has only been accomplished in one other experiment (Yunger *et al.* 2002; Kelt *et al.* 2004). We also asked whether any predator-induced effects on short-term deer mouse foraging behaviour are reflected in predation

pressure on seeds for longer periods of time (months rather than days) and under more natural conditions.

METHODS

Study system

We established experiments in semi-arid *Festuca scabrella* and *Festuca idahoensis* dominated grasslands in the Blackfoot Valley in western Montana (47°01' 13.11" N, 113°07' 59.21" W). These grasslands are composed of a relatively diverse assemblage of mostly native species (J.L. Maron & D.E. Pearson, unpublished data). Average precipitation is 32 cm y^{-1} . The dominant native ungulates are elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). These species winter in high numbers in the Blackfoot Valley; many elk and mule deer move to higher elevations in late spring. We focus on how deer mice, montane voles and Columbian ground squirrels influence vegetation because these are the most abundant rodent species at our sites. Other small mammals occur at low numbers and only at some sites (Maron *et al.* 2010). Although the mammalian predator community is diverse (Maron *et al.* 2010), our observations, game cameras and snow tracking indicate that the most abundant and active mammalian predators are coyotes (*Canis latrans*), short-tailed weasels (*Mustela erminea*) and badgers (*Taxidea taxus*; J.L. Maron & D.E. Pearson unpublished data). Raptors are also diverse, but occur at low densities (J.L. Maron & D.E. Pearson, personal observations). Snakes appear absent from our sites.

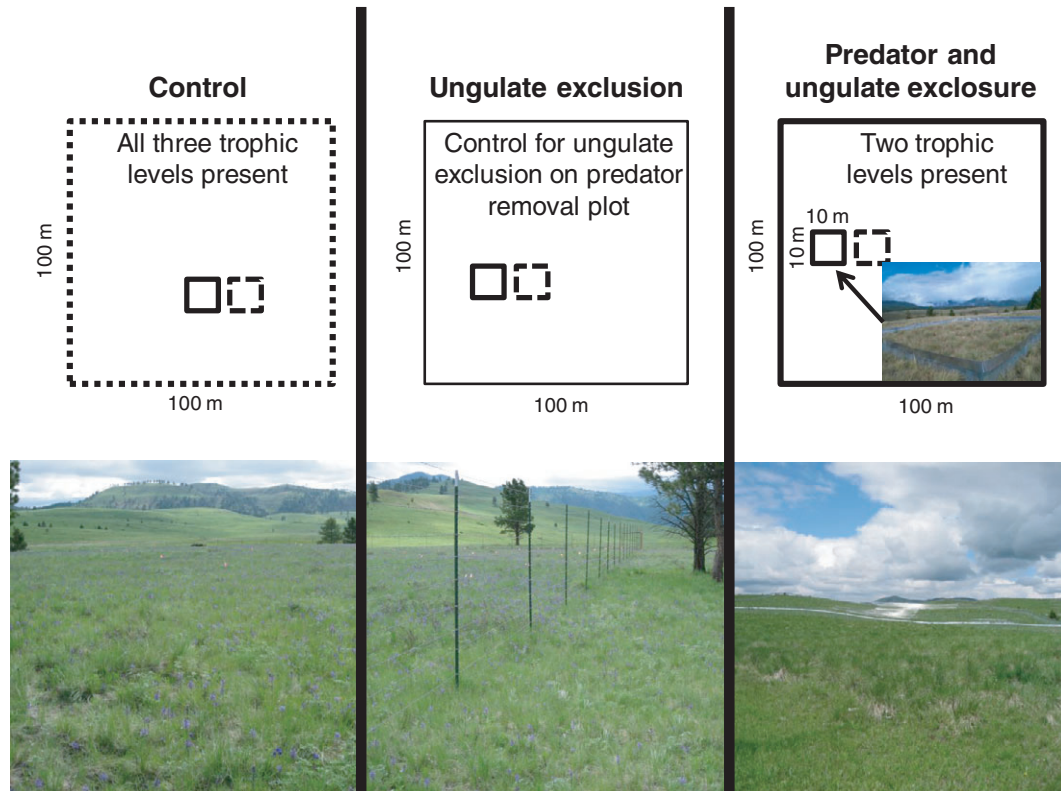


Figure 2 Schematic showing an experimental block (each block was replicated across four sites). Each block is composed of three 1-ha plots. Control plots have a 3-level treatment (predators, consumers and plants present), predator exclusion plots are a 2-level treatment (consumers and plants only). As predator exclusion treatment plots also by necessity exclude ungulates, ungulate only exclusion plots allow separation of the direct effects of ungulates on vegetation from the indirect of predators on vegetation. Nested within each 1-ha plot is a 10 m × 10 m rodent exclusion subplot (small square with solid line) and a paired control subplot (small square with dashed line). This allows determination of rodent impacts on vegetation and how this varies depending on the presence or absence of predators and/or ungulates.

Predator and/or ungulate exclusion plots and rodent exclusion subplots within them

We established four replicate experimental blocks, with blocks separated from each other by an average of 23 km (minimum distance between blocks = 7.5 km). Three blocks were established in September 2002 and a fourth was added in September 2005. Each block consists of three 100 m × 100 m plots that have similar vegetation characteristics and are separated from each other by at least 100 m. We randomly assigned one of the following three treatments to each plot: (1) predator and ungulate exclusion, (2) ungulate exclusion only and (3) control. These treatments can be visualised in the context of a 3-level trophic level food chain, where the control is the 3-trophic level reference and the predator exclusion is a 2-level trophic treatment (Fig. 2). The ungulate only exclusion treatment controls for the fact that the predator exclusion plot also necessarily excludes ungulates. Hence, it enabled us to separate the direct effects of ungulates on vegetation from the potential indirect effects of predators on vegetation. In our experiment, the 1-trophic level treatment (exclusion of small mammals and predators) involves 10 m × 10 m rodent exclusion subplots that we nested within each larger 1-ha treatment plot. This design enabled us to examine how the impact of rodents on vegetation was influenced by the presence or absence of predators and or ungulates (Fig. 2).

Predator exclusion plots are surrounded by game fencing (Bekaert Industries, Kortrijk, Belgium) topped with two strands of high tension

wire (total fence height = 2.6 m). We excluded raptors by stringing overhead parallel strands of 0.025 mm diameter stainless steel wire, spaced 20 cm apart. From September 2002–August 2005, we excluded all predators except weasels from predator exclusion plots. In September 2005, we retrofitted predator exclusion fences to exclude both short- and long-tailed weasels (*M. erminea* and *Mustela frenata*, respectively; hereafter ‘weasels’). See Maron *et al.* (2010) for details of fence construction. To exclude ungulates, we strung 2.4 m tall 10 stranded barbed wire fence (strand spacing = 0.24 m) to fence posts with no overhead wires. Predators freely pass through this ungulate exclusion fence (Maron *et al.* 2010). On control plots, no fence was erected but we installed 2-m tall fence posts approximately every 20 m along each perimeter to emulate raptor perch sites created by fence posts around the other plots. There is no livestock grazing on any of our experimental plots.

We have used a combination of snow tracking and smoked track plates to assay predator activity across each 1-ha treatment plot. Although weasels have occasionally breached the predator exclusion fence, our monitoring indicates that the experimental treatments strongly suppress predator and/or ungulate access to plots (Maron *et al.* 2010).

Within each 1-ha plot, in summer 2003 we randomly located a 10 m × 10 m subplot around which we constructed a rodent exclusion fence. We subsequently paired this subplot with a nearby equally sized unfenced subplot which served as a control. We constructed rodent enclosures of 0.625 cm × 0.625 cm wire mesh

fencing that was buried 40 cm deep and extended 60 cm above ground. Each fence is topped with 20 cm of aluminium flashing to prevent entry by climbing rodents. We maintain baited snap traps within enclosures to ensure rodent exclusion.

Plant sampling

In July 2008, at peak plant biomass, we quantified differences in above-ground plant production across each 1-ha treatment plot at all four sites. We harvested all above-ground vegetation within 0.4 m × 0.4 m quadrats placed at 40 randomly chosen locations that were stratified across each 1-ha plot. We repeated this sampling in July 2010, but used 0.5 m × 0.5 m quadrats to sample 25–30 locations, again stratified across each 1-ha plot.

To examine how rodent impacts on plant biomass varied across our larger treatment plots, in summer 2010 we also sampled from six 0.5 m × 0.5 m quadrats that were placed in randomly selected locations stratified across each 10 m × 10 m rodent enclosure and rodent enclosure control subplot. For all sampling, vegetation was cut at ground level, sorted by graminoids, forbs, present year's growth for shrubs, and litter (2010 only), bagged, oven-dried at 60 °C and weighed. Shrubs were never sampled in or out of rodent enclosure subplots. They were only found in biomass samples across 1-ha plots, only at two sites, and composed very low total biomass. For this reason, we do not report shrub biomass here.

Seed depots and seed cages to assess post-dispersal seed predation

We quantified how predators and/or ungulates influenced deer mouse foraging behaviour using seed depots and seed cages. We focus on deer mice because *Peromyscus* can exhibit behavioural plasticity in their foraging patterns in response to predation risk (e.g., Morris & Davidson 2000). In August (2007, 2009 and 2010) or early September (2008), when ground squirrels were hibernating, we deployed large Petri dishes (15 cm diameter × 15 mm tall) filled with 40 *Lupinus sericeus* seeds mixed in with sand. Petri dishes were placed at 25 randomly selected points stratified across each treatment plot. We used *L. sericeus* seeds because they occur naturally on plots and previous work has shown that they are favoured by *P. maniculatus* (Bricker *et al.* 2010, J.L. Maron & D.E. Pearson, unpublished data). We placed dishes out on treatment plots in mid-day, retrieved them 48 h later and counted the number of seeds remaining per dish. Seed trays placed in rodent enclosures showed little sign of seed consumption by birds or insects.

To determine how predator and/or ungulate exclusion influenced post-dispersal seed predation over months rather than days, we placed *Lithospermum ruderale* seeds into paired cages open or closed to deer mice. We used *L. ruderale* seeds because this species is common at our sites, it produces large, white, conspicuous seeds that are easy to see on the ground and deer mice readily consume them (Bricker *et al.* 2010, J.L. Maron & D.E. Pearson, personal observation). Cages were 25 cm × 25 cm × 15 cm deep constructed of 0.625 cm × 0.625 cm wire mesh sunk into the ground 10 cm deep with a wired on top. Mouse access cages had two 5 cm × 5 cm openings cut in each side. In June 2010, we installed 10 pairs of these seed cages across each 1-ha treatment plot using a random stratified design. Each cage in a pair was placed c. 0.5–1.0 m apart, with one cage randomly selected to be open to mice and the other cage closed. In early August 2010, we scattered 20 locally collected *L. ruderale* seeds onto the soil surface

inside each cage and in mid-September 2010, we counted the number of seeds remaining in each cage.

Analyses

We performed two different analyses to examine whether predators indirectly influenced plant productivity. First, using plant biomass data collected across each 1-ha treatment plot in 2008 and 2010, we compared mean graminoid or forb biomass (log transformed) among our three treatments (control, predator and ungulate exclusion and ungulate exclusion only) using a mixed model repeated measures ANOVA with year as the repeated measure, site as a random factor and treatment a fixed factor. If predators have strong indirect effects on plant production, then we would expect plant biomass to be reduced on predator exclusion plots compared with ungulate only exclusion plots. Thus, we first made this comparison. If predator plus ungulate exclusion plots were no different from ungulate only exclusion plots, we lumped data from these two plots together and tested these against control plots. In a separate analysis, involving only data on litter accumulation in 2010 (the only year we collected these data), we used a two-way ANOVA (with treatment as a fixed factor and site as a random factor) to test for predator and/or ungulate exclusion effects on litter biomass (log transformed). As we did for graminoids and forbs, we first tested to see if litter biomass differed between predator and ungulate only treatment plots. If there was no difference, we combined data from these two plots and tested these values against values from control plots.

Second, we asked whether the impact of rodent exclusion on plant production was different across our three treatment plots. If predators have strong negative direct effects on rodent numbers or behaviour, then the impacts of rodent exclusion should be greater on predator exclusion plots compared with the other two treatments. Alternatively, if predator effects are weak but ungulates, by modifying cover or food availability, influence rodent behaviour, then rodent effects on vegetation should be greater on ungulate exclusion plots compared with controls. To test these hypotheses, we used a split-plot ANOVA with treatment (i.e. predator and/or ungulate exclusion or control) applied at the whole plot level and ±rodent exclusion at the split-plot level. We tested for the main effects of these factors and the interaction. Similar to the tests described above, these comparisons were performed on mean biomass data calculated for each rodent enclosure or rodent enclosure control subplot.

We analysed deer mouse foraging data in several ways. We first tested whether the mean number of *L. sericeus* seeds left in each Petri plate after 48 h was different across 1-ha treatment plots. As a measure of how treatment influenced spatial patterns of mouse foraging, we tested whether the mean number of Petri plates that showed evidence of mouse foraging (defined as trays missing ≥ 5 *L. sericeus* seeds), or the mean number of seeds left in those Petri plates that showed evidence of mouse foraging varied among treatments. We used a two-way repeated measures ANCOVA for these analyses with year as the repeated measure, site as a random factor and treatment as a fixed factor. We used the number of unique mice caught on each plot (1–2 weeks before the feeding trial was run) as a covariate to statistically control for variation in mouse density among plots. This enabled us to ask, independent of mouse density, how treatment might influence foraging behaviour. As voles are known to feed on seeds occasionally, and potentially compete with deer mice, we first tried running models with both deer mice and vole numbers as covariates. Adding vole numbers

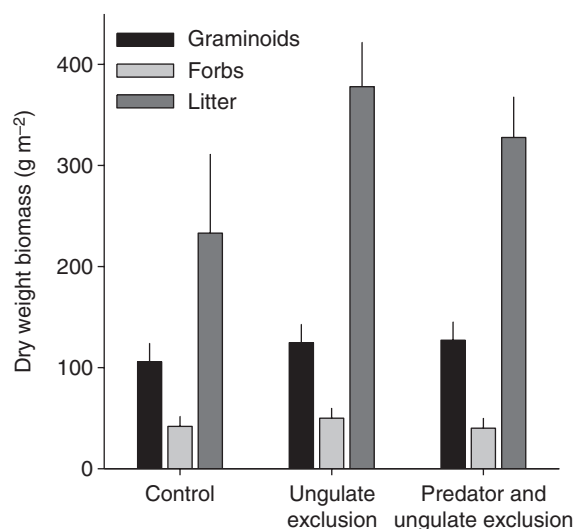


Figure 3 Direct effects of ungulates, and indirect effects of predators on least square mean (+SEM) above-ground dry weight biomass of graminoids and forbs. Least square means from a repeated measures ANOVA with year as the repeated measure (see Methods for details). For litter, mean (+SEM) above-ground dry weight biomass is shown based on 2010 data only.

as a second covariate did not improve model fit and in no case was this covariate significant. As such, we dropped voles from the analysis and only used deer mice as a covariate. Deer mouse and vole abundance were determined from mark-recapture live trapping on permanently marked 10 × 10 grids (100 traps, 10 m spacing between traps) on each 1-ha treatment plot. We placed one Sherman live trap (7.6 cm × 8.9 cm × 22.9 cm; H. B. Sherman Traps, Tallahassee, FL, USA) at each station and checked the traps each morning and evening Monday–Friday, which resulted in eight trapping sessions per sampling period (see Maron *et al.* 2010 for details). In these models, there were no significant interactions between mice caught and treatment or year, so these interactions were not included.

To examine how seed predation varied across our treatment plots, we used a split-plot ANOVA as described above. The response variable was the mean number of seeds censused in seed cages that were either open or closed to rodents. All analyses were performed in the Proc Mixed module within SAS V9.2 (SAS Institute, Cary, NC, USA).

RESULTS

Predators had no significant indirect effects on primary production. For example, there were no significant differences in above-ground plant biomass between 1-ha plots that had both predators and ungulates excluded compared with those with only ungulates excluded (Fig. 3; see Appendix S1 in Supporting Information for ANOVA table). Comparing predator + ungulate and ungulate only exclusion plots combined to control plots, ungulates had a significant impact on graminoid biomass but not forb biomass (see Table S2). In all of the above tests, there were no significant differences between years and no year by treatment interaction (see Tables S1 and S2). In terms of litter, in 2010 there were no significant differences in litter biomass between 1-ha plots that had both predators and ungulates excluded compared with those with only ungulates excluded ($F_{1,3} = 1.41$, $P = 0.32$), but there were significant differences in litter accumulation on plots where ungulates were excluded (predator and ungulate

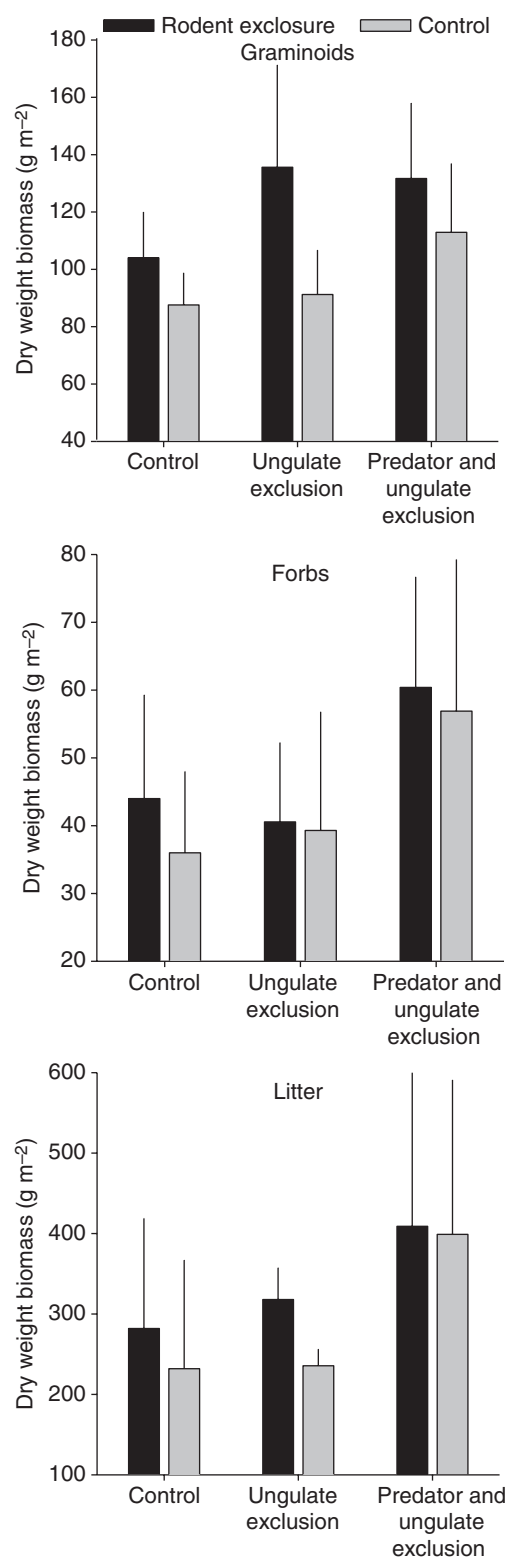


Figure 4 Mean (+SEM) above-ground dry weight biomass of graminoids (top panel), forbs (middle panel) and litter (bottom panel) in and out of rodent enclosures embedded within 1-ha control, ungulate exclusion and ungulate plus predator exclusion plots. Effects of rodent exclusion on graminoid and litter biomass were significant (or marginally significant for litter), but the magnitude of this effect did not differ across control, ungulate only, and predator and ungulate exclusion plots.

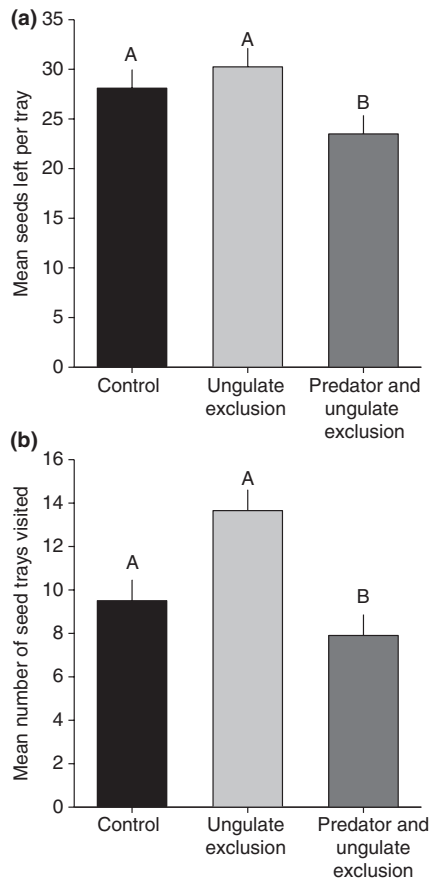


Figure 5 Least square mean (+SE) (a) number of *L. sericeus* seeds left in trays and (b) number of seed trays visited (as defined in Methods) after 48 hours of exposure to deer mice on each 1-ha treatment plot. Least square means calculated from ANCOVA with mice numbers per plot as covariate (see Methods for details). Different letters above bars indicate significant differences by *post-hoc* test.

exclusion plots combined) compared with control plots ($F_{1,7} = 9.8$, $P < 0.02$).

Comparing primary production in and out of rodent enclosures, we found that rodents significantly decreased graminoid (Fig. 4; $F_{1,9} = 13.52$, $P < 0.005$) and marginally decreased litter biomass ($F_{1,9} = 4.29$, $P = 0.065$) but had no impacts on forb biomass (Fig. 4; $F_{1,9} = 0.9$, $P = 0.37$). The magnitude of these effects did not vary significantly across 1-ha treatment plots (Fig. 4; graminoids, $F_{2,9} = 1.13$, $P = 0.36$; forbs, $F_{2,9} = 0.03$, $P = 0.97$; litter, $F_{2,9} = 0.25$, $P = 0.78$), indicating that predators and/or ungulates did not alter the strength of rodent effects on vegetation biomass.

The number of *L. sericeus* seeds that deer mice removed from seed trays varied significantly among our larger treatment plots (Fig. 5; see Table S3), as did the number of seed trays visited by mice (Fig. 5; see Table S3), even after controlling for the highly significant positive relationships between deer mouse density and number of seeds remaining per tray (see Table S3) and the number of seed trays visited (see Table S3). There was no difference among years (for number of seeds removed per tray or the number of trays visited, see Table S3), although there was a significant treatment by year interaction for number of seeds remaining per tray, but not for number of trays visited (see Table S3). *Post-hoc* comparisons revealed that the number of seeds remaining per tray was significantly lower and the number of

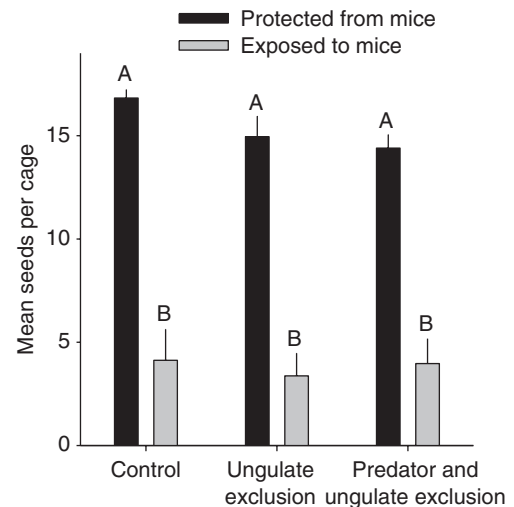


Figure 6 Intensity of post-dispersal seed predation on *L. ruderalis* seeds on 1-ha control, ungulate exclusion and ungulate plus predator exclusion plots. Mean (+SEM) seeds left in cages protected or exposed to deer mice after 1.5 months in the field. Different letters above bars indicate that cages open to rodents had significantly fewer seeds left in them compared with paired cages protected from mice. However, the magnitude of this effect did not differ for cages on control, ungulate only, and predator and ungulate exclusion plots.

seed trays visited was significantly higher on predator exclusion plots compared with ungulate exclusion plots or control plots (*post-hoc* tests, $P < 0.03$). There were no significant differences in seeds remaining per tray or the number of seed trays visited on control versus ungulate only exclusion plots (*post-hoc* test, $P > 0.05$). There was no difference among treatment plots in the mean number of seeds per tray when only those trays that were fed upon were analysed ($F_{2,7.03} = 0.28$, $P = 0.77$).

Post-dispersal seed predation on *L. ruderalis* seeds was intense. Across all plots and sites, on average there were 75% fewer seeds in cages open to rodents compared with closed cages (Fig. 6; $F_{1,15} = 202$, $P < 0.0001$). However, behavioural differences reflected in short-term feeding trials across treatment plots were not apparent in longer-term effects of mice on seed survival. That is, there was no difference in the intensity of seed predation (i.e. the difference in seed number between cages open and closed to mice) across our three larger treatments (Fig. 6; $F_{2,15} = 0.64$, $P = 0.54$).

DISCUSSION

In terrestrial systems, smaller scale experiments have primarily demonstrated that predators can have cascading effects that influence plant performance (Schmitz *et al.* 2000; Halaj & Wise 2001; Shurin *et al.* 2005; Mooney 2007), with more limited effects on primary productivity (Shurin *et al.* 2005; Schmitz 2006). As most of this work has involved small predators and invertebrate consumers, some have argued strongly that larger vertebrate predators may be underappreciated drivers of trophic cascades in terrestrial habitats (Beschta & Ripple 2009). However, uncertainty continues to pervade this issue partly because there have been few large-scale long-term experiments that have examined whether vertebrate predators have cascading indirect effects in terrestrial systems (but see Sinclair *et al.* 2000; Meserve *et al.* 2003). Our experiment addressed this gap by simulating the extinction of all avian and mammalian carnivores from a system.

In doing so, we were able to examine how predators influence an important ecosystem variable – primary production – while also exploring whether these or other effects might occur through trait- or density-mediated interaction pathways.

The key result that emerged from our 8-year study is that indirect effects of an entire vertebrate predator assemblage on plant productivity and seed predation were remarkably weak, despite strong consumer effects on both plant biomass and seed survival. Why might this be so? Our previous results from this experiment showed that predators do not substantially influence either ground squirrel or deer mouse abundance (Maron *et al.* 2010). As such, density-mediated indirect effects would not be expected to pass through these species. In contrast, weasels suppress montane vole populations in our system (Maron *et al.* 2010), thus predators could potentially transmit density-mediated indirect effects through voles. However, we found no evidence for this. While rodents significantly suppressed graminoid biomass, the magnitude of this effect was not different in the presence or absence of predators. This lack of indirect predator effect results from predators having weak effects on the abundance of consumers that impact vegetation (deer mice and ground squirrels) and strong effects on a consumer (montane voles) that does not substantially suppress plant production. The significant effect of rodent exclusion on grass and litter production is likely driven by ground squirrels rather than voles. Ground squirrels are typically the most abundant small mammal of the three we study (Maron *et al.* 2010). They are an order of magnitude larger than voles and actively maintain open interstitial spaces between bunchgrasses. As well, ground squirrels eat the inflorescences of many forbs (J.L. Maron & D.E. Pearson, unpublished data).

Density-mediated interactions, however, are not the only means by which trophic cascades might propagate through a system. Predators can also exert strong indirect effects through trait-mediated pathways (Preisser *et al.* 2005). Our finding that predator suppression has limited impacts on primary productivity suggests that any unmeasured trait-mediated effect of predators on herbivorous voles and ground squirrels were not strong enough to transmit to significant impacts on primary producers.

For granivorous deer mice, we found some evidence for predators influencing foraging behaviour. We found that the number of seeds left in trays (an estimate of per capita foraging intensity) was significantly lower on predator exclusion plots compared with the other two treatments. This result is similar to what was found by Yunker *et al.* (2002). As we also found that many more seed trays were foraged on within predator removal plots compared with the other two treatment plots, it appears that mice were active over larger areas in the absence of predators. When we restricted our analyses to compare seed removal only across those trays that were encountered by mice, we found no differences among treatments. This suggests that if mice encountered trays, foraging intensity was similar across treatments. Thus, differences in overall seed removal across the treatment plots were largely due to mouse encounter rates with depots. Although our seed offerings were limited to 40 seeds per tray, mice rarely consumed all the seeds in a dish. Thus, estimates of foraging intensity were not constrained due to depletion of seeds in seed trays. Although the absolute number of deer mice (but not voles) on each plot significantly affected seed removal and seed tray encounter rates, even after statistically controlling for mouse numbers (by using mouse density as a covariate) we still found a significant effect of predator exclusion on deer mouse foraging behaviour.

Notably, this effect was strong despite the fact that we could not control for other factors that potentially act as sources of variation in deer mouse foraging among plots, such as cover, shrub density, microclimate, etc. Finally, predators affected spatial dispersion of foraging but not mouse foraging intensity. In other systems, space use patterns of mice can influence their predation rate on bird nests (Schmidt & Ostfeld 2003) and in our system, predator-driven impacts on mouse spatial foraging patterns has the potential to indirectly influence plant spatial distributions.

Seed offerings provide a convenient and rapid assessment of short-term behavioural responses of granivores to variation in predation risk. However, little is known about how such assays relate to longer-term patterns of granivory. Adding seeds to the soil surface within cages that controlled rodent access provided a measure of how short-term foraging behaviour compared with longer-term impacts on seed survival under more natural conditions. Predation rates of *L. ruderalis* seeds after six weeks were quite high, a result confirmed by longer-term experiments (Bricker *et al.* 2010; M. Bricker, D.E. Pearson and J.L. Maron, unpublished data). However, the magnitude of predation on seeds did not vary across plots with and without predators in our longer-term seed cage experiments. Thus, the behavioural responses mice exhibit in short-term feeding experiments can attenuate over longer time periods and under more realistic foraging conditions. This conclusion has been echoed in other studies (Kelt *et al.* 2004; Zwolak *et al.* 2010; but see Pearson & Callaway 2008).

Ungulate exclusion strongly affected both graminoid biomass and litter accumulation (litter was principally composed of graminoids, personal observation), with much stronger effects on litter. The difference in grass production between ungulate exclusion and control plots ranged from 23.1 to 33.7 g/m², whereas the difference in litter accumulation between ungulate exclusion and control plots ranged from -28 to 205 g/m². It is likely that ungulate effects on litter represent the accumulated impacts of herbivory across several seasons. In fact, the year before we sampled litter biomass (2009) grass production and flowering was unusually high (J.L. Maron & D.E. Pearson, personal observation). It is well appreciated that in semi-arid grasslands such as those we work in, graminoid litter often takes several seasons to decompose (Vossbrinck *et al.* 1979) and domestic and wild grazing can reduce long-term litter accumulations (Naeth *et al.* 1991).

This study is one of only a handful of large-scale, long-term, replicated experiments to explore how strongly vertebrate predators indirectly influence terrestrial plant production. However, the spatial scale of our work necessitated a relatively small sample size ($n = 4$). Although this compromises statistical power, even at the level of trends we found no obvious signature that predators might have indirect effects on primary production (Figs. 3 and 4). For example, the difference in primary production between rodent exclusion and paired control subplots is *less* on plots where predators are excluded compared with ungulate only exclusion plots. This trend is in the opposite direction of what one would predict from a classic trophic cascade, where consumers should have greater impacts on vegetation on predator exclusion plots compared with plots open to predators. Our results are somewhat comparable with those obtained in a similar experiment conducted in a semi-arid scrub community in Chile, where it was found that predators had weak cascading effects on plants (Gutiérrez *et al.* 1997; Meserve *et al.* 2003). In Chile, the relative strength of top-down versus bottom-up effects varied largely as a function of El Niño Southern Oscillation events. During peaks in

resource abundance fuelled by high rainfall years, the strength of top-down control increased (Meserve *et al.* 2003). Our system does not exhibit the strong interannual pulses of rainfall that drive large-amplitude variation in primary production characteristic of desert or semi-desert systems. However, in our system, primary production is limited by rainfall and this may in-turn limit rodent populations from the bottom-up. For example, in grasslands similar to ours, ground squirrels and deer mice populations can be food-limited (Dobson & Oli 2001; Pearson & Fletcher 2008). Thus, there may be limited scope for predators to exert a strong top-down influence, possibly due to the nature of resource limitation of the herbivores in our grasslands (Schmitz 1993). Manipulation of resource inputs in this system could provide an interesting test for how resources might influence the strength of trophic cascades (Schmitz 2008). More generally, our results serve as an important counterpoint to small scale studies involving simpler food webs and suggest that cascading indirect effects of predators may be less pervasive in terrestrial systems than some have suggested. The challenge for the future is to determine the conditions under which impacts of predators are propagated through terrestrial food webs and the conditions where these impacts may be large or small. Larger-scale experiments in complex natural systems will be critical if we are to meet this challenge.

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REFERENCES

Beckerman, A.P., Uriarte, M. & Schmitz, O.J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc. Natl. Acad. Sci. USA*, 94, 10735–10738.

Beschta, R.L. & Ripple, W.J. (2009). Large predators and trophic cascades in terrestrial ecosystems of western United States. *Biol. Conserv.*, 142, 2401–2414.

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B. *et al.* (2005). What determines the strength of a trophic cascade? *Ecology*, 86, 528–537.

Bricker, M., Pearson, D. & Maron, J.L. (2010). Small mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. *Ecology*, 91, 85–92.

Brown, J.S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.*, 22, 37–47.

Brown, J.S., Kotler, B.P., Smith, R.J. & Wirtz, W.O. II (1988). The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*, 76, 408–415.

Carpenter, S.R. & Kitchell, J.F. (1993). *The Trophic Cascade in Lake Ecosystems*. Cambridge University Press, Cambridge, UK.

Dobson, F.S. & Oli, M.K. (2001). The demographic basis of population regulation in Columbian ground squirrels. *Am. Nat.*, 158, 236–247.

Dyer, L.A. & Letourneau, D.K. (1999). Trophic cascades in a complex, terrestrial community. *Proc. Natl. Acad. Sci. USA*, 96, 5072–5076.

Fukami, T. *et al.* (2006). Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol. Letts.*, 9, 1299–1307.

Gomez, J.M. & Zamora, R. (1994). Top-down effects in a tritrophic system: parasitoids enhance plant fitness. *Ecology*, 75, 1023–1030.

Gutiérrez, J.R., Meserve, P.L., Herrera, S., Contreras, L.C. & Jaksic, F.M. (1997). Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia*, 109, 398–406.

Halaj, J. & Wise, D.H. (2001). Terrestrial trophic cascades: how much do they trickle? *Am. Nat.*, 157, 262–281.

Kauffman, M.J., Brodie, J.F. & Jules, E.S. (2010). Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology*, 91, 2742–2755.

Kelt, D.A., Meserve, P.L., Nabors, K., Forister, M.L. & Gutiérrez, J.R. (2004). Foraging ecology of small mammals in semiarid Chile: the interplay of biotic and abiotic effects. *Ecology*, 85, 383–397.

Kotler, B.P., Brown, J.S. & Hasson, O. (1991). Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, 72, 2249–2260.

Kotler, B.P., Brown, J.S. & Bouskila, A. (2004). Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. *Ecology*, 85, 917–922.

Letourneau, D.K., Dyer, L.A. & Vega, G. (2004). Indirect effects of a top predator on a rain forest understory plant community. *Ecology*, 85, 2144–2152.

Maron, J.L., Estes, J.A., Croll, D.A., Danner, E.M., Elmendorf, S.C. & Buckalew, S. (2006). An introduced predator transforms Aleutian Island plant communities by disrupting spatial subsidies. *Ecol. Monogr.*, 76, 3–24.

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, 3719–3729.

McLaren, B.E. & Peterson, R.O. (1994). Wolves, moose and tree-rings on Isle Royal. *Science*, 266, 1555–1558.

Meserve, P.L., Kelt, D.A., Milstead, B. & Gutiérrez, J.R. (2003). Thirteen years of shifting top-down and bottom-up control. *Bioscience*, 53, 633–646.

Mooney, K.A. (2007). Tritrophic effects of birds and ants on a canopy food web, tree growth, and phytochemistry. *Ecology*, 88, 2005–2014.

Morris, D.W. & Davidson, D.L. (2000). Optimally foraging mice match patch use with habitat differences in fitness. *Ecology*, 81, 2061–2066.

Naeth, M.A., Bailey, A.W., Pluth, D.J., Chanasyk, D.S. & Hardin, R.T. (1991). Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. *J. Range Manage.*, 44, 7–12.

Pearson, D.E. & Callaway, R.M. (2008). Weed biocontrol insects reduce native plant recruitment through second-order apparent competition. *Ecol. Appl.*, 18, 1489–1500.

Pearson, D.E. & Fletcher, R.J. Jr (2008). Mitigating exotic impacts: restoring native deer mouse populations elevated by an exotic food subsidy. *Ecol. Appl.*, 18, 321–334.

Peckarsky, B.L. *et al.* (2008). Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology*, 89, 2416–2425.

Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501–509.

Ripple, W.J. & Beschta, R.L. (2007). Restoring Yellowstone's aspens with wolves. *Biol. Conserv.*, 138, 514–519.

Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biol. Conserv.*, 102, 227–234.

Schmidt, K.A. & Ostfeld, R.S. (2003). Mice in space: space use predicts the interaction between mice and songbirds. *Ecology*, 84, 3276–3283.

Schmitz, O.J. (1993). Trophic exploitation in grassland food chains: simple models and a field experiment. *Oecologia*, 93, 327–335.

Schmitz, O.J. (2006). Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology*, 87, 1432–1437.

Schmitz, O.J. (2008). Herbivory from individuals to ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, 39, 133–152.

- Schmitz, O.J., Hambäck, P. & Beckerman, A.P. (2000). Trophic cascades in terrestrial systems: a review of the effect of top predator removals on plants. *Am. Nat.*, 155, 141–153.
- Schmitz, O.J., Krivan, V. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.*, 7, 153–163.
- Shurin, J.B., Gruner, D.S. & Hillebrand, H. (2005). All wet or dried up? Real differences between aquatic and terrestrial food webs. A cross-ecosystem comparison of the strength of trophic cascades *Proc. R. Soc. B*, 273, 1–9.
- Sinclair, A.R.E. *et al.* (2000). Testing hypotheses of trophic level interactions: a boreal forest ecosystem. *Oikos*, 89, 313–328.
- Spiller, D.A. & Schoener, T.W. (1994). Effects of top and intermediate predators in a terrestrial food web. *Ecology*, 75, 182–196.
- Terborgh, J., Feeley, K., Silman, M., Nunez, P. & Balukjian, B. (2006). Vegetation dynamics of predator-free land-bridge islands. *J. Ecol.*, 94, 253–263.
- Vossbrinck, C.R., Coleman, D.C. & Woolley, T.A. (1979). Abiotic and biotic factors in litter decomposition in a semiarid grassland. *Ecology*, 60, 265–271.
- Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.
- Yunger, J.A., Meserve, P.L. & Gutiérrez, J.R. (2002). Small mammal foraging behavior: mechanisms for coexistence and implication for population dynamics. *Ecol. Monogr.*, 72, 561–577.
- 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, 1124–1131.

SUPPORTING INFORMATION

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

Appendix S1 Results from rMANOVAS (Tables S1–S3).

Table S1 Table from rMANOVA comparing mean graminoid or forb biomass (log transformed) among treatments (control, predator and ungulate exclusion and ungulate exclusion only).

Table S2 Table from rMANOVA comparing mean graminoid or forb biomass (log transformed) between predator and ungulate exclusion and ungulate exclusion only plots combined with control plots.

Table S3 Table from rMANCOVA comparing mean: (a) *L. sericeus* seeds left in seed trays and (b) number of seed trays visited (defined as trays missing ≥ 5 *L. sericeus* seeds) among treatments (control, predator and ungulate exclusion, and ungulate exclusion only).

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