# Title: Energetic compensation breaks down over time in a desert rodent community

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**Original submission:** This submission analyzes long-term data on rodent community abundance and energy use from the Portal Project. Sections of this timeseries have been analyzed in numerous other publications, but this is the first to analyze data from 2007-2020 on energetic compensation on experimental and control plots.

**No prior publication:** While sections of the Portal Project data have been analyzed in numerous other publications, the key data for this submission have not been published elsewhere. This submission is posted as a preprint on bioRxiv at [bioRxiv].

**Animal welfare:** Rodent censuses were conducted with IACUC approval.

**Open research:** All data and code to reproduce these analyses are archived on Zenodo at [Zenodo].

**Analytic methods:** All analyses were conducted in R version [R version].

# Abstract

# Key words: energetic compensation, zero-sum dynamic, environmental fluctuations, functional complementarity, dispersal limitation

# Introduction

The question of whether, and under what circumstances, community-level properties are robust to changing species composition is key for understanding how communities are structured and how community function may respond to future perturbations. In communities of consumers with a shared resource base, energetic compensation can occur when declines in resource use – measured as metabolic flux, or energy use – from some species are offset by compensatory gains from others (Ernest and Brown 2001; Ernest et al. 2009). When it occurs, energetic compensation is consistent with a zero-sum competitive dynamic, in which resources not being used by one species are readily absorbed by other competitors, and any increases in abundance from one species must come at the direct expense of resources being used by other species (Van Valen 1973, Ernest et al. 2008). By definition, energetic compensation also renders community-level energy use relatively stable despite species-level fluctuations (Houlahan et al. 2007; Ernest et al. 2008).

For energetic compensation to be possible, some, or all, of the species in a community must share similar resource use traits and broader environmental requirements such that, if one species declines in abundance, other species can access the leftover resources and increase in abundance to compensate. This can occur under a neutral scenario, where all species in a community are functionally identical, or via functional redundancy or complementarity in a niche-structured community (Hubbell 2001; Houlahan et al. 2007; Thibault et al. 2010). In the latter case, while competitors are unlikely to be fully identical in all aspects of the niche, there may be areas of partial overlap that allow for compensation under some circumstances (Chesson 2001; Loreau 2004). In this scenario, energetic compensation may be contingent on environmental conditions that allow complementary, but not identical, species to compensate for each other (Loreau 2004, Fetzer et al. 2015). If shifting conditions over time affect these species differently and alter the extent to which they can compensate for each other, energetic compensation may wax and wane as conditions change. This would mean that zero-sum dynamics (and their implications for community structure and evolutionary dynamics) are intermittent over time, and that the robustness of assemblage-level function to species-level variability fluctuates with shifting conditions.

Some of the strongest empirical evidence regarding energetic compensation comes from long-term manipulative field experiments. Experimentally removing a subset of species from a community, and comparing the community-level energy use of manipulated communities to unmanipulated assemblages, allows for direct assessment of energetic compensation even as the total resource availability fluctuates over time (Thibault et al 2010). Manipulations of desert rodent communities, including experiments at Fray Jorge in Chile and the Portal Project in southeastern Arizona, have revealed that strong energetic compensation can occur in these communities, contingent on the presence of functionally complementary groups of species in the local and regional species pools (Ernest and Brown 2001; Thibault et al 2010; Kelt et al 2015).

Long-term monitoring has also demonstrated that shifting environmental conditions over time have profound effects on the structure and composition of these communities, with potential implications for energetic compensation. Since the beginning of the project in 1977, the Portal Project has documented several major transitions in the rodent and plant communities linked to environmental shifts (Dipo decline paper, Thibault on floods, LDA). Over the 1980s and 1990s, changing weather patterns in southwestern North America contributed to a habitat transition from grassland to desert scrub. This appears to have driven a community-wide shift in the rodent community favoring shrubland-associated species over grassland-affiliates, including kangaroo rats (genus *Dipodomys*). These shifts may also have helped enable the establishment of new and previously rare species at the site, including the invasive forb *Erodium ciculatum* and the pocket mouse *Chaetodipus baileyi.* Once it established at the site, *C. baileyi* greatly increased the community’s capacity for energetic compensation for the removal of kangaroo rats. Prior to *C. baileyi’s* arrival, non-kangaroo rat species (collectively, “small granivores”) absorbed only ~20% of the energy made available by experimentally removing kangaroo rats from the assemblage; once *C. baileyi* became abundant in the system, it drove this compensatory response to an average of 52%, and occasionally >X%.Following an extended and severe drought from 2008-2010, the rodent community has reorganized once again, in the first major change since *C. baileyi*’s establishment at the site (Christensen et al 2019). In this most recent configuration, *C. balieyi* remains present in the community but is relatively scarce on unmanipulated control plots, although other species of small granivores, including the desert pocket mouse *Chaetodipus penctillatus*, are more abundant than in previous states of the system.

Here, we investigate how shifting conditions affect the functional overlap among species, and therefore the dynamics of energetic compensation, using the recent reorganization of the Portal rodent community as a case study. If conditions have changed such that *C. baileyi* is no longer capable of maintaining high abundances at the site, even on plots where kangaroo rats have been removed, energetic compensation may have broken down with the decline in *C. baileyi*. However – especially if the increasing relative abundance of smaller granivores, chiefly *C. penctillatus*, reflects a shift in conditions favoring those species – other species may now be able to access a greater proportion of the sitewide resources than they have been in the past, and may therefore maintain some degree of energetic compensation despite a decrease in *C. baileyi’s* contribution. To situate these shifts in rodent community dynamics in broader environmental context, we also explore trends in climatic and habitat conditions surrounding the most recent community reorganization event.

# Methods

## All data and code are available at [www.github.com/diazrenata/squareone](http://www.github.com/diazrenata/squareone).

## The Portal Project

The Portal Project consists of a set of 24 fenced experimental plots located approximately 7 miles east of Portal, AZ, USA, on unceded land of the Chiricahua Apache. Beginning in 1977, kangaroo rats (*D. spectabilis, D. merriami, and D. ordii*) have been experimentally excluded from a subset of these plots, while all other rodents are allowed free access through small holes cut in the plot fencing. Other plots, with larger holes, are freely accessible to all species, including kangaroo rats. Rodents on all plots are censused monthly, and the plant communities are censused twice a year. Precipitation and temperature data have been collected using automated weather stations beginning in X [weather methods]. For additional details on the site and methodology of the Portal Project, see [data paper preprint].

## Data

We use data for 4 control plots (to which all rodents have access) and 5 exclosure plots (from which kangaroo rats are removed, but all other species have access), from January 1988 until January 2020. The experimental treatments for some plots have changed over time, and we restricted our analysis to the subset of plots that have had the same treatments for the longest period of time. To compare how energetic compensation has shifted over different time periods, we broke this timeseries into three time periods corresponding to major transitions in the rodent community (Ernest and Brown 2001, Christensen LDA). The first is from 1988-1996, when *C. baileyi* first arrived at the site. The second is from 1996 until the community reorganization event in 2010. The last is from 2010 until the interruption in data collection caused by the COVID-19 pandemic.

## Rodent community energy use

For all variables, we combined data for all plots within a treatment in each census period and calculated treatment-level means. This is necessary to calculate energetic compensation (below), and we treated other variables in the same way to maintain consistency. We calculated the degree of energetic compensation for kangaroo rat removal, and the overall impact of kangaroo rat removal on community-level energy use, for each census period. We defined energetic compensation as the proportion of the energy made available by removing kangaroo rats from the community that is taken up via compensatory increases in non-kangaroo rat granivorous species (“small granivores”, including *species*. We calculated this as [equation], where *SGE* is the amount of energy used by small granivores on exclosure plots, *SGC* is energy use by small granivores on control plots, and *KRC* is the amount of energy used by kangaroo rats on control plots. This quantity is distinct from the overall impact of kangaroo rat removal on total energy use, which we calculated as [equation], where *TEC* and *TEE* are the total energy use of all species on control and exclosure plots, respectively. We also calculated the proportion of treatment-level energy use accounted for by all small granivores, and by *C. baileyi* specifically, for each treatment in each census period.

We used generalized least squares (using the R package *nlme*) and generalized linear models to test how these quantities have shifted over the three time periods described above, using the general model form *response ~ time period*. For energetic compensation and total energy use, we used generalized least squares models, accounting for temporal autocorrelation. Because the proportions of community energy use accounted for by small granivores, and specifically *C. baileyi*, are bounded from 0-1 and are therefore not appropriate for generalized least squares, we used generalized linear models with a negative binomial link function. Because *C. baileyi* was not present at the site prior to 1996, we restricted the analysis of *C. baileyi* proportional energy use to 1996-2020.We calculated estimates and contrasts for each variable across time periods using the R packages *emmeans*.

*Plant community composition*

We explored whether there have been shifts in the composition of the plant community over time that may provide context for the observed transitions in the rodent community. We used a version of the model presented in Christensen et al (2019) to test for reorganization events in the plant community. Briefly, this model uses Latent Dirichlet Allocation to distill the timeseries of individual species’ abundances into a handful of “topics”, or combinations of species that often occur together in a particular ratio, and characterizes the state of the community at each time step as a combination of *topics*. It then uses Bayesian change-point analysis to estimate if, and when, the topic composition of the community changes over time. We modified the model in Christensen et al (2019) to accommodate annual (rather than monthly) censuses, and the very high species richness of the plant communities (>100 species of plants, compared to 21 rodent species). For additional details, see Appendix X. This system experiences distinct summer and winter rainy seasons, with distinct plant communities in each season. We therefore tested for compositional shifts in the summer and winter communities separately.

We also specifically examined the dynamics of the invasive winter annual *E. ciculatum.* *E. ciculatum* became highly abundant at the site following the same habitat shift that appears to have precipitated *C. baileyi*’s establishment at the site (). If *E. ciculatum* and *C. baileyi* benefitted from similar environmental conditions in the 1990s, changes in *E. ciculatum* may be circumstantial indications that the conditions experienced on the plots have shifted away from the conditions that once benefitted those species.

*Environmental variables*

To explore how climatic conditions have changed over the course of the study, we calculated 6, 12, and 18 month SPEI drought indices for all months from 1988-2020, using Thornthwaite PEVT (recent droughts paper, SPEI paper). We also calculated anomalies in the mean, maximum, and minimum temperature, total precipitation, and NDVI for each month relative to the 40-year PRISM normals.

# Results

*Rodent community energy use*

*Plant community composition*

*Environmental variables*

# Discussion

# Acknowledgements

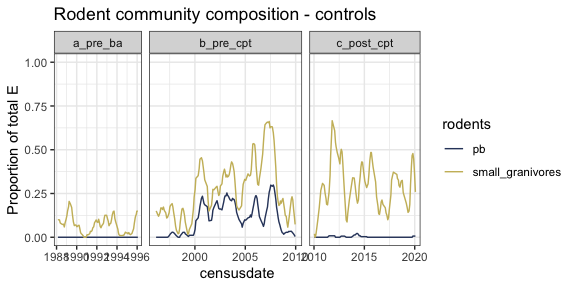
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# Literature cited

# Tables

# Figure legends

# Figures



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