# 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

Determining the circumstances under which community-level properties are sensitive to changing species composition, and how this sensitivity changes over time, is key for understanding how communities are structured and how community function may respond to future perturbations. For communities of consumers with a shared resource base, the total metabolic flux (‘total energy use’, *Etot*) of a community reflects the total amount of resources being taken up by that assemblage, and is an important metric of community function (Ernest et al. 2008; White et al. 2004; non-weec refs). The extent to which a community’s *Etot* is robust to changing species composition, and specifically declines or losses of particular species, depends on both the initial composition of the community, and on the potential for compensation from the species that remain. Species loss can affect *Etot* directly through the loss of the energy use accounted for by the species that are lost. However, if the remaining species in a community are sufficiently similar to the lost species, these remaining species may be able to exploit a large proportion of the resources originally used by the species that were lost, and offset the decline in *Etot* directly caused by species loss. This phenomenon is known as energetic compensation (Ernest and Brown 2001; Kelt 2015). When it occurs, near-complete 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, strong energetic compensation also renders community-level energy use relatively stable despite species-level fluctuations (Houlahan et al. 2007; Ernest et al. 2008).

Changing conditions over time may alter the sensitivity of a community’s *Etot* to the loss of particular species, either through changes to baseline community composition – and therefore the direct impact of species loss on *Etot* – or through changes in the degree of energetic compensation achieved by the remaining species. These distinct pathways are difficult to disentangle from short-term or observational data, and indeed are sometimes treated interchangeably (Ernest and Brown 2001; Thibault et al 2010; Bledsoe and Ernest 2019). However, they have different implications for community structure and function. Changes in energetic compensation over time signal changes in the competitive dynamics of an assemblage, either driven by metacommunity processes or by changes in the functional overlap among the species already present in an assemblage. If the species present in a local community lack the traits necessary to exploit the resources made available through species loss, but species with the appropriate traits are present in a larger regional species pool, the necessary species may disperse to the local community and greatly increase energetic compensation (as documented in Ernest and Brown 2001).Energetic compensation may also wax and wane, even within the same set of species, if shifting conditions affect the species in an assemblage in different ways and alter the extent to which they can compensate for each other (Chesson 2001; Loreau 2004). Fluctuations in energetic compensation, especially within a consistent set of species, would mean that zero-sum dynamics, and their implications for short-term population dynamics and long-term eco-evolutionary processes, are intermittent and context-dependent. However, changes in the sensitivity of *Etot* to species loss may also occur without changes to energetic compensation, if the baseline community composition changes. That is, if the proportion of *Etot* accounted for by the species that are eventually lost differs under different conditions, the loss of those species will naturally result in different impacts to *Etot*, independent of changes to energetic compensation.

Here, we investigate how shifting conditions affect the sensitivity of *Etot* to species loss, using a 30-year experiment on desert rodents to disentangle the effects of changes to dispersal limitation, functional overlap, and baseline community composition on *Etot*. In this study system, kangaroo rats – the largest, and behaviorally and competitively dominant, species in the rodent community – have been removed from experimental plots since 1977. Comparing species- and community-level energy use between manipulated and unmanipulated plots allows for direct assessment of how *Etot* responds to species loss, as well as the extent to which energetic compensation and baseline community composition account for this response (Ernest and Brown 2001; Thibault et al. 2010). Long-term monitoring of this experiment has documented repeated shifts in the habitat and species composition of this system, resulting in distinct time periods characterized by different habitat conditions and configurations of the rodent community (Christensen et al. 2018). By making comparisons across these time periods, we explored how changes to dispersal limitation, functional overlap between species, and baseline community composition have contributed to changes in energetic compensation and *Etot* over time*.*

Specifically, in 1996, an abrupt reorganization event occurred in the rodent community when a new species of pocket mouse, *Chaetodipus baileyi*, established at the site (Ernest and Brown 2001; Christensen et al. 2018). *C. balieyi* is more similar in size, and presumably other traits, to kangaroo rats than are the other species found at the site, and its rise to dominance at the site drove a pronounced increase in energetic compensation (Ernest and Brown 2001).Following a second reorganization event ca. 2010, *C. baileyi* has become relatively scarce, but remains present in the community (Christensen et al. 2018). Finally, over the course of this experiment, the habitat at the study site has transitioned from desert grassland to scrub, driving a shift in baseline rodent community composition away from kangaroo rats and favoring other, smaller, granivores (Ernest et al. 2008).

# 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 (*Dipodomys 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. 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. To measure the overall impact of kangaroo rat removal on *Etot*, we calculated the ratio of treatment-level *Etot* for kangaroo-rat exclosure plots relative to unmanipulated control plots (Thibault et al 2010; Bledsoe and Ernest 2019). This quantity is distinct from energetic compensation, which we defined 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 (all granivorous species other than kangaroo rats; *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). To compare these variables across time periods, we used generalized least squares models (the R package *nlme*; Pinheiro et al. 2020), accounting for temporal autocorrelation, using the form *response ~ time period* + *CORCA1(census period)*, and calculated estimates and contrasts using the R package *emmeans* (Lenth 2021). To evaluate change in baseline community composition over time, we calculated the proportion of treatment-level energy use accounted for by kangaroo rats on control plots in each census period. Because proportional abundance is bounded 0-1 and is therefore not appropriate for generalized least squares, we compared values across time periods using a generalized linear model with a quasibinomial link function. Finally, we calculated the proportional energy use of d. 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 compared *C. baileyi* proportional energy use over time and across treatments using a quasibinomial generalized linear model of the form *response ~ time period. \* treatment.*

# Results and Discussion

The overall effect of kangaroo rat removal on *Etot* has shifted repeatedly in this system, driven at different times by changes to energetic compensation through dispersal, changes in compensation due to changing functional overlap among the same species, and shifts in baseline community composition. In the first transition, in 1996-97, energetic compensation increased dramatically following the arrival of *C. baileyi,* from an average of 18% to 54%. Over roughly the same time period – but more gradually – the proportion of *Etot* on control plots accounted for by kangaroo rats decreased, from an average of 92% to 71%. These combined changes, and especially the increase in energetic compensation driven by *C. baileyi*, resulted in an increase in the ratio of *Etot* on exclosure relative to control plots from 29% to ~70%. This transition demonstrates the importance of dispersal limitation and the regional species pool to the dynamics of energetic compensation and the maintenance of *Etot*, as has been previously discussed (Ernest and Brown 2001; Thibault et al 2010).

Following the reorganization event in 2010, however, energy use in this community has shifted into a yet another configuration. Energetic 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 prior to *C. baileyi*’s establishment at the site. This decline in compensation coincides with a precipitous decline in *C. baileyi* abundance sitewide, from X% to X% of energy use on exclosure plots, and from X to X on control plots. No other species of small granivore has made compensatory gains to offset the decline in *C. baileyi*, resulting in a breakdown of the energetic compensation effect observed in the 1990s and 2000s.

Unlike the 1996 transition, the 2010 decline in energetic compensation cannot be attributed to extinctions or colonizations in the local species pool. Rather, the 2010 transition highlights the importance of fluctuating conditions and shifting functional overlap within a consistent assemblage to the dynamics of energetic compensation. In this most recent configuration, *C. baileyi* remains present in the community, and the amount of resources available on exclosure relative to control plots has not changed (Christensen et al. 2019a). Despite this, some aspect of the system has shifted such that *C. baileyi* is no longer capable of exploiting these resources and maintaining high enough population abundances on exclosure plots to compensate for kangaroo rat removal. We suggest that this study site constitutes marginal habitat for *C. baileyi*, and that, while conditions in the 1990s and early 2000s brought the site close enough to *C. baileyi*’s niche requirements for *C. baileyi* to establish and dominate the community, conditions since the mid-2000s once again limit *C. baileyi*’s abundance at the site. *C. baileyi* established at the site following a period of unusual weather and changing habitat conditions that also benefitted other species of shrubland-associated small granivores and led to pronounced changes in the annual plant communities that form the primary resource base for these rodents (Allington, …). *C. baileyi*’s decline occurred immediately following a period of low plant productivity and low rodent abundance community-wide. 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). Regardless of the proximate cause of *C. baileyi*’s decline, the fact that *C. balieyi* remains in the system, but no longer compensates for kangaroo rats, illustrates that shifting conditions can have profound effects on energetic compensation by modulating the degree of functional overlap within a consistent set of species.

This breakdown in energetic compensation also demonstrates that, in a strongly niche-structured community, changing conditions cause the strength of zero-sum competitive dynamics to fluctuate over time. With *C. balieyi’s* decline, there are now considerable resources available on exclosure plots that are not being exploited by any rodents.

*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. This may reflect a constraint imposed by limiting similarity. *C. baileyi* appears more functionally similar to kangaroo rats than are the other small granivores in this community, and, at this site, *C. baileyi* is competitively subordinate to kangaroo rats. Across the Southwest, *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 this site – unlike kangaroo rats, and other species of small granivore that occur more consistently in the local community – its dominance in the system could be intermittent and dependent on windows of opportunity when local conditions temporarily align with its requirements. To the extent that limiting similarity prevents functionally analogous species from specializing on precisely the same habitats, the long-term maintenance of energetic compensation

*.* Alt sitewide,

Although energetic compensation has broken down due to the decline in *C. baileyi,* shifts in overall rodent community composition have decoupled the dynamics of energetic compensation from the dynamics of *Etot* more broadly. 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.

In contrast, *C. baileyi’s*, resulting in a breakdown of the energetic compensation effect observed in the 1990s and 2000s (Figure We note that *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). Limiting similarity may prevent the functionally similar *C. baileyi* and kangaroo rats from specializing on precisely the same habitats; indeed, *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, 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 (blue), and *C. baileyi* (gold)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