

Energetic compensation is historically contingent and not supported for small mammals in South American or Asian deserts

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Abstract. Understanding the nature of faunal assembly and community structure remains central to ecology. Research in North American deserts and some tropical forests provides evidence of energetic compensation and zero-sum dynamics, suggesting that species in some natural assemblages may be replaced with limited impact on ecosystem function. Experimental removal of a dominant small mammal (degu, *Octodon degus*) from replicate plots in semiarid coastal thorn-scrub habitat in north-central Chile revealed no evidence for energetic or functional compensation; energy consumption remained significantly lower on degu exclusions relative to control plots after 17 years of exclusion. This occurred in spite of the fact that the geographic species pools for South American sites generally are similar in size to those of most North American sites (mean and median number of species, 16.3 and 21.5 vs. 21.0 and 20, respectively). A macroecological assessment of energetically equivalent species at 394 arid sites in North America, the Gobi Desert, and South America indicated that the number of potentially equivalent species was lower than (Gobi) or similar to (South America) that found in North America, but when segregated by trophic groups, these faunas differed markedly. North American sites included large numbers of granivorous species whereas South American sites were dominated by omnivores. The more general trophic strategy in the latter sites would be expected to facilitate compensatory responses within local faunas, suggesting either that our site is anomalous or that other factors are governing local dynamics. Further research is needed to understand the generality of compensatory dynamics within natural systems, as this mechanism has direct relevance to discussions on ecological resilience in the face of ongoing environmental change.

Key words: community ecology; degu; deserts; energetic compensation; functional redundancy; historical contingency; north-central Chile; *Octodon degus*; species coexistence; species redundancy; trophic strategy; zero-sum dynamics.

INTRODUCTION

Ecological systems face a barrage of abiotic exigencies, from seasonal patterns in climate to multi-decadal atmospheric drivers, interspersed with episodic events such as drought and storms. Global climate change (GCC) is poised to amplify some of these (Post 2013), leading to extensive discussion over ecological responses to GCC and to synergistic impacts of multiple threats to biodiversity (e.g., Brook et al. 2008, Powell and Lenton 2013), potentially with global implications (Brook et al. 2013). Understanding how ecological assemblages will respond to current and pending threats is an increasingly

urgent theme in ecology. In particular, as species adjust to extrinsic stressors and some species are locally or regionally extirpated, the extent to which remaining species will compensate, either demographically or functionally, is of great ecological and conservation interest. The nature of species interactions is likely to play important roles in determining the extent to which different species are impacted by GCC (Cahill et al. 2013, Post 2013). Such interactions link landscape dynamics and spatial ecology with local patterns and processes such as niche structure and niche construction, and ecological compensation and compensatory dynamics. Natural ecological communities interface across various spatiotemporal scales (Holyoak et al. 2005), and desert rodents, in particular, are good candidates for metacommunity dynamics (Stevens and Tello 2012). A related question is the extent to which biodiversity in

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general, and individual species in particular, may stabilize ecological dynamics or yield ecological or functional redundancy. Available literature supports the role of diversity (Chapin et al. 1998, Loreau et al. 2001, Kinzig et al. 2002), but debate persists around the role of individual species (e.g., Symstad et al. 1998). Here we focus on the latter set of themes, and address the extent to which functional compensation characterizes arid-zone assemblages of small mammals.

Understanding the factors underlying the structure of ecological assemblages over time and space has generated controversy over multiple decades (Andrewartha and Birch 1954, Cody and Diamond 1975, Ricklefs and Schluter 1993). One area of emphasis has been the individuality of species: are all species unique and ecologically distinct, or are there “ecological equivalents” that perform similar roles, and that potentially could compensate for biodiversity losses in the face of anthropogenic extinctions? Niche theory (Vandermeer 1972) argues that no two species may use resources in the same manner in the same place at the same time; however, this does not preclude overlap in use of some resources or similar or complementary use of similar resources in allopatric species. Hence, many groups of species similar in some key niche parameter co-occur less frequently than expected by chance, and distribute allopatrically across landscapes (Cody 1974, Brown 1975, Terborgh and Weske 1975, Grant 1986, Kelt et al. 1996). Many examples exist of overlap on one niche axis balanced by dissimilarity on one or more other axes.

Near Portal, Arizona, USA, J. H. Brown and colleagues have excluded granivorous kangaroo rats (*Dipodomys*) from a series of replicate sites (Brown 1998), and for nearly two decades, other granivorous rodents at this site (*Baiomys*, *Chaetodipus*, *Perognathus*, *Peromyscus*, *Reithrodontomys*) exhibited limited compensation in terms of consumption of energy resources left in the absence of kangaroo rats; this changed in 1995–1996, when Bailey’s pocket mouse (*C. baileyi*) successfully established on these exclusion plots. Within three years, this species consumed about 67% to >80% of the energy resources that would have been used by kangaroo rats (based on observed densities on control plots; Ernest and Brown 2001*a, b*). Such “zero-sum dynamics” have also been documented in tropical forest (Hubbell 2001, Ernest et al. 2009), but the generality of this remains uncertain (Houlahan et al. 2007).

We have studied a site in semiarid north-central Chile for 25 years, and for 19 of these years we excluded a key small-mammal species, *Octodon degus* (“degu” hereafter), from replicate sites as part of an experimental assessment of the role of biotic and abiotic regulation of semiarid ecosystems (Gutiérrez et al. 2010, Meserve et al. 2011; see Plate 1). According to zero-sum dynamics, we hypothesized that exclusion of the largely folivorous degu would lead to compensatory changes in other small-mammal species. In

contrast to expectations, population sizes of Darwin’s leaf-eared mice (*Phyllotis darwini*) and olive-colored akodont (*Abrothrix olivaceus*) did not increase markedly on degu exclusions relative to control plots (Meserve et al. 1993*a*, 1996, Gutiérrez et al. 2010). This analysis failed to account for differential energy consumption, however, and was limited to individual species. Here we expand these earlier efforts to evaluate whether our site conforms to the expectations of zero-sum ecology. Because our site has not experienced immigration of new species, we assume that any compensatory changes on degu-exclusion plots will reflect incremental changes in energy use by component species. Small (not significant) changes in population numbers combined with greater longevity, for example, could result in greater net changes in energy use than in population numbers. As one example, degus are only slightly more abundant on predator exclusion grids at our site, but they experience greater survival there, relative to control grids (Meserve et al. 1993*b*). This could result in larger (older) degus and greater overall biomass, which would translate to greater energy consumption in spite of similar population sizes.

We hypothesize that total energy use by small-mammal assemblages on degu-exclusion grids will be similar to that on control plots via incremental increases in energy use by component species. Such changes would not conflict with niche theory because we already know that these species co-occur successfully and that they differ in body size and other ecological features. This is somewhat different from the situation documented for Portal, Arizona, where substantial energetic compensation occurred only after the relatively large *C. baileyi* established in *Dipodomys* exclusion plots; note that at that site, *C. baileyi* remain rare on control plots, suggesting that their historical absence probably was caused by competition with similar-sized or larger kangaroo rats, augmented by a sorting effect (Chase and Leibold 2003) whereby the regional presence of *Dipodomys* may have inhibited the immigration of *C. baileyi* to the Portal site. Failure to document similar energy use would indicate a lack of energetic compensation. At our site this could reflect the different niche or trophic structure of component species (e.g., primarily herbivores and omnivore/insectivores) and the lack of immigration of “degu-equivalent” species. We evaluated the likelihood of the latter but expanded this to consider all small-mammal species at our site by tallying the number of potentially equivalent (PE) species, in energetic terms, in the regional species pool. We then expanded this in a more general assessment of the potential for immigration of such PE species at other sites in arid regions of South America as well as Asia and North America.

The Heteromyidae comprise a dominant and highly diverse radiation in North American deserts, and they are largely granivorous (Brown et al. 1979, Reichman and Price 1993). Consequently, the trophic structure of



PLATE 1. A young degu (*Octodon degus*), a key small mammal species found in areas of Chile with a mediterranean climate. Experimental removal of degus from replicate plots in semiarid coastal thorn-scrub habitat in north-central Chile revealed no evidence of energetic or functional compensation. Photo credit: P. L. Meserve.

these faunas differs from that of other deserts, which have greater representation by folivorous, omnivorous, and carnivorous small mammals (Kelt et al. 1996, Fox 2011, Kelt 2011). Because other deserts lack such a serendipitous radiation (Mares 1979, 1993b) we predicted that sites in other deserts would exhibit fewer PE species than those in North America.

METHODS

Fray Jorge

Since 1989, we have studied small mammals, plants, and predators in a national park in north-central Chile. This 10000-ha semiarid site has been protected from grazing and woodcutting since 1947, and was designated as a UNESCO Man and the Biosphere (MAB) reserve in 1977. Given this protection, the site has a mature vegetative community that hosts a largely intact biota. We established 16 75 × 75 m plots and allocated them randomly to four experimental treatments ($n = 4$ plots per treatment). These included exclusion of predators with fencing and polyethylene netting; exclusion of a common small mammal, the degu; exclusion of predators and degus; and control plots where all taxa had free access (Meserve et al. 2003, Gutiérrez et al. 2010). In the face of very limited vegetative responses to the exclusion of degus, we converted four degu exclusions in 2007 to exclusions of invasive lagomorphs (*Lepus europaeus*, *Oryctolagus cuniculus*). Hence, data reported here comprise 19 years (1989–2007). All sites were sampled monthly with live traps; small mammals were uniquely marked with ear tags or leg bands. All field methods and handling procedures were approved by the Institutional Animal Use and Care Administrative Advisory Committee at both the University of California, Davis, and Northern Illinois University, and met guidelines recom-

mended by the American Society of Mammalogists (Sikes et al. 2011, 2012).

Energy use at Fray Jorge

We assessed energetic compensation (following Ernest and Brown 2001a) in degu exclusion and control plots. We calculated minimum number known alive (MNKA; Krebs 1966, Hilborn et al. 1976) for 6-month time periods (May–October, November–April) and calculated energy use per species as $E_i = \text{MNKA}_i \times aM_i^{0.75}$, where i indexes species, a is a scaling constant ($a = 5.69$), and M is the mean body mass of individuals of species i during the given time period. We calculated energetic compensation as $C = (E_C - E_{-D})/E_{D(C)}$, where E_C and E_{-D} are total energy use by non-degu species on control and degu exclusion (–D) plots, respectively, and $E_{D(C)}$ is energy use by degus on control plots (see Ernest and Brown 2001a). Our approach differs from that of Ernest and Brown (2001a) in two ways. We calculated MNKA for 6-month periods whereas Ernest and Brown used the average of six monthly estimates, and we used the mean mass of individuals during each 6-month period instead of a single value per species over all time periods; neither of these changes should be analytically important. We compared energy use on control and degu-removal plots using repeated-measures analysis of variance (rmANOVA) in SAS (Proc GLM; SAS Institute 2008). It is important to note here that all other species in the region had full access to degu exclusion plots; hence, exclusion of one folivore did not equate to exclusion of other folivores or granivore/folivores (e.g., lagomorphs, *Abrocoma*, *Phyllotis*). To confirm that any differences between treatments were due to compensatory dynamics, we assessed energetic compensation on degu exclusion plots with a paired t test (Proc TTEST; SAS Institute 2008).

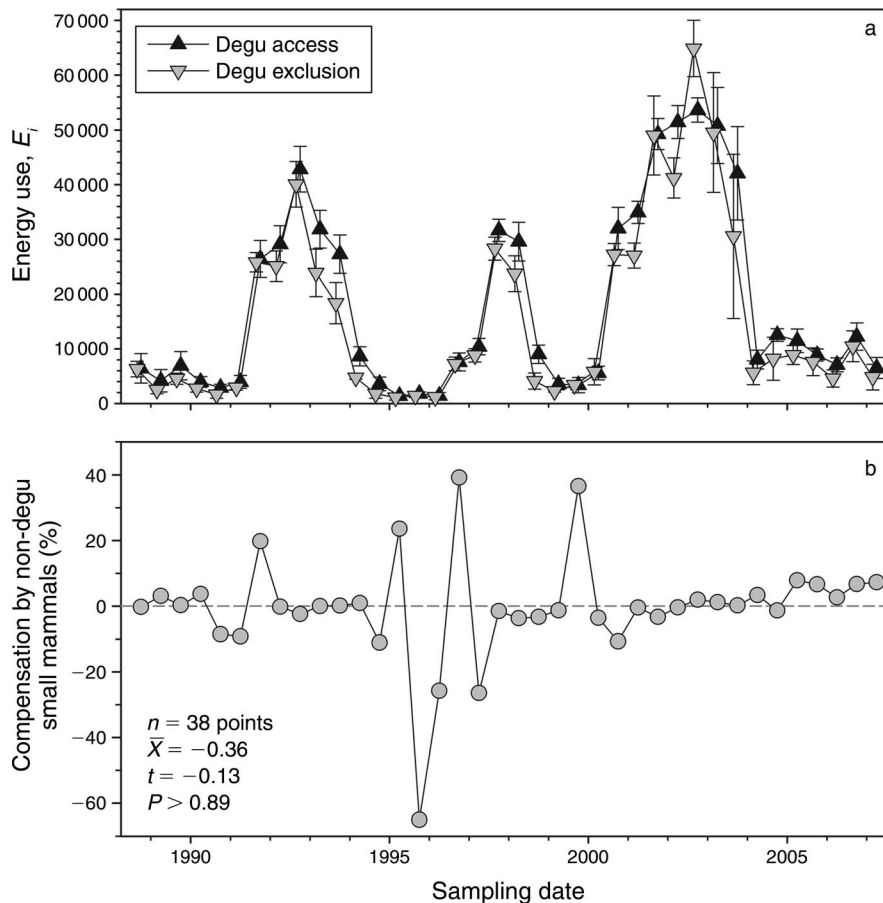


FIG. 1. Temporal variation in energy use across all species and plots (four 75×75 m plots per treatment) in semi-arid coastal thorn-scrub in Fray Jorge, north-central Chile, 1989–2007. (a) Total energy use (mean \pm SD) on control (degu [*Octodon degus*] access) and experimental (degu exclusion) grids. Energy use per species was calculated as $E_i = MNKA_i \times aM_i^{0.75}$, where i indexes species, a is a scaling constant ($a = 5.69$), and M is the mean body mass of individuals of species i during the given time period. (b) Energetic compensation by non-degu small mammals, calculated as $C = (E_C - E_{-D})/E_{D(C)}$ where E_C is total energy use across all non-degu species in control plots, E_{-D} is total energy use by non-degu species on degu exclusion plots, and $E_{D(C)}$ is energy use by degu on control plots. Statistical tests indicate no significant differences between control and degu-exclusion plots.

Potentially equivalent species

We defined potentially equivalent (PE) species as those species in the regional pool for a site that were trophically similar and that were within 10% of the mass of focal species. We extracted data on the composition of local assemblages and geographic species pools (Kelt et al. 1995) for arid lands in North America ($n = 201$ sites), the Gobi Desert ($n = 97$), and South America ($n = 96$) from Meserve and Glanz (1978), Pearson and Ralph (1978), Kelt et al. (1996), and M. D. Rodríguez and R. A. Ojeda (*personal communication*; see also Rodríguez (2011)). All species are listed in Appendix A, and the composition of local sites and their associated species pools are provided in the Supplement. For each species at every site, we determined the number of PE species in the site-specific pool with the proviso that no PE species was counted more than once. Distributions of PE species were compared using Kolmogorov-Smirnov two-sample tests and Kuiper's tests (Proc NPAR1WAY;

SAS Institute 2008); because our a priori expectations were that North America would have similar numbers of PE species to those in Asian deserts but greater than South America, these comparisons were limited to North America vs. Gobi and vs. South America. Finally, we assessed whether the number of PE species at Portal and Fray Jorge were in the extreme tail of the North and South American distributions by tallying the number of sites in the data set with as many or more PE species as these two sites; for this analysis we treated site #29 from Brown and Kurzius (1987) as representing the Portal site; site #29 is located about 1 km NW of the Portal site and species composition reflects that for the long-term Portal grids (J. H. Brown, *personal communication*).

RESULTS

Evidence for energetic compensation at Fray Jorge

Small mammals at Fray Jorge fluctuate greatly in response to temporal variation in rainfall (Meserve et al.

1993a, 1996, 2003, Gutiérrez et al. 2010). Where degus have been excluded (Fig. 1), energy consumption has remained lower than that of degu-access plots (rmANOVA, $F_{1,6} = 30.32$, $P = 0.0015$). Moreover, compensatory energy use by other species is trivial ($t_{38} = -0.13$, $P > 0.89$), suggesting that in nearly two decades and in the face of enormous demographic fluctuations that result in widespread immigration from other habitats in the park (Meserve et al. 2003, Milstead et al. 2007), other species do not consume resources left in the absence of degus.

Potentially equivalent species

North American sites potentially have more equivalent species than sites in the Gobi Desert, and although the range of PE species is similar to that of South American arid sites, the latter has fewer sites with very few PE species (Fig. 2, Table 1). The median and mean number of PE species in North America is much greater than that of the Gobi Desert, but not greatly different from that of South American sites (Table 2). In contrast, the distribution of trophically defined PE species at North American sites differed from that in both the Gobi Desert and South American sites (Table 1). Only North American sites had any carnivorous PE species, the Gobi lacked omnivorous PE species, and South America lacked any granivorous PE species. Note that this is not to say that these trophic groups do not exist in these regions, but merely that species pools lack species to replace local losses in these groups. North American sites had many more granivorous PE species than did Gobi sites, and all three regions had a median of zero folivores, and mean values below 1. South American sites had more omnivorous PE species than did other regions.

Among North American sites, Portal (as represented by site #29 in Brown and Kurzius 1987) is exceeded by only two other sites in total PE species (Table 3). Additionally, this site is in the extreme tail for carnivores and marginally so for granivores and omnivores. In contrast, Fray Jorge appears representative of other South American sites, reaching the 51st and 57th percentiles for omnivores and all species combined, respectively.

Given the preeminent role of interspecific competition underlying community assembly (Bowers and Brown 1982, Brown and Heske 1990, Brown et al. 2002) and energetic compensation (Ernest and Brown 2001b, Ernest et al. 2008), and recognizing the arbitrary nature of our 10% body size limit for PE species, we expanded the definition of PE species to include all species up to 110% of the body size of each focal species, and we recalculated distributions for each continent and each trophic guild (Appendix B). This is a more liberal definition of which species have the potential to compensate, but provides context for the preceding analysis. The result of this definition of PE was to greatly increase the number of PE species at sites, but

this was particularly notable for folivores and granivores. The median number of folivorous PE species in North America (11) was greater than that in South America (0), and extended to higher values (61 vs. 48 species, reflecting the larger species pool of North American sites); however, both continental distributions were much greater than that for the Gobi Desert (median 0 species, range 0–4). North America had vastly more granivorous PE species (median 30 species) than did the Gobi (median 0), and South American sites lacked any such species. South America had many more omnivore PE species (median 26) than North America (median 14), and the Gobi lacked these entirely; the distribution for South American sites (range, 16–27 species) was well above that for North America (0–16 species). Finally, this broadened definition of PE included some carnivorous PE species at South American sites (unlike the earlier analyses). The net result was that the Gobi Desert had many fewer PE species (range 0–4 species, median 0) than either South America (range 16–48 species, median 28) or North America (range 9–61 species, median 44).

DISCUSSION

The extent to which species have unique ecological roles has been debated extensively (Chase and Leibold 2003, Soberon 2007). The broader role of biodiversity in promoting or sustaining ecological functionality is widely accepted (Kinzig et al. 2002, Loreau et al. 2002, Hooper et al. 2005), and although functional redundancy has been the subject of numerous reports (e.g., Lawton and Brown 1994, Rosenfeld 2002, Wohl et al. 2004, Guillemot et al. 2011), the role of individual species has received less attention (Gitay et al. 1996, Symstad et al. 1998, Thibault et al. 2010). Basic niche theory (Vandermeer 1972, Schoener 2009) highlights the prediction that no species that co-occur can have the same realized niche. Indeed, even for the heteromyid rodents studied by Ernest and Brown (2001a) and presented as examples of energetic equivalence (Ernest et al. 2008), Thibault et al. (2010) concluded that these species were complementary to each other rather than equivalent or redundant. Nonetheless, the dynamics at Portal raise the question of the permeability of local assemblages and whether species invade by occupying otherwise “vacant niches” (e.g., Herbold and Moyle 1986; K. Rohde, *personal communication*) or by coopting niche space from one or more preexisting species, and the extent to which energetic equivalence (if not ecological redundancy) characterizes natural systems.

Using a similar long-term exclusion in an evolutionarily independent region, we documented no evidence of energetic compensation over 19 years in northern Chile; energy consumption in removal plots remained lower than or similar to that documented in control plots with full access by all species. This is similar to earlier results from Portal (Brown and Munger 1985, Brown et al. 1986), and it might be that a longer duration of degu

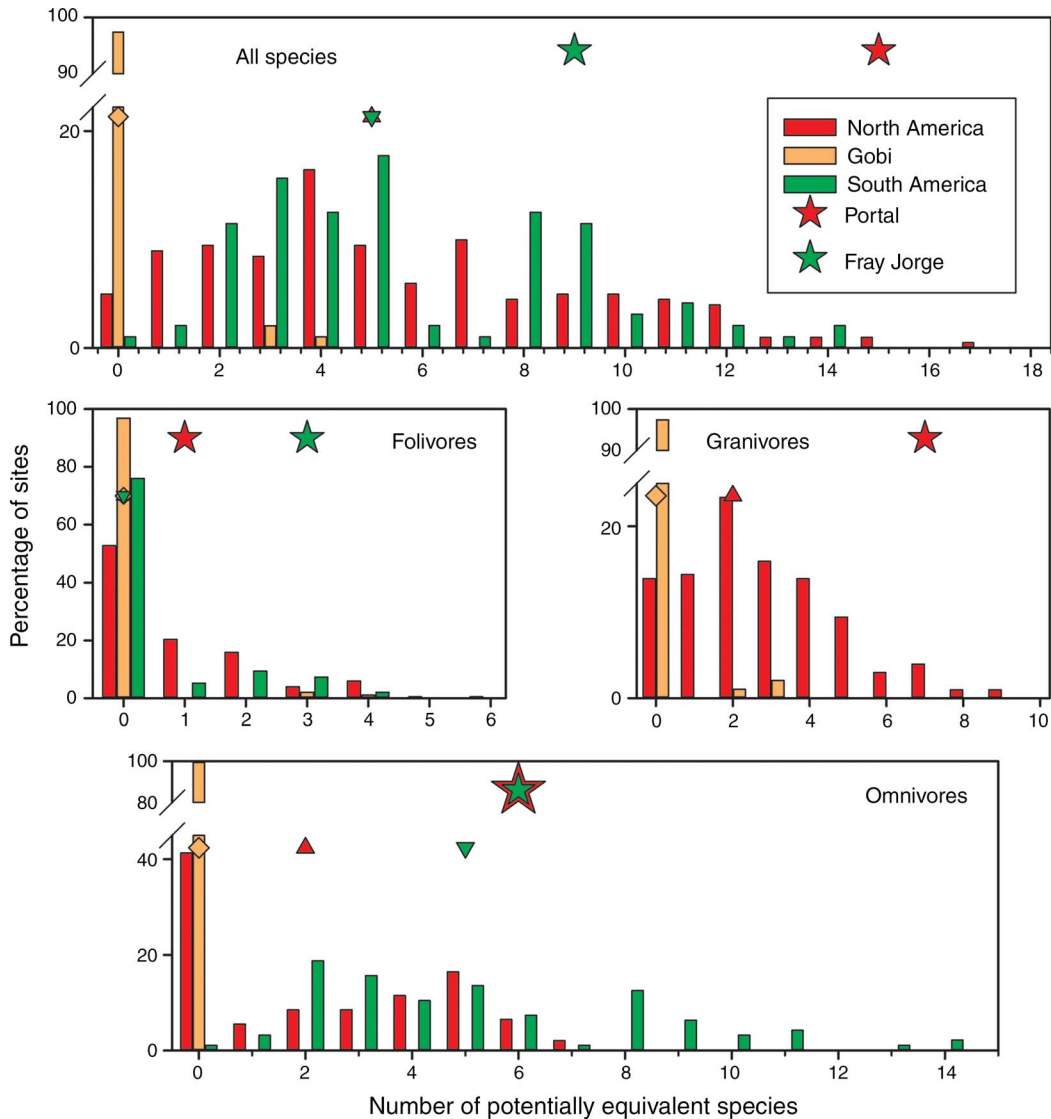


FIG. 2. Distribution of potentially equivalent (PE) species in three regions. Triangles represent the median values for each region. Stars indicate the number of potentially equivalent species at two focal sites Portal, Arizona, USA (representing the North American region); Fray Jorge, north-central Chile (representing the South American region). Note that the median number of all PE species was identical for Portal and Fray Jorge, that for folivorous PE species was zero in all deserts, and that of granivorous PE species was zero in Gobi and South American sites; Gobi and South American sites lacked carnivorous PE species (Table 2).

exclusion would reverse this pattern, as observed at Portal (Ernest and Brown 2001a). Such an experiment is not possible, but in an effort to address this possibility, we evaluated the number of potentially equivalent species (PE) in the geographic species pool for multiple sites in two arid regions of the Northern Hemisphere and throughout arid regions of South America.

If the patterns observed at Portal were a product of the unique diversification of the largely granivorous heteromyid rodents, then we would expect that, on average, sites in North America would have more PE species than other arid regions. Although this prediction was not supported in a comparison between North and South America, it was for the Gobi. In contrast to

comparisons of total PE species, this prediction was overwhelmingly supported for granivorous PE species, which were 33 times more likely in North American sites than Gobi sites, and were entirely missing from South American sites (see Mares and Rosenzweig 1978, Mares 1993a). Somewhat unexpectedly, omnivores were the dominant PE species in South American sites, and they were nearly as common as granivorous ones in North America, calling into question the overriding importance of the heteromyid radiation or of granivore diversity in general (but see further discussion).

In contrast to observed dynamics at Portal, where the abundance and diversity of granivorous rodents may have allowed for the compensatory dynamics docu-

TABLE 1. Tests of the distribution of potentially equivalent (PE) small-mammal species in North America (NA), the Gobi Desert, and South America (SA).

Trophic group and region	Kolmogorov-Smirnov		Kuiper	
	<i>D</i>	<i>P</i>	<i>K_a</i>	<i>P</i>
All species				
NA vs. SA	0.108	0.434	1.227	0.495
NA vs. Gobi	0.716	<0.0001	5.794	<0.0001
Folivores				
NA vs. SA	0.233	0.0017	1.878	0.0226
NA vs. Gobi	0.442	<0.0001	3.489	<0.0001
Granivores				
NA vs. Gobi	0.572	<0.0001	4.627	<0.0001
Omnivores				
NA vs. SA	0.426	<0.0001	3.434	<0.0001
NA vs. Gobi	0.587	<0.0001	4.749	<0.0001

Notes: None of our sites in the Gobi or South American regions included any carnivorous PE species; no South American sites included any granivorous PE species (Table 2), so we did not compare this trophic group with North America. Here *D* and *K_a* are Kolmogorov-Smirnov and Kuiper test statistics, respectively. Tests were qualitatively identical if six South American sites lacking any species (see Appendix B) were removed from analysis.

mented by Ernest and Brown (2001*a, b*), folivorous PE species are uncommon in South American sites, and this could underlie the lack of response to the exclusion of degus at our site in Chile. The abundance of omnivorous PE species, however, might be expected to allow for ecological response, but this was not observed.

These patterns were greatly amplified when we used a more liberal definition of PE species that included all smaller species (not only those within 10% of the body mass of target species). In particular, for granivorous species, median sites in North America have 30 PE for any locally occurring taxon, whereas Gobi and South American sites have none. Using either definition of PE species, South American sites exceed those in North America only for omnivorous species, which reflects either the more catholic diets of South American small mammals or our ignorance of their dietary preferences.

These intercontinental differences may be rooted in the distinct geographical and evolutionary histories of each region, the result of which are very different

radiations of independent mammal lineages in distinct environments over different periods of time (Kelt et al. 1996, Shenbrot et al. 1999). The unique role of the heteromyid radiation in North America is well-known (Mares 1993*b*, Kerley and Whitford 1994, Kelt et al. 1996), and has resulted in large pools of ecologically similar species for many locations in North American deserts, even if only a subset of these co-occurs locally (Brown and Kurzius 1987, Kelt et al. 1996). The Heteromyidae probably originated in the Oligocene, with subfamilies well-established by the Miocene (Alexander and Riddle 2005, Hafner et al. 2007), and is complemented by a smaller assortment of muroid rodents, most of which are omnivorous or folivorous. Asian deserts are populated primarily by murid (gerbil-line) and dipodid rodents that diverged by the middle Miocene (Pavlinov et al. 1990, Shenbrot et al. 1995). Asian deserts are older than those of North America, e.g., Miocene (Guo et al. 2002) or perhaps Eocene (Bosboom et al. 2014) vs. Pleistocene (Webb 1977, Axelrod 1979) and possibly Miocene (Riddle 1995, Hafner et al. 2007), but both evidently are quite young in comparison with the Atacama Desert of coastal South America, which may date to the Jurassic (Hartley et al. 2005) and includes some of the most hyperarid regions on Earth. Small-mammal assemblages there comprise species that have immigrated either from Mediterranean Chile, by trans-Andean immigration via deep valleys that descend on the western slopes of the Andes and provide corridors between arid habitats of the Altiplano and lower elevations, or possibly along a north-south “desertic corridor” on the western flanks of the Andes (Meserve and Kelt 1990, Marquet 1994, Moreno et al. 1994). South American arid regions considered here (Marquet 1994, Kelt et al. 1996) include areas of the Atacama as well as the dry Altiplano of Peru, Bolivia, and northern Chile and Argentina. South American arid lands include both caviomorph and sigmodontine radiations, which evidently lack species able to survive without free water (Mares 1977, Bozinovic and Gallardo 2006).

At Fray Jorge, we excluded a large-bodied folivore. Our quantification of energetic compensation might be flawed if our sampling there failed to include the full range of folivores or if our experimental exclusions

TABLE 2. Descriptive statistics for the distribution of potentially equivalent (PE) small-mammal species in North America (NA), the Gobi Desert, and South America (SA).

Trophic group	Mean no. PE species			Median no. PE species		
	NA	Gobi	SA	NA	Gobi	SA
All species	5.493	0.103	5.781	5	0	5
Carnivores	0.189	0	0	0	0	0
Folivores	0.935	0.103	0.542	0	0	0
Granivores	2.746	0.082		2	0	
Omnivores	2.284	0	5.240	2	0	5

Notes: Blank cells indicate that no South American sites exhibited any granivorous PE species. See Appendix B for comparable data using a more liberal definition of PE species.

TABLE 3. Number of potentially equivalent small-mammal species (PE) at Portal, Arizona, USA, and Fray Jorge, north-central Chile, relative to all sites in the continental data sets (regional pool).

Trophic group	Portal (site, 10 spp.; pool, 28 spp.)			Fray Jorge (site, 7 spp.; pool, 11 spp.)		
	No. PE spp.	No. sites	% sites	No. PE spp.	No. sites	% sites
All species	15	3/201	1.5	9	55/96	57.3
Carnivores	2	6/201	3.0	0	96/96	100
Folivores	1	95/201	47.3	3	96/96	100
Granivores	7	12/201	6.0	0		
Omnivores	6	17/201	8.5	6	49/96	51

Notes: Values are the number and percentage of sites out of the total number of regional arid sites ($n = 201$ for North America; $n = 96$ for South America) for which the number of species is equal to or greater than that of the focal site (Portal or Fray Jorge). Boldface type indicates those sites that were in the extreme 10% of the observed distribution.

hindered access by other folivores in addition to degus. For example, trophic overlap may not be limited to those species sampled by small-mammal traps (Keesing 2000, Pringle et al. 2014). However, we do not believe this to be a concern at our site. Introduced lagomorphs and native guanaco (*Lama glama*) readily access both control and degu removal plots but do not appear to favor any of our treatments. Guanacos are generalist herbivores (e.g., Baldi et al. 2004), although in the Chilean Andes they selected for perennial grasses and legumes (Cortés et al. 2003). However, the guanaco population at Fray Jorge is quite limited (as few as eight individuals; Cook M. 2013) and seems unlikely to have a substantial impact at the scale of these exclusions. Invasive lagomorphs could compete with small mammals in this region of Chile, although Jaksic (1998:167, translated from Spanish) emphasized that *Oryctolagus* (by far the more abundant invasive lagomorph at our site) “do not appear to compete for forage with folivorous rodents, due to their complementary spatial distribution.” In the north-central Chilean Andes, *Lepus* has a broader trophic niche than three native rodents, but dietary overlap was greatest among the rodent species (López-Cortés et al. 2007). In 2007, we established four lagomorph exclusions to evaluate the relative top-down influence of native and invasive folivores on introduced and native plants. These grids have been sampled identically to other grids and between 2007 and 2012, energy consumption was not different when compared with control plots (rmANOVA $F_{1,6} = 0.08$, $P = 0.79$). These data do not support a hypothesis that invasive lagomorphs forage differentially in degu-exclusion plots, and we argue that they are unlikely to be responsible for the lower energy consumption documented among rodents there.

Two other large-bodied folivorous rodents, the moon-toothed degu (*O. lunatus*) and Bennett’s chinchilla rat (*Abrocoma bennetti*), are similar in size to degus or larger. Neither of these is abundant at our site, however (Meserve et al. 1993a, 1995), and in any case they gain occasional access to degu exclusions via breaches caused by the tunneling activity of coruro

(*Spalacopus cyanus*), which are not influenced by our fencing and respond irruptively in wet years (hence, this influence is sporadic in nature). *O. lunatus* is quite rare in our study area and appears to be a riparian/mesic specialist (our study plots are semiarid shrub) and *Abrocoma* is an uncommon resident on most of our study plots. Importantly, degus are removed from treatment plots monthly, but neither *O. lunatus* nor *A. bennetti* are removed from these grids, yet their densities remain very low on all sites where they occurred (Gutiérrez et al. 2010).

Finally, reflecting the continental pools from which they are derived, the trophic structure at Fray Jorge is very different from that at Portal. Whereas the latter includes a number of species known to emphasize seeds in their diet, the former has fewer species overall, and these are notable for being more evenly distributed across trophic “space,” as shown by Meserve (1981: Fig. 1) in a triangular presentation based on proportional consumption of insects, seeds, and foliage. Fray Jorge supports one carnivore (*Thylamys elegans*), one omnivore (*A. olivaceus*), and one carnivore/omnivore (*A. longipilis*). Two species are largely folivorous (*O. degus*, *A. bennetti*), and two are largely granivorous (*P. darwini*, *Oligoryzomys longicaudatus*). However, closer attention to temporal changes in diets (Meserve 1981: Tables 2–4) show that *Phyllotis* and both *Abrothrix* species consume large amounts of foliage through the year, notably that of *Chenopodium petiolare*, a preferred forage species of degus (up to 22%, 26%, and 46% for *A. longipilis*, *A. olivaceus*, and *Phyllotis*, respectively). The more “balanced” trophic structure at Fray Jorge may underlie the lack of compensatory responses, and indeed had we been able to exclude a different species (e.g., *Phyllotis*), our results might differ. Hence, these results do not disallow or even doubt the importance of compensatory dynamics in arid-adapted assemblages of small mammals, but they do call attention to the need for further studies to better understand the generality of this phenomenon.

Whether Portal or Fray Jorge is more representative of small-mammal assemblages will require data from additional sites, but using our metric, at least, Portal

appears to be atypical among arid sites within North America. In contrast, Fray Jorge appears to be representative of South American arid lands. This suggests that most sites in North America may be less predisposed to the type of energetic compensation documented at Portal, whereas most sites in South American arid lands are likely to reflect patterns documented at Fray Jorge. Houlahan et al. (2007) argued that zero-sum dynamics do not apply generally to species abundances; our data question the extension of such assumptions to biomass and energy consumption as well. These intercontinental comparisons also underscore the role that historical contingency plays in contemporary ecological structure and possibly function (Ricklefs and Schluter 1993), as well as the need for additional long-term data sets to allow for broader generalization of ecological patterns.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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