

# Biotic interactions and community dynamics in the semiarid thorn scrub of Bosque Fray Jorge National Park, north-central Chile: A paradigm revisited



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## ABSTRACT

In 1989, we initiated a long-term field experiment in a semiarid thorn scrub community in north-central Chile. We posited that biotic interactions, particularly predation, interspecific competition, and herbivory assumed a primary top-down role in affecting small mammals and annual plants here. Using a multi-factorial design we selectively excluded vertebrate predators (principally carnivores and raptors) and a large small mammal herbivore, the degu (*Octodon degus*), from replicated 0.56 ha exclosures located in a valley near the coast in Bosque Fray Jorge National Park. Evidence initially supported effects of predator exclusion on *O. degus* but not for other small mammals in the assemblage (e.g., *Phyllotis darwini*, *Abrothrix olivaceus*). Subsequent years of monitoring have documented that predation has temporary effects on degu numbers, but that populations of this and other small mammals are much more strongly influenced by environmental bottom-up factors (i.e., rainfall). Further, our experimental manipulation has provided no evidence for negative interspecific competition effects on numbers of any small mammal in this assemblage. Degu exclosures, however, have had negative indirect effects on exotic annuals; native annuals appear to outcompete exotics especially during drought years. The effect is magnified in all-small mammal exclosures. Since about 2002, selective exclosures of lagomorphs and small mammals have resulted in changes in cover of some perennial shrubs. Also notable has been a fundamental shift in the small mammal composition following the last major El Niño Southern Oscillation (ENSO) event in 2000–2002; degus now comprise a majority of small mammal biomass in the assemblage, and their numbers have become more stable and less temporally variable. This appears to have been caused by a shift in rainfall periodicity from strong interannual fluctuations in response to periodic ENSOs, to a more equitable pattern with more consistent annual rainfall. This represents one of the first documented cases of system-wide biotic phase shifts to a relatively modest change in rainfall regime. This may be indicative of ongoing climate change in the Chilean semiarid region, and we expect that further changes in the community will occur if those trends continue.

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## 1. Introduction

In the 1970's and 1980's, community ecologists emphasized the importance of biotic interactions affecting community membership and composition. Exhaustive reviews by Schoener (1983), Connell (1983), Sih et al. (1985), and others highlighted important effects

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of predation, interspecific competition, and herbivory in various communities. Semiarid desert communities received particular attention because of the work of James H. Brown and others on diverse small mammal assemblages in North America that had been the focus of the IBP project (e.g., [Orians and Solbrig, 1978](#)). For example, Brown and his colleagues identified a major role of interspecific competition among granivorous rodents (e.g., [Brown et al., 1979, 1986; Munger and Brown, 1981](#)). However, the generality of such patterns was hindered by the lack of experimental studies elsewhere (with the exception in South America of those in marine systems, e.g., [Menge and Sutherland, 1976; Moreno and Sutherland, 1982](#)), as well as lack of evidence for strong granivory among South American (and Australian) small mammals ([Mares and Rosenzweig, 1978; Meserve, 1981a,b; Morton, 1985](#)). In an application to the U.S. National Science Foundation in 1988 for support to implement a large-scale experimental study of biotic interactions in a semiarid community in north-central Chile, we noted that in their exhaustive reviews of the literature: “neither [Schoener \(1983\)](#) nor [Connell \(1983\)](#) listed any experimental studies of interspecific competition for South America”. Further, in our reviews of the literature then, we found “only two previous manipulative studies of interspecific competition [in small mammals] ... and ... “no experiments examining the role of predation in higher vertebrates” in South America. More than a quarter century later, much has changed.

In 1987, for several reasons we posited that biotic interactions were important in the semiarid zone of north-central Chile, where we had worked in a relatively undisturbed natural site, Bosque Fray Jorge National Park (hereafter BFJNP). First, we noted an unusual abundance of vertebrate predators here. Second, in a pilot study in 1973–1975 we found patterns in small mammal species abundances ([Meserve, 1981a,b; Meserve and Le Boulengé, 1987](#)) that suggested interspecific competition might be important; for example, for every trophic specialization in the small mammal assemblage (herbivorous, granivorous, insectivorous), there was one common and one rare species. Further, some species maintained fairly constant populations from year to year whereas others fluctuated dramatically ([Meserve and Le Boulengé, 1987](#)). Finally, whereas an important small mammal herbivore, the Chilean degu (*Octodon degus*), was thought rare to uncommon here (e.g., [Fulk, 1975](#)), we found it to be quite common in this semiarid community near the northern end of its range ([Meserve and Le Boulengé, 1987](#)). So, when we began work at BFJNP in 1989, we implemented a large-scale field experiment which focused on assessment of the role and magnitude of 3 major classes of biotic interactions: 1) predation; 2) interspecific competition; and 3) herbivory ([Meserve et al., 1993a](#)).

## 2. Materials and methods

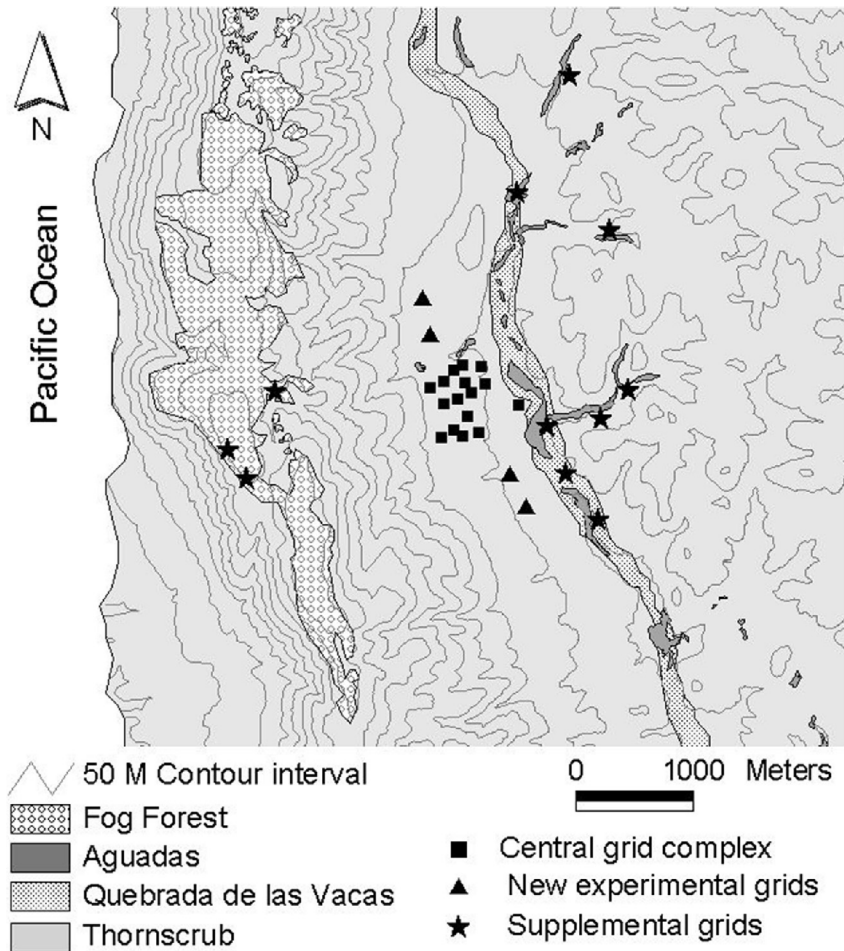
BFJNP (71°40' W, 30°38' S) is a ca. 10,000 ha World Biosphere Reserve about 380 km N of Santiago, Chile and 150 km S of the southern edge of the hyperarid Atacama Desert ([Fig. 1 C. Armas et al., 2015](#)). The park is dominated by semiarid thorn scrub vegetation, and coastal hills support remnant fog forests, all of which has been protected from grazing and disturbance since 1941 ([Squeo et al., 2004](#)). The thorn scrub includes spiny drought-deciduous and evergreen shrubs and understory herbs on a primarily sandy substrate ([Muñoz and Pisano, 1947; Muñoz, 1985; Gutiérrez et al., 1993a](#)). The climate is semiarid Mediterranean with 90% of the mean annual 125 mm (1989–2013) precipitation falling in winter months (May–Sept.), and warm, dry summers. Since 1989, there have been 6 El Niño/high rainfall events in this region: 1991–92 (233–229 mm), 1997 (330 mm), 2000–2002 (236–339 mm), 2004 (168 mm), 2006 (147 mm), and 2011 (160 mm); intervening years

have been dry (11–95 mm). Small mammals here include several caviomorph rodents such as *O. degus* (Molina, 1782) (ca. 120–180 g), *O. lunatus* (Osgood, 1943) (ca. 160–200 g), and *Abrocoma bennetti* Waterhouse, 1837 (150–250 g), several smaller (20–80 g) sigmodontine rodents such as *Abrothrix olivaceus* (Waterhouse, 1837), *Abrothrix longipilis* (Waterhouse, 1837), *Phyllotis darwini* (Waterhouse, 1837), and *Oligoryzomys longicaudatus* (Bennett, 1832), and a mouse opossum *Thylamys elegans* (Waterhouse, 1839) ([Meserve, 1981a, b](#)). Numerous small mammal predators include owls (*Tyto alba* [Scopoli, 1769], *Speotyto cunicularia* [Molina, 1782], *Bubo magellanicus* [Lesson, 1828], *Glaucidium nanum* [King, 1828]) and the culpeo fox (*Lycalopex culpaeus* [Molina, 1782]). Predator numbers are unusually high because the park contains the largest remaining intact scrub habitat in north-central Chile ([Bahre, 1979](#)).

Our manipulations utilize a long-term “press” approach (sensu [Bender et al., 1984](#)) to examine biotic interactions; that is, they are sustained and long-term. The initial experimental complex consisted of 16 small mammal live-trapping grids (75 × 75 m = 0.56 ha) in thorn scrub habitat in a valley near the coast (“Quebrada de las Vacas,” 240 m elev.; “Central grid complex” in [Fig. 1](#)) previously studied (1975) and [Meserve \(1981a,b, Meserve and Le Boulengé, 1987\)](#). The design included 4 treatments, each with 4 randomly assigned grids (see [Kelt and Meserve, 2014](#) for details): 1) controls with low fencing and holes in the fencing permitting access by both predators and small mammals (+D +P); 2) predator exclusions with tall fencing and suspended overhead polyethylene netting, but with ground-level holes to allow access only by small mammals (including degu; +D -P); 3) degu exclusions with low fencing lacking holes but that allowed free access by smaller mammals (-D +P); and 4) degu + predator exclusions with tall fencing and netting but without holes (-D -P). In 2001, given lack of vegetative changes or small mammal responses to degu exclusions for over 12 years, we converted the -D -P grids to all-small mammal enclosures (-SM) by removing the original netting and fencing, and installing low (1.5 m) hardware cloth fencing topped with metal flashing. All fencing was buried at least 50 cm to prevent subterranean access, although occasional burrowing by the fossorial coruro (*Spalacopus cyanus*) provided access for small mammals (these were removed during monthly surveys). Finally, in 2008, we randomly assigned the 4 -D +P and another 4 grids (“New experimental grids” [Fig. 1](#)) formerly used for food addition experiments ([Meserve et al., 2001](#)) to either lagomorph (-L) or lagomorph + small mammal exclusions (-L -SM).

Sampling methods are as follows (see also [Meserve et al., 1995, 1996; Gutiérrez et al., 1993a,b; 1997; Jaksic et al., 1997; Kelt and Meserve, 2014](#)): 1) Small mammals are trapped for 4 days/month/grid (5 × 5 stations, 15 m interval, two traps/station). Animals removed from the all-small mammal exclusions are released ~1 km away. We estimate population size with minimum number known alive (MNKA; [Hilborn et al., 1976](#)); 2) Perennial shrub cover is measured every 3 months using a point intercept method (0.5 m intervals) on 4 permanent 75-m parallel transects/grid; 3) Ephemeral (annuals + geophytes) cover is measured monthly in the growing season (April–Aug. to Oct.–Dec.) on 10 random 1.5-m segments subdivided into 30 points (5 cm intervals) on the transects; 4) Soil samples (n = 20 random samples [3 cm d × 5 cm depth = 35.35 cm<sup>3</sup>] grid-1) are collected every 4 months, and seeds separated by sieving; and 5) Fox scats and owl pellets are collected monthly from the site and nearby roosts; predators are monitored monthly with sightings and olfactory lines.

We have employed various approaches to data analysis. Initially, we used repeated measures analysis of variance (rmANOVA, PROC GLM; SAS 1990a, b, [Potvin et al., 1990; Von Ende, 2001](#)), and mixed-model rmANOVA (PROC MIXED; [Wolfinger and Chang, 1995](#); SAS



**Fig. 1.** Location of study area, grids, and major habitats in Fray Jorge. Light-shaded areas are predominantly thorn scrub habitat. Sixteen grids in the Central Grid Complex have been trapped since 1989; 4 other grids (New Experimental Grids) were used for food addition experiments in 1997–2001 and are currently being used for selective lagomorph or all-mammal (lagomorph + small mammal) exclusions. Supplemental Grids were used to sample other habitats between 1996 and 2003 (Milstead et al., 2007).

1996). Small mammal survivorship was analyzed with PROC LIFETEST (SAS 1990b) and nonparametric log-rank tests (Lee, 1980; Fox, 2001). Results of these analyses on small mammals and predators were reported in Jaksic et al. (1997), and Meserve et al. (1993b, 1995, 1996, 1999, 2001, 2003).

Previtali et al. (2009a, b) investigated the effects of predator/competitor exclusions using Log Response Ratios (LRRs), calculated as the log of the ratio of the density of the target species in the competitor or predator exclusion treatment over its density in the control ( $LRR = \ln(N_t \text{ exclusion}/N_t \text{ control})$ ; Schmitz et al., 2000; Berlow et al., 2004). We assumed that biotic interactions (competition, predation) would vary depending on the duration of wet or dry phases since this relates directly to resources availability. Consequently, we categorized each year based on whether wet vs. dry conditions (i.e., above vs. below the annual mean) prevailed in that year and the preceding year. Thus, we defined each year as part of a Dry–Dry, Dry–Wet, Wet–Wet, or Wet–Dry phase. Given the lag in demographic responses to resource availability, we posited that Dry–Wet years would have high resource availability (current year), but low population densities (due to the preceding dry year). Similarly, Wet–Dry years should have low resources (current, dry year), but high population densities (in response to the preceding wet year), and so on.

We assessed behavioral (foraging) responses to predator removal using “giving up densities” (GUDs) from foraging trays

(Yunger et al., 2002, 2007; Kelt et al., 2004a,b,c). This allowed us to evaluate whether experimental treatments have had functional effects on small mammal foraging independent of their numerical responses to manipulation of predator and/or interspecific competition.

For plant responses, we estimated cover (angular transformed) and seed densities (log-transformed) and used annual peak values (due to varying length of the annual growing season) to allow balanced between-year analyses with rmANOVA (Gutiérrez et al., 1997). Elsewhere we compared plant densities and biomass across our experimental treatments (log-transformed; Gutiérrez and Meserve, 2000). Recently, C. Armas (2015) reanalyzed trends in perennial shrub cover, and herein we briefly report some of those findings.

Prior to manipulations we documented no significant between-treatment differences (small mammals: pre-test period = March–May 1989; plants: 1989).

### 3. Results

#### 3.1. Biotic factors

The major results reported here for biotic interaction effects are primarily from 1989 to 2001 when all of the treatments were operational. *O. degus* responded positively to predator exclusions



(Previtali et al., 2009a,b), with greater LRRs during prolonged droughts (i.e., Dry–Dry years, 1994–1996, and 1999; Fig. 2). Other species (*Phyllotis* and *A. olivaceus*) showed only slight or even negative effects of predator exclusions. Degu survival probabilities were significantly greater on predator exclusions than control grids (Previtali et al., 2009a). Although we documented behavioral changes in *Octodon* and other species under predator exclusion conditions (Lagos et al., 1995; Yungler et al., 2002, 2007; Kelt et al., 2004a), generally these are not manifested in numerical responses to predation.

*Octodon* negatively impact trophically dissimilar species such as *A. olivaceus* (Meserve et al., 1996; Yungler et al., 2002; Kelt et al., 2004a; Previtali et al., 2009a,b), *Oligoryzomys* (Milstead, 2000), and *Thylamys* (Meserve et al., 2001). Surprisingly, degus may have a facilitative influence on *Phyllotis*, with which it has more trophic overlap; this species exhibited higher densities in control grids than degu exclusions (Yungler et al., 2002).

Vegetative responses to herbivore (i.e., degus) and/or predator exclusions have been heterogeneous (Gutiérrez et al., 1997; Gutiérrez and Meserve, 2000; Madrigal et al., 2011). Perennial cover showed no significant treatment responses through 2001, but diversity increased on degu exclusions. Some species showed greater cover in plots excluding degus (e.g., *Baccharis paniculata* D.C., *Chenopodium petiolare* H.B.K.) or predators (e.g., *Proustia cuneifolia* D. Don). *C. petiolare* is a suffruticose perennial and an important degu food (Meserve, 1981b). Ephemerals (annuals + geophytes) showed no significant main treatment effects on cover or diversity, but total biomass was significantly

higher in plots accessible to degus and predators (Gutiérrez and Meserve, 2000). Overall, consumptive effects of degus were relatively small, whereas their indirect activities appeared to increase ephemeral biomass. Seed densities of annual species, including those of *Erodium* spp. and *Moscharia pinnatifida* R. et P., were higher in degu-access grids (Gutiérrez et al., 1997). Widespread, adventitious herbs (e.g., *Erodium*) may be facilitated by disturbance due to runway development and activity as well as digging under bushes (Madrigal et al., 2011). These observations suggest that degus exert complex effects on vegetation, including both depression and facilitation of plants and seeds.

After installation of the -SM treatments in 2003, some plants responded immediately and dramatically in the following year; cover by *Plantago hispidula* R. et P. in -SM treatments increased ~4X's over that in control grids. Although this species is an important food of herbivorous rodents in the study area (Meserve, 1981b), seed densities were similar in -SM and control treatments. Consequently, the best explanation for the increase of *P. hispidula* here and not in degu exclusion grids was absence of herbivory by non-degu species, most likely the herbivorous *Phyllotis*. However, this difference in cover was not maintained in subsequent years, so the general importance of this effect is unclear. Another immediate response was that *Adesmia bedwellii* Skotts., a perennial shrub comprising ~8% of shrub cover at our study site, produced significantly more new leaves and buds in -SM plots. Other shrubs (e.g., *Porlieria*, *Proustia*) have not shown these responses, indicating that the impacts of small mammals on perennial shrub species were selective.

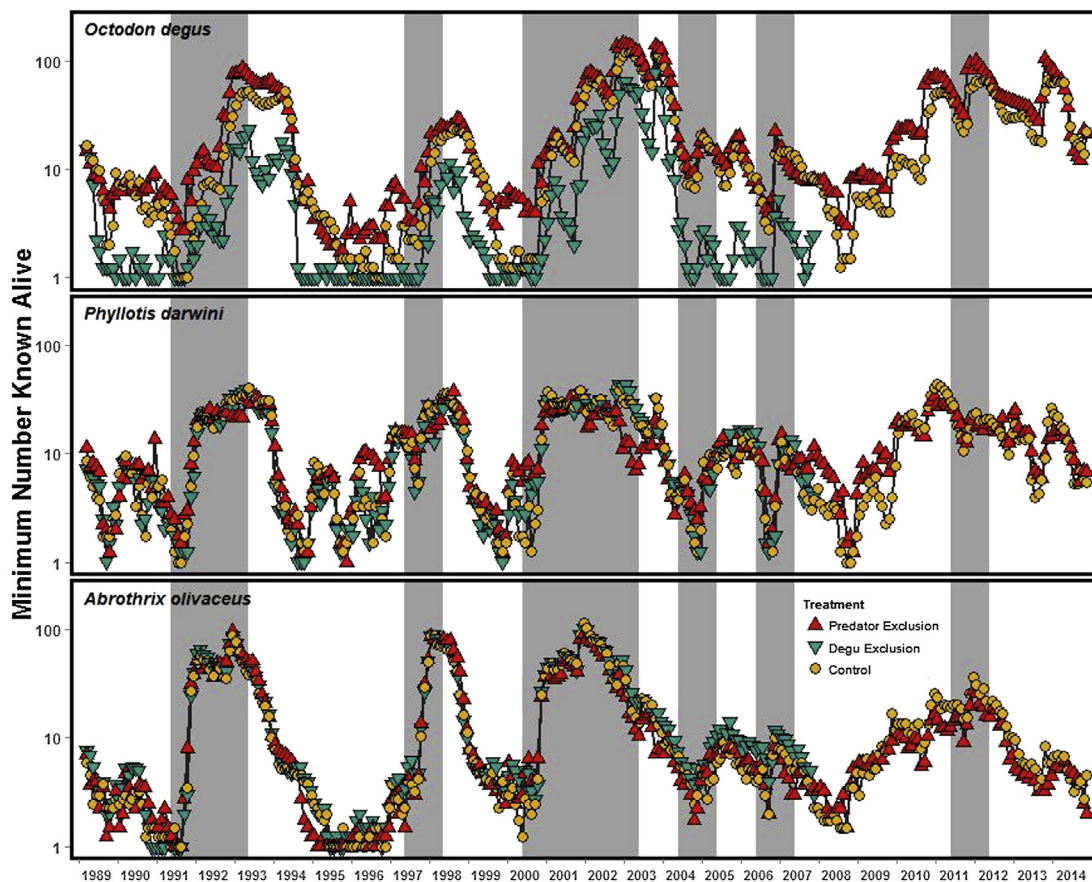


Fig. 2. Population trends for the 3 principal (core) small mammals (*Octodon degus*, *Phyllotis darwini*, and *Abrothrix olivaceus*) in 3 experimental treatments (degu exclusion = -D +P; predator exclusion = +D -P; and control grids (+D +P) in the thorn scrub in Fray Jorge between 1989 and 2013. Shaded areas denote wet years as defined in the text.

Reanalysis of shrub cover patterns by C. Armas (2015) has revealed some dramatic changes in overall shrub cover since about 2002. Whereas shrub cover had been similar between control and experimental grids until then, controls (+D +P) demonstrated a monotonic decline in cover of some shrub species; for example, *A. bedwellii*, a shrub with deciduous foliage, and *C. petiolare* have declined drastically in control (+D +P) grids (Armas, 2015). These trends are due most likely to the increased herbivory and indirect activities of *O. degus* since this is the principal species that has increased since 2000 in the study area (see below).

### 3.2. Abiotic factors

Rainfall has dramatic effects on numbers of small mammals (Fig. 2), and the distinct demographic responses of principal small mammal species reflected different life history traits (Meserve et al., 1995; Previtali et al., 2009a,b). Short-lived multiparous sigmodontine rodents with short gestations (e.g., *P. darwini* and *A. olivaceus*) respond rapidly to high rainfall episodes whereas longer-lived seasonally uniparous caviomorphs with longer gestation (e.g., *O. degus*) typically increase more slowly and with a discernible time lag with respect to periods of peak rainfall (Meserve et al., 2011).

Effects of high rainfall on plants is also apparent (Fig. 3). Ephemerals respond rapidly to rainfall pulses, and cover by these species varied from 0% during an extreme La Niña event (1998, 11 mm ppt) to 80–86% during El Niño/high rainfall years (1991, 1997, 2002). Decreases during ensuing years of multi-year high rainfall events (i.e., 1992, 2001–02) suggest nutrient depletion (Gutiérrez et al., 1993b, 1997). Maximum seed densities reached 41,832 m<sup>2</sup>, similar to that reported from North American deserts (Inouye 1991), but they do not track rainfall as closely as does ephemeral cover (Gutiérrez and Meserve, 2003). Similar ephemeral responses have been documented elsewhere in semiarid Chile (Dillon and Rundel, 1990; Gutiérrez and Meserve, 2000). On the other hand, perennial shrub cover has varied from 38.6% to 64.4% in 26 years, similar to values of 50 and 35 years ago (Muñoz and Pisanó, 1947; Meserve, 1981a; Gutiérrez et al., 1993a, 2010), and does not show dramatic year-to-year fluctuations (Fig. 3).

Against this background, recently we have noted major changes

in the rainfall regime of BFJNP. Although the probability of extreme drought in this region has roughly doubled in the last 50 years (Jiménez et al., 2011), annual rainfall at our site has increased moderately and variation has decreased since about 2000 (Meserve et al., 2011). Between 1989 and 1999 rainfall averaged 111.4 ± 103.8 mm (±1 SD), but from 2000 to 2013 it was 137.1 ± 84.5 mm). If rainfall during the extended ENSO/high rainfall event of 2000–2002 is not included, the mean has declined slightly, but more importantly, annual variation has declined dramatically (101.57 ± 39.62 mm). Accompanying this change has been a dramatic shift in the small mammal composition (Meserve et al., 2011). Whereas *O. degus* formerly comprised a relatively small proportion of the small mammal biomass here, it now dominates the assemblage (Fig. 4). Further, species diversity (Shannon–Weiner *H'*) has increased modestly from the 1989–1999 period to the 2000–2013 period (1.18 versus 1.31, respectively; Satterthwaite's  $t_{36.79} = -1.84$ ,  $P = 0.0745$ ) but temporal variation in *H'* has decreased significantly (CV = 0.226 versus 0.138; Satterthwaite's  $t_{27.47} = 3.62$ ,  $P = 0.0012$ ; updated from Kelt and Meserve, 2014). These latter changes are due most likely to increased abundance of *O. degus* relative to other small mammal species.

### 4. Discussion

With the advantage of a quarter century of fieldwork, hindsight provides an opportunity to address several questions. First, why did we focus almost wholly on biotic interactions at this semiarid site in our initial design? Doubtless, we were influenced by the arguments of Diamond and Case (1986) and Sih et al. (1985) as well as Schoener (1983) and Connell (1983) that more ecological field experiments and studies of biotic interactions were needed, and especially in South America. Further, we operated within the context of prevailing ecological paradigms then; critical transitions, spatial vs. temporal subsidies, trophic cascades, top-down vs. bottom-up control, and climate change/global warming were topics on the still-distant horizon. Finally, we phrased our initial questions and field experiments within logistical and temporal constraints. More simply put, in a national park harboring a unique semiarid community, we were understandably precluded from large scale modifications of the physical environment through vegetation

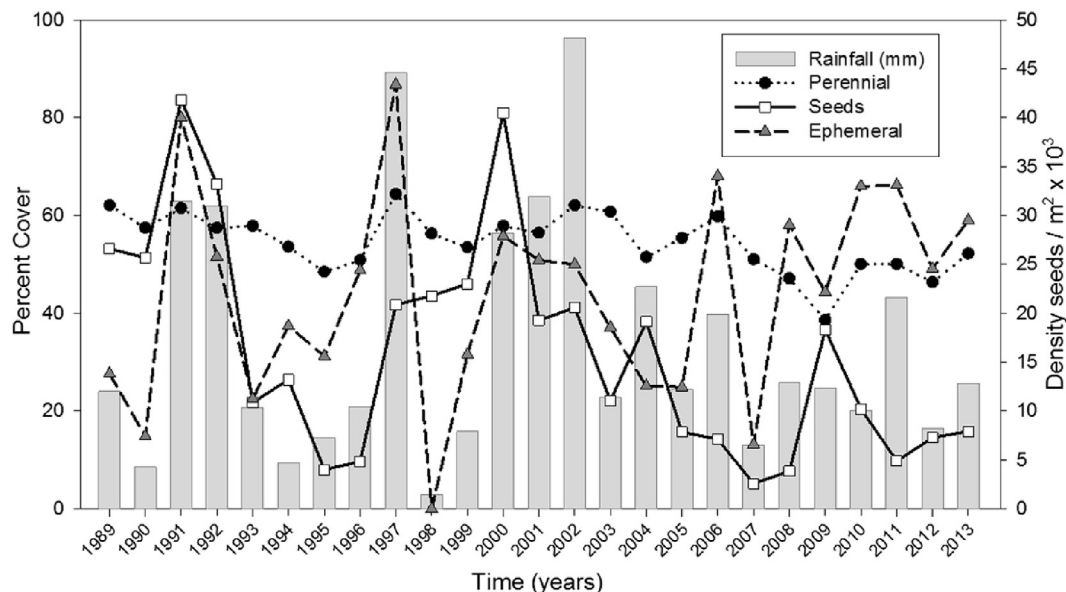
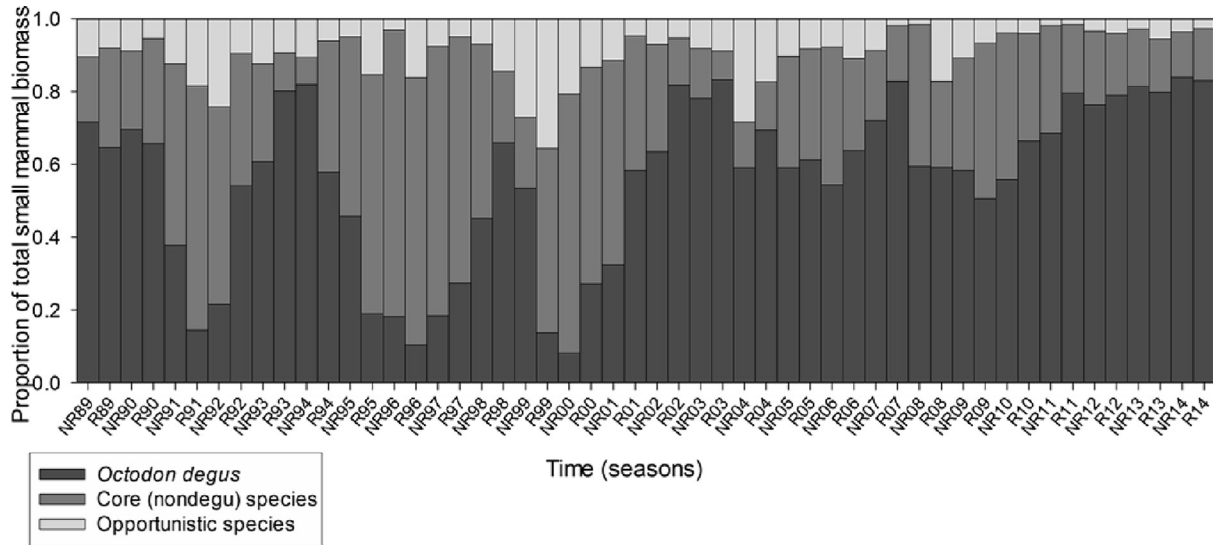


Fig. 3. Precipitation, peak annual cover of perennial shrubs and ephemerals, and peak seed densities in the thorn scrub in Fray Jorge for 25 years.



**Fig. 4.** Proportion of small mammal biomass made up of *Octodon degus*, other core species (*Phyllotis darwini*, *Abrothrix olivaceus*, and *Thylamys elegans*), and opportunistic species (*Abrothrix longipilis* and *Oligoryzomys longicaudatus*) from 1989 through 2013 for nonreproductive (NR) and reproductive (R) seasons. The nonreproductive season includes small mammal data from March through September, whereas the reproductive season includes data from October through February.

tailoring or water supplementation; further, within the temporal constraints of the standard 2–3 year funding timelines, we expected definitive results on the question of biotic interactions within that time frame. We simply did not envision that 7 NSF awards totaling over \$1.65 million U.S., and more than 70 publications later, we still would be working in this system 26 years later.

Second, why were we surprised by the magnitude of small mammal responses to environmental variation? Given previous accounts of small mammal outbreaks and explosive flowering in arid regions here (e.g., [Fulk, 1975](#); [Pearson, 1975](#); [Bahre, 1979](#)), we should have expected large magnitude responses to changes in rainfall. Perhaps because ENSO/high rainfall events are relatively uncommon here (about every 5–7 years), we did not anticipate their impact within a 3-year project time frame. In either case, we failed to foresee the overwhelming magnitude of abiotic influences in this system; as we have found, however, pulses of high rainfall act to “reset the clock” in terms of the importance of biotic factors. That is, predation, interspecific competition, and herbivory may only be important at certain times within the long-term oscillation of ENSO’s here. Initially, we attempted to explain the system’s behavior with a heuristic paradigm of alternating or shifting top-down vs. bottom-up control ([Meserve et al., 1999, 2001, 2003](#); [Gutiérrez and Meserve, 2000](#)). We argued that the importance of “top-down” biotic interactions should be greatest during periods when high rainfall “released” primary producers, and thus, their various consumers. During prevailing dry periods and droughts, nutrient and moisture limitation reduced primary productivity, and hence, the impact of various consumer groups was relatively minor. However, [Previtali et al. \(2009a\)](#) showed that the top-down influence of predators had strongest effects primarily when prey numbers were low near the end of prolonged droughts or during early increase phases; data from Aucó, roughly 115 km SSE of BFJNP, also implicated predation in density-dependent dynamics of *Phyllotis* ([Lima et al., 2001, 2002](#)). But in neither case did predators or herbivores “control” their respective resources. Predation neither limited small mammal increases nor accelerated their declines during and following high rainfall periods; conversely, herbivory has assumed greater importance. In addition, since about 2000 we have begun to observe that long-term changes in abiotic (or physical) factors appear to be altering the role of some biotic

interactions such as herbivory here.

This leads to a third question; has something changed fundamentally in the system? Contrasting patterns from 1989 to 1999 with those since 2000, it appears so. We have noted a dramatic shift in the small mammal assemblage since about 2000 when rainfall became more equitable. Even if mean annual rainfall is viewed as having declined slightly since 2002 (e.g., if we exclude the 2000–02 ENSO/rainy period), interannual variation has declined dramatically. We have suggested that the lack of pronounced droughts during this period has enabled a formerly less abundant herbivore, the degu, to become much more dominant in the small mammal assemblage ([Meserve et al., 2011](#)). In turn, this appears to have driven changes in the plant community. Since perennial shrub and ephemeral cover has not increased dramatically in response to the changes in rainfall patterns, we suggest that alteration of the rainfall regime from pronounced dry–wet oscillations to a more equitable pattern has most strongly influenced the dynamics of a relatively long-lived, seasonally-uniparous rodent, the degu, and in turn a cascading effect on their plant resources ([Meserve et al., 2011](#)). Although this might be viewed as a transient phenomenon, the persistence and monotonic nature of the changes suggest a fundamental phase shift, and perhaps ultimately, a critical transition ([Scheffer, 2009](#)). On a regional scale, climate change may be having unanticipated impacts on the small mammal and plant communities here. Interestingly, whereas the perennial shrub community is demonstrating dramatic changes, the ephemeral plant community seems not to have been affected in a pronounced way suggesting that seed banks and spatial heterogeneity in the assemblage may experience spatio-temporal buffering to both climate change and small mammal herbivory.

In summary, the initial paradigm that we posited in 1987 for a dominant role for biotic interactions in this system is overly simplistic, and needs to be modified to one in which the importance of those interactions is viewed within the context of the abiotic or physical environment. Similarly, J. H. Brown’s long-term research in Arizona has underscored an overarching role of climatic variability; severe storm events there have had strong (albeit temporary) impacts on the mammal assemblage ([Valone et al., 1995](#); [Brown et al., 1997](#); [Thibault and Brown, 2008](#)), and longer-term climate changes appear to be converting vegetation at this site from desert



grassland to desert shrubland (Brown et al., 1997). In Australia, Chris Dickman and his associates have documented dramatic biotic responses to rainfall (Letnic and Dickman, 2010; Dickman et al., 2011; Pastro et al., 2013). Hence, the emphasis of ecology in the 1970s and early 1980s on biological interactions, and the implicit assumption of equilibrium conditions, were clearly simplistic starting points from which a much more comprehensive understanding of ecosystem dynamics at our Chilean site has emerged. As in the American Southwest (Brown et al., 1997), changes in the rainfall regime in north-central Chile appear to be influencing regional and local dynamics. These changes likely are a consequence of ongoing climate change (Jaksic, 2001; Kelt and Meserve, 2014) and have led to dramatic changes in the small mammal assemblage and in turn, the extent of herbivore impacts on the vegetative community. What will be the potential consequences for region as a whole? Ironically, for much of it which has already been strongly altered by overgrazing, clearing, and replanting with exotic shrubs such as *Atriplex* spp., there may be relatively few consequences because the natural fauna has already been impacted by loss and conversion of habitat to near-monocultures of species that often are exotic. But for the relatively small remaining native plant community such as harbored by BFJNP, the consequences may be severe; further, they will be exacerbated by on-going intrusions of livestock from surrounding areas that create disturbance and provide opportunities for invasion of exotic plants. Climate change here is likely to produce surprising and unexpected effects that were unanticipated some 26 years ago when we initiated work in this system.

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