# 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 4.0.3.

# Abstract

Energetic compensation can occur in a community when declines in abundance from some species are offset by compensatory gains in others such that community-level metabolic flux is maintained, consistent with a zero-sum competitive dynamic. For energetic compensation to occur in niche structured communities, species must overlap in both their resource use and their match to broader biotic and abiotic conditions. Over time, shifting conditions may modulate the degree of functional overlap between species and cause energetic compensation to shift or break down, even within a consistent set of species. Using a 40-year manipulative experiment on competition in desert rodents, we explored how changing environmental conditions and associated changes in rodent community composition have affected energetic compensation. We find that, while this system has displayed strong energetic compensation in the past, energetic compensation has broken down following a drought and community reorganization event in 2010. These results demonstrate that energetic compensation is a shifting, contingent phenomenon that depends strongly on metacommunity effects, including niche tracking, dispersal, and species pool constraints. Zero-sum compensatory dynamics, and the maintenance of assemblage-level function despite species’ declines, may therefore manifest over long timescales, driven by metacommunity and even macroevolutionary processes.

# 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 granivorous rodents (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 at times >75% (Figure 1a, Ernest and Brown 2001; Thibault et al. 2010).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). *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 small granivores sitewide 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). All analyses were conducted in R version 4.0.3 (R Core Team 2020).

## 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 (exclosures), while all other rodents are allowed access through small holes cut in the plot fencing. Control plots, with larger holes, are 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 used 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, which is approximately when the most recent reorganization event occurred (Christensen et al. 2018); and from January 2010 until January 2020, when data collection was interrupted by the COVID-19 pandemic. For each individual rodent captured, we estimated the individual-level metabolic rate as 5.69 \* (*m*0.75), where *m* is body mass in grams (White et al. 2004). We calculated treatment and species-level energy use as the sum of the appropriate individuals’ metabolic rates. All data were accessed using the R package *portalr* (Christensen et al. 2019b).

## 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 energy use by small granivores (*Baiomys taylori, C. baileyi, Chaetodipus hispidus, Chaetodipus intermedius, C. penicillatus, Perognathus flavus, Peromyscus eremicus, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys fulvescens, Reithrodontomys megalotis,* and *Reithrodontomys montanus*). We calculated this as (*SGE - SGC)/KRC* where *SGE* and *SGC* are the amount of energy used by small granivores on exclosure and control plots, respectively, 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 the ratio of total energy use, by all species, on exclosure plots to total energy use on control plots (see also Thibault et al. 2010). To compare these variables across time periods, we used generalized least squares models (*nlme*; Pinheiro et al. 2020), accounting for temporal autocorrelation, using the form *response ~ time period* + *CORCA1(census period)*. 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. Because these values are bounded from 0-1 and are therefore not appropriate for generalized least squares, we tested for change over time using generalized linear models with quasibinomial link functions, of the form *response ~ 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 July 1997-2020.We calculated estimates and contrasts across time periods and treatments using *emmeans* (Lenth 2021).

*Plant community composition*

We explored whether there have been shifts in plant community composition 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 (*LDATS*; Simonis et al. 2020,based on the model presented in Christensen et al. 2018), to identify if, and when, there have been shifts in the overall species composition of the winter and summer annual plant communities (corresponding to distinct winter and summer rainy seasons). For the complete model description, including adjustments to accommodate the high species richness and low sampling frequency of the annual plant communities, see Christensen et al. (2018) and Appendix 1.

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, and has since been a major driver of plant community dynamics (Allington et al. 2013). 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 and treatments using a quasibinomial generalized linear model of the form *response ~ time period + treatment*.

*Environmental variables*

To explore how climatic conditions have changed over the course of the study, we calculated 12-month Standardized Precipitation Evapotranspiration indices (SPEI) for all months from 1989-2020, using the Thornthwaite method to estimate potential evapotranspiration (*SPEI*, Beguería and Vicente-Serrano 2017; Slette et al. 2019; Cárdenas et al. 2021). We also calculated anomalies in the monthly NDVI (from Landsat 5, 7, and 8, obtained via *portal*r; Maesk et al. 2006; Vermote et al. 2016; Christensen et al. 2019b), total precipitation, and mean, maximum, and minimum temperature.

# Results and Discussion

Since the 2010 community reorganization event, energy use at Portal has shifted into a new configuration. *C. baileyi* is currently still present in the system, but it has declined on both control and exclosure plots, from 72% (95% interval of 69-75%) of total energy use on exclosures to 25% (22-28%), and from 11% (9-13%) to near 0% on controls (for both treatments, 1996-2010 contrast with 2010-2020 *p* < 0.001; for complete results of all models, see Appendix S2). Other small granivores have not increased their energy use to compensate, and compensation has declined from 54% (46-63%) from 1997-2010 to 21% (12%-31%; contrast *p* <0.001) since 2010 – a level not significantly greater than the 18% (9-28%; contrast *p =* 0.9) observed up until the mid-1990s. However, small granivores now account for a larger proportion of community-level energy use than at the beginning of the study (29% on control plots, compared to 8% prior to 1997; contrast *p* < 0.001), and removing kangaroo rats from the system now results in a smaller loss of energy use (energy use on exclosures 46% of controls since 2010, compared to 29% prior to 1997; contrast *p* = 0.039) even though there has not been an increase in the proportion of that loss that is offset by other species.

These changes simultaneously highlight the shifting, context-dependent nature of energetic compensation driven by the near-kangaroo-rat-analog *C. baileyi*, and illustrate relative consistency in the degree of resource partitioning between kangaroo rats and other, less similar, species of small granivore*.* That is, even though long-term habitat shifts have benefitted small granivores, we do not detect an increase in the proportion of resources used by kangaroo ratsthat small granivores, other than *C. baileyi,* are able to exploit (Figure 1). This may reflect a degree of consistent partitioning between these groups, even as the baseline distribution of resource use within the community has changed. One possible axis of consistent differentiation may relate to spatial partitioning of foraging zones. Kangaroo rats readily forage 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 use resources located in the remaining open microhabitats, which may be too risky for small granivores to access even once kangaroo rats are removed – leaving a relatively consistent, and limited, zone of overlap in resource use between the two groups.

In contrast, *C. baileyi’s* demonstrated capacity to exploit 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 resource availability on exclosure plots remains comparable to that on controls (Christensen et al. 2019a). However, *C. baileyi* no longer occurs in high enough abundances to compensate for kangaroo rats. It may be that Portal constitutes marginal habitat for *C. baileyi*, and that conditions at the site from the mid-1990s until 2010 temporarily brought the site close enough to *C. baileyi*’s niche requirements for it to establish and eventually dominate the small granivore community. *C. baileyi*’s decline occurred immediately following a period of low plant productivity and low rodent abundance community-wide, and in the decade since, the site has experienced two long and severe droughts interspersed with an unusually wet period (Christensen et al. 2018; Figure 2). These extreme conditions may themselves limit *C. baileyi’s* fitness at the site, or the rodent population crash in 2010 may have temporarily overcome incumbency effects and triggered a reorganization event tracking longer-term shifts in conditions (Thibault and Brown 2008; Christensen et al. 2018). Circumstantially, we note that *E. ciculatum* became abundant in this system at the same time as *C. baileyi*, and, like *C. baileyi,* has declined sharply since 2010 (Figure 2; Appendix 2). This could reflect shifts in conditions towards and away from shared requirements between the two species – although it may be coincidental, or part of a more complex consumer-resource dynamic (Allington et al. 2013). We do not detect other pronounced shifts in climate or the plant community around 2010 (Appendices S1, S3), although numerous relevant factors may not be captured by our data.

*C. baileyi* stands out as the only small granivore in this community known to compensate appreciably for kangaroo rats, and the major species with the most inconsistent history in this system. *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). *C. baileyi* was not found in this community for at least the two decades from 1977-1996, and is the only major species to fail to recover following the community-wide population crash in 2010. Limiting similarity may prevent the functionally similar *C. baileyi* and kangaroo rats from specializing on precisely the same habitats, and *C. baileyi* may be better adapted to exploit habitats where kangaroo rats are less prevalent. *C. baileyi* has been observed to prefer denser, shrubbier microhabitats than kangaroo rats, and to trade off in dominance with kangaroo rats across adjacent habitats (Rosenzweig and Winakur 1969; Price 1978; Ernest and Brown 2001). If *C. baileyi* is not specialized to endure the full range of conditions that occur at Portal – unlike kangaroo rats, and other species of small granivore found at the site – its dominance in the system could be intermittent and dependent on windows of opportunity when local conditions temporarily align with its requirements.

Regardless of the specific drivers of *C. baileyi*’s decline at Portal, the fact that *C. baileyi* no longer compensates for kangaroo rats demonstrates that energetic compensation is a dynamic, context-dependent phenomenon even within the same set of species. This highlights the importance of a metacommunity perspective on energetic compensation, and particularly the interrelated constraints of dispersal limitation, niche tracking, and regional species pools (Leibold et al. 2017). Dispersal limitation was the most apparent barrier to energetic compensation from 1977-1996, when *C. baileyi* was not yet present in the system. Since 2010, niche tracking has come to the forefront as a constraint on compensation, as *C. baileyi* remains part of the assemblage but fails to compensate for kangaroo rats under current conditions. Theoretically, another species similar to *C. baileyi*, but better equipped for Portal’s current state, 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 diverse, to supply functionally similar species whose traits track local conditions as they shift over time (Kelt 2015; Leibold et al. 2017). If limiting similarity discourages functionally similar species from coexisting within the same assemblage, or from specializing on precisely the same habitats, sustained energetic compensation may depend even more strongly on repeated colonization events from many different 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 decadal-scale fluctuations in energetic compensation observed at Portal also illustrate nuances in how zero-sum dynamics manifest in natural assemblages. Portal does not exhibit a constant, unrelenting zero-sum constraint of the type sometimes associated with compensatory dynamics, and compensation like that observed at Portal may not be apparent from short-term fluctuations in species’ abundances (Hubbell 2001, Houlahan et al. 2007, Vasseur and Gaedke 2007). Rather, there are long periods of time when there are unused resources available in the system, ending when species eventually join the system and absorb those resources. These dynamics are more consistent with a zero-sum constraint at a metacommunity or even macroevolutionary level (Van Valen 1973, Leibold et al. 2017), in which compensation occurs as species disperse or evolve to exploit pockets of unused resources. Compensatory dynamics of this type are difficult to detect from purely observational, or even short-term experimental, data (Houlahan et al 2007). In a rapidly changing world, long-term manipulative studies, including the Portal Project, continue to provide unique insights into the pathways by which ecological dynamics can buffer assemblage-level properties against changes across levels of organization.

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**Figure legends**

Figure 1. Dynamics of energy use and rodent community composition over time. Lines represent 6-month moving averages of energetic compensation (a), the ratio of energy use on exclosure plots to control plots (b), and the share of community energy use accounted for by all small granivores, and *C. baileyi* specifically, on control (c) and exclosure (d) plots. Dotted vertical lines mark the boundaries between time periods used for statistical analysis. Horizontal lines are time-period estimates from generalized least squares (a, b) and generalized linear (c, d) models, and the semitransparent envelopes mark the 95% confidence intervals.

Figure 2. Dynamics of (a) drought and (b) *E. ciculatum* proportional abundance at the site. Dotted vertical lines mark boundaries between time periods. (a) 12-month SPEI index for each month from 1989-2020. Values greater than 0 (blue) indicate wetter than average conditions, and values less than 0 (red) indicate drier conditions. Values between -1 and 1 (horizontal lines) are considered within normal variability for a system, while values < -1 constitute drought (Slette et al. 2019). (b) Lines are the proportional abundance of *E. ciculatum* in the winter annual plant community for each census year for exclosure (green) and control (purple) plots. Horizontal lines are time-period estimates from a quasibinomial generalized linear model, and the semitransparent envelopes mark the 95% confidence interval.

# Figure 1

Diagram

Description automatically generated with medium confidence

**Figure 2**

