

# Elk herbivory alters small mammal assemblages in high-elevation drainages

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## Summary

1. Heavy herbivory by ungulates can substantially alter habitat, but the indirect consequences of habitat modification for animal assemblages that rely on that habitat are not well studied. This is a particularly important topic given that climate change can alter plant–herbivore interactions.

2. We explored short-term responses of small mammal communities to recent exclusion of Rocky Mountain elk (*Cervus elaphus*) in high-elevation riparian drainages in northern Arizona, where elk impacts on vegetation have increased over the past quarter century associated with climate change. We used 10-ha elk exclosures paired with unfenced control drainages to examine how browsing influenced the habitat use, relative abundance, richness and diversity of a small mammal assemblage.

3. We found that the small mammal assemblage changed significantly after 5 years of elk exclusion. Relative abundance of voles (*Microtus mexicanus*) increased in exclosure drainages, likely due to an increase in habitat quality. The relative abundances of woodrats (*Neotoma neomexicana*) and two species of mice (*Peromyscus maniculatus* and *P. boylii*) decreased in the controls, while remaining stable in exclosures. The decline of mice in control drainages was likely due to the decline in shrub cover that they use. Thus, elk exclusion may have maintained or improved habitat for mice inside the exclosures while habitat quality and mouse abundance both declined outside the fences. Finally, small mammal species richness increased in the exclosures relative to the controls while species diversity showed no significant trends.

4. Together, our results show that relaxation of heavy herbivore pressure by a widespread native ungulate can lead to rapid changes in small mammal assemblages. Moreover, exclusion of large herbivores can yield rapid responses by vegetation that may enhance or maintain habitat quality for small mammal populations.

**Key-words:** *Cervus elaphus*, deer mice, exclosure, habitat quality, herbivory, indirect effects, northern Arizona, Rocky Mountain elk, small mammals, voles

## Introduction

Individual species can indirectly affect co-occurring heterospecifics by altering their habitat (Jones, Lawton & Shachak 1997; Pringle 2008). These species, referred to commonly as ecosystem engineers, have the ability to modify resources available to other species in a community (Jones, Lawton & Shachak 1994, 1997; Fox-Dobbs *et al.* 2010). Habitat modifiers can increase the richness and abundance of sympatric species if they create new habitats (Crooks 2002), or if they increase habitat

heterogeneity by creating a mosaic of engineered and non-engineered patches on the landscape (Jones, Lawton & Shachak 1997). Habitat modifiers can also decrease the richness and abundance of co-occurring species if they lower overall habitat quality (Keasing 1998; McCauley *et al.* 2006, 2008; Ogada *et al.* 2008). These negative effects are particularly poorly understood because they are less dramatic than the wholesale destruction or creation of habitat that some engineering species impose. Experiments that test the impacts of these habitat modifiers on other members of the community are critically needed (Wright & Jones 2004; Suominen & Danell 2006; Pringle *et al.* 2007).

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Ungulates can act as ecosystem engineers through their strong impacts on general features of habitat (Persson 2003). Due to their high energy requirements and increased density compared with historic density in many locales (Côté *et al.* 2004; McGraw & Furedi 2005), species such as deer and elk (family: Cervidae) can strongly modify vegetation structure (McNaughton, Ruess & Seagle 1988; Russell, Zippin & Fowler 2001; Rooney & Waller 2003; Danell *et al.* 2006; Martin 2007). Reductions in vegetative cover due to ungulate browsing have the potential to reduce the abundance and diversity of species that rely on the three-dimensional structure of vegetation as habitat (Grant *et al.* 1982; Smit *et al.* 2001). For example, large herbivores can reduce bird abundance and diversity by decreasing the cover of shrubs and saplings (McShea & Rappole 1997; Berger *et al.* 2001; Martin 2007; Ogada *et al.* 2008; Martin & Maron 2012). Alternatively, large herbivores can increase the abundance and diversity of co-occurring species when their activities create habitat (Feber *et al.* 2001; WallisDeVries & Raemakers 2001). Whether large herbivores increase or decrease abundance and diversity of co-occurring species will likely depend on several factors including herbivore density, productivity and the specific life history requirements of the co-occurring species (Crooks 2002; Rooney & Waller 2003; Côté *et al.* 2004; Rooney *et al.* 2004; Pringle *et al.* 2007).

One factor that has great potential to influence the impacts of large herbivores on vegetation and habitat is climate change (Post & Pedersen 2008; Olofsson *et al.* 2009; Brodie *et al.* 2012). Changes in temperature and precipitation can influence plant tolerance to herbivory, plant quality and quantity for herbivores, and the response of herbivores to plants (Post & Pedersen 2008; Wookey *et al.* 2009; Brodie *et al.* 2012). In our system of snow melt drainages within high-elevation forest in Arizona, USA, climate change has led to dramatic declines in snowfall over the last 25 years (Martin 2007; Martin & Maron 2012). These declines in snowpack have been coincident with declines in deciduous tree abundance and other components of vegetation (Martin 2007; Martin & Maron 2012). Change in vegetation and habitat structure appears driven not by the direct effects of reduced snowpack on vegetation, but instead by snowfall influences on elk (*Cervus elaphus*) herbivory (Martin & Maron 2012). Specifically, deep snow at our site, as in other locales, causes elk to move to lower elevations, which reduces herbivore pressure on plants (Sweeney & Steinhoff 1976; Brown 1994; Brodie *et al.* 2012). Long-term declines in snow fall have enabled elk to spend more time browsing during winter at our high-elevation sites, increasing their negative impacts on vegetation. Excluding elk from drainages where vegetation has declined in concert with declining snowfall has led to rapid recovery of vegetation (Martin & Maron 2012).

Here, we examine how these changes in vegetation from elk herbivory, as influenced by climate change, influence rodent communities. While there has been much concern

about how climate change might directly influence the phenology, abundance or distribution of species (Parmesan 2006; Kelly & Gouldey 2008; Moritz *et al.* 2008; Sinervo *et al.* 2010), less work has examined the potential for indirect climate change effects through altered plant–animal interactions. Small mammal populations are often influenced by microhabitat characteristics such as protective cover and vegetation complexity (Birney, Grant & Baird 1976; Dueser & Porter 1986). We know from a handful of studies that ungulates can influence small mammal assemblages by changing habitat characteristics, although the vast majority of research has examined impacts of domestic grazers (Schmidt *et al.* 2005; Steen, Myserud & Austrheim 2005; Torre *et al.* 2007; Appendix S1, Supporting information). Thus, if climate change is altering the strength of elk herbivory on vegetation, there is great potential for climate change impacts to indirectly influence rodent assemblages. To test this, we compared rodent populations in drainages that had been recently fenced (starting in autumn 2004) and where vegetation was rapidly recovering from high herbivory (Martin & Maron 2012) with unfenced drainages where vegetation has continued to decline due to reduced snowfall and increased herbivory (Martin & Maron 2012).

## Materials and methods

### STUDY SITES

Our study sites were a series of parallel high-elevation (2300 m) drainages along the Mogollon Rim in Coconino National Forest in north-central Arizona, USA. The canopy vegetation in these drainages is characterized by aspen (*Populus tremuloides*, Michx.), canyon maple (*Acer grandidentatum*, Nutt.), New Mexico locust (*Robinia neomexicana*, A. Gray), Gambel oak (*Quercus gambelii*, Nutt.), white fir (*Abies concolor*, Gordon), Douglas fir (*Pseudotsuga menziesii*, Mirb.), white pine (*Pinus monticola*, Douglas) and ponderosa pine (*Pinus ponderosa*, Douglas). The woody understory vegetation includes Utah serviceberry (*Amelanchier utahensis*, Koehne), blue elderberry (*Sambucus nigra*, Linnaeus) and other shrubs in the family Rosaceae. Dominant herbs include western brackenfern (*Pteridium aquilinum*, Linnaeus), Owl's claws (*Hymenoxys hoopesii*, A. Gray), spreadfruit goldenbanner (*Thermopsis divaricarpa*, A. Nelson) and Canadian white violet (*Viola canadensis*, Linnaeus). Further description of the study site can be found in Martin (1998, 2007).

The large mammalian herbivores that use these drainages are Rocky Mountain elk (*Cervus elaphus nelsoni*, Linnaeus), mule deer (*Odocoileus hemionus*, Rafinesque) and Coues white-tailed deer (*Odocoileus virginianus couesi*, Zimmermann). Rocky Mountain elk were by far the most abundant large herbivore in our system (in 2007 and 2008, they produced 97% of the ungulate scat piles on our study drainages, unpublished results). Rocky Mountain elk were introduced to northern Arizona from Yellowstone National Park in 1913 (Arizona Game & Fish Department 2010), roughly 30 years after the native elk subspecies (*Cervus elaphus merriami*, Linnaeus) became extinct (Truett 1996). We commonly see elk on our sites, as well as evidence of heavy herbivory in the drainages (Martin 2007; Martin & Maron 2012).

The small mammals that use these high-elevation drainages include: rock squirrel (*Spermophilus variegatus*, Erxleben), American red squirrel (*Tamiasciurus hudsonicus*, Erxleben), Mexican woodrat (*Neotoma mexicana*, Baird), northern pocket gopher (*Thomomys talpoides*, Richardson), grey-collared chipmunk (*Tamias cinereicollis*, J.A. Allen), Mexican vole (*Microtus mexicanus*, Saussure), brush mouse (*Peromyscus boylii*, Baird), deer mouse (*Peromyscus maniculatus*, Wagner) and Merriam's shrew (*Sorex merriami*, Dobson). Deer mice and brush mice are similar in size and appearance and were only successfully distinguished after early summer 2006.

To determine how elk herbivory affects small mammal communities, we identified three pairs of drainages (six drainages total) in large canyons near the rim of the Mogollon Plateau. Each drainage pair within a canyon was separated by *c.* 200 m, and canyons containing pairs of drainages were separated by *c.* 2 km. We randomly assigned one drainage from each pair to receive an ungulate exclusion treatment (see Appendix S2, Supporting information for detailed locations). This consisted of a 2.5-m tall fence that was attached to metal fence posts 0.3 m above ground level to allow predator access. Fences had two strands of high-tension wire above them to bring the fence to a height of 3 m. Each fence enclosed a 10-ha section of drainage, which comprised the majority of each drainage. Fences were constructed during fall 2004, and paired control drainages were left unfenced. The fences excluded elk but not black bears (*Ursus americanus*, Pallas), coyotes (*Canis latrans*, Say) and mountain lions (*Puma concolor*, Linnaeus). White-tailed deer occasionally entered the enclosures; however, their numbers were fairly low and impacts minimal.

#### TRAPPING PROTOCOL

We captured small mammals during the summers of 2004–2009 using both Sherman (8 × 9 × 23 cm) and Tomahawk (13 × 13 × 41 cm) live traps. In each summer, we had three primary trapping sessions (in May, June and July) with each session lasting 4 days and three nights. Sherman traps were placed on a permanently marked 10 × 25 trapping grid (250 traps total with 10-m spacing) located at the centre of each enclosure and control drainage. Trapping grids encompassed the more mesic drainage bottoms to halfway up the xeric ridges and thus included a range of vegetation and habitat features. In addition to Sherman traps, 25 Tomahawk traps were placed on the trapping grid so we could catch the larger rodents. These were placed on alternating grid lines at every third and seventh trap station.

During each trapping period, traps were baited with a combination of rolled oats and bird seed scented with peanut butter (Shermans) or unshelled peanuts (Tomahawks) and were covered with closed-cell foam for protection from heat and cold. Traps were checked once in early morning and once before night fall of each day. We simultaneously trapped animals on each drainage of a pair, and traps were moved to the next drainage pair after each 3-day, four-night trapping session was completed. During the entire study, drainage pairs were always trapped in the same order each summer beginning with the most easterly pair and ending with the westernmost pair. All trapped animals were given a uniquely numbered metal Monel ear tag (National Band and Tag Company, Newport, KY, USA). Because shrews and northern pocket gophers were rarely captured, they were not included in the analyses.

#### RELATIVE ABUNDANCE, DIVERSITY AND SPECIES RICHNESS

We calculated the relative abundance of all species (in all drainages and for all primary trapping sessions) as the number of unique individuals captured divided by sampling effort (Beauvais & Buskirk 1999; Appendix S3, Supporting information). We used unique individuals rather than rate of all captures to eliminate any biases induced by individuals that avoid or seek out traps. We estimated relative abundance using an index rather than a population estimator such as those provided in Program MARK (White & Burnham 1999) because we were primarily interested in the relative difference in abundance between treatments as opposed to an absolute estimate of abundance. In addition, examining paired differences allowed us to take full advantage of the paired-plot design: trapping dates were held constant within a pair allowing us to control for weather, day length, moon cycles, etc., and thus the overall trapping environment between pairs. We calculated relative abundance for each species separately as mean paired differences across the three trapping periods (enclosure–control) by year (see Appendix S3, Supporting information for detailed description of methods).

We determined whether elk exclusion influenced small mammal species richness and diversity (Shannon's  $H'$ , calculated as  $-\sum(\rho_i \times \ln \rho_i)$  with  $\rho_i$  as the proportion of unique captures for each species out of the total number of unique animals captured) by calculating paired differences in these variables for each drainage pair within each trapping period and year. For this analysis, we only examined 2006–2009 data because deer mice and brush mice were only successfully differentiated after May 2006. We predicted that all of the small mammal species we trapped often in the smaller Sherman traps (voles, deer mice, brush mice, chipmunks and rats) would increase in abundance inside of the enclosures due to an increase in their food resources (e.g. grasses, herbs, increased berry and seed production from increased plant production in enclosures, etc.).

#### RED SQUIRREL SURVEYS

Red squirrels were abundant in the drainages (E. Parsons, pers. obs.), but we did not capture them often in our traps. Thus, as an alternative method to estimate red squirrel relative abundance, in July of each summer from 2006 to 2009, we counted the number of middens along thirteen 100-m transects located along every other trap line on each trapping grid. Middens at our field site are a combination of stored food resources and collections of conifer litter that has accumulated from feeding (Uphoff 1990). A red squirrel may often have multiple smaller middens near its largest primary midden; therefore, we only counted large primary middens. Furthermore, we only counted active middens where there was evidence of recent use (i.e. fresh cone parts). The number of active primary middens is a good index of relative abundance for red squirrels because they are often centrally located within an individual's territory, and the stored resources are critical for over-winter survival (Réale *et al.* 2003). We predicted that enclosures would not affect red squirrel abundance (or midden number), because the primary food source (fir cones) would not likely be affected by elk browsing.

## MICROHABITAT SELECTION

In summer 2007, we estimated the per cent cover of grasses, forbs, shrubs, woody debris, bare ground and deciduous litter in a 5-m-radius circle around a randomly chosen subset of trapping points where deer mice were either captured or not ( $n = 99$  each), and also around 84 randomly selected trapping points where brush mice were either captured or not ( $n = 42$  each).

Shrub cover, an important habitat characteristic for small mammals, was similar in 2007 as compared with the long-term average from 2004 to 2009 (unpublished results); thus, habitat characteristics of 2007 are a good representation of average conditions across the length of the study. We chose deer and brush mice because we had a relatively large number of captures of each compared with the other species. Per cent cover of deciduous litter is correlated with the number of maple and aspen stems, and thus represents an index of microhabitat that is dominated by these deciduous species (Appendix S4, Supporting information). See Martin (1998) for further details regarding vegetation sampling design.

## STATISTICAL ANALYSES

We used ANCOVA with ordinary least squares estimation to test whether paired differences in small mammal relative abundance, richness and diversity between ungulate exclusion and control drainages changed significantly between 2004 and 2009. Such a change would indicate that small mammal species progressively got more or less abundant on one of the three paired drainages through time. We used these paired differences in the relative abundance of each small mammal species as dependent variables, and we treated the identity of each drainage pair as a fixed factor and year as a covariate. We included the interaction between year and drainage identity to test whether the slopes for each drainage pair differed. We removed interaction terms from the model when they were not significant. When interactions were significant, we conducted ANOVA by drainage pair to determine where the difference occurred. Levene's test was used to test for homogeneity of variances, and all models were checked to make sure that residual errors were normally distributed.

To test whether year explained more variation in paired differences in relative abundance using a curvilinear model instead of a linear model, we log transformed paired differences and conducted the same analyses as above (see Appendix S5, Supporting information for details). To determine whether observed changes in paired differences were due to changes occurring in exclosures or control drainages (i.e. a positive change in paired differences could be due to an increase in exclosures, a decrease in controls or both), we regressed both exclosure and control relative abundance estimates against paired differences and examined the significance and coefficients of determination. We also used forward stepwise regression to determine which species or combination of species explained the most variation in paired differences in species richness.

To determine whether the number of red squirrel middens changed in exclosures relative to controls, we used generalized estimating equations (GEE) using a poisson distribution with a log-link function (Torre *et al.* 2007) because the middens are repeated count data. We specified plot as the subjects variable, year as the within (repeated) subjects variable, midden number as the dependent variable, and treatment and year and their

interaction as predictors. We used generalized linear models to look for individual treatment effects within each year.

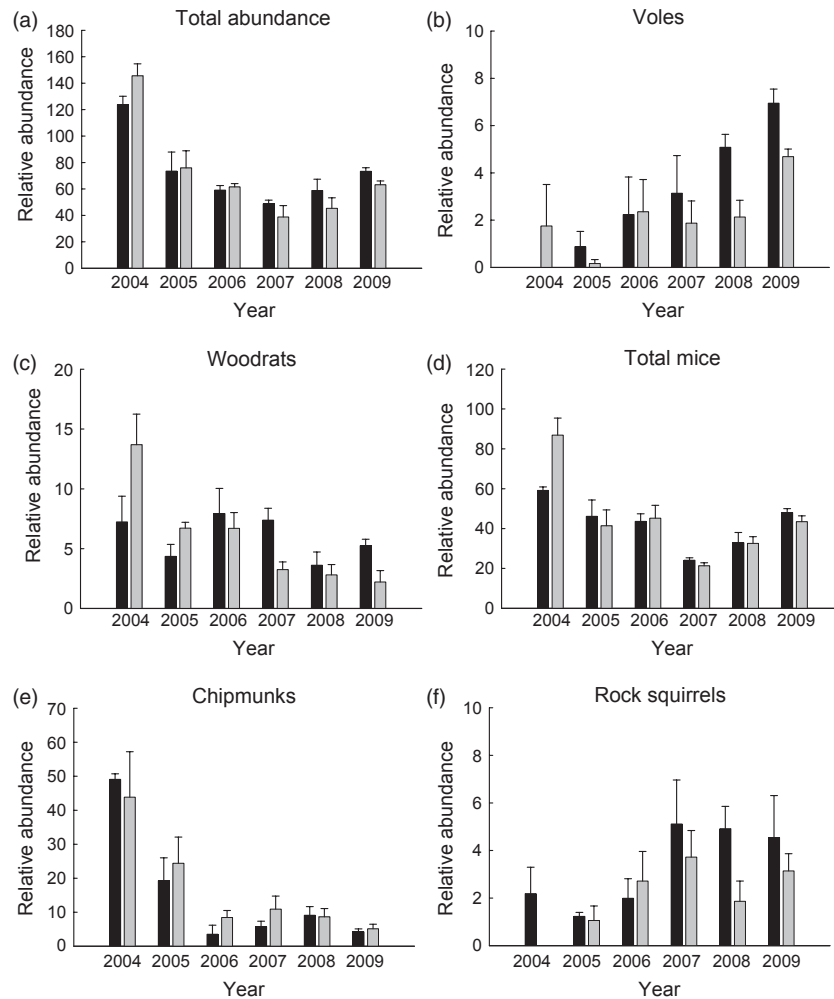
Finally, to determine which microhabitat variables were selected by brush and deer mice, we used logistic regression (Hosmer & Lemeshow 2000; Manly *et al.* 2002) with presence-absence data for each species as dependent variables, and arcsin square-root transformed vegetation variables as covariates. Elk exclusion treatment was also included as a categorical fixed factor to determine whether there was an effect of treatment on the selection of habitat variables (e.g. mice might select different habitat types inside vs. outside of the exclosures). We used a forward stepwise procedure (Sergio, Pedrini & Marchesi 2003) with the enter value of 0.10 and removal value of 0.15 because the more traditional enter value of 0.05 may fail to identify important variables (Mickey & Greenland 1989; Hosmer & Lemeshow 2000). Furthermore, we tested all statistical models for normality and homogeneity of variances to make sure model assumptions were met. All statistical analyses were conducted using spss version 17 (SPSS, Chicago, IL, USA).

## Results

## Small Mammal Response

We captured seven small mammal species and a total of 4153 animals of 109 400 trap nights between May 2004 and July 2009 (Appendix S6, Supporting information). Paired differences (exclosure-control) in the total relative abundance of all animals increased on exclosure drainages as compared with control drainages between 2004 and 2009 ( $F_{1,14} = 12.11$ ,  $R^2 = 0.54$ ,  $P = 0.004$ ; Fig. 1a). Specifically, animals were more abundant on control drainages in the beginning and became more abundant on exclosures by the end (Fig. 1a). The increase in paired differences in total abundance on exclosures relative to controls was driven mostly by a decline on control drainages. Control abundance explained 64.2% of the variation and was negatively associated with paired differences ( $F_{1,14} = 19.47$ ,  $P = 0.001$ ) while exclosure abundance explained only 32.2% of the variation and was only marginally positively associated with paired differences ( $F_{1,14} = 3.65$ ,  $P = 0.08$ ). Changes in paired differences in total abundance between 2004 and 2009 were significantly related to paired differences in the relative abundance of voles (voles:  $F_{1,14} = 9.97$ ,  $P = 0.007$ ; drainage pair:  $F_{2,14} = 0.35$ ,  $P = 0.71$ ) and woodrats (woodrats:  $F_{1,14} = 6.29$ ,  $P = 0.025$ ; drainage pair:  $F_{2,14} = 1.04$ ,  $P = 0.38$ ), but not to any of the other small mammal species.

Paired differences in the relative abundance of voles increased within exclosures relative to controls through time ( $F_{1,14} = 6.94$ ,  $R^2 = 0.44$ ,  $P = 0.02$ ; Fig. 1b). Paired differences were positively associated with exclosure relative abundance ( $F_{1,14} = 16.58$ ,  $R^2 = 0.62$ ,  $P = 0.001$ ), but not significantly associated with control relative abundance ( $F_{1,14} = 0.61$ ,  $P = 0.45$ ). Paired differences in woodrat relative abundance increased on two of the three drainage pairs (significant drainage pair\*year interaction



**Fig. 1.** Mean ( $\pm$  SEM) relative abundance (number of individuals captured) for (a) small mammal, (b) vole, (c) woodrat, (d) all mice, (e) chipmunk and (f) rock squirrel by year. Black bars represent enclosure drainages; grey bars represent non-fenced control drainages.

$F_{2,12} = 3.80$ ,  $P = 0.05$ ; Fig. 1c). When we tested each drainage pair separately, woodrat paired differences increased on both Buck Springs drainages ( $F_{1,4} = 58.2$ ,  $R^2 = 0.94$ ,  $P = 0.002$ ) and McClintock drainages ( $F_{1,4} = 8.33$ ,  $R^2 = 0.68$ ,  $P = 0.045$ ), but not on Dane ridge drainages ( $F_{1,4} = 0.24$ ,  $P = 0.86$ ). The increase in paired differences was mostly driven by declines in relative abundance in the control drainages; control abundance was negatively associated with paired differences ( $F_{1,14} = 33.12$ ,  $R^2 = 0.44$ ,  $P < 0.001$ ).

We also found an increase in paired differences in the relative abundance of both *Peromyscus* species combined on enclosures compared to controls ( $F_{1,14} = 6.95$ ,  $R^2 = 0.4$ ,  $P = 0.02$ ; Fig. 1d). Similar to woodrats, this increase in paired differences was mostly explained by a decrease in control drainages. Control abundance explained 76.8% of the variation in paired difference and was negatively associated with paired differences ( $F_{1,14} = 40.13$ ,  $P < 0.001$ ).

Paired differences in the relative abundance of deer mice showed no significant trends across years

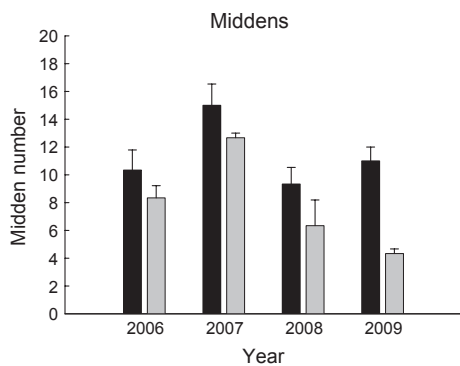
( $F_{1,8} = 0.99$ ,  $P = 0.35$ ), whereas changes in brush mice across years depended on the particular drainage pair (year\* drainage pair:  $F_{2,6} = 5.81$ ,  $P = 0.039$ ). Paired differences in relative abundance of brush mice declined on the McClintock drainages ( $F_{1,2} = 14.26$ ,  $P = 0.064$ ), but did not change in either of the other two drainage pairs (Buck Springs ridge:  $F_{1,2} = 1.58$ ,  $P = 0.34$ ; Dane ridge,  $F_{1,2} = 3.02$ ,  $P = 0.23$ ).

Chipmunks showed no change inside of the enclosures relative to the control drainages between 2004 and 2009 ( $F_{1,14} = 0.092$ ,  $P = 0.77$ ; Fig. 1e). However, when an outlier in 2004 was removed, paired differences increased significantly over time ( $F_{1,13} = 4.69$ ,  $P = 0.05$ ). Paired differences in relative abundance for rock squirrels interacted with year (drainage pair\*year:  $F_{2,12} = 3.46$ ,  $P = 0.065$ , Fig. 1f). Rock squirrel paired differences decreased on Buck Springs drainages ( $F_{1,4} = 6.44$ ,  $P = 0.064$ ), but not on Dane drainages ( $F_{1,4} = 2.67$ ,  $P = 0.18$ ) or McClintock drainages ( $F_{1,4} = 0.32$ ,  $P = 0.60$ ). During this same time period, we found a highly significant treatment\*year interaction for red squirrel middens

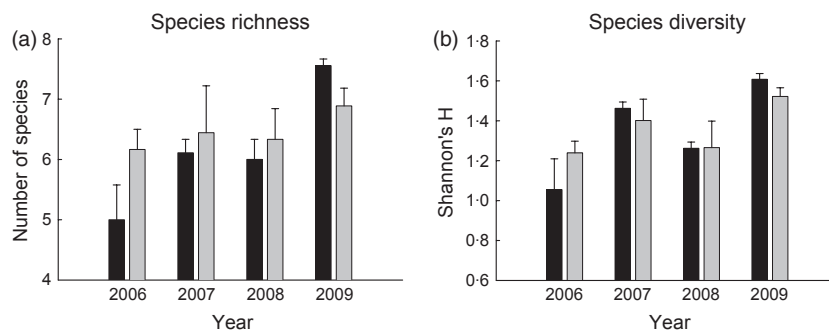
between 2006 and 2009 (Wald = 898.12, d.f. = 3,  $P < 0.001$ ), with significantly more middens on exclosures relative to control drainages in 2009 (Wald  $\chi^2 = 8.09$ , d.f. = 1,  $P = 0.004$ ; Fig. 2). This difference in midden number was partially explained by a decrease in control drainages; control midden abundance explained 38% of the variation in midden paired differences and was negatively associated with paired differences ( $F_{1,10} = 6.08$ ,  $P = 0.033$ ). Finally, year explained a greater proportion of the variation in untransformed than log-transformed paired differences in relative abundance for total abundance, total mice and voles (Appendix S5, Supporting information).

#### SPECIES RICHNESS AND DIVERSITY

Paired differences in small mammal species richness increased between 2006 and 2009 on exclosure drainages compared with control drainages ( $F_{1,8} = 4.59$ ,  $P = 0.065$ ; Fig. 3a). This change was driven by an increase in species richness in exclosures as paired differences were positively associated with exclosure richness ( $F_{1,8} = 9.7$ ,  $R^2 = 0.56$ ,  $P = 0.014$ ), but not control richness ( $F_{1,8} = 1.4$ ,  $R^2 = 0.17$ ,



**Fig. 2.** Mean ( $\pm$  SEM) number of red squirrel middens, 2006 through 2009. Black bars represent exclosure drainages; grey bars represent non-fenced control drainages. Differences (exclosure–control) increased through time, and there were significantly more red squirrel middens in exclosures compared with control drainages in 2009.



**Fig. 3.** Mean ( $\pm$  SEM) in (a) species richness between June 2006 and July 2009 and (b) species diversity (Shannon's H) during the same time period.

$P = 0.27$ ). Also, forward stepwise regression showed that paired differences in species richness were significantly associated with paired differences in woodrats ( $F_{1,10} = 5.45$ ,  $R^2 = 0.59$ ,  $P = 0.042$ ), which was the only species in the model. Finally, species diversity (Shannon's H) did not change between fenced and control drainages during the same time period ( $F_{1,8} = 2.15$ ,  $P = 0.18$ ; Fig. 3b).

#### MICROHABITAT SELECTION

Shrubs, woody debris and deciduous cover were all important predictors of abundance for both species of *Peromyscus* (deer mice:  $\chi^2 = 43.88$ , d.f. = 3,  $R^2 = 0.27$ ,  $P < 0.001$ , brush mice:  $\chi^2 = 19.83$ , d.f. = 3,  $R^2 = 0.29$ ,  $P < 0.001$ ). Specifically, deer mice selected habitats high in shrub cover and woody debris (shrubs,  $\beta = 1.39$ , Wald = 3.72, d.f. = 1,  $P = 0.05$ ; woody debris,  $\beta = 4.39$ , Wald = 15.41, d.f. = 1,  $P < 0.001$ ), and avoided habitats high in deciduous litter ( $\beta = -2.52$ , Wald = 17.18, d.f. = 1,  $P < 0.001$ ). Interestingly, brush mice selected all three cover types (shrubs,  $\beta = 2.6$ , Wald = 6.35, d.f. = 1,  $P = 0.01$ ; woody debris,  $\beta = 5.0$ , Wald = 8.11, d.f. = 1,  $P = 0.004$ , deciduous litter,  $\beta = 2.21$ , Wald = 4.6, d.f. = 1,  $P = 0.03$ ). Paired differences in shrub cover increased significantly between 2004 and 2009 (year:  $F_{1,14} = 8.71$ ,  $P = 0.011$ ; drainage pair:  $F_{2,14} = 4.1$ ,  $P = 0.04$ ;  $R^2 = 0.56$ ). Paired differences in shrub cover were positively associated with paired differences in the relative abundance of mice (Year:  $F_{1,14} = 26.04$ ,  $P < 0.001$ ; drainage pair:  $F_{2,14} = 1.22$ ,  $P = 0.32$ ;  $R^2 = 0.69$ , Appendix S7, Supporting information). Furthermore, paired differences in shrub cover were explained both by an increase inside ( $F_{1,16} = 9.27$ ,  $P = 0.008$ ,  $R^2 = 0.37$ ) and a decline outside of the exclosures ( $F_{1,16} = 11.65$ ,  $P = 0.004$ ,  $R^2 = 0.42$ ). Finally, elk exclusion did not influence selection for these three habitat variables ( $P = 0.14$ ), and no interactions between treatment and the habitat variables were significant in any of the models.

#### Discussion

Differences in the understory vegetation between exclosure and control drainages were visually dramatic in

2009. Cover of maple, aspen, New Mexico locust and various graminoids was greatly increased inside the exclosures as compared with outside (Martin & Maron 2012; Appendix S8, Supporting information). This difference in vegetation and habitat had large effects on the small mammal community, with these effects manifest over a relatively short 5-year time period (Fig. 1). Paired differences in voles increased significantly inside of all three exclosures due solely to increasing vole abundance inside the exclosures (Fig. 1b). However, mice, woodrats and the number of red squirrel middens declined on control drainages while remaining stable inside of exclosures during the same time period. Finally, the relative abundance of chipmunks and rock squirrels did not change on either exclosures or controls between 2004 and 2009. These results suggest that during this 5-year time period, the relative impacts of elk on small mammals differed among species.

Changes in small mammal communities may occur in areas where large mammalian herbivores are excluded because of asymmetrical competition (e.g. Keesing 1998, 2000). Asymmetrical competition may also explain why voles at our field site exhibited such a marked increase inside of the exclosures in such a short time period (Fig. 1b). Voles are mainly herbivorous (Lin & Batzli 2001), and they have a significant amount of grass in their diet (Haken & Batzli 1996). Similarly, a significant proportion of the summer diet of elk is also grass (Kufeld 1973), and we found higher grass cover inside of the exclosures in 2009 compared with control drainages (Appendix S8, Supporting information). The lack of changes in chipmunks or rock squirrels, however, implies that either elk did not affect the food resources of these species during the duration of this study, or some other factor (e.g. predators, disease, cover, etc.) is more important in the short term in influencing population dynamics for these species than is elk.

Not only did elk exclusion lead to increases in vole populations, but it also led to increased species richness of small mammals inside exclosures as compared with control drainages, an effect that increased through time (Fig. 3a). Other studies have shown higher small mammal species richness inside of ungulate exclosures (Eccard, Walther & Milton 2000). In fact, in a search of the literature, we found that out of 15 studies that quantified impacts of large herbivores (cattle in 12 of 15 studies) on small mammal richness, 9 or 60% showed unambiguous increases in species richness in areas where ungulates were excluded, while only 1 (7%) showed a decline inside exclosures and 5 (33%) showed no effect (Appendix S1, Supporting information). While we found no significant increase in small mammal diversity, 4 (50%) of eight studies in our literature review that also quantified impacts on diversity found increased small mammal diversity in areas where ungulates were excluded. However, half (four studies) found no effects on diversity while zero studies showed an increase in diversity. Although this pattern may be influenced by herbivore identity and density, study

duration and other interacting factors (such as disturbance), we suggest that large herbivorous mammals may commonly reduce the richness or diversity of smaller mammals through engineering effects on their habitat.

Across all the species studied, the effects of elk on small mammal numbers could not simply be explained by an increase in animal abundance inside exclosures, where vegetation rapidly recovered in the absence of elk herbivory (Martin & Maron 2012). The difference in relative abundance of woodrats, mice and the number of red squirrel middens on exclosures vs. control drainages was explained by declines on the control drainages with little change inside exclosure drainages. This decline in animal numbers through time on control drainages is likely explained by the continued degradation in habitat quality during the course of the study. We found that paired differences in shrub cover increased, and this was explained not only by an increase in shrub cover inside the exclosures, but a decline in shrub cover on control drainages. Furthermore, we found a strong association between paired differences of mice and shrubs, and logistic regression models showed that both *Peromyscus* species selected habitats high in shrub cover. Collectively, these results suggest that at least for mice, elk removal may have ameliorated the negative effects of habitat deterioration outside of the fences.

The decline in habitat quality on control drainages mirrors patterns we observed in drainages across the entire high-elevation habitat (which spans over 24 km along the Mogollon Rim; Martin 2007; pers. obser.). Thus, our results are not driven by the fact that we excluded elk from some drainages, which increased browsing pressure on nearby unfenced controls. Our fenced drainages represent a tiny fraction of available habitat for elk (30 hectares is <0.01% of the area of Coconino National Forest). Rather, long-term data does point towards an interaction between climate change and ungulate browsing as being an important driver of community structure at this site (Martin 2007; Martin & Maron 2012). Snowpack has declined for many years in the study area (Martin 2007; Martin & Maron 2012), and this has likely facilitated greater browsing pressure by elk at higher elevations during winter (Wambolt 1998; Campbell *et al.* 2005; Brodie *et al.* 2012). This has led to reductions in important deciduous tree species, including maple and aspen, as well as other changes in vegetation (Martin 2007; Martin & Maron 2012). Therefore, it is likely that declines in these tree species and associated declines in cover and food resources outside the fences have contributed to the declines in mice and woodrats (and possibly red squirrels), while habitat quality has been maintained or improved inside the fences.

Our results demonstrate that large wild ungulates can structure ecologically important co-occurring animal assemblages. These findings may have widespread significance, since large native ungulate abundance is much higher now than historically in many parts of the

United States (McShea, Underwood & Rappole 1997; Alverson, Waller & Solheim 1988; Allombert, Stockton & Martin 2005), and since climate change impacts on snow depth and hence winter herbivory will likely only increase through time. To the extent that these factors generally have a negative impact on small mammal abundance, richness and diversity, then small mammal communities may be impoverished in many regions. As well, herbivore-driven changes in habitat are likely to affect other species beyond small mammals. In our system, for example, breeding bird numbers as well as nest predation on those birds also differs substantially among fenced and unfenced drainages (Martin & Maron 2012). Thus, an important challenge for the future is understanding how animal populations respond to changes in habitat that might be driven by the direct effects of climate change (e.g. Moritz *et al.* 2008) as well as indirect effects stemming from altered ecological interactions. Moreover, as small mammals can have significant impacts on plant communities in their own right (Brown & Heske 1990), changes in small mammal distribution and abundance may feed back in important ways to influence community change (Rooney & Waller 2003; Goheen *et al.* 2004).

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## Supporting Information

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

**Appendix S1.** Studies that quantified the effects of large herbivores on small mammal community richness.

**Appendix S2.** The location and names of study drainages.

**Appendix S3.** Detailed description of methods for calculating paired differences in relative abundance.

**Appendix S4.** Details of the measurement of correlation between deciduous litter cover and the number of deciduous trees.

**Appendix S5.** A comparison of the coefficients of determination for linear models and log-transformed models for explaining changes in paired differences over time.

**Appendix S6.** Small mammal trapping summary results: 2004–2009.

**Appendix S7.** Positive association between changes in shrub cover and changes in mouse relative abundance.

**Appendix S8.** Differences in understory vegetation between exclosures and non-fenced controls in 2009.