# 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 (max 200)

# 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 so 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 variable over time, and that the robustness of assemblage-level function to species-level changes 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-wide energy use of manipulated communities to unmanipulated assemblages, allows for direct assessment of energetic compensation even as total resource availability and species composition fluctuate over time (Thibault et al 2010). Manipulations of desert rodent communities, including experiments at the Fray Jorge Biosphere Reserve in central 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 shifts in climate and habitat conditions (Valone et al. 1995, Thibault and Brown 2008, Christensen et al. 2018). Over the 1980s and 1990s, changing weather patterns in southwestern North America contributed to a habitat transition from grassland to desert scrub (Brown et al. 1997). This drove a community-wide shift in the rodent community favoring shrubland-associated species over grassland-affiliates, including kangaroo rats (genus *Dipodomys*) (Ernest et al. 2008). These shifts may also have helped enable the establishment of new and previously rare species at the site, including the invasive annual *Erodium ciculatum* and the pocket mouse *Chaetodipus baileyi* (Ernest and Brown 2001; Allington et al. 2013)*.* *C. baileyi* greatly increased energetic compensation for kangaroo rats (Ernest and Brown 2001; Thibault et al. 2010). Prior to *C. baileyi’s* arrival in the mid-1990s, 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 compensation increased to an average of 52%, and occasionally >X%.During a period of community-wide low rodent abundance associated with low plant productivity from 2008-2010 and severe drought from 2010-2012, the rodent community reorganized once again, in the first major change since the 1990s (Christensen et al 2018). In this configuration, *C. balieyi* remains present in the community but is relatively scarce, although other species of small granivores, chiefly the desert pocket mouse *Chaetodipus penctillatus*, are proportionally more abundant than in previous states of the system.

Here, we investigate how shifting conditions affect 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, even on plots where kangaroo rats have been removed, compensation may have broken down with the decline in *C. baileyi*. However – especially if the increasing relative abundance of other small granivores reflects a shift in conditions favoring those species – other species may now be able to access more resources than they have been in the past, and may therefore maintain some degree of compensation. To situate these shifts in rodent community dynamics in broader 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 (genus *Dipodomys*) have been experimentally excluded from a subset of these plots (exclosures), while all other rodents are allowed free access through small holes cut in the plot fencing. Control plots, with larger holes, are freely accessible to all rodents, including kangaroo rats. Rodents on all plots are censused monthly. The plant communities on the plots are censused twice a year, and precipitation and temperature data have been collected with automated weather stations since 1989. For additional details on the site and methodology of the Portal Project, see Ernest et al. (2019).

## Data

We use data for 4 control and 5 exclosure plots 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 (Ernest et al. 2019). We broke this timeseries into three time periods corresponding to major transitions in the rodent community: from January 1988 to June 1997; from July 1997, which is the first census period in which *C. baileyi* was captured on all exclosure plots at the site (Bledsoe and Ernest 2020), until January 2010 (Christensen et al. 2018); and from January 2010 until January 2020, when data collection was interrupted by the COVID-19 pandemic.

## Rodent community energy use

For all variables, we combined data for all plots within a treatment in each monthly census period and calculated treatment-level means. This is necessary to calculate energetic compensation, and we treated other variables in the same way to maintain consistency. We defined the degree of energetic compensation for kangaroo rat removal 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 rodents (“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 (Ernest and Brown 2001). 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 (see also Thibault et al. 2010). We also calculated the proportion of treatment-level energy use accounted for by all small granivores, and by *C. baileyi* specifically, on control and exclosure plots in each census period. To test how these variables have shifted across time periods, for energetic compensation and total energy use, we used generalized least squares models (*nlme)*, accounting for temporal autocorrelation, using the form *response ~ time period* + *CORCA1(census period)*. 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. C. baileyi* was not present at the site prior to 1996, and 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 package *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 combination of topic modeling and change-point analysis to identify if, and when, there have been shifts in the species composition of the winter and summer annual plant communities (Christensen et al. 2018). In brief, we used Latent Dirichlet Allocation to reduce the dimensionality of the full matrix of species abundances over time to a timeseries of a few (2-5) “topics” comprising mixtures of species that occur together in consistent proportions. We then fit a change-point model to the timeseries of *topic* proportions over time, to detect if, and when, the community has transitioned between different regimes of species composition. For the complete model methodology, see Christensen et al. (2018) and Appendix 1. Because this system features distinct summer and winter plant communities corresponding to summer and winter rainy seasons, we tested for shifts in the summer and winter communities separately.

We also examined the dynamics of the invasive winter annual *E. ciculatum.* *E. ciculatum* became abundant at the site following the same habitat shift that preceded *C. baileyi*’s establishment at the site (Allington et al. 2013). If *E. ciculatum* and *C. baileyi* benefitted from similar environmental conditions in the 1990s, changes in *E. ciculatum* may be circumstantial clues that the conditions experienced on the plots have shifted away from the conditions that once benefitted those species. We calculated the proportional abundance of *E. ciculatum* in the winter annual community on control and exclosure plots in each census year, and tested for changes across time periods using a quasibinomial generalized linear model of the form *e\_cicu\_prop\_abundance ~ time\_period \* treatment*.

*Environmental variables*

To explore how climatic conditions have changed over the course of the study, we calculated 12-month SPEI indices for all months from 1989-2020, using Thornthwaite PEVT (Slette et al. 2019; Cárdenas et al. 2021). We also calculated anomalies in the mean, maximum, and minimum temperature, total precipitation, summer (April-September) and winter (October-March) precipitation, days above 35C, and NDVI for each month relative to the 30-year normals.

# Results and Discussion

Since the 2010 community reorganization event, the dynamics of energetic compensation at Portal have shifted into a new configuration for the system (Figure 1; Appendix 4). 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 (Figure 2; Appendix 4). Other small granivores have not increased their share of energy use on exclosure plots to compensate for kangaroo rat removal. However, the totaldecline in energy use caused by kangaroo rat removal has shrunk relative to the decline observed prior to 1996 (Figure 1). Kangaroo rats now account for a smaller proportion of community-level energy use than at the beginning of the study (Figure 2), 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 proportionof that loss that is compensated for by other species.

These joint shifts demonstrate relative consistency in the degree of overlap in resource use between 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 (Figure 2), there has been no detectable increase in the proportion of resources used by kangaroo ratsthat small granivores are able to exploit once kangaroo rats are removed (Figure 1). This may reflect some degree of stable niche partitioning between these species, even as habitat conditions and the baseline distribution of resource availability shifts. One such axis of relatively consistent 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 restrict their foraging to sheltered areas to reduce predation risk (Kelt 2011). Even as the overall amount of shrub cover sitewide has increased, kangaroo rats may continue to exploit resources located in the remaining open microhabitats, which may be too risky for small granivores to access 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 (Figure 1). *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. 2019). However, under current conditions, *C. baileyi* – more so than the other major rodent species –has lost its ability to exploit these resources. Portal may constitute marginal habitat for *C. baileyi*. *C. baileyi* has been previously observed to prefer slightly different habitats to kangaroo rats (Rosenzweig and Winakur 1969; Price 1978), and 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 (Ernest and Brown 2001), and shifts in conditions in recent decades may have moved the site away from *C. baileyi*’s preferred conditions once again. In addition to the period of low plant productivity that immediately preceded the community reorganization event in 2010, the site has since experienced two periods of extended and severe drought (Appendix 3). These extremes may limit *C. baileyi’s* fitness at the site directly, especially as *C. baileyi* has been reported to prefer shrubby or wooded habitats over open ones (Price 1978). The community-wide population crash associated with low plant productivity and drought from 2008-2012 may also have temporarily overcome incumbency effects and created an opportunity for the rodent community to reorganize tracking more long-term shifts in environmental conditions (Thibault and Brown 2008; Christensen et al. 2018). 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* (Appendix 2)*.* This could reflect shifts in conditions towards and away from shared environmental requirements between the two species – although it may be coincidental, or part of a more complex consumer-resource feedback within the broader community (Allington et al. 2013). Our data do not show other pronounced shifts in climate or plant community composition around 2010 (Appendices 1 and 3), but numerous factors relevant to the rodent community may not be fully captured 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.

It is notable that *C. baileyi* is the only small granivore known to be capable of compensating for kangaroo rat removal, and has the least consistent temporal history at Portal of the major rodent species. These characteristics may be linked: *C. baileyi* is more similar in body size, and presumably other traits, to kangaroo rats than are the other small granivores, and *C. baileyi* is strongly affected by competition with kangaroo rats (Thibault et al. 2010). Limiting similarity may prevent *C. baileyi* and kangaroo rats from specializing on precisely the same habitats, and *C. baileyi* may be more closely adapted to exploit habitats where kangaroo rats are less dominant. Previously, *C. baileyi* and kangaroo rats have been reported to dominate in adjacent, complementary habitats (Rosenzweig and Winakur 1969; Price 1978). At the beginning of the study, *C. baileyi* may have been absent from the system due to the combined effects of competition from kangaroo rats and a relatively low affinity for the habitat at the site. Conditions in the early 1990s, combined with the patches of unused resources present on kangaroo-rat exclosure plots, may have created a window of opportunity for *C. baileyi* to establish in the system. Over time, conditions at the site may have again shifted too far from *C. baileyi*’s preferred habitat for *C. baileyi* to remain dominant in the system, even as kangaroo rats and other small granivores, particularly *C. penctillatus* – species with a longer observed, and potentially evolutionary, association with this site throughout a range of environmental conditions – have endured.

The dynamic, context-dependent energetic compensation observed at Portal highlights the importance of a metacommunity perspective on energetic compensation, and particularly the interrelated constraints of dispersal limitation and niche tracking (Leibold et al. 2017). Originally, compensation at Portal was delayed due to dispersal limitation, as *C. balieyi*  - the only species with the traits necessary to compensate for kangaroo rat removal - was absent. Since 2010, niche tracking has come to the forefront as a constraint on 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 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 high, 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 (Kelt 2015; Leibold et al. 2017). To the extent that limiting similarity prevents functionally similar species from coexisting within the same assemblage, or from evolving to specialize on precisely the same habitats, sustained energetic compensation may depend strongly on repeated colonization events from many similar, but non-identical, species from a large regional species pool. Particularly as ecosystems globally move into novel climatic spaces and experience accelerating rates of species loss and turnover (Williams and Jackson 2007; Dornelas et al. 2014), maintenance of 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 demonstrate nuances in how, and at what scales, zero-sum dynamics manifest in natural assemblages. Portal does not exhibit a temporally consistent zero-sum constraint of the type sometimes associated with compensatory dynamics (Hubbell 2001, Houlahan et al. 2007), and 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 of compensation at Portal play out over longer timescales (see also Vasseur and Gaedke 2007) and are more consistent with a zero-sum constraint considered at a metacommunity or even macroevolutionary level (Van Valen 1973, Leibold et al. 2017). Although there are long periods of time when there are unused resources available in the system, 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 even longer timescales, evolution) more consistently than in local-scale, short-term population fluctuations. In a 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.

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# Figure legends

# Figures





**Appendices**

1. LDATS on plants – methods and results
2. Erodium - results
3. Climate - results
4. GLS/GLM results and contrasts

**Miscellany**

* Figure legends
* Appendices