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Global climate change and small mammal populations in north-central Chile

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Since 1989 we have monitored small mammal populations at a semiarid site in north-central Chile with a large-scale live-trapping grid complex. Selective exclusions of vertebrate predators or putative small mammal competitors, or both, have yielded relatively small or mostly transitory effects, or both, on small mammal population dynamics and plant community composition. During the study period 5 El Niño–high rainfall episodes have occurred lasting 1–3 years. Resident or core small mammals such as *Abrothrix olivaceus*, *Phyllotis darwini*, and *Octodon degus* experience dramatic fluctuations during and following rainfall pulses. Temporary resident or opportunistic species such as *Oligoryzomys longicaudatus* and *A. longipilis* disappear from the thorn scrub for varying periods of time. All species persist in more mesic nearby habitats near dry stream courses (aguadas). Since a 3-year high rainfall event in 2000–2002 mean annual rainfall has increased in this region, mainly due to a lack of prolonged droughts. Under these conditions, and building on a qualitative model proposed by Noy-Meir, long-lived species might become more abundant. Changes in the small mammal assemblage are consistent with these predictions; *O. degus*, a caviomorph rodent with a long life span, now comprises a more constant proportion of the small mammal biomass in the thorn scrub, and we have documented reduced variation in species diversity. Increased rainfall, a predicted consequence of global climate change in this region, might be leading to changes in small mammal assemblage structure and composition and ultimately will result in a more stable, less oscillatory assemblage in the thorn scrub. Additionally, invasive groups such as introduced lagomorphs and ephemeral plants might become more abundant in this community. The long-term consequences of changes in rainfall patterns due to El Niño Southern Oscillations (ENSOs), with important teleconnections to global-scale phenomena, will lead to diverse changes at the community level here.

Key words: Chile, El Niño, El Niño Southern Oscillation (ENSO), global climate change, population fluctuations, semiarid small mammals

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Long-term studies are important for identifying the importance and strength of biotic interactions and abiotic effects such as those due to global climate change (GCC—Müller et al. 2010). The former can be subtle and difficult to detect at short timescales, requiring carefully designed experiments and long-term monitoring to tease apart multiple interactions and distinguish between top-down and bottom-up control (Hunter and Price 1992; Meserve et al. 2003; Power 1992). The latter necessitates baseline data on preexisting conditions and sustained monitoring during periods of climate variation.

Whereas small-scale “pulse” studies often yield definitive results regarding the role of biotic interactions such as competition and predation, they can be less useful in predicting long-term consequences of broadscale processes such as GCC where “press” (i.e., long-term) studies are more appropriate. Although evidence for GCC is now so pervasive as to be irrefutable (Intergovernmental Panel on Climatic Change



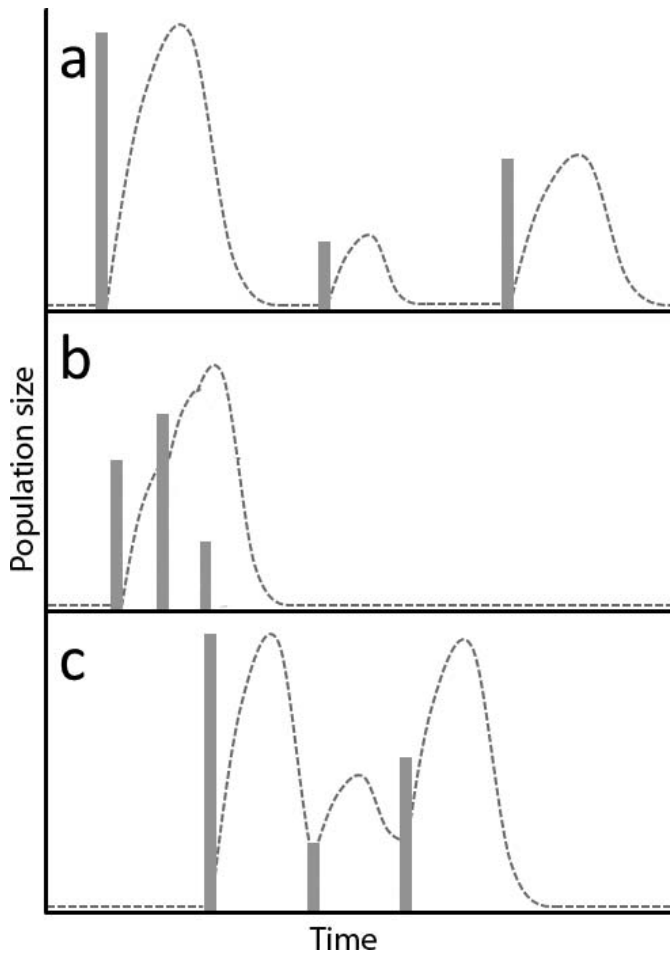


FIG. 1.—Graphical representation of biotic responses (gray lines) to rainfall pulses (vertical bars; modified from Noy-Meir 1973:figure 2). a) Widely separated pulses yield biotic responses as a function of the amount of rainfall. b) Clustered pulses can result in a cumulative biotic response that is larger than would be expected from any single pulse. c) Pulses with intermediate spacing should exhibit separate but partially cumulative responses. The extent to which these are cumulative should be a function of life history, with shorter-lived species treating these as separate pulses (as in panel a) and longer-lived species treating these as sequential or cumulative pulses (as in panel b or c).

2007; Walther et al. 2002), there remain limited numbers of long-term studies that allow for tracking organismal responses to this change, particularly in arid–semiarid parts of the Southern Hemisphere. These regions are of special interest because increased frequency, duration, and magnitude of El Niño Southern Oscillation (ENSO) events are one facet of ongoing GCC (Diaz et al. 2001; Easterling et al. 2000; Herbert and Dixon 2002; Mann et al. 2000; Timmermann et al. 1999). In western South America increasing rainfall tends to occur during ENSO warm phases, especially in southwestern Peru and north-central Chile; concurrently, low rainfall occurs elsewhere, such as in Australia and southern Africa. Although dispute remains about linkages between ENSO and GCC (e.g., Diaz et al. 2001; Kleeman and Power 2000), evidence suggests that GCC already has altered the ENSO phenomenon (Fedorov

and Philander 2000; Kerr 2004). Several stepwise shifts in climate appear to have occurred in the past 30 years, including one around 1976 when the eastern Pacific Ocean became warmer (World Meteorological Organization 1992). Between 1976 and 1998 El Niños were larger, more persistent, and frequent; the 2 largest El Niños of the 20th century occurred in this period (Gergis and Fowler 2009). The implications of such changes for semiarid regions are diverse (Holmgren et al. 2006; Jaksic 2001). Increased rainfall leads to dramatic changes in ephemeral plant cover (Dillon and Rundel 1990; Gutiérrez et al. 2000a), but in multiple-year El Niño–high-rainfall events ephemeral plant cover actually can decrease in subsequent years (de la Maza et al. 2009; Gutiérrez et al. 2000b). Various organismal groups increase dramatically following El Niños, including small mammals (Lima et al. 2002, 2006; Meserve et al. 1995), their vertebrate predators (e.g., Arim and Jaksic 2005; Farias and Jaksic 2007; Jaksic et al. 1997), and birds (Jaksic and Lazo 1999). The responses appear to be a consequence of upwardly cascading effects of rainfall on productivity in regions that are extremely arid (Holmgren et al. 2001, 2006). A similar pattern holds for plant and animal groups elsewhere when unusually high rainfall occurs during El Niño years (North America—Brown and Ernest 2002; Thibault et al. 2010) or La Niña years (Australia—Letnic et al. 2004, 2005). Negative biological consequences of more frequent El Niño–high-rainfall events also include a greater impact of introduced species (e.g., Arroyo et al. 2000; Gutiérrez et al. 2007; Hobbs and Mooney 2005).

Nearly 40 years ago Noy-Meir (1973:28) emphasized that rainfall is “the master input” in arid and semiarid environments, and he presented a model for biological responses to rainfall pulses. According to this model system responses are determined largely by the temporal distribution of a resource (rain; Fig. 1). When inputs are widely spaced, the biotic response is expected to be simple pulses in productivity that are a function of the quantity of available resources. Thus, smaller rainfall events should result in lower responses than larger ones. Ample evidence supports this facet of the model, especially the remarkable vegetative responses to high rainfall often associated with El Niño years (Gutiérrez et al. 2000a, 2000b; Holmgren et al. 2006). If multiple rainfall events occur in clusters, the net response might be cumulative across each event. Finally, if multiple rainfall pulses occur with intermediate frequency, the response might be composite but only partially cumulative.

Although the model developed by Noy-Meir (1973) was for ephemeral plants, it is applicable to higher trophic levels in a rainfall-limited system. The key feature to such systems is the interval between rainfall events as a function of the response time of the producer or consumer. Putting this in the context of consumer species, the salient question is how the duration of the interval between resource pulses will affect the consumer responses, depending on the life-history traits of the given organism. Species with high reproductive output and short life spans should treat separate rainfall pulses (and resulting vegetative growth) as independent events (Fig. 1a). Even with

sequential rainfall pulses, these species might not exhibit cumulative responses as long as little overlap exists among cohorts between rainfall periods. In contrast, species with lower reproduction and longer life spans should show cumulative responses to rainfall pulses, whether sequential (Fig. 1b) or separated by short intervals (Fig. 1c). The crucial feature here is the length of the organism's life span relative to the interval between rainfall events. If rainfall events are rare relative to the life span of a species, this species should treat sequential rainfall pulses as independent events in demographic terms.

Generally, caviomorph rodents have much lower reproductive output rates than do sigmodontine rodents (Weir 1974). Consequently, we predict that sigmodontine species should respond rapidly to rainfall events, but their relatively short life spans (most individuals at our site do not survive more than a year—Meserve et al. 1995) should limit the overlap between cohorts, and thus their demographic responses, to clumped rainfall events. In contrast, caviomorph rodents, with life spans > 3 years (Meserve et al. 1995; Previtali et al. 2010), might be expected to respond cumulatively to clumped rainfall events. Specifically, in a system with normally rare and widely spaced rainfall events that is changing to one with more closely timed El Niño–high rainfall events due to GCC, we predict that caviomorph rodents would be more likely to respond with sustained demographic growth than would sigmodontine rodents. A common caviomorph at our site is *Octodon degus*, which has a long gestation (90 days—Woods and Boraker 1975) and, generally, single small litters at this locality (Meserve and Le Boulengé 1987).

In 1989 we initiated a large-scale manipulation in a national park and World Biosphere Reserve in the north-central Chilean semiarid zone. Building on earlier work (Meserve 1981a, 1981b; Meserve and Le Boulengé 1987) and using a reductionist, multifactorial approach, we initially focused our attention on the role of biotic interactions in the community, specifically vertebrate predation, small mammal herbivory, and interspecific competition among small mammals. Manipulations targeted principal predators (i.e., owls [*Tyto alba*, *Athene cunicularia*, *Bubo magellanicus*, and *Glaucidium nanum*] and culpeo foxes [*Lycalopex culpaeus*]—Jaksic et al. 1992, 1997) and the principal small mammal herbivore, the degu (*O. degus*), a medium-sized (~ 120 – 150 g) caviomorph rodent. Other small mammals, such as the uncommon 150- to 250-g chinchilla rat (*Abrocoma bennettii*; also a caviomorph), several smaller (20–80 g) sigmodontines such as the olive grass mouse (*Abrothrix olivaceus*), the long-haired grass mouse (*Abrothrix longipilis*), Darwin's leaf-eared mouse (*Phyllotis darwini*), and the long-tailed rice rat (*Oligoryzomys longicaudatus*), and 1 marsupial, the elegant mouse opossum (*Thylamys elegans*), were unmanipulated (Meserve et al. 1995, 1996).

In this paper we review some key findings of this research program and then turn our attention to expectations in the face of changing patterns of rainfall in northern Chile. Our research program initially focused on the thesis that small mammals

were strongly affected by predation. Although this hypothesis was not strongly supported (Meserve et al. 1996; Previtali et al. 2009), another hypothesis—that plants were significantly affected by degu herbivory and their indirect activities—was partially verified (Madrigal et al. 2011). Overall, we have emphasized the overarching role of abiotic factors keyed to high rainfall events usually associated with warm ENSO phases (i.e., El Niños—Lima et al. 2006; Previtali et al. 2009, 2010). Our results show that effects exerted by these extrinsic factors are significant and pervasive, and we have concluded that they are leading to significant changes in community composition and function. Finally, given that climate change is predicted to result in more frequent rainfall events in northern Chile (Fiedler 2002; Holmgren et al. 2006; but see Comisión Nacional del Medio Ambiente 2006), we hypothesize that as a result, the caviomorph rodent, *O. degus*, characterized by long life spans, should increase in numbers and remain at a higher relative abundance in our system than many of the smaller, short-lived sigmodontine rodents (*Phyllotis* and *Abrothrix*). Overall, we expect that increasing annual rainfall and decreased interannual variation will affect the dynamics and variability of small mammal assemblages in the northern Chilean semiarid zone.

MATERIALS AND METHODS

Study site.—The study area is in Bosque Fray Jorge National Park ($30^{\circ}38'S$, $71^{\circ}40'W$) on the coast of the Pacific Ocean in north-central Chile. This 10,000-ha park contains semiarid thorn scrub vegetation and remnant fog forests that have been protected from grazing and disturbance since 1941. The flora of the lower elevational scrub zone includes spiny drought-deciduous and evergreen shrubs and understory herbs on a primarily sandy substrate (Gutiérrez et al. 1993). The climate is semiarid Mediterranean with 90% of the precipitation occurring in winter months (May–September); summer months (December–March) are warm and dry. Although annual rainfall has averaged 131 mm since 1989, in this period 5 El Niño–high-rainfall events have occurred: 1991–1992 (233 and 229 mm), 1997 (330 mm), 2000–2002 (209, 236, and 356 mm), 2004 (168 mm), and 2006 (147 mm). Intervening years were dry and included 2 La Niña events in 1998 and 2007 (11 and 48 mm, respectively).

Data collection.—In 1989 we established an experimental complex of sixteen 75×75 -m (0.56-ha) small mammal livetrapping grids in thorn scrub habitat in an interior valley of the park (Quebrada de las Vacas, 240 m elevation; Central Grid Complex; Fig. 2). The original design included 4 treatments each with 4 randomly assigned grids: low mesh fencing with holes in the fencing at ground level to allow all small mammal and predator access (controls); high fencing and overhangs, with netting overhead, and holes in the fencing to exclude predators but allow small mammal access, including degus (predator exclusions); low fencing but without holes to exclude degus but not other small mammals or predators (degu exclusions); and high fencing, with overhangs and netting but

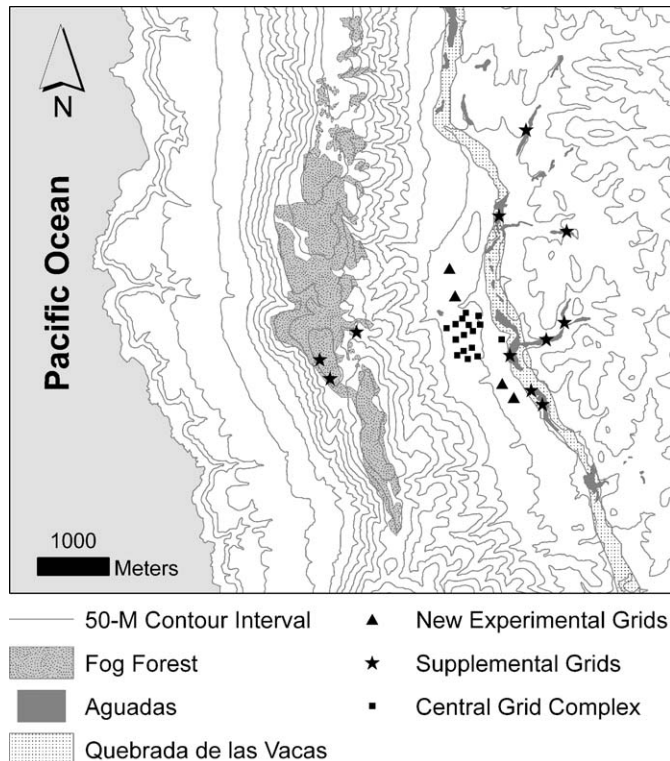


FIG. 2.—Location of study area, grids, and major habitats in Fray Jorge. Light-shaded areas are predominantly thorn scrub habitat. Sixteen grids in the Central Grid Complex have been trapped since 1989; 4 other grids (New Experimental Grids) were used for food-addition experiments in 1997–2001 and are 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.

without holes to exclude both predators and degus (degu + predator exclusions—Meserve et al. 1995, 1996, 2003).

Replicated monitoring methods used for small mammals on a monthly schedule are as follows (Meserve et al. 1996). Small mammals are trapped for 4 days month⁻¹ grid⁻¹ (5 × 5 stations, 15-m interval, 2 traps/station). Livetrapping procedures and handling of small mammals followed guidelines specified by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal and Use Committees at Northern Illinois University and the University of California, Davis. Monthly trappability for most species is remarkably high (>90%), justifying use of minimum number known alive (Hilborn et al. 1976) to estimate population size (Shenbrot et al. 2010; Thibault et al. 2010).

Between 1996 and 2004 we supplemented monthly monitoring on the Central Grid Complex with sampling on a series of identically sized unfenced grids established in peripheral habitat (Milstead et al. 2007; Supplemental Grids; Fig. 2). Habitats sampled included fog forest, shallow ravines (aguadas), and river bottoms (quebradas; Fig. 2). Except for frequency, trapping procedures were identical to those used on the Central Grid Complex.

Other components of the community that were monitored include perennial shrub cover, ephemeral cover (annuals +

geophytes), soil seed densities, and predator diet + activity. Since 2004 we have been monitoring insects and birds (Gutiérrez et al. 2010).

Data analysis.—We have reported on competition among small mammals and effects of predation on them elsewhere (Jaksic et al. 1997; Meserve et al. 1993, 1996, 1999, 2003; Previtali et al. 2009). Here, we focus on emergent trends in plants, predators, and control grid populations of small mammals in response to apparent changes in rainfall conditions since about 2000.

Within the context of the Noy-Meir (1973) model for productivity in arid regions, sequential pulses of rainfall should yield qualitatively different biological responses than other combinations. Parenthetically, 3 consecutive years of high rainfall should serve to amplify the differences between caviomorph and sigmodontine rodents. Although we have only 1 such 3-year period, it is useful to view small mammal responses to this event in the context of the several multiple-year rainfall events that have occurred since 1989.

To assess the influence of the duration of rainy events we characterized each rainfall year (May–April) as being either below the long-term mean annual rainfall of 131 mm or as the 1st, 2nd, or 3rd year of a rainy cycle (e.g., rain = 0, 1, 2, or 3). We compared relative changes in minimum number known alive by species in these 4 periods using a mixed-model analysis of variance (SAS Proc Mixed—SAS Institute Inc. 1999) in which our response variable (minimum number known alive for a given species) was a function of rain, month, the interaction of rain*month, and minimum number known alive in the preceding month. We treated rain, year, and month as classification variables, and nested year within rain as a random effect. We ran all models using 2 covariance structures. To account for potential autocorrelation we used a 1st-order autoregressive structure (type = ar(1)), and we compared this with Akaike's information criterion (AIC—Burnham and Anderson 2002) with models using the default variance components structure (type = vc). Using difference in AIC scores (Δ AIC) to compare models, those lacking the rain*month interaction consistently performed poorly (Δ AIC > 200). Two of 5 species were modeled better with an autoregressive covariance structure, but 1 of these was only slightly better than a model with the simpler variance components structure. In all cases results were qualitatively identical with either covariance structure, so we present only the latter results. We extracted least-squares mean minimum number known alive (and SE) for graphical purposes and quantitatively compared these with *t*-tests using the DIFF option in SAS (SAS Institute Inc. 1999).

Finally, because rainfall patterns in the 1st and 2nd decades of this study have differed, we assessed the influence of this on species diversity at our site using the Shannon–Wiener diversity index (H'). We calculated the coefficient of variation for H' from 1989 through 1999 and from 2000 through 2010 and tested for reduced diversity in the latter period using a *Z*-test (Zar 1999).

RESULTS

Plant responses.—Annual perennial shrub cover varied between 38.6% and 64.4% over the last 21 years, similar to values recorded 50 and 35 years ago (Gutiérrez et al. 1993; Meserve 1981a; Muñoz and Pisano 1947). Ephemeral plant cover, however, varied dramatically from as low as 0% during a La Niña event (1998, 11 mm rainfall) to as high as 80–86% during El Niño years (e.g., 1991, 1997, and 2000). Decreases in ephemeral cover in ensuing years of multiple-year high rainfall events (i.e., 1992 and 2001–2002) could be due to nutrient depletion effects (Gutiérrez et al. 1997, 2000b) and lagged increases of degu populations and their indirect facilitation of exotic and native ephemerals (Madrigal et al. 2011). Maximum seed densities of 63 plant species reached 41,832 seeds/m², similar to values from North American deserts (Inouye 1991); however, and not surprisingly, seed densities did not track rainfall as closely as did ephemeral cover (Gutiérrez and Meserve 2000). Similar responses have been documented elsewhere in semiarid Chile (Dillon and Rundel 1990; Gutiérrez et al. 2000a). Plant species richness at our site rose with increasing productivity and plant cover, which in turn was positively related to rainfall; however, productivity was related more closely to diversity indices such as H' and J' (evenness) than to species richness as such (A. Gaxiola, Pontificia Universidad Católica de Chile, pers. comm.). de la Maza et al. (2009) used normalized difference vegetation index data from 1984 to 2003, which included 4 El Niño–high rainfall events, to show that increased rainfall led not only to increased plant primary productivity but also a longer growing season. Greening-up was accelerated, but a delay in the productivity peak occurred in high rainfall years. Finally, the decrease in vegetation (senescence) proceeded more rapidly, thus restricting further vegetation growth. As noted, a possible mechanism for this is decreased nutrient availability due to increased competition among plants (Gutiérrez et al. 1997).

Predator responses.—As indexed by pellet counts (owls) and olfactory line activity (foxes), trends in numbers of principal small mammal predators roughly paralleled those of their prey. Although foxes were principal predators of *A. bennettii*, followed by *O. degus*, they also were more omnivorous and showed less numerical fluctuation over time than did owls (Previtali et al. 2009). Major predators on *P. darwini* included burrowing owls (*A. cunicularia*) and barn owls (*T. alba*). Burrowing owls are principally insectivorous and feed opportunistically on small mammals when the latter are abundant, whereas barn owls are more obligate small mammal predators (Jaksic 1998a; Jaksic et al. 1997) and show greater changes in abundance over time (Previtali et al. 2009).

Small mammal responses.—Similar to plants, responses of small mammals to El Niño–high-rainfall events were variable but largely dependent on their individual residency status and life-history characteristics. Milstead et al. (2007) distinguished between core species (i.e., *O. degus*, *P. darwini*, *A. olivaceus*, and *T. elegans*), which are permanent residents of the thorn scrub (although they show demographic fluctuations there),

and opportunistic species (i.e., *O. longicaudatus* and *A. longipilis*), which are temporary residents of the thorn scrub, persisting otherwise in peripheral habitats such as aguadas, river bottoms (both areas of more mesic vegetation due to standing or subsurface water), or fog forest on coastal ridges (Fig. 2).

Octodon degus showed protracted responses to high rainfall, often increasing only in subsequent years after an initial wet one (Fig. 3). Analysis of several life-history traits for this species revealed that their variation is associated more with longer term patterns (e.g., rainfall phases or change since 1999) than with annual fluctuations in rainfall or density (Previtali et al. 2010). Unlike for other rodents (most sigmodontines), degu increases often were incremental, reaching densities as high as 213.8 individuals/ha after a prolonged El Niño–high-rainfall period in 2000–2002 (Fig. 3).

Phyllotis darwini and *A. olivaceus* are smaller than degus, and as sigmodontine rodents they exhibit rapid rates of increase due to frequent, large litters and high frequency of movements during periods of high rainfall. *P. darwini* showed annual oscillations regardless of precipitation totals, although numbers were higher in wet years (Fig. 3). Maximum densities were about 60–80 individuals/0.56-ha grid, and increases usually occurred within about 3–4 months of the onset of precipitation.

Similar to *P. darwini*, *A. olivaceus* showed rapid increases about 3–4 months after precipitation onset in wet years (Fig. 3). Unlike *P. darwini*, however, populations of *A. olivaceus* lacked annual oscillations, and they declined to very low levels during dry years, even disappearing for varying lengths of time. Because of this they might be characterized more accurately as a quasi-core species (Milstead et al. 2007). Physiologically, *A. olivaceus* appears less arid-adapted than *P. darwini* (Cortés et al. 1988) and has a more mesic geographic range than the latter (Iriarte 2008). Whereas both *A. olivaceus* and *P. darwini* are permanent residents in peripheral aguada habitats near the upland thorn scrub, they are rare or absent in fog forest (Milstead et al. 2007).

Two other sigmodontines, *O. longicaudatus* and *A. longipilis*, are only temporarily resident in the thorn scrub (Milstead et al. 2007). In thorn scrub *O. longicaudatus* showed highly sporadic numbers, often (but not always) during pulses of higher rainfall (Fig. 4); there were long periods of absence of this species.

Abrothrix longipilis demonstrated a different pattern than *O. longicaudatus*, with slower periods of increase during wet years and protracted declines in subsequent dry years (Fig. 4). Precipitation pulses of 168–147 mm in 2004 and 2006 did not trigger increases in this species. Both *O. longicaudatus* and *A. longipilis* maintain high numbers in both fog forest and aguadas, with survival of up to 4 years for the latter (P. L. Meserve, pers. obs.); thus, these habitats probably represent sources and the thorn scrub sinks (sensu Pulliam 1988).

Thylamys elegans, another core species, showed roughly similar annual oscillations of about the same magnitude irrespective of precipitation amount (Fig. 4). This insectivorous species is about equally abundant elsewhere in peripheral

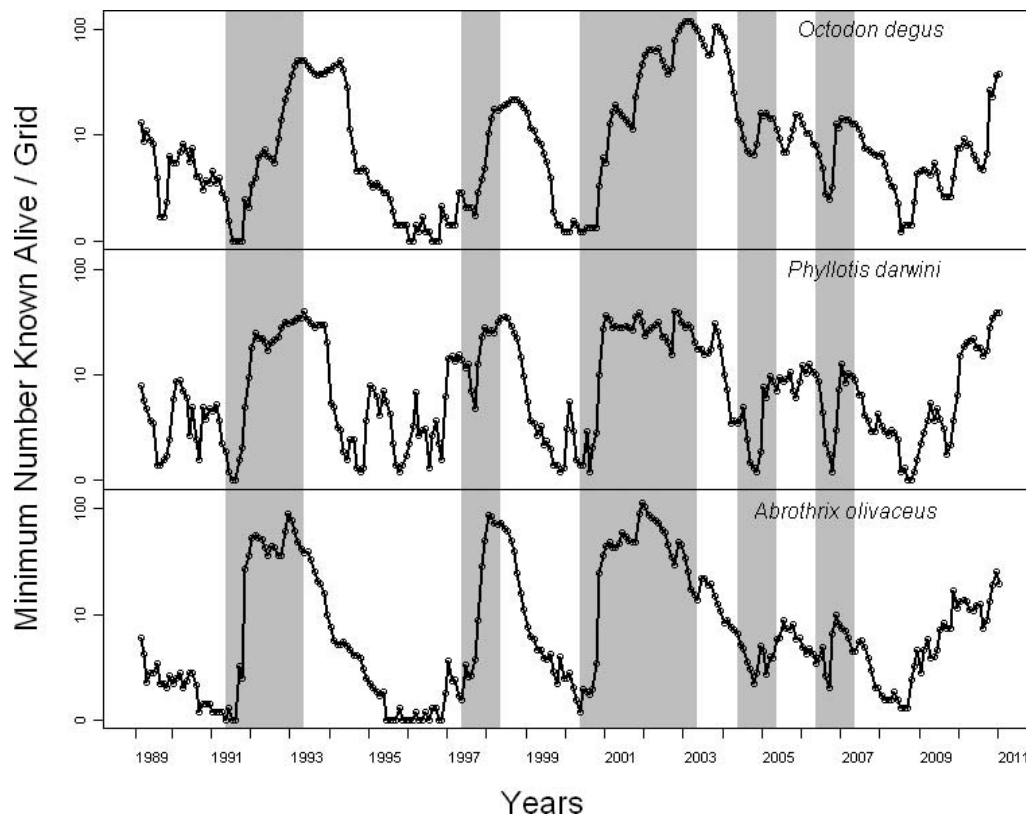


FIG. 3.—Population responses by 3 core species (*Octodon degus*, *Phyllotis darwini*, and *Abrothrix olivaceus*) on control grids in the thorn scrub habitat in Fray Jorge between 1989 and 2010. Densities are numbers of individuals/0.56-ha grid as estimated by use of minimum number known alive (Hilborn et al. 1976).

habitats, including aguadas and fog forest (Milstead et al. 2007), and thus appears to be a habitat generalist.

Potential impact of climate change.—El Niño Southern Oscillation—rainy years have been more frequent in the later half of our study period (since 2000), and this has been accompanied by 2 clear trends. First, all 5 species examined—the 3 core species *O. degus*, *P. darwini*, and *A. olivaceus*, and the 2 opportunistic ones, *A. longipilis* and *O. longicaudatus*—responded demographically to rainfall events, but their responses differed in ways that generally match our predictions from the Noy-Meir (1973) model of biotic responses to pulsed resources in arid systems (Fig. 1).

For *O. degus* and *A. longipilis* this analysis indicated no demographic response to the 1st year of rainy events. Visual interpretation of trends (Figs. 3 and 4) suggests that this reflects a delayed response rather than the absence of any such response. In contrast, however, the other 3 species demonstrated clear numerical increases in response to rains in the 1st rainy year. Patterns among these 2 groups of species diverged further with a 2nd sequential year of rain. Both *A. longipilis* and *O. degus* exhibited increases in numbers, but *O. longicaudatus* declined marginally, and both *A. olivaceus* and *P. darwini* increased only marginally. In the single 3-year rainy period (2000–2002) only *O. degus* continued to increase in numbers. *A. longipilis* remained unchanged from 2nd year numbers (although this may reflect mingling of 2nd-year data from 1992–1993 and 2001–2002; Fig. 4), *O. longicaudatus*

and *P. darwini* declined marginally, and *A. olivaceus* declined substantially, from 2nd-year densities (Fig. 5).

Even more compelling than these demographic patterns, however, are changes in the proportions of small mammal biomass comprised by *O. degus* and other core species, compared to those of opportunistic species, since about 2001 (Fig. 6). In particular, the proportion of core small mammal biomass comprised by *O. degus* has been >40% since then. Thus, biomass proportions in the thorn scrub are increasingly dominated by core species (mostly *O. degus*), with corresponding reductions in the role of opportunistic ones. Shannon diversity values in the thorn scrub also have fluctuated much less over the past 11 years (since 2000) than during 1989–1999 (mean coefficient of variation [CV] = 0.095 versus 0.220, $Z = 11.85$, $P < 0.01$; Fig. 7). This indicates that the small mammal assemblage in the thorn scrub is not experiencing dramatic changes in diversity as it did prior to 2000.

DISCUSSION

Despite major differences in the demography of the component species in this small mammal assemblage (or perhaps because of these differences), some general patterns emerge. Core species exhibit patterns of population change that result in their long-term persistence in the thorn scrub despite most showing dramatic fluctuations in response to rainfall variation. In contrast, opportunistic species demonstrate

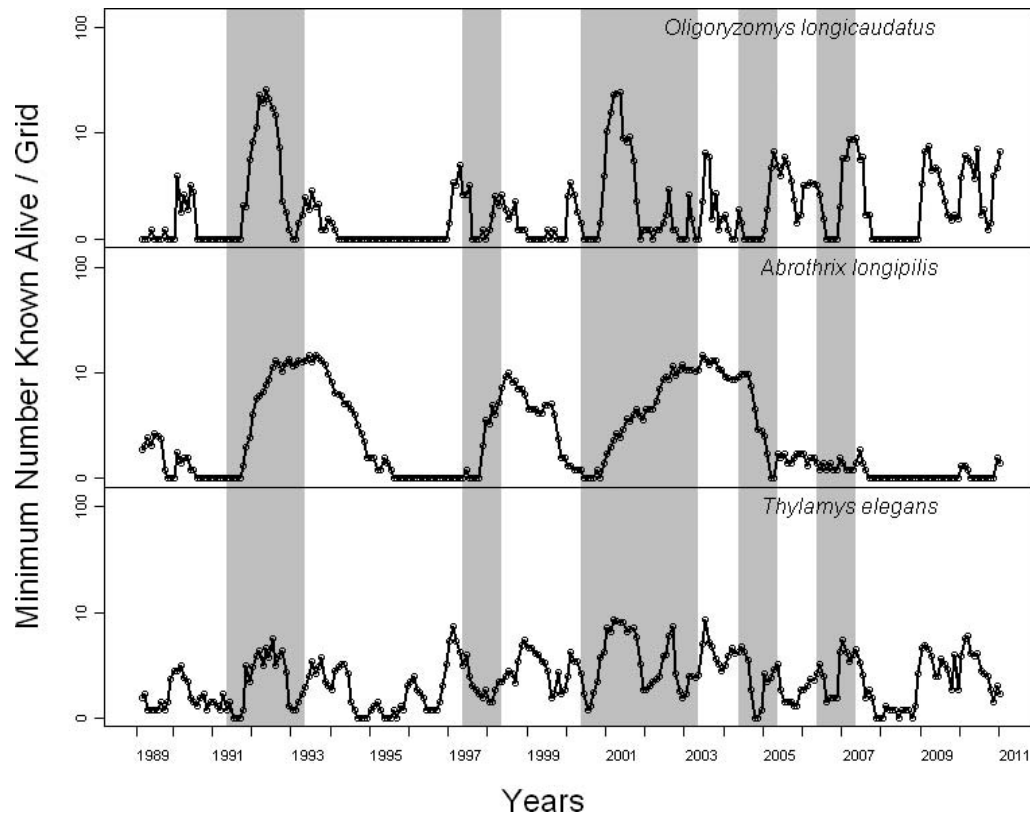


FIG. 4.—Population responses of 2 opportunistic species (*Oligoryzomys longicaudatus* and *Abrothrix longipilis*) and a core species (*Thylamys elegans*) on control grids in the thorn scrub habitat in Fray Jorge between 1989 and 2010. Densities are numbers of individuals/0.56-ha grid as estimated by use of minimum number known alive (Hilborn et al. 1976).

sporadic fluctuation and occurrence in the thorn scrub and can disappear from that habitat for months to years.

In semiarid ecosystems variation in the amount of precipitation is a critical driving factor for primary productivity

(Chesson et al. 2003; Holmgren et al. 2006; Noy-Meir 1973). Spatial and temporal subsidies also can play an important role in explaining fluctuations of major consumer groups (Anderson et al. 2008; Polis et al. 1996, 1997). In our system

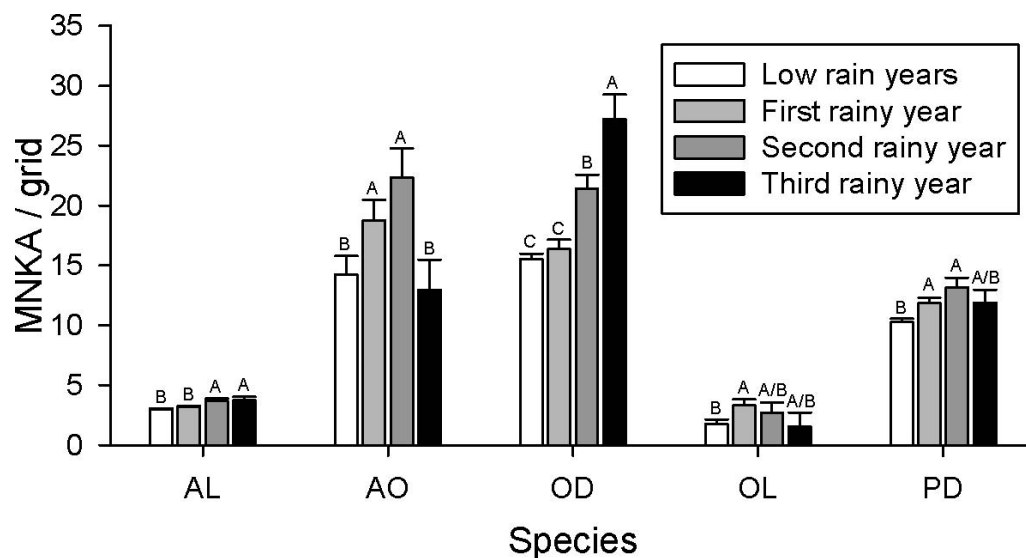


FIG. 5.—Least-square means ($\pm$ SE) of the minimum number known alive (MNKA) for 5 species of small mammals in 4 rainfall periods. Different letters above bars indicate significant differences (within species) based on a mixed-model analysis of variance (using DIFF option within the LSMEANS statement in SAS [SAS Institute Inc. 1999]). AL = *Abrothrix longipilis*, AO = *A. olivaceus*, OD = *Octodon degus*, OL = *Oligoryzomys longicaudatus*, PD = *Phyllotis darwini*.

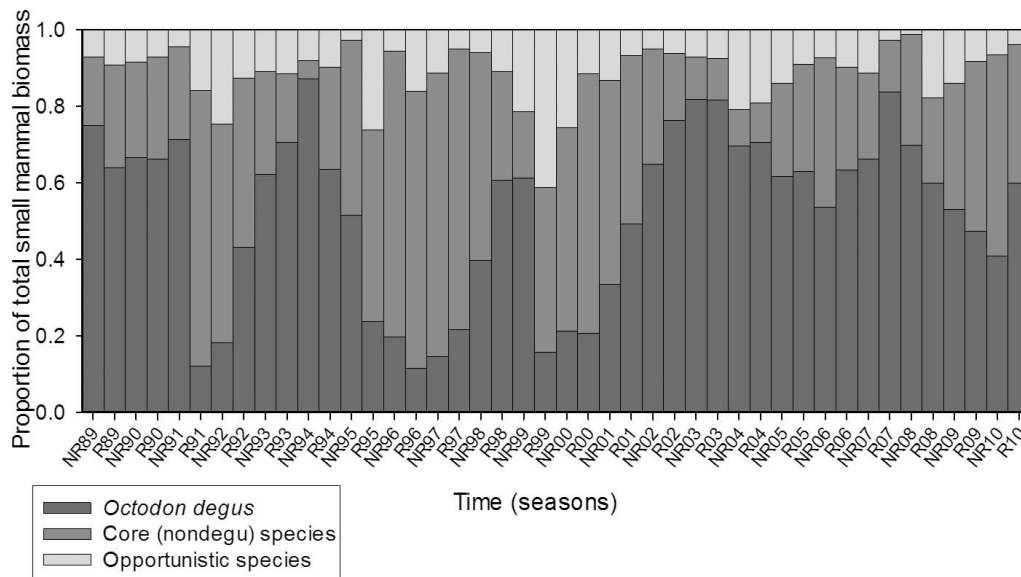


FIG. 6.—Proportion of small mammal biomass made up of *Octodon degus*, other core species (*Phyllotis darwini*, *Abrothrix olivaceus*, and *Thylamys elegans*), and opportunistic species (*Abrothrix longipilis* and *Oligoryzomys longicaudatus*) from 1989 through August 2010 for nonreproductive (NR) and reproductive (R) seasons. The nonreproductive season includes small mammal data from March through September, whereas the reproductive season includes data from October through February.

spatial subsidies are manifested by rapid increases in small mammal numbers in the thorn scrub during wet years augmented by immigration from peripheral habitats where year-round populations persist (Milstead et al. 2007). Temporal subsidies are reflected by large increases in food availability following high rainfall. Elsewhere we showed that food supplementation led to higher numbers and biomass of most core species (i.e., *O. degus*, *P. darwini*, and *A. olivaceus*) during dry periods, but not during El Niño–high-rainfall periods (Meserve et al. 2001). Thus, food is a critical limiting factor, but rainfall is the proximate influence in this system.

At the same time, the propensity for pulsed systems to return to a predictable stable point depends on the geographical context of the system. Small mammal communities in the southwestern United States experience relatively slow compositional changes and stable patterns of energy use (Ernest et al. 2008; Thibault et al. 2004; White et al. 2004), although extreme climatic events can have dramatic effects that greatly influence apparent long-term patterns (Thibault and Brown 2008; Thibault et al. 2010). In marked contrast, semiarid systems in Australia and South America show radical changes in abundance patterns over short time spans and relatively few

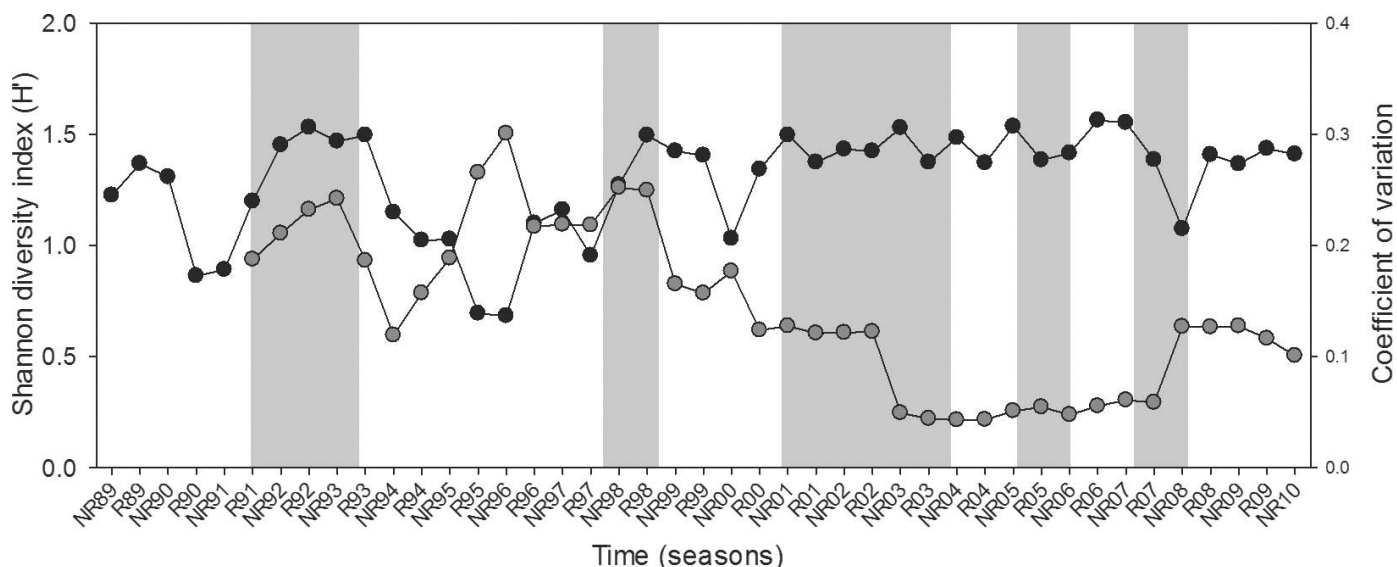


FIG. 7.—Shannon diversity (black symbols) of small mammals in Fray Jorge for 6-month nonreproductive and reproductive season from 1989 through August 2010 (same time periods as in Fig. 6). The gray symbols are coefficient of variation (CV) values for a running 3-year window. Hence, the 1st value (R91) represents the CV for NR89–R91, the 2nd CV value is for R89–NR92, and so on.

compositional changes in the long term (Dickman et al. 1999; Letnic et al. 2004, 2005; Meserve et al. 2003). Part of the explanation for geographic differences lies in the size of the species pools, which is especially limited in the northern Chilean semiarid zone (Meserve and Glanz 1978). Other evidence suggests that unlike southwestern United States deserts, Chilean semiarid small mammal assemblages are not strongly structured by competition (J. Goheen, University of Wyoming, pers. comm.). The same can be true for rodents in the Negev Desert (Shenbrot and Krasnov 2002; Shenbrot et al. 2010).

In our system we expected to see marked compositional changes in response to the increased frequency of high rainfall events probably driven by GCC. Recent changes in the small mammal assemblage generally match our predictions, but with some caveats. Overall, since 2000 our site has experienced more stable biomass proportions and species diversity, presumably reflecting changes in rainfall patterns favoring more mesic core species. Until recently, rainfall had been declining in the northern Chilean semiarid zone, continuing a gradual aridity trend over the past 1,000 years (Bahre 1979; Villalba 1994). Rainfall in Fray Jorge averaged 209 mm/year in 1940–1949, 185 mm in 1960–1969, 127 mm in 1970–1979, and 111 mm in 1990–1999 (Fulk 1975; Meserve et al. 2003). However, since 2000, rainfall has averaged 150 mm annually; the 3 largest El Niño events of the past 100 years have occurred since 1982 (Gergis and Fowler 2009).

Patterns of rainfall have shifted halfway through the 20 years of our study. In the 1st decade our site experienced a single 2-year rainy period in 1991–1992 followed by a 1-year rainy period in 1997. In contrast, the 2nd decade was marked by a prolonged 3-year rainy period and 2 subsequent 1-year rainy periods. The Noy-Meir (1973) model predicts that as the interval between rainfall events decreases, the effects of these pulses could be additive (or multiplicative). For rodents with different life spans we predicted that the multiple-year rainfall events should be perceived by the short-lived species as sequential pulses because populations of these species with low overlap between cohorts should decrease in size in the interval between rainy periods. In contrast, the longer-lived caviomorph rodents might perceive multiple-year rainy periods as a cluster of resource pulses. Because *O. degus*, the primary caviomorph at our site, lives longer than most sigmodontines, we predicted that it should respond cumulatively to 2nd and 3rd years of rainfall. Demographic responses at our site appear to support this prediction. *O. degus* showed a delayed response to rainfall, but it appeared to increase even more with additional rainy years. In contrast, 2 other core species (*A. olivaceus* and *P. darwini*) did not appear to increase numerically after the 1st year of rains, and *A. olivaceus* even declined in the 3rd year of our single 3-year rainy period. The 2 opportunistic species analyzed demonstrated smaller quantitative responses to rainy periods, but they also agreed with our predictions. That is, the short-lived *O. longicaudatus* increased numerically in the 1st year of rainy periods but failed to increase further with longer events, and

the longer-lived *A. longipilis* showed a delayed population increase until the 2nd year, like *O. degus*, but maintained its population size in the 3rd year of rainfall. Although the conclusions that we can draw from these analyses are limited (i.e., only one 3-year rainy period and two 2-year cycles, one of which comprised the first 2 years of our 3-year cycle), they are suggestive. More compelling perhaps is the increase in the relative importance of *O. degus* in the 2nd decade of our study, presumably in response to more frequent rainy years. As a result, temporal variability in assemblage composition and mean diversity were reduced in the 2nd half of our study (Fig. 7), with implications for how this system responds to GCC.

Holmgren and Scheffer (2001) suggested that El Niño events can present opportunities for restoration of degraded semiarid systems; at the same time, cascading-upward effects of increased productivity triggered by high rainfall might attenuate top-down control or even destabilize it (Holmgren et al. 2006; Scheffer et al. 2008). Also, Holmgren et al. (2001, 2006) emphasized that more frequent El Niño events might reverse or ameliorate the general desertification of much of north-central semiarid Chile (Bahre 1979; Holmgren and Scheffer 2001). El Niño has facilitated outbreaks of small mammals and influenced agriculture elsewhere (Fuentes and Campusano 1985; Holmgren et al. 2006; Jaksic 2001; Jaksic and Lima 2003; Pearson 1975).

A broader consequence of GCC and more frequent El Niños can be a greater impact of introduced species (Arroyo et al. 2000; Gutiérrez et al. 2007; Hobbs and Mooney 2005). Introduced plants comprise 18% of the Chilean flora and 27% of herbaceous plants alone. Some naturalized species (e.g., *Erodium*, *Medicago polymorpha*, and *Malva nicaeensis*) constitute up to 45% of the vegetation in Chilean matorral (Arroyo et al. 2000; Figueroa et al. 2004). Changes in the proportions of exotic species have been attributed to the effects of exotic grazers (Holmgren 2002) and fire (Kunst et al. 2003; Sax 2002; but see Holmgren et al. 2000). In Fray Jorge, where fire and most livestock have been absent since at least 1944, exotic plants comprise up to 21% of the herbaceous species and 19% of the seed bank species (Gutiérrez and Meserve 2000). In contrast to plants, only 24 (4%) of 610 vertebrate species in continental Chile are introduced (Iriarte et al. 2005; Jaksic 1998c). However, negative impacts of introduced murid rodents (*Rattus rattus*, *R. norvegicus*, and *Mus musculus*) and lagomorphs (*Oryctolagus cuniculus* and *Lepus europaeus*) have been documented (murids [Lobos et al. 2005; Milstead et al. 2007] and lagomorphs [Jaksic 1998a, 1998c]). Jaksic (1998a) described positive effects of rabbits and hares on indigenous vertebrate predators, including pumas, diurnal hawks, and owls, but also noted the apparent lack of strong predator utilization of them until the late 1980s. In Fray Jorge lagomorph populations historically have been low, but concurrent with the prolonged El Niño–high-rainfall event of 2000–2002 and a sharp decrease in the numbers of foxes due to an outbreak of parvovirus, rabbit and hare numbers increased dramatically in the park. Recent experimental work immediately outside the

park demonstrated significant effects of excluding rabbits and hares, including a 90% increase in survival of *Prosopis chilensis* (an arborescent shrub largely extirpated from arid northern Chile), increases in tall native grasses (e.g., *Bromus berterianus*), and decreases in native and exotic prostrate ephemerals (Gutiérrez et al. 2007; Manrique et al. 2007). Additional exclusion of herbivores under conditions of simulated high rainfall increased overall plant productivity and favored native species (Manrique et al. 2007). Access by lagomorphs reduced native grass biomass and facilitated invasive grasses; thus, lagomorph grazing can affect plant community structure and composition by influencing competitive dynamics between native and exotic plant species.

Although most future climatic scenarios have predicted stronger and more extreme El Niño events (Fiedler 2002; Holmgren et al. 2006; Jaksic 1998b), some forecast decreased winter rainfall in semiarid northern Chile (Comisión Nacional del Medio Ambiente 2006). Such an alternative climate scenario could occur here, but our understanding of interactions between GCC and ENSO, and, in turn, between ENSO and local environments, continues to improve. As we reported earlier (Previtali et al. 2010), El Niño differentially influences productivity across the elevational gradient in the Chilean Andes (Squeo et al. 2006) and can reduce substantially the production of fog from the Pacific Ocean (Garreaud et al. 2008), an important contributor to local moisture in this semiarid region (del-Val et al. 2006; Kummerow 1966). Given this, it seems clear that any influence of GCC on El Niño events is likely to influence the availability of water throughout northern Chile, and results from our long-term site indicate that the ecological consequences of such changes will not be trivial.

Overall, more frequent and intense El Niños have the potential to alter community dynamics significantly in the northern Chilean semiarid zone. Such perturbations could lead to significant changes over time in community membership and interspecific interactions, including increased opportunities for invasive species that heretofore have been largely unimportant due to the region's aridity.

RESUMEN

Desde 1989, hemos estudiado las poblaciones de micromamíferos en un sitio semiárido en el norte de Chile, mediante un complejo de grillas de trampeo-vivo a gran escala. La exclusión selectiva de depredadores vertebrados y/o posibles competidores micromamíferos ha resultado en efectos pequeños y/o mayormente transitorios en la dinámica de micromamíferos y en la composición de la comunidad de plantas. Durante el período de estudio, han habido 5 eventos lluviosos o El Niño con duración de 1 a 3 años. Los micromamíferos residentes o centrales tales como *Abrothrix olivaceus*, *Phyllotis darwini*, y *Octodon degus* mostraron marcadas fluctuaciones durante y posteriormente a los pulsos de lluvias. Las especies oportunistas o de residencia transitoria tales como *Oligoryzomys longicaudatus* y *A. longipilis* desaparecen del ambiente de matorral espinoso por períodos variables de

tiempo. Todas las especies persisten en ambientes cercanos más mésicos asociados a lechos de arroyos secos (aguadas). Después de 3 años lluviosos consecutivos entre el 2000 y 2002, el promedio anual de precipitaciones ha aumentado en esta región, principalmente debido a una ausencia de sequías prolongadas. Bajo estas condiciones y usando un modelo cualitativo propuesto por Noy-Meir, especies de larga vida pueden llegar a ser más abundantes. Los cambios del ensamble de micromamíferos son consistentes con estas predicciones, el roedor caviomorfo con una historia de vida larga, *O. degus*, ahora constituye una proporción más constante de la biomasa de micromamíferos del matorral espinoso, y ha habido una reducción en la variación de la diversidad de especies. El aumento en las lluvias, que está pronosticado como una consecuencia del cambio climático global para esta región, puede estar causando cambios en la estructura y composición del ensamble de micromamíferos, y eventualmente resultará en un ensamble más estable y menos fluctuante en el matorral espinoso. A su vez, los grupos invasores como los lagomorfos y plantas efímeras introducidas pueden intensificar su establecimiento en esta comunidad. Por lo tanto, las consecuencias a largo plazo de los cambios en los patrones de lluvias debidos a El Niño Oscilación del Sur (ENOS) con importantes teleconexiones a fenómenos de escala global, causarán aquí cambios diversos al nivel de la comunidad.

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