# Introduction

1. Framing: Energetic compensation, complementarity, and shifting conditions
   1. Energetic compensation (EC) can occur within an assemblage when declines in the abundance of one species or group of species are offset by gains from other species, such that the total proportion of available resources being used by the assemblage remains unchanged. When observed, energetic compensation is consistent with a zero-sum competitive dynamic, and by definition renders assemblage-level function (in terms of resource use) resilient to fluctuations at smaller levels of organization.
   2. For EC to occur, all or at least some of the species in an assemblage must be sufficiently similar in their resource use and broader environmental requirements that replacement species can increase in abundance to absorb resources made available due to declines in other species. This may happen via neutrality - if all species in an assemblage are functionally identical - or via functional redundancy or complementarity in a niche-structured community. That is, while species are unlikely to be fully identical in all dimensions of their niche requirements, there may be areas of partial overlap that allow for EC.
   3. When EC occurs via functional complementarity in a niche-structured system, it is contingent on biotic and abiotic conditions allowing similar but not identical species to functionally substitute for each other. If these species differ in their responses to shifting environmental conditions, EC may wax and wane as conditions change, even within the same set of species. This would mean that zero-sum dynamics (and their effects on community structure and evolution) are intermittent over time, and that the stability of assemblage-level function fluctuates with shifting conditions.
2. Empirical approaches to EC
   1. EC is challenging to detect in observational timeseries. [May reference compensatory dynamics lit here]
   2. Some of the strongest evidence regarding EC comes from long-term experimental manipulations of desert rodent communities. When observed in these systems, EC appears to be niche-structured and determined in large part by the species and traits available in the assemblage. (Kelt, Ernest)
   3. At Portal, very weak energetic compensation occurred in the first 16 years following kangaroo rat removal. Smaller granivores increased in abundance on exclosure relative to treatment plots, but only compensated ~15% for the missing kangaroo rats. In the late 1990s, a new species of pocket mouse, PB, established at the site. PB became the dominant species on exclosure plots, and, driven by its high abundances, small granivore compensation for kangaroo rats increased to ~70%. PB is more similar in size to kangaroo rats than other small granivores and competes with them strongly, suggesting that it shares similar traits, particularly related to resource use, to kangaroo rats. While these traits were missing from the exclosure plots, EC was not possible, but once they joined the assemblage, EC occurred.
3. Shifting conditions at Portal
   1. PB’s establishment at the site, and the resulting EC, coincided with major environmental transitions. Over the 1980s and 1990s, and especially following a period elevated winter rainfall associated with the early 1990s El Nino cycle, shrub cover increased dramatically at the site, as did the relative abundance of shrubland-associated rodent species. While it has never been clear why PB established at the site when it did, PB has also been reported to like bushy habitat (old studies), and the transition to shrubland may have made it possible for dispersing individuals to establish a population at the site in the mid-1990s. Finally, PB’s dominance at the site was firmly established following a period of drought, which may have overcome incumbency effects favoring long-term resident species.
   2. Other reorganization events at the site have also corresponded with a combination of gradual and rapid environmental shifts. The decline of DS coincided with a transition from grassland to shrubland, combined with sheet flooding from tropical storm Octave (Brown and Valone). Among the plant community, the invasive Erodium established at the site in the mid-1990s, aided by shifting climate and plant community conditions (Allington).
   3. The most recent such reorganization event, and the first to occur since PB rose to dominance, occurred following a severe drought in 2010.The post-drought rodent community differs from previous eras at Portal. First, PB has declined precipitously, but remains present at the site (Christensen, Bledsoe). Second, the new species composition features a larger proportion of smaller pocket mice (PP), even on control plots, than has been previously observed at Portal (Christensen).
   4. These changes to the rodent community have the potential to qualitatively alter the dynamics of EC at Portal.
      1. If no other species picks up to compensate for the PB decline, EC could have declined.
      2. However, if the increase in PP abundance on controls reflects a shift in conditions favoring PP, PP may be able to access a greater proportion of the sitewide resources than it was able to from 1980-1996 and drive a stronger compensatory response than was observed previously.
      3. Finally, the reduction in kangaroo rat proportional abundance on control plots naturally shrinks the magnitude of the possible net difference in energy use between control plots and exclosure plots. The dynamics of the *compensatory* response may therefore be more different from the dynamics of the *net* effect of kangaroo rat removal than they have been in previous time periods.
4. Here we investigate:
   1. How the community reorganization event following the 2010 drought has affected EC. Specifically,
      1. Has another species – PP – picked up to compensate for PB, or has EC waned with PB’s decline?
      2. What are the *net* and *compensatory* effects of kangaroo rat removal in this new community configuration?
   2. We also explore recent shifts habitat conditions to situate the most recent reorganization in broader context.

**Methods**

1. Time periods
   1. Rodent data from 1988-2020: longest period of continuous plot treatments. Only longterm plots.
   2. Split the timeseries into three time periods: 1988-1996 (pre-PB), 1996-2010 (PB dominance), and 2010-2020 (post-changepoint). Explore the sensitivity to different division points.
2. Rodent community energy use
   1. For all variables, pool plots of the same treatment and look at the dynamics of the treatment-level means. This is necessary to calculate quantities like energetic compensation.
      1. If the between-plot variability becomes a sticking point, I have a GAM method one could argue for. It shows qualitatively the same dynamics. It’s not perfect, but there isn't a more established method available.
   2. Variables:
      1. PB energy use as a proportion of treatment-level total energy use on treatments and controls
      2. Energetic compensation on treatments as (SGE\_trt - SGE\_ctrl) / DipoE\_ctrl
      3. Total energy use on treatments as a proportion of total energy use on controls
   3. Compare each of these variables over the different time periods using generalized least squares or generalized linear models. Use `emmeans` to estimate time-period-level means and SE, and to test significance of between-time-period pairwise comparisons using [I think the default is Tukey] correction for multiple comparisons.
      1. PB energy use: This variable is bounded 0-1 and often close to 0, so GLS does not work. Use GLM with quasibinomial link. Time period restricted to 1996-2020, because PB is not present prior to 1996 (and the 0s break the GLM). No autocorrelation term because autocorrelation terms for a GLM are not well-implemented, and the qualitative dynamics are so pronounced that it would be very hard for autocorrelation to change the effects.
      2. Energetic compensation: GLS accounting for temporal autocorrelation
      3. Total energy: GLS accounting for temporal autocorrelation
3. Exploratory analyses of habitat conditions
   1. Climate
      1. SPEI drought index with thornthwaite potential evapotranspiration on 6, 12, 18, 60 month timescales (following recent droughts paper)
      2. Individual timeseries of mean/max/min temperature, total precipitation, winter and summer precipitation, and NDVI
         1. I favor plots of the timeseries with seasonality removed via decomposition, but have also looked at the anomalies.
         2. Fit GAM smooths for visualization.
   2. Plants
      1. Community composition on winter and summer annuals
         1. LDATS
            1. This approach has the advantage that it is explicitly designed for temporal analysis of community composition, and it doesn’t depend on an a priori specification of when (or if) to break up the timeseries. I’m pretty confident in the crossvalidation method for this application now and am formalizing it as a package.
            2. Use a modified version of the method in Christensen (LDATS) to explore whether there have been transitions in the winter and summer plant communities coincident with the rodent transitions.
            3. Modifications, to accommodate the shorter time series and higher dimensionality:

Perform model selection using leave-one-out crossvalidation

Do not include a seasonal term

* + - 1. Because LDATs is Very New, we also compare the plant communities across different time periods using partially constrained correspondence analysis. This is more traditional and follows Supp and Christensen. However, using ordination to compare across time periods requires us to define the time periods a priori (and does not seem to me to be a usual application).
         1. (abundance matrix ~ treatment + time period + random(plot)). Unconstrained, or aggregating across treatments, or using year or 5-year window instead of time period, give qualitatively similar results.
         2. Visualize the dispersion/aggregation of the time periods in CCA space.
    1. We also specifically examined the dynamics of Erodium, because Erodium’s establishment at the site (like PB’s) occurred following a habitat shift and was probably aided by that shift. If Erodium and PB share similar environmental requirements, changes in Erodium could be circumstantial indications that the conditions on the plots have shifted away from the conditions that benefitted these species in the 1990s.
       1. Total abundance and proportion of winter annuals. Can just visualize, or fit a GLS/GLM respectively (matching rodent methods).

**Results**

1. Rodent community energy use: <https://github.com/diazrenata/squareone/blob/spring/analyses/rodents/rodent_energy.md>
   1. PB on controls and exclosures
      1. Controls: Pre-cpt, 10% (8/12%); Post-cpt, 0%
      2. Exclosures: Pre-cpt, 65% (62/68%); Post-cpt, 25% (21/28%)
   2. Compensation
      1. Pre-Baileys, 17% (6/27%); Pre-cpt, 52% (44/60%); Post-cpt, 21% (12/31%)
         1. Pre-Baileys and post-cpt not significantly different
   3. Total energy use
      1. Pre-Baileys, 25% (16/34%); Pre-cpt, 67% (59/75%), Post-cpt 46% (37/55%)
2. Habitat conditions
   1. Climate
      1. SPEI
      2. NDVI
      3. Precip & temp variables [most go in supplement]
   2. Plants
      1. LDATS
      2. Ordination
      3. Erodium

**Discussion**

1. In the years following the 2010 drought, there has been a qualitative shift in the EC observed at Portal.
   1. PB has declined sitewide, but most on the controls.
   2. Despite a sitewide shift favoring small granivores, no other small granivore species has taken on the functional role of PB. EC has declined and is now qualitatively similar to what was observed before PB arrived.
   3. However, the sitewide shift has affected the *net* effect of kangaroo rat removal. Because kangaroo rats now account for less of the total energy used on control plots, their removal – even un-compensated for – now creates less of a discrepancy in energy use between treatment and control plots than at the beginning of the experiment.
   4. These shifts have coincided with a period of longer and more severe droughts than have been observed previously during the study.
2. It is notable that PB is the only major rodent species to have declined, and not recovered, following the 2010 drought.
   1. Portal may constitute marginal habitat for PB. The conditions from 1995-2010 may have brought Portal within PB’s fundamental niche.
      1. This might partially explain why it took 15 years to establish at the site.
      2. Erodium arrived (in large numbers) and declined simultaneous with PB. To the extent that Erodium and PB have similar environmental tolerances, this may reflect a shift in the conditions experienced on the plots towards and then away from those tolerances.
      3. The drought(s) may *be* the shift in conditions, or they may be just triggers that knock out incumbency effects.
   2. PB’s decline at the site may be linked to the same characteristics that enabled it to functionally substitute for kangaroo rats under earlier conditions. That is, body size and presumably other trait similarities to kangaroo rats.
      1. PB may be evolved for Portal-adjacent habitats where it doesn’t have to compete as strongly with kangaroo rats, and may therefore not have the evolutionary history at Portal that the other major species do.
      2. PB’s decline at Portal may have been exacerbated by the experimental setup. PB has always been more abundant on exclosure plots, often more strongly so than other small granivores that may compete less directly with kangaroo rats. Especially if stressful conditions meant that PB was essentially restricted to 8 1-ha kangaroo-rat-free islands in a matrix full of kangaroo rats, PB could be kept to lower abundances than it would be if there were a larger swath of kangaroo-rat-free habitat available. However, this explanation on its own is insufficient to explain the decline: there must also have been *some* shift that would mean that the amount of habitat that was available from 1996-2010 was no longer sufficient.
3. Regardless of the proximate cause of PB’s decline, the fact that PB has declined, and no other species has taken its place, is an important update to our understanding of EC at Portal and more broadly.
   1. First, it highlights the joint constraints of dispersal and niche tracking on EC.
      1. Dispersal was an obvious constraint in 1996. Now, the dispersal limitation **on PB** is absent, but the environmental constraints come to the forefront.
      2. This can fit into the CAFÉ framework as an additional nuance to dispersal limitation. That is, for function to be maintained over time and shifting conditions, dispersal must be more rapid to account for niche tracking. Eventually, the species pool becomes another relevant constraint.
   2. Second, implications for zero-sum dynamics on short and long-term ecological and evolutionary dynamics.
      1. EC fluctuates over decadal timescales and at the level of species colonizations and extinctions, rather than finescale covariation in abundances.
      2. These dynamics may be consistent with a Van Valen-inspired framework. We do not observe new rodent species evolving, but the long delays observed at Portal do constitute evolutionary or metacommunity opportunity.
   3. Third, implications for assemblage-level functional resilience to global change.
      1. EC depends hugely on whether the correct traits are present or able to disperse in rapidly from the species pool. At Portal at least, dispersal is slow relative to the pace of opportunities opening up.
      2. To the extent that the traits that make you a good analog make you less likely to be already present in the community – or to be deeply evolved in the community – EC may be even more limited.
      3. The outcomes under novel environmental conditions will depend on how those new conditions match up to the tolerances and traits available from the species pool, and how easily species can disperse to track appropriate conditions.