# 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 drove 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 removing kangaroo rats from the assemblage; once *C. baileyi* became abundant in the system, this compensatory response increased 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 proportionally more abundant than in previous states of the system.

Here, we investigate how shifting conditions affect 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 with automated weather stations, beginning in 1989. 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 on control plots, and by *C. baileyi* on both control and exclosure plots, 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, of the form *proportional\_energy\_use ~ time period \* treatment.* 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 and, where appropriate, treatments, 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 dynamics 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 proportion of *topics*. It then fits a change-point model to the timeseries of topic proportions at each time step, to identify if and when the species composition of the community has changed 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 immediately preceded *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 1989-2020, 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 30-year PRISM normals.

# Results

*Rodent community energy use*

All rodent community energy variables have changed significantly over the three time periods. Small granivores increased their share of community energy use on control plots from 7% prior to 1996, to an average of 23-25% from 1996-2020 (1996-2010 and 2010-2020 not significantly different), and – unsurprisingly – consistently account for nearly all energy use on kangaroo rat exclosure plots. Although *C. balieyi* is still present in the system, the proportion of energy use accounted for by *C. baileyi* has declined on both control and exclosure plots, from an average from 10% from 1996-2010 to <0.01% after 2010 on controls and from 65% to 25% on exclosures. Energetic compensation by all small granivores for kangaroo rat removal has declined from an average of 52% from 1996-2010, to an average of 22% (GLS significance, contrast *p* value > 0.001). This is not significantly greater than the degree of compensation observed prior to *C. baileyi*’s arrival at the site in 1996, an average of 17% from 1988-1996 (contrast p = .75). The ratio of total energy use on exclosure plots, to total energy use on control plots, has also declined from an average of 67% to 46% - although it remains higher than the 25% observed from 1988-1996 (1996-2010 compared to 2010-2020 contrast p = 0.001, 1988-1996 compared to 2010-2020 contrast p = 0.005).

*Plant community composition*

The change-point model of topic compositions identified an abrupt transition in the winter plant community, around 1996, and a second, more gradual and variable, transition over the latter portion of the time series. The model does not identify any coherent shifts in species composition in the summer plant community. *E. ciculatum* has declined sharply in abundance, coinciding with the 2010 drought, from an average of 35% of community abundance on control plots to 8%, and from 60% to 18% on exclosure plots.

*Environmental variables*

The site has experienced numerous periods of drought over the course of the study, with two unusually long and severe droughts occurring since 2010. Mean, minimum, and maximum temperatures have tended upwards, as have the number of days with maximum temperature > 35C.

# Discussion

Since the 2010 drought, the dynamics of energetic compensation at Portal have shifted into a new configuration for the system. Energetic compensation by all small granivores for kangaroo rat removal has declined to levels comparable to those observed up until the mid-1990s Unlike the 1980s and early 1990s, *C. baileyi* is currently still present in the system, but it has declined in abundance on both control and exclosure plots. Without large populations of *C. baileyi,* no other species of small granivores have increased to absorb the available resources and compensate for kangaroo rat removal. However, the *total* decline in energy use caused by kangaroo rat removal since 2010 has shrunk relative to the decline observed prior to 1996. This is because kangaroo rats now account for a smaller proportion of community-level energy use than at the beginning of the study, and so removing kangaroo rats from the system results in a smaller loss of energy use – even though there has been no increase in the *proportion* of that loss that is compensated for by other species.

First, these joint shifts illustrate some degree of consistency in the degree of overlap in resource use among kangaroo rats and small granivores other than *C. baileyi.* Even though a sitewide habitat transition towards shrubland has favored small granivores over kangaroo rats, resulting in small granivores controlling a larger proportion of resources sitewide than at the beginning of the study, there has been no detectable increase in the proportion of resources *used by kangaroo rats* that small granivores are able to exploit once kangaroo rats are removed. This may reflect some degree of stable partitioning of niche space among these species, even as habitat conditions and the baseline distribution of resource availability shifts. One such axis of relatively consistent niche differentiation may relate to spatial partitioning of foraging zones. Kangaroo rats are relatively well-suited to foraging in open areas between clumps of vegetation, while smaller granivores often rely on dense vegetation as an antipredator defense, and restrict their foraging to sheltered areas. Even as the overall amount of shrub cover sitewide has increased, kangaroo rats may continue to control resources located in the remaining open microhabitats, which are too risky for small granivores to forage in even once kangaroo rats are removed.

In contrast, *C. baileyi’s* capacity to take advantage of resources made available by removing kangaroo rats has decreased dramatically since 2010, resulting in a breakdown of the energetic compensation effect observed in the 1990s and 2000s. *C. baileyi* is still present in the system, and potential resource availability on exclosure plots remains comparable to that on control plots (Christensen et al 2020). However, some aspect of the system must have shifted such that *C. baileyi* – more so than the other major rodent species –has lost its ability to exploit these resources. It may be that Portal constitutes marginal habitat for *C. baileyi*, and *C. baileyi* is only able to achieve large abundances at the site under certain environmental conditions. *C. baileyi* has been previously observed to prefer slightly different habitats to kangaroo rats (rat natural history papers cited in E&B 2001), and indeed was not found at Portal for at least the two decades from 1977-1996. Conditions at the site in the early 1990s may have helped dispersing individuals of *C. baileyi* to establish populations (this has been said), and shifts in conditions in recent decades may have moved the site away from *C. baileyi*’s preferred conditions once again. Since 2010, the site has experienced two periods of extended and severe drought. These extremes may themselves limit *C. baileyi’s* fitness at the site more strongly than they limit species for whom Portal appears to constitute more core habitat, and which may be better equipped to tolerate the full range of conditions experienced there. Or, community-wide population crashes following droughts may constitute moments in time when incumbency effects are erased and there are opportunities for the rodent community to reorganize to track more subtle, long-term shifts in environmental conditions (Christensen et al 2019). Circumstantially, we note that *E. ciculatum* became highly abundant in this system at the same time as *C. baileyi,* and has subsequently declined simultaneously with *C. baileyi.* This could reflect a shift in conditions towards and away from shared environmental requirements between the two species – although it may also be coincidental, or part of a more complex consumer-resource feedback within the broader community context (Allington). Our data do not show additional pronounced shifts in climate, habitat, or resource availability around 2010, but numerous factors relevant to the rodent community – e.g. predation, plant phenology, or nuanced weather conditions – are not well described by our data streams. Regardless of the specific drivers of *C. baileyi*’s decline at the site, the fact that *C. baileyi* is no longer functionally compensating for kangaroo rats demonstrates that energetic compensation is a shifting, contingent phenomenon even within the same set of species.

The dynamic, context-dependent energetic compensation observed at Portal highlights the importance of a metacommunity perspective on energetic compensation, and particularly the joint constraints of dispersal limitation and niche tracking (CAFÉ). Originally, energetic compensation at Portal was delayed due to dispersal limitation – that is, because *C. balieyi*, the only species with the traits necessary to compensate for kangaroo rat removal, was not part of the local species pool. Since 2010, niche tracking has come to the forefront as a constraint on energetic compensation. *C. baileyi* remains present in the assemblage, but lacks the traits necessary to allow it to compensate for kangaroo rats under recent conditions. Theoretically, a new species with the appropriate traits could join the community and reinstate energetic compensation – although it is not clear if such a species exists, or how long it might take for it to disperse to the site. In general, for energetic compensation to be maintained long-term, dispersal must be sufficiently rapid, and the regional species pool sufficiently large and functionally diverse, to supply functionally similar species whose traits track local conditions as they shift over time. Particularly as ecosystems globally move into novel climatic spaces and experience accelerating rates of species loss and turnover (), assemblage-level function may be highly contingent on whether these metacommunity processes keep pace with environmental change.

The intermittent, decadal-scale fluctuations in energetic compensation observed at Portal also suggest important nuances in how, and at what scales, zero-sum dynamics manifest in natural assemblages. Portal does not demonstrate a constant, consistent zero-sum constraint of the type sometimes associated with compensatory dynamics (Hubbell, Houlahan). Compensation like that observed at Portal may not necessarily be apparent from short-term patterns of covariation in species’ abundances (e.g. Houlahan et al 2007). Rather, the dynamics shown at Portal emerge over longer timescales (see also Vasseur) and are more consistent with a zero-sum constraint considered at a metacommunity or even macroevolutionary level (CAFÉ?; Van Valen 1973). Although there are long periods of time when there are unused resources available in the system – either because species have been removed from the system or because local species are not fully equipped to exploit the available resources as conditions shift – new species do eventually join the system and absorb those resources. Zero-sum dynamics may therefore manifest at the level of colonizations and extinctions (and, over longer timescales, evolution) more consistently than in local-scale population fluctuations. In an increasingly rapidly changing world, long-term manipulative studies, such as the Portal Project, continue to provide unique insights into if, and how, ecological dynamics can buffer assemblage-level properties against changes across levels of organization.

# Acknowledgements

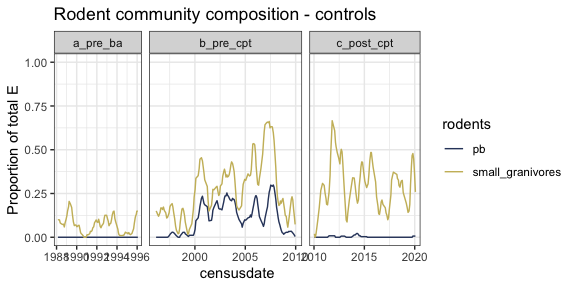
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# Literature cited

# Tables

# Figure legends

# Figures



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