# 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 in 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 (4 CC, 5 EE).
   2. Split the timeseries into three time periods: 1988-1996 (pre-PB), 1996-2010 (PB dominance), and 2010-2020 (post-changepoint).
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.
   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 (SmallGranivoreEnergy\_trt - SmallGranivoreEnergy \_ctrl) / DipoEnergy\_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.
      1. PB energy use: Use GLM with quasibinomial link. Time period restricted to 1996-2020.
         1. This variable is bounded 0-1 and often close to 0, so GLS does not work. 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. 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. Visualization of SPEI drought index with thornthwaite potential evapotranspiration on 12 month timescales
         1. Following recent droughts paper
      2. Visualizations of individual timeseries of other variables (supplement):
         1. Mean/max/min temperature, total precipitation, winter and summer precipitation, days above 35 C, and NDVI
         2. Anomalies from PRISM normals for mean/max/min temp, precipitation, and NDVI (h/t Glenda)
         3. Differences from long-term means for winter and summer precip and hot days (days > 35C)
   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, especially coincident with the rodent transitions in 1996 and 2010.
            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. Correspondence analysis (supplement):
         1. Because LDATs is Very New, we also compare the plant communities across different time periods using correspondence analysis. CA generally gives the same impression as LDATS.
         2. 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).
         3. Partially constrained correspondence analysis as: (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.
         4. 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. Erodium abundance as a proportion of total winter annual abundance, comparing across time periods using a GLM (same arrangement as for PB energy use, above).

**Results**

1. Rodent community energy use: <https://github.com/diazrenata/squareone/blob/main/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: <https://github.com/diazrenata/squareone/blob/main/analyses/climate/drought_results.md>
         1. 2010-2020 has included two long, severe drought periods separated by a relatively wet period. Of course, there have been other droughts since 1996, including a single extended, severe drought in the early 2000s, that did not make PB crash.
      2. NDVI [supplement]: <https://github.com/diazrenata/squareone/blob/main/analyses/climate/ndvi_results.md>
         1. NDVI had a long low period associated with the 2010 drought, but has since entered a high period (including recent periods of very high NDVI relative to past time periods)
      3. Other climate variables [supplement]: <https://github.com/diazrenata/squareone/blob/main/analyses/climate/precip_results.md>
         1. There looks like a – weak – signal of low precipitation and increasing minimum temperature and hot (>35C) days since the early 2000s.
         2. These shifts are nowhere near as pronounced as the shift towards low precipitation and higher temperatures seen from the 1980s-1990s.
         3. Whatever story there is here, I think is consistent with and more intuitive in the drought index. But, these are here for transparency.
   2. Plants
      1. LDATS: <https://github.com/diazrenata/squareone/blob/main/analyses/plants/annuals_ldats_results.md>
         1. LDATS identifies one changepoint, approx. 1996, for the winter annuals, and no changepoints for the summer annuals. The winter transition is from a community dominated by hapl grac (75%) to one dominated by erod cicu (44%) and astr nutt (22%).
      2. Ordination [supplement]: <https://github.com/diazrenata/squareone/blob/main/analyses/plants/annuals_ca_results.md>
         1. Ordination shows a difference in the pre-1996 and post-1996 communities, and a less compelling difference between pre-2010 and post-2010, for winter; approx. 20% of variance explained by time period. For summer, the differences between all 3 time periods are either absent or much less compelling; approx. 9% of variance explained by time period.
         2. I am not really comfortable hanging much interpretation on this analysis.
      3. Erodium: <https://github.com/diazrenata/squareone/blob/main/analyses/plants/erodium_results.md>
         1. Erodium drops on both controls and exclosures ca. 2010.
         2. Erodium’s proportional abundance is significantly higher from 1996-2010 than pre-1996 or post-2010 for both controls and exclosures. Mean proportions on controls in each time period: 2%; 35%; 7%; on exclosures: 4%; 60%; 18%.

**Discussion**

1. [Narrative-ish summary of results] 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 decade featuring longer and more severe droughts than have been observed previously during the study. We do not detect a pronounced shift in the overall plant community associated with the 2010 drought, but Erodium specifically – which had similar establishment dynamics to PB – declined sharply with the 2010 drought.
2. [~Speculation on proximate and ultimate reasons for PB’s decline] It is notable that PB is the only major rodent species to have declined, and not recovered, following the 2010 drought.
   1. Everyone’s abundance crashed, but most species recovered. PB did not go fully extinct at the site, and so has a starting population that could, in principle, have recovered as well. As of 2015, there are still comparable food resources available on exclosure plots (see Christensen plot switch).
   2. We suggest that Portal may constitute marginal habitat for PB based on its environmental tolerances, and that shifts away from PB’s ~optimal conditions have rendered it less able to compensate for or compete with kangaroo rats.
      1. The conditions from ~1995-2010 may have brought Portal close enough to PB’s environmental tolerances that it was able to establish and even coexist with kangaroo rats on control plots.
         1. This might partially explain why it took 15 years to establish at the site – if conditions prior to ~1995 were not as good for PB, potential colonization events might have fizzled.
      2. Conditions since ~2010 may no longer be as good for PB, preventing it from reaching high abundances on exclosures (even though the resources are still available) or coexisting with kangaroo rats on control plots.
         1. Driven by both the fundamental niche (i.e., PB would not succeed under these conditions period) and reduced competitive performance in the broader community context.
      3. Specific shifts
         1. The drought from 2008-2010 and in the 20teens may *be* the shift in conditions, or the 2010 drought might have been a trigger that knocked out an incumbency effect.
         2. There are not other obvious regime shifts in the climate data or the plant community-wide abundance data. However, we do not necessarily expect our data streams to fully capture the range of variables that determine individual species’ match to the system.
         3. Circumstantially, Erodium arrived (in large numbers) and declined 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.
      4. PB’s decline at Portal may have been accelerated 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 the exclosures, as 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. In the 1990s, PB came up from zero starting on the exclosures. Something must be different now, that prevents PB from doing the same again.
   3. At a deeper level, 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.
      1. PB may be evolved for Portal-adjacent habitats where it doesn’t have to compete as strongly with kangaroo rats. Because niche differentiation is happening via habitat partitioning, it can have similar body size and resource-uptake traits to kangaroo rats. This same niche differentiation along habitat tolerances may contribute to PB being only compatible with a subset of the environmental conditions that occur at Portal.
3. The fact that PB has declined, and no other species has taken up its functional role, 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 limiting constraint on the EC observed starting 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. 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.