**Context dependence and historical contingency in zero-sum dynamics**

Keywords

**Zero-sum dynamics**

*Defined* Closely related to energetic compensation. When the species in an assemblage (community) share a pool of common resources and compete strongly, such that declines in resource use from one species are compensated for by increases in resource use by other species resulting in no net change in community-level resource use. May be part of neutral dynamics, where many species are functionally substitutable, or via trait/niche structure, where *certain* functionally analogous species trade off with each other.

*Significance* A common assumption of neutral theory and evolutionary dynamics (Van Valen/Red ueen?). At ecological timescales, means that the functional status of a community may be more resilient to perturbation than individual species. May also provide some structure to biodiversity change, if even high rates of turnover are operating within a strong limiting resource/energetic constraint.

*Evidence* Difficult to test for. Especially difficult to evaluate over time via observational data, because the total amount of energy available may change. Observationally, compensatory dynamics as measured via variance ratios appear rare, but abundance is not the best currency, ratios are indirect, and may not adequately capture differences in the temporal scale at which synchronous and compensatory dynamics occur. Experimental evidence is good but rare. Experimental evidence is mixed (Portal v Fray Jorge). May occur with long time lags and contingent on niche-related processes.

**Context dependence**

*Defined* The strength, direction, or outcome of ecological processes often depends on environmental or biotic conditions

*Significance* Makes prediction hard; need to engage with what pieces of context are relevant

**Historical contingency**

*Defined* A special kind of context dependence, where not only does the effect depend on current conditions but on historical conditions. May be via (detectable) legacy effects, such as indirect interactions mediated by habitat structure, incumbent advantage; or, may emerge even in otherwise comparable systems via stochasticity and priority effects.

*Significance* Adds lags to systems and a specific kind of context to be aware of?

Knowledge gaps

To what extent are zero-sum dynamics a) a consistent feature of certain systems or b) dependent on niche and metacommunity processes?

An overarching energetic/resource constraint may transcend species differences, such that many species can exploit a resource base comparably effectively and trade off with each other. This would result in an efficient and fairly fluid community, with compensatory dynamics detectable between populations at short timescales, relatively stable aggregate properties despite highly variable species dynamics, and intense competitive pressure contributing to evolutionary dynamics (as in Van Valen’s Red ueen). However, to the extent that species differ in which resources they can use effectively, shifting environmental and metacommunity conditions may become increasingly important in determining when zero-sum dynamics are relevant in a system, and zero-sum phenomena like energetic compensation may be context-dependent and inconsistent over time. Compensatory dynamics may only be evident when there are sets of species, either present in a system or able to disperse to the system from the regional pool, with sufficient resource niche overlap to compensate for each other. This depends jointly on environmental conditions and on the set of species present in the local and regional species pools. If such sets of species are not present, or if dispersal is low, energetic compensation may be inconsistent and occur with long temporal lags. If shifting environmental conditions modulate different species’ ability to exploit resources, zero-sum constraints may weaken and fade. If zero-sum dynamics are thus highly dependent on environmental and metacommunity context, their signature consequences – strong negative covariances between species at the population level, highly stable aggregate metrics relative to variable population dynamics, and potential implications for macroevolutionary dynamics – may be inconsistent over time.

Incorporating temporal lags and metacommunity context may help us better detect *when* communities are operating with a zero-sum constraint, explore how an active zero-sum constraint manifests in species dynamics and assemblage-level properties, and formulate more nuanced expectations for how zero-sum constraints may manifest in community assembly, ecosystem function, and evolutionary dynamics.

Some of the most compelling evidence of zero-sum dynamics, evinced as energetic compensation following the removal of a group of species, derives from long-term monitoring and experimental manipulations of the rodent community near Portal, AZ. In 1977, the behaviorally and energetically dominant kangaroo rats were removed from experimental plots. While smaller granivorous species increased in abundance following kangaroo rat removal, indicating some degree of interspecific competition, smaller granivores were unable to fully exploit the resources left unexploited by the banished kangaroo rats. Fully 18 years after the initial experiment, a new species established at the site. This species, which is more similar to kangaroo rats in size and appears to compete strongly with kangaroo rats, appears to perform many functions analogous to kangaroo rats; once it established on exclosure plots, the total energetic flux on those plots increased to nearly match control plots, and abundances of other small granivores declined. In this example, a zero-sum effect occurred contingent on species’ traits and metacommunity dynamics, which introduced a long lag from the initial perturbation to the compensation.

Over subsequent decades, Portal has undergone additional changes in habitat conditions and species composition. We have also implemented new experimental manipulations. We can combine additional years of long-term monitoring of experimental and control plots, and repeat implementations of the original experiment, to test whether the compensation observed in the 1990s and early 2000s has endured despite environmental change and shifts in species composition, and whether this effect is additionally contingent on *historical* conditions.

Evidence/analysis

* Comparison of old exclosures to old controls: have the effects seen in the 1990s persisted? Energy matching.
* Comparison of new exclosures to old controls: does PB (or another species) again come in and compensate?
* Comparison of new exclosures to old exclosures: is zero sum behavior historically contingent? Either on detectable legacy effects or on not-obvious differences between old and new exclosures
* **Maybe** do covariance ratios and test the strength over time?

Possible outcomes

* Compensation/zero-sum – match between PB and Dipo – may have faded over time; PB may be still leaving resources on the table, and may fail to compensate for removed Dipo *even though it is in the species pool*; means it is highly highly contingent on environment-species matching. Suggests to me a kind of weak, loose constraint? And probably not a lot of stability in aggregate/function.
* Compensation may persist over time
* Compensation might be happening *from another species*
* Either of those two, suggest that at least for this system zero-sum is strong; aggregate is indeed more stable; zero-sum might play a strong role in evolutionary dynamics.

So here’s a thing, I don’t actually think the evidence under “zero sum” in ZSTNAM is…evidence of zero sum?

They frame zero sum as specifically a *steady state of energy supply*. This is a necessary assumption if you’re going to try and use covariance ratios or other observational data, or comparing variability in E over time to variability in species’ populations.

* Variability in species composition should be greater than aggregate E
* Negative covariances in energy use should exist among species
* Compensatory size shifts

The thing is… IDK, I don’t really put a lot of stock in covariance ratios. If the total amount of energy varies over time, you’re trying to pull out compensation between pairs from overall synchrony.

As opposed to… experimental evidence. Where you reduce the density of one species and see if other species compensate. *This* to me is compelling; that removing kangaroo rats 🡪 PB stepped in (eventually). But also compelling is that it took so long, and other species didn’t do it. *In 1977, PP was not in a competitive zero-sum with krats*. *There is significant niche structure keeping them from accessing the same pool of resources, and limiting the assemblage’s ability to rapidly bounce back from perturbation. There’s metacommunity and nichey stuff.*

But right, like a size shift over time doesn’t mean we’re at energy steady state or that energy use is somehow tightly constraining stuff.

* The 1977 and 1988 results are actually probably evidence of overlap but not zero-sum. By definition removing krats should have 🡪 small granivores compensate. This did not occur for 18 years, and so for 18 years you had smgran abundance limited by something other than krat presence.
* PB vs krats might be competing, but this is a pairwise dynamic, not a community-wide dynamic
* So far, functional replacement in this community seems to have been highly contingent on metacommunity (dispersal).
* The more we see that energetic compensation, even within this community, is contingent on
  + Environmental conditions
  + Metacommunity/species pool
  + Legacy effects

The less I think of this as evidence of a community-wide zero-sum dynamic, and the more I think of it as evidence that

* + Competition and compensation are occurring at the functional group level
  + Zero-sum is probably inadequate to describe the constraints at ecological or evolutionary scales
  + Resilience to perturbations such as species loss is going to be highly contingent on dispersal providing the right traits; there could be long time lags

*Energetic compensation is context-dependent and historically contingent*

vs

*Energetic compensation endures over time despite shifting environmental and historical context*

Energetic compensation: reductions in one species offset by another. Implies a strong competitive interaction. Sometimes interpreted as evidence of zero-sum dynamics. Can make community-level energy use more stable over time and in response to perturbation than population dynamics. Evidence very limited and best obtained via manipulative experiments.

E. compensation at Portal demonstrated. Unclear if a common phenomenon, even among desert rodents.