

## Bottom-up control of consumers leads to top-down indirect facilitation of invasive annual herbs in semiarid Chile

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**Abstract.** The abundance of exotic plants is thought to be limited by competition with resident species (including plants and generalist herbivores). In contrast, observations in semiarid Chile suggest that a native generalist rodent, the degu (*Octodon degus*), may be facilitating the expansion of exotic annual plants. We tested this hypothesis with a 20-year data set from a World Biosphere Reserve in mediterranean Chile. In this semiarid environment, rainfall varies annually and dramatically influences cover by both native and exotic annual plants; degu population density affects the composition and cover of exotic and native annual plants. In low-rainfall years, cover of both native and exotic herbs is extremely low. Higher levels of precipitation result in proportional increases in cover of all annual plants (exotic and native species), leading in turn to increases in degu population densities, at which point they impact native herbs in proportion to their greater cover, indirectly favoring the expansion of exotic plants. We propose that bottom-up control of consumers at our site results in top-down indirect facilitation of invasive annual herbs, and that this pattern may be general to other semiarid ecosystems.

**Key words:** bottom up; ecosystem invasibility; exotic annual plants; facilitation; native annual plants; *Octodon degus*; semiarid coastal Chile; top down.

### INTRODUCTION

Biological invasions are recognized as important consequences of global change (e.g., climate change, disturbance in anthropogenic habitats, and synergistic effects of biotic exchanges). Because of the wide array of ecological and economic impacts that alien species have on invaded areas, this topic has attracted increasing attention from ecologists. The role of species interactions (competitive interactions in particular) in the expansion of exotic species is a central issue and underlies many popular hypotheses of their effects on native species (Levine et al. 2004). By definition, native and exotic plant species should compete whenever their niches (in particular, strategies for the acquisition of resources) overlap sufficiently (MacDougal et al. 2009), but these interactions may be mediated by other interactions, which may be pivotal to the success or failure of invasion. In semiarid ecosystems, years of extreme drought are characterized by an almost total absence of native annual plant germination (Vidiella and Armesto 1989, Ward 2009). When winter precipitation exceeds germination thresholds, however, annual plants initiate a short but intense race to successfully complete

growth and reproduction, often in only a few weeks (Mulroy and Rundel 1977). Eurasian annual plants that have successfully invaded many semiarid ecosystems of the Americas (e.g., *Erodium cicutarium*, *Schismus arabicus*) are drought tolerant, but, under more benign conditions, are less competitive than native herbs (Seabloom et al. 2003). Key to their success is their ability to grow under conditions of limited nutrient and water conditions, which probably is responsible for their proportionally higher cover in very dry years (Brooks and Berry 2006). Exotic annual species may even become dominant in semiarid ecosystem which suggests that other relevant processes are involved in the invasion; one such process is disturbance activities of humans and livestock grazing (HilleRisLambers et al. 2010).

Native herbivores may influence the expansion of exotic annuals in wet years through top-down control of native species (Maron and Vilà 2001). For example, the lack of coevolved relationships with native herbivores can enable exotic species to have a competitive advantage relative to native vegetation (Keane and Crawley 2002). Exotic species may be less impacted by herbivores in the new ecosystem as the latter are expected to be less efficient at consuming alien species. This classical perspective likely is particularly suited to specialist herbivores living in close association with one or more species of native plants (Levine et al. 2004). In contrast, a predominant negative effect may characterize

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generalist herbivores that impact plants in proportion to their density (Levine et al. 2004). By this mechanism, generalist herbivores may influence invasion dynamics by altering interactions among plants. Invasive species that are poor competitors may be facilitated by generalist herbivores due to their consumption of native vegetation, thereby reducing the competitive environment for the invasive species. Indirectly, both scenarios suggest that top-down regulation of vegetation by generalist herbivores would lead to a relatively steady equilibrium between native and exotic plants in the absence of other influences. Nevertheless, the underlying mechanisms by which generalist herbivores facilitate or hinder the expansion of exotic plants remain largely unknown; in particular, the influence of factors that control or govern interactions between herbivores and plants has received limited investigation (Maron and Vilà 2001).

Mediterranean Chile is one of the most invaded ecosystems of the world, making management of exotic species a major challenge for the conservation of biodiversity and the maintenance of ecological functions (Arroyo et al. 2000). We have surveyed the abundance of a native generalist rodent, the degu (*Octodon degus*), and the abundance of native and exotic annual plants for 20 years at a protected site in north-central Chile, near the northern border of the Mediterranean biome in Chile (Gajardo 1994). These surveys have been conducted within an experimental study including plots from which degus have been excluded, and control plots that allowed full access by degus. Degus are one of the larger and more abundant folivores in semiarid Chile and may have a key role in top-down regulation of plants during wet periods, when their populations may increase up to 30-fold (Meserve et al. 2003). Here we evaluate whether this generalist herbivore influences the expansion of exotic annual plants in semiarid Chile. If competition with native annuals hinders expansion by exotic species, then the latter must either overcome significant constraints in years of higher rainfall (when both groups of plants respond favorably to more benign conditions), or they must exhibit significant expansion in years of low water availability when competition with native species is reduced. During years of high precipitation and high density of degus, we predict that exotic annuals should be facilitated by degus through their consumption of more abundant native annual plants. Our experimental exclusion of degus has spanned several periods of dramatic variation in precipitation, allowing us to account simultaneously for the influence both of herbivore activity (top-down regulation) and precipitation (bottom-up regulation). Our approach emphasizes a holistic (e.g., community scale) view, assuring a more robust perspective for understanding how interactions that are regulated by bottom-up and top-down control may affect the invasion of exotic annual plants in a semiarid ecosystem.

## MATERIALS AND METHODS

### Study area

Our study area is in Bosque Fray Jorge National Park (71°40' W, 30°38' S; Fray Jorge hereafter), located on the coast of Chile approximately 100 km south of La Serena and 350 km north of Santiago (see Plate 1). This 10 000-ha park contains semiarid thorn scrub vegetation and remnant fog forest which have been protected from grazing and disturbance since 1941. The flora of the lower elevation scrub zone includes spiny drought-deciduous and evergreen shrubs and understory herbs on a primarily sandy substrate (Gutiérrez et al. 1993). The dominant shrub species are the evergreen *Porlieria chilensis* (Zygophyllaceae, 30% cover), the semi-deciduous *Adesmia bedwellii* (Papilionaceae, 5% cover), and the drought-deciduous *Proustia pungens* (Asteraceae, 6% cover). The climate is semiarid mediterranean with 90% of the 130 mm annual precipitation falling in winter (May–September). The El Niño Southern Oscillation (ENSO) promotes strong interannual variability of precipitation. Summer months are warm and dry. The small mammal assemblage is moderately diverse, and includes the rodents *Octodon degus*, *Abrocoma bennetti*, *Abrothrix longipilis*, *Abrothrix olivaceus*, *Phyllotis darwini*, *Oligoryzomys longicaudatus*, and the mouse opossum, *Thylamys elegans*. *Octodon degus* is a generalist herbivore species (folivore–granivore), and one of the largest and most abundant rodents in the system (Previtali et al. 2009, 2010).

### Sampling design and data recorded

In 1989, we established 16 75 × 75 m plots (0.56 ha) in a homogeneous habitat within a coastal valley, each separated by >50 m. Plots were randomly assigned to four treatments, two of which are relevant to this study. Four control plots have low (1 m) fencing buried 40 cm into the ground and provided with 2.5-cm holes at ground level every 2 m to allow access by all small mammals (henceforth, degu access [+D] plots). Four other plots had similar fencing but without holes at ground level, thereby excluding degus but allowing access by most other species (except a larger, rare rodent, *Abrocoma*; henceforth degu exclusion [–D] plots). The independent variable in our analyses was the mean minimum number of small mammals known alive (MNKA; individuals/ha) on control and exclusion plots, assuming a 7.5-m buffer around trapping grids. MNKA was calculated monthly from 1989 to 2008. Cover of annual plants was measured on four permanent 75-m transects separated by 15 m in each plot. Ten 1.5-m segments were randomly selected on each transect, and subdivided into 30 points at 5-cm intervals. The same segments were sampled each year. Percent cover was determined as (number of individual plants per point/total number of sampling points) × 100 (Mueller-Dombois and Ellenberg 1974). Data reported correspond to the maximum cover value reached by plants in

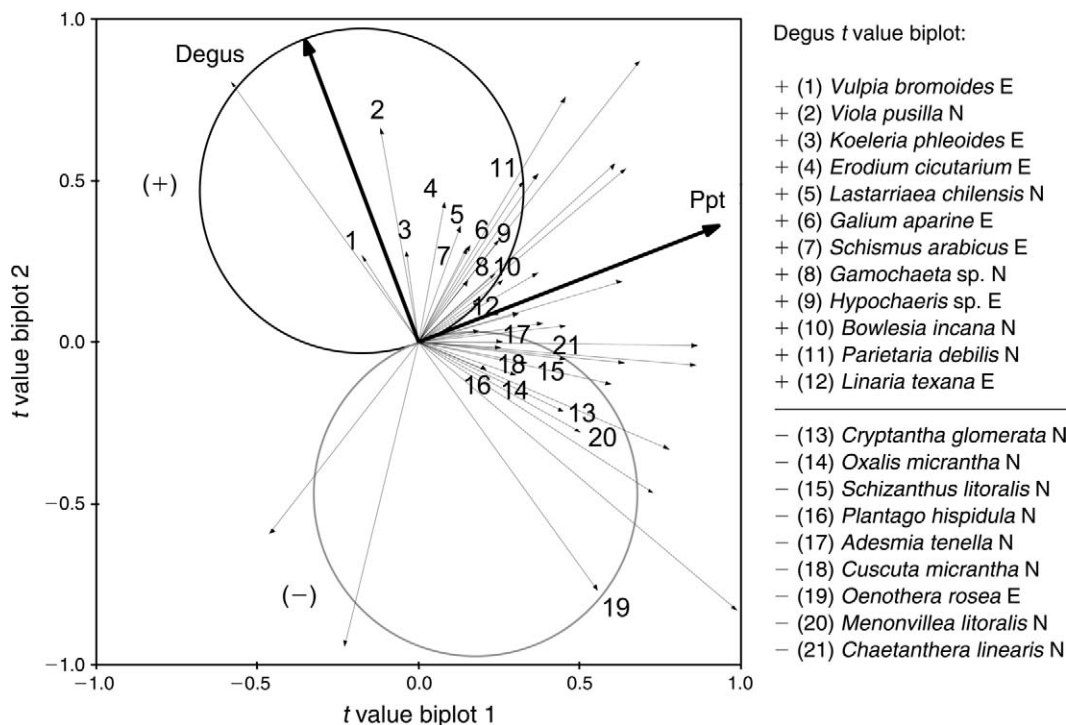


FIG. 1. A  $t$  value biplot for the relationship between degus and annual plants at Fray Jorge (Chile). Species arrows fully falling within a Van-Dobben circle indicate a significant relationship between the focal species and the abundance of degus. Relationships may be positive (black circle) or negative (gray circle) and are based on  $t$  values of regression coefficients of species expressed as linear combinations of degu abundance. Annual plant species that are significantly associated with degu abundance are listed in the legend. E and N indicate exotic and native species, respectively; Ppt stands for precipitation.

each year (early September). As more than one individual may be intercepted per sampling point, cover values could exceed 100%.

#### Statistical analyses

To extract principal trends in annual plant assemblages, we ordered log-transformed values of plant abundance with a Principal Components Analysis (PCA) by using a matrix of inter-species correlations. PCA was selected since the length of the first ordination axis in a previous (not shown) detrended correspondence analysis (DCA) was  $\leq 2$  SD (ter Braak and Šmilauer 2002). We subsequently pursued a direct ordination using redundancy analysis (RDA), with precipitation (Ppt) and degu density (Degu) as potential predictors affecting the coordinates of sampling points in the ordination diagram. Permutations for the Monte Carlo test were conducted in CANOCO 4.5 (Lepš and Šmilauer 2003), and restricted according to the data structure, with eight independent plots replicated across 20 years. The variability associated with potential random effects among grids was accounted for and included as a covariable (nominal). Temporal dependency in data due to repeated measures was accounted for in the restriction of permutations (e.g., years of study) at the whole-plot level. In support to the direct ordination analysis we constructed a  $t$  value biplot for

degu density (Degu), which allowed us to test and plot the relationship between the predictor and each dependent variable (species) in a multivariate plot. This analysis assumes that the relationship between the predictor variable and each species is significant ( $P < 0.05$ ) if  $t$  values of respective regression coefficients are  $> 2$  units. Predictor variables are represented by a vector whereas significant relationships with species in the diagram are indicated with circles to distinguish positive from negative relationships (Van Dobben circles; see ter Braak and Šmilauer 2002). Species vectors fully falling within a Van Dobben circle indicate species that respond significantly to the predictor variable (see Lepš and Šmilauer 2003).

The effects of precipitation and degu density on total cover by native and alien plants were separately assessed with generalized additive models (GAMs) assuming a maximum quadratic degree of the response function, a Poisson distribution of residuals of the dependent variable (appropriated for counts or percent cover data) and a logit link function. We used a deviance-based  $F$  computed with total deviance (obtained in a null model by 9999 random permutations of annual assemblages) and the residual deviance of the fitted models (the difference between the deviances of the null model and the fitted model in the numerator, and the residual



deviance of the fitted model in the denominator; Lepš and Šmilauer 2003).

To test whether the positive effects of degus on exotic plant cover is an indirect function of their negative effects on native plant cover, we computed a new dependent variable, relative exotic species cover = (exotic plant cover)/(total annual plant cover), and analyzed temporal shifts in the relative abundance of exotic species owing to Ppt and Degus using linear mixed models (LMM). We accounted for random effects among years and among plots, and fixed effects of Degus and Ppt. As required by LMM, we categorized the continuous variables Degus and Ppt. We categorized Ppt as high (above the average) or low (below the average). We categorized Degus by pooling all density values into three equal categories (low, moderate, high). Fixed effects were tested using Fisher's  $F$  statistic whereas repeated measures and random effects were tested by using the Wald  $Z$  statistic in an estimates of covariance parameters analysis. We adjusted the error degrees of freedom by the Satterthwaite method. We used the diagonal type of covariance for repeated measures, and the variance components type of covariance for random effects among grids.

#### RESULTS

The distribution of species assemblages in the RDA plot disclosed a pattern similar to that observed in a previous PCA, with precipitation and degu density significantly associated with the first and second axes, respectively (Ppt  $\lambda = 0.15$ ,  $F = 32.34$ ,  $P < 0.001$ ; Degus  $\lambda = 0.06$ ,  $F = 13.92$ ,  $P < 0.0001$ ). Annual plant assemblages on homologous canonical (RDA) and indirect (PCA) ordination axes were significantly correlated (axis 1,  $r = 0.794$ ,  $P < 0.001$ ; axis 2,  $r = 0.555$ ,  $P < 0.001$ ), and canonical axes were all significant ( $F = 24.515$ ,  $P = 0.0001$ ) supporting the relevant influence of the highlighted predictors in structuring the annual species assembly. RDA results further reflected those of the PCA in emphasizing the role of degu herbivory (Appendix B; Fig. 1); of the whole pool of exotic annuals (15 species), the seven most abundant species (together  $>88\%$  of total exotic plants cover) exhibited significant positive associations with degu density, as shown by the results of the  $t$ -value biplot analysis (Fig. 1; e.g., *Vulpia bromoides*, *Erodium cicutarium*, *Schismus arabicus*, *Linaria texana*, *Galium aparine*, *Koeleria phleoides*). In contrast, the most dominant native annual species such as *Plantago hispidula*, *Moschardia pinnatifida*, *Oxalis micrantha*, and *Schizanthus litoralis* together were negatively associated with degu density. Rare exotic species (e.g., *Erodium botrys*, *Erodium malacoides*, *Sonchus oleraceus*, *Malva parviflora*, or *Malva nicaensis*) did not show any significant response to degus; a single rare one (i.e., *Oenothera rosea*) was negatively associated with the rodent.

Bivariate regression models supported the decisive role of degu density on the spatial distribution of native vs. exotic annual plants. As shown by nonlinearity tests,

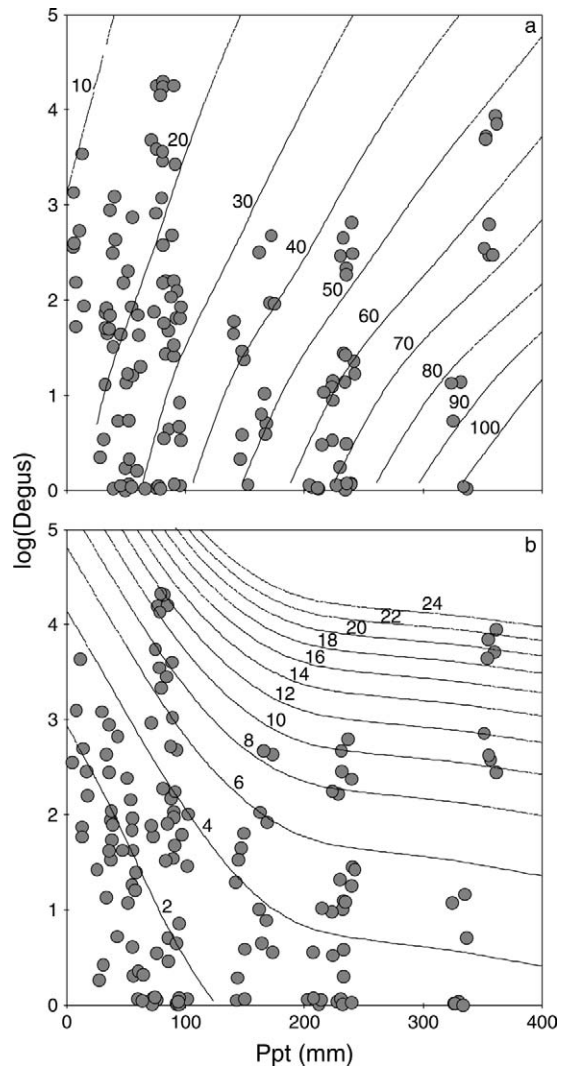


FIG. 2. Bi-dimensional contour plots showing values of (a) exotic and (b) native annual plant cover as function of Ppt and Degus. Isolines represent consistent values of annual plants cover across the plot. Degus (minimum number known alive [MNKA]/ha) was log-transformed.

cover of both native and exotic plants showed a significant nonparametric response (Ppt,  $F = 8.66$ ,  $P = 0.0037$ ; Degus,  $F = 8.34$ ,  $P = 0.0044$ ) to both precipitation and degu abundance (Fig. 2) suggesting that a nonlinear response model depicts better their responses (model:  $Y = s[\text{Ppt}]^2 + s[\text{Degus}]^2$ ; where  $s$  represents a smoothing function). Ppt and Degus jointly explained  $\approx 48\%$  of total deviance ( $F_{4, 155} = 5.57$ ,  $P < 0.001$ ) for native annual plants and  $\approx 65\%$  of total deviance ( $F_{3, 8, 155.2} = 14.32$ ,  $P < 0.0001$ ) for exotic annual plants. Cover of both native and exotic plant species was driven primarily by precipitation at lower values of this variable, highlighting the importance of water limitation in this semiarid ecosystem. Above approximately 100 mm of precipitation, however, degu



PLATE 1. The semi-arid scrubland of Fray Jorge National Park, Chile, in the (upper image) dry season and (lower image) wet season. Photo credit: D. A. Kelt.

density assumed predominance, leading to the segregation of native and exotic plant species. Under high levels of precipitation native annual plants were more abundant at lower levels of degu density (Fig. 2a) whereas exotic species were more abundant at higher degu densities (Fig. 2b).

Results of the LMM conducted on the relative abundance of exotic species in the community supported these models (Fig. 3). Ppt, Degus, and their interaction were significantly associated with the relative abundance of exotic species in the community (Ppt,  $F_{1,20.630} = 31.311$ ,  $P < 0.0001$ ; Degus,  $F_{2,18.727} = 15.04$ ,  $P < 0.0001$ ; Ppt  $\times$  Degus,  $F_{2,18.952} = 14.701$ ,  $P < 0.0001$ ). When degu densities were low, variation in precipitation did not influence the relative abundance of exotic plants. However, at medium and especially high densities of degus, exotic plants increasingly are favored by elevated rainfall. Random effects among plots did not show any significant influence on the relative abundance of exotic species (Wald  $Z = 0.648$ ,  $P = 0.517$ ) whereas effects among years pointed to some marginally significant influence (Appendix C: Table C1).

#### DISCUSSION

These results underscore the alternating role of bottom-up and top-down control in the expansion of exotic annual plants in this semi-arid ecosystem. Exotic

species that have colonized semi-arid Chile (e.g., *E. cicutarium*, *S. arabicus*, *K. phleoides*) are poor competitors in benign conditions but are highly drought tolerant, usually inhabiting bare sandy soils in mediterranean Eurasia, where they can grow and develop avoiding more competitive species (e.g., mesic perennial grasses). Semi-arid ecosystems of the Americas provide opportunity for the survival and resilience of such alien plants since unpredictable precipitation can prevent the successful establishment of highly competitive native herbs. In fact, their expansion in these arid and semi-arid ecosystems has been explicitly associated with their ability for avoiding competition by native annual plants during dry periods (Brooks and Berry 2006).

In semi-arid Chile, low water availability limits the emergence and growth of native annuals, which should favor the expansion of exotic plants (Gutiérrez 1992). As water becomes more abundant ( $>100$  mm) dominant native vegetation (e.g., *Plantago hispidula*, *Oxalis micrantha*, *Bromus berterianus*) rapidly monopolizes space, and less competitive species are competitively limited (Manrique et al. 2007). A similar pattern has been reported for serpentine grassland communities in California, where addition of nutrients and water triggers the dominance of a few native strong competitors (perennial grasses) that suppress less competitive species, including exotic taxa (Going et al. 2009). However, our results do not support the high drought tolerance of invaders (e.g., *Erodium cicutarium*) as a key mechanism underlying their success in colonizing this semi-arid system. In contrast, the lack of significant differences in the relative abundance of alien species to variation in rainfall at low density of degus (Fig. 3) suggests that in the absence of significant top down regulation, these species capture a proportional quota of resources such that their persistence in this system does not depend on the avoidance of competition with native plants in dry years. In contrast, they become increasingly abundant in years of higher rainfall,

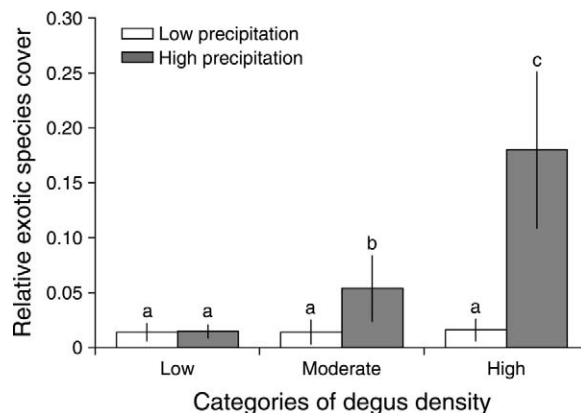


FIG. 3. Relative exotic species cover (exotic plant cover/total annual plant cover; mean  $\pm$  95% CI) under low (white) and high (gray) levels of precipitation and low, moderate, and high abundance of degus. Different letters indicate significant differences at  $P < 0.05$  (LSD test).

presumably aided by disturbance processes that impact the dominant native vegetation (Burke and Grime 1996). Human activities provide well-documented disturbances that favor alien species over a broad range of natural systems (Hobbs and Huenneke 1992, Domènech and Vilà 2006, Chytrý et al. 2008). However, Fray Jorge is a World Biosphere Reserve that has been protected from grazing since 1941; expansion of exotic species into such a well-preserved ecosystem that is relatively free of human disturbance argues for another type of disturbance. Huissman and Olf (1998) provided a theoretical model which underscored the importance of a generalist consumer for the coexistence of plant diversity and indirectly for associated specialist consumers. Here, the key role of the generalist resided in its negative effects on dominant plant species. The generalist consumer may impact native plant species in proportion to their greater abundance and cover, independent of the fact that the absence of coevolved relationships between the former and the pool of exotic species could also bias foraging pressures against native annual plants. Our results support such a scenario in which degus are generalist consumers that may facilitate the access and establishment of less competitive (exotic) species by impacting the dominant native plants. However, foraging is not the only mechanism by which degus may alter native vegetation. Runways and other direct activities of these rodents may also impact native vegetation (Gutiérrez and Meserve 2000). While we suspect that the net positive effects of degus on exotic annual plants likely is a function of both direct and indirect impacts on native species, more research is needed to shed light on these uncertainties. As degu populations vary with the availability of resources, both of the above effects likely vary proportionally, such that this positive indirect interaction should be temporally heterogeneous in response to variation in rainfall. Thus, we hypothesize that direct bottom-up control of degu populations by vegetative growth in response to elevated rainfall, may lead to indirect top-down facilitation of exotic annual plants by proportional consumption and disturbance of exotic as well as native annual plants. It is by this two-phase process that the degu, a generalist herbivore, may indirectly favor the invasibility of this semiarid ecosystem.

In closing, we note that recent high-resolution climatic models suggest an increasing frequency of El Niño events in the face of global climate change (Timmermann et al. 1999). High-rainfall events have increased in frequency in our study area in recent decades (Trenberth and Hoar 1997, Tudhope et al. 2001). If this pattern continues, top-down control may become increasingly important in structuring vegetation in this region (Previtali et al. 2010), potentially facilitating the expansion of exotic species and resulting in a dramatic compositional change of annual plant communities, with unknown impacts on consumer groups and ecosystem properties.

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#### APPENDIX A

Descriptive statistics (*Ecological Archives* E092-024-A1).

#### APPENDIX B

Ordination plots from indirect and direct gradient analyses (*Ecological Archives* E092-024-A2).

#### APPENDIX C

Estimates of covariance parameters in a linear mixed model (*Ecological Archives* E092-024-A3).