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

# Authors: Renata M. Diaz1 and S. K. Morgan Ernest2

1. School of Natural Resources and Environment, University of Florida, Gainesville, FL. Corresponding author. renata.diaz@weecology.org

2. Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL.

**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

Understanding the ecological processes that may maintain community-level properties in the face of species loss, and how these processes change over time, is key to understanding the relationship between community structure and function and predicting how communities may respond to perturbations in the Anthropocene. Using a 30-year experiment on desert rodents, we show that the impact of species loss on community-level energy use has changed dramatically over time, through the combined effects of shifting baseline community composition and fluctuations in energetic compensation. Although strong energetic compensation, initially driven by the dispersal of functionally complementary species to the local community, occurred in this system from 1996-2010, since 2010, energetic compensation has broken down due to decreasing functional overlap within the same set of species. Over the course of the experiment, changes in sitewide community composition have decoupled the dynamics of energetic compensation from the overall impact of species loss on community-level energy use. These results highlight the importance of explicitly long-term, metacommunity, and eco-evolutionary perspectives on compensatory dynamics, zero-sum constraints, and the link between species-level fluctuations and community function in a changing world.

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

# Introduction

Determining the extent to which community-level properties are affected by changes to species composition, and how this changes over time, is key for understanding how communities are structured and how community function may respond to future perturbations (Gonzalez and Loreau 2009). 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 processed by that assemblage, and is an important metric of community function (Lawton 1994). 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 affects *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 (Walker 1992, 1995; Ernest and Brown 2001; Rosenfeld 2002; Gonzalez and Loreau 2009). 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 compensation also renders community-level properties relatively stable despite species-level fluctuations (Ernest et al. 2008).

Changing conditions over time may change the degree to which species loss affects *Etot,* 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 (e.g. Ernest and Brown 2001 compared to Thibault et al. 2010, Leibold et al. 2017). 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. That is, 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 (Ernest and Brown 2001; Leibold et al. 2017).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 (Loreau 2004; Fetzer et al. 2015). 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 impact of species loss on *Etot* 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 effects on *Etot*, independent of changes to energetic compensation.

Here, we investigate how shifting conditions affect how *Etot* responds 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 species loss impacts *Etot*, 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). 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). By making comparisons across these time periods, we explored how changes to dispersal insufficiency, functional overlap between species, and baseline community composition have contributed to changes in energetic compensation and *Etot* over time*.*

# 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 2019), 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 a “total energy ratio” as the ratio of treatment-level *Etot* for kangaroo-rat exclosure plots relative to unmanipulated control plots, i.e. *EtotE/EtotC* where *EtotE* and *EtotC* are total energy use on exclosures and controls, respectively (Thibault et al 2010; Bledsoe and Ernest 2019). The total energy ratio 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 (*KRC/EtotC*). 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 of the form *response ~ time period*. Finally, we calculated the proportional energy use accounted for by *,* specifically,exclosure and controld (*CBE/EtotE* and *CBC/EtotC*, respectively). *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

    The impact of kangaroo rat removal on *Etot* has changed repeatedly over time, through a combination of abrupt shifts in energetic compensation driven by *C. baileyi*, and long-term changes in baseline community composition sitewide (Figure 1). The first shift occurred around 1996, when *C. baileyi* - which had not previously been observed at the site - established in the community (Figure 1D; see also Ernest and Brown 2001). *C. baileyi* rapidly became dominant on exclosure plots and dramatically increased energetic compensation (Figure 1B), from an average of 19% (95% interval 9-29%) from 1988-1996 to an average of 55% (46-63%; contrast *p* < 0.001; for complete results of all models, see Appendix 1) from 1996-2010. With *C. baileyi*’s addition to the community, the total energy ratio (on exclosures relative to controls; Figure 1A) increased from 30% (20-39%) to 68% (60-77%, contrast *p* < 0.001). In the second shift, beginning around 2010, *C. baileyi*’s abundance sitewide dropped precipitously (Figure 1D). *C. baileyi*’s proportional energy use dropped from an average of 72% (70-75%) to 25% (22-28%, contrast *p* < 0.001) on exclosure plots, and from 12% (10-14%) to essentially 0 on control plots (contrast *p* < 0.001). Other species of small granivore did not make compensatory gains to offset the decline in *C. baileyi* (Figure 1B)*.* As a result, energetic compensation declined from an average of 55% (46-63%) to 22% (12-32%, contrast *p* < 0.001), a level not significantly different from the 19% (9-29%, contrast *p* = .9) observed prior to *C. baileyi*’s establishment at the site. Somewhat paradoxically, while the total energy ratio also dropped following *C. baileyi*’s decline, from an average of 68% (60-77%) from 1996-2010 to 46% (37-56%, contrast *p* = 0.002) from 2010-2020, it remained higher than its average of 30% (20-39%, contrast *p* = 0.04) from 1988-1996 (Figure 1A). Over the course of the experiment, rodent community composition shifted sitewide, such that in later years, kangaroo rats account for a lower proportion of baseline Etot than they did at the beginning of the study (Figure 1C). From 1988-1996, kangaroo rats accounted for 92% (90-94%) of *Etot* on controls; in later time periods, this dropped to an average of approximately 70% (1988-1996 compared to later time periods, *p* < 0.001; 1996-2010 and 2020-2020 not significantly different, *p =* .86). Because the proportion of *Etot* directly lost to kangaroo rat removal was smaller from 2010-2020 than from 1988-1996, the total energy ratio was higher from 2010-2020 than it was from 1988-1996 - even though there was not a detectable difference between the two time periods in the proportion of lost energy being offset through energetic compensation.

# Discussion

    The dynamics of rodent community energy use at Portal illustrate that the effect of species loss on *Etot* fluctuates over time, and that the processes driving these fluctuations have also changed over time. First, while the shift in 1996 highlighted dispersal limitation as a constraint on energetic compensation, the shift in 2010 demonstrates that changing functional overlap, within the same set of species, can have major consequences for energetic compensation (Figure 1B, D). The 1996 increase in compensation, driven by *C. baileyi*’s establishment at the site , was a clear and compelling example of colonization from the regional species pool overcoming dispersal limitation. That is, while the small granivore species originally present in the community did not possess the traits necessary to exploit the resources made available through kangaroo rat removal, *C. baileyi* supplied those traits and substantially restored community function on exclosure plots. In contrast, following the transition in 2010, *C. baileyi* remained present in the community, butceased to operate as a functional replacement for kangaroo rats. This is consistent with fluctuating conditions modulating the degree of functional overlap between similar, but non-identical, competitors. Kangaroo rats and *C. baileyi* are relatively similar in size and are demonstrably capable of using similar resources. However, *C. baileyi* prefers different, shrubbier microhabitats than kangaroo rats, and the two groups have been found to trade off in dominance over adjacent habitats (M’Closkey 1982; Price 1978l Rosenzweig and Winakur 1969). We suggest that this study site, which has historically been dominated by kangaroo rats, constitutes marginal habitat for *C. baileyi*, and that, while conditions from 1996-2010 aligned sufficiently with *C. baileyi*’s requirements to create substantial functional overlap between kangaroo rats and *C. baileyi*, conditions since 2010 have caused this overlap to break down. Specifically, *C. baileyi*’s decline occurred immediately following a period of low plant productivity and low rodent abundance community-wide (Appendix 2; Christensen et al. 2018). In the decade following, the site experienced two long and severe droughts interspersed with an exceptionally wet period (Appendix 2; Christensen et al. 2018). These extreme conditions may themselves have limited *C. baileyi’s* fitness at the site, or the community-wide low abundance event may have temporarily overcome incumbency effects and triggered a community reorganization tracking longer-term habitat shifts (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 community, but no longer compensates for kangaroo rats, illustrates that changing conditions can have profound effects on energetic compensation by modulating the degree of functional overlap within a consistent set of species.

Second, the difference in the total energy ratio between 1998-1996 and 2010-2020 demonstrates that changes in baseline community composition can decouple energetic compensation from the overall impact of species loss on community function. As the habitat at the site became shrubbier, small granivores increased their share of *Etot* on control plots (Figure 1C; Brown et al. 1997). However, despite favorable habitat conditions for small granivores, once *C. baileyi* was no longer abundant in the small granivore community, there was no longer a detectable increase in the share of energy being used by kangaroo rats on control plots (*KRC*) successfully exploited by small granivores on kangaroo rat removal plots (Figure 1B). This may reflect some degree of consistent resource partitioning between kangaroo rats and small granivores (other than *C. baileyi*), possibly related to spatial foraging zones. Kangaroo rats are large and bipedal and readily forage in open, exposed microhabitats, while smaller granivores rely on vegetation cover as an antipredator defense and restrict their foraging to sheltered microhabitats (Kelt 2011). Even while shrub cover at the site increased, kangaroo rats may have continued to use resources located in open areas. These resources may have remained inaccessible to small granivores, even on plots where kangaroo rats were removed - leading to an increase in the overall proportion of resources being used by these small granivores (Figure 1C), but no increase in their capacity to compensate for kangaroo rat removal (Figure 1B). While kangaroo rat removal resulted in a smaller loss of *Etot* from 2010-2020 than it did from 1988-1996 (Figure 1A), this difference was driven by a shift in baseline community composition tracking long-term changes in habitat, and not a change in the compensatory dynamic between kangaroo rats and the remaining species in the community.

Overall, the long-term changes in energy use among the Portal rodents underscore the importance of multiple metacommunity processes to the maintenance of community function following species loss (see also Leibold et al. 2017). For energetic compensation to be possible, there must be substantial functional overlap between the species that are lost and at least some of the species that remain. Although a single colonization event may be enough to allow for compensation temporarily, as conditions fluctuate, species that are capable of compensation under some conditions may no longer perform that function. Particularly if limiting similarity prevents similar competitors from specializing on precisely the same habitats (Rosenfeld 2002), this type of temporary, context-dependent compensation may be common. In niche-structured systems undergoing changing conditions, multiple colonization events, supplying different species with the appropriate traits to perform compensation under different conditions, may be required to maintain energetic compensation over time. Depending on dispersal rates and the composition of regional species pools, repeated colonization events tracking changing conditions may be unlikely or even impossible . At Portal, dispersal limitation introduced a 20-year lag between the initiation of the experiment and the beginning of energetic compensation driven by *C. baileyi*. Theoretically, another species capable of compensating for kangaroo rats, and better-suited to conditions at the site since 2010, could colonize the site and restore energetic compensation – but it is unclear whether such a species exists or how long it might take for it to disperse to the site. More broadly, as ecosystems globally undergo reductions in habitat connectivity and regional beta diversity, and move into novel climatic spaces, maintenance of community function via energetic compensation may become increasingly rare and context-dependent (Dornelas et al. 2014; Williams and Jackson 2007).

The decadal-scale variation in energetic compensation documented here adds important nuance to our understanding of how zero-sum dynamics operate in natural assemblages. Theories invoking zero-sum dynamics, and tests for compensatory dynamics in empirical data, often treat a zero-sum dynamic as a strong and temporally consistent constraint on population dynamics (Hubbell 2001; Houlahan et al. 2007). In this framing, any resources made available through species loss should immediately be taken up by other species. This is not consistent with the type of zero-sum dynamics that occur at Portal, as there have been extended periods of time when there are substantial resources available on exclosure plots that are not being used by any rodent species. Rather, the dynamics at Portal are more consistent with a zero-sum constraint operating at metacommunity, or, more broadly, evolutionary scales (Leibold et al. 2017; Van Valen 1973; Terry and Rowe 2015). That is, while strong niche structure may weaken zero-sum effects over short timescales or within a closed local assemblage, new species may disperse, or evolve, to take advantage of available resources. These types of dynamics may not be apparent from observational timeseries or short term experiments, but can be detected through long-running manipulative experiments such as the Portal Project. Moving forward, a long-term, metacommunity, and even macroevolutionary approach may be necessary to fully understand how zero-sum constraints manifest in community dynamics; how energetic compensation and shifting baselines jointly contribute to dynamics of community function; and how, and when, community-level properties are maintained in the face of species extinctions and changing conditions over time.

# Acknowledgements

The Portal Project has been supported by numerous NSF grants, most recently [LTREB], and has been sustained over the decades via the dedicated efforts of dozens of researchers and volunteers. RMD was supported in part by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138 and DGE-1842473. SKME [].

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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 kangaroo rats on control plots (c), and by C. baileyi (d), on control (gold) and exclosure (blue) 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 or credible intervals.

# Figure 1

