Ecology: ECY21-1030

Maintenance of community function through compensation breaks down over time in a desert rodent community

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General Comments

We appreciate the time and attention the Editor and Reviewers have put into refining this manuscript. In response to the reviewers' comments, we have:

1. **Expanded and clarified the description of the field and statistical methods, in the main text and supplementary materials**
2. **Added supplementary materials 1) including an analysis examining biomass in place of energy use and 2) to the extent possible, exploring the effects of variability between plots within the same experimental treatment on these results. Both analyses produce qualitatively the same results as those presented in the main text.**
3. **Made numerous textual revisions to refine and add nuance to the framing and interpretation of results.**
4. **Finally, because these changes added length to the main text, we have tightened the language throughout, removed unnecessary references, and shortened the acknowledgements to comply with the page limit.**

RESPONSE TO EDITOR

COMMENT

Your revisions should address the specific points made by each reviewer. Both provide constructive suggestions to improve the ms. I agree that an explanation of mathematical procedures will avoid confusion over the R code, as suggested by Rev #1, and that a figure of body mass of the rodents involved in this study would be very useful, as suggested by Rev #2.

Response:

We have expanded the details of the statistical methods in the main text (lines 141-178 in the "clean" manuscript) and the supplementary materials (Appendices S1-S3), with specific attention to the points (temporal autocorrelation and effects of experimental treatments on *C. baileyi* proportional energy use) raised by Reviewer 1. We agree with Reviewer 2 that biomass is also a relevant currency for this study, and have included a supplementary analysis (Appendix S3) and figure using biomass, rather than energy use. Results for biomass are nearly identical to those for energy use, so we were comfortable including this analysis in the supplement rather than as part of the main text.

RESPONSE TO REVIEWER 1

COMMENT

This manuscript studies the link between community function and structure by measuring the changes of a desert rodent community in Arizona. An interesting feature of this study is the long time series (over 30 years) gathered on these desert rodents within an experimental setting that includes exclosures.

I found the manuscript interesting and well written. Overall, I have only minor concerns that need to be addressed about the manuscript.

Response:

Thank you!

COMMENT

1.1 - Make sure all acronyms used on the manuscript are defined. For example, "SG" is never defined.

Response:

We have included definitions for "SG", "KR", and "CB", in addition to "Etot", in the main text (lines 157, 158, 169).

COMMENT

1.2 - L39: Define "community function".

Response:

We have added a short definition of community function in this context (line 42).

COMMENT

1.3 - L104-105: "...the habitat at the study site has transitioned from desert grassland to scrub..."

Why? Is it because of the rodent community or because of other environmental constraints? Please give more details. This information is important because if it is caused by the rodent species themselves, it could have important implication for the rodent community structure.

Response:

This is an excellent point. The habitat transition at this site occurred primarily from the late 1980s-early 1990s, driven by a period of high winter rainfall associated with the early 1990s La Niña cycle that encouraged the growth of woody shrubs (Brown et al. 1997). The change occurred site (and region)-wide, and not differentially on different plots as a result of ecosystem engineering by the rodents. We have summarized this in the text as "shifting environmental conditions" (lines 104-107).

Brown, J. H., T. J. Valone, and C. G. Curtin. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceedings of the National Academy of Sciences 94:9729–9733.

COMMENT

1.4 - L111-112: Move this small paragraph to the end of the Method section.

Response:

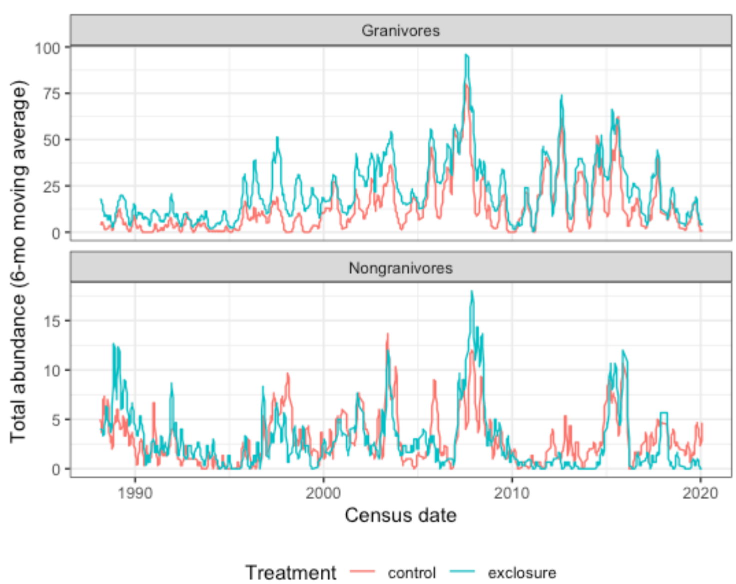
Done (now at lines 177-178).

COMMENT

1.5 - L114-120: Could the exclosure with small holes prevent other species (e.g. larger predators of rodents) to enter in the exclosure thus influencing the dynamic of the rodent community and potentially the environment (see my comments above)? Please explain.

Response:

The primary predators to rodents in this system are coyotes, birds of prey, and snakes. The plot fencing is low (0.5m) and does not appear to impede coyotes or aerial predators. The fences may affect some snakes, but we have observed snakes using the holes cut in the fences for the rodents, and they are also able to enter the plots by going over the fences or climbing along vegetation. While we do not have direct data on predator presence or predation pressure on plots with different treatments, we can use the response of non-granivorous rodents (*Neotoma albigula, Onychomys leucogaster, Onychomys torridus, Sigmodon fulviventer, Sigmodon hispidus, Sigmodon ochrognathus*) to kangaroo rat removal to disentangle differences between the treatments driven by competition from treatment artefacts, such as predation pressure. Non-granivores should not be strongly affected by competitive release due to kangaroo rat removal, but should be similarly affected by any reductions in predation pressure caused by the exclosure treatments. Like past investigators at Portal (Munger and Brown 1981), we do not observe an increase in non-granivore rodent abundance on exclosure plots (in contrast to a consistent increase in small granivore abundance on these plots); see plot, below.



Munger, J. C., and J. H. Brown. 1981. Competition in Desert Rodents: An Experiment with Semipermeable Exclosures. Science 211:510–512.

COMMENT

1.6 - L126-130: On these lines a description of the time periods used for comparison are presented. This description should explain in details why the boundaries of each time period was selected as they were.

Response:

We selected these time period boundaries following the demarcation points for transitions in the rodent community identified in previous studies (specifically, Bledsoe and Ernest 2019, for the first, and Christensen et al. 2018, for the second). We explored using slightly different boundaries to assess impacts on our results. For the first transition, we examined using the first observation of *C. baileyi* at the site (June 1996). For the second transition, we used the results presented Christensen et al. (2018) to identify the timing of the second boundary. Christensen et al. (2018) identified a 95% credible interval for the second transition that spans a 16 month period from June 2009 to September 2010. We examined the impact of using the beginning, middle (January 2010, the boundary used in the main text), or end of that 16-month window as the boundary for the second transition. Using these different boundaries did not have a qualitative effect on the overall results. We have expanded the discussion of the choice of time-period boundaries in the text (lines 125-135).

Bledsoe, E. K., and S. K. M. Ernest. 2019. Temporal changes in species composition affect a ubiquitous species' use of habitat patches. Ecology 100:e02869.

Christensen, E. M., D. J. Harris, and S. K. M. Ernest. 2018. Long-term community change through multiple rapid transitions in a desert rodent community. Ecology 99:1523–1529.

COMMENT

1.7 - L131: "5.69 * (m^0.75)". In the context of the study, it is important to explain the meaning of this equation and of the different values in this equation.

Response:

We have expanded the explanation of this metabolic scaling relationship. Because of space constraints, we direct readers to the original paper applying this relationship in this system (White et al. 2004) for details (lines 135-138).

White, E. P., S. K. M. Ernest, and K. M. Thibault. 2004. Trade-offs in Community Properties through Time in a Desert Rodent Community. The American Naturalist 164:670–676

COMMENT

1.8 - L153: "... using the form response ~ time period + CORCAR1(census period)..."

What does this mean exactly? Especially the CORCAR1() part. This would be clearer if mathematical equations were used to describe the model instead of R code.

Response:

Thank you for raising this question; it is clear that we did not sufficiently explain our rationale for incorporating temporal autocorrelation into the models nor how we accounted for temporal autocorrelation in those models. Our data consists of monthly censuses, which are then combined

into decadal-scale time periods for analysis. There is temporal autocorrelation between values for census that are close to each other in time. To account for this, we included a temporal autocorrelation error structure in our analyses of compensation and total energy use; this is implemented in R via the `CORCAR1()` constructor for generalized least squares models fit with the `nlme` package. Accounting for temporal autocorrelation improves model fit considerably (see Appendices S1, S2, S3). We have expanded our explanation of the inclusion of temporal autocorrelation in the main text (lines 162-164) and supplement (Appendices S1, S2, S3), and direct readers to the online data and code repositories for details of the code.

We note that we were unable to incorporate temporal autocorrelation into our models for *Dipodomys* or *C. baileyi* proportional energy use, because we prioritized using the appropriate model family over including autocorrelation, and we were not successful in finding methods implemented in R for incorporating temporal autocorrelation into generalized linear models (appropriate for proportion data bounded 0-1). We proceeded with GLMs that do not account for autocorrelation, in part because the differences between time periods for these variables are so pronounced that we were not concerned about being misled over subtle effects due to autocorrelation.

COMMENT

1.9 – Following up on comment 8, I strongly believe that presenting pseudo-code (or R code) in a manuscript as was done here may lead to confusion and result in misunderstanding of the model that was actually used and as such I recommend using mathematical equation instead. For example, in the explanation giving prior to the pseudo-code presented on L164-165 (response ~ time period * treatment), it is not clear what the relationship between the different parts of the explanatory variable in model. In R, the code presented means that the "response" is modelled with the "time period" variable, the "treatment" variable and the interaction between "time period" and "treatment", while in the explanation given, the text seems to imply (although this is not clear) that only "time period" and "treatment" are interacting. Obviously, this has important implication in the results and the interpretation given to the model. Note that if only the interacting terms were to be considered, ":" should be used instead of "*" in R.

Response:

We appreciate this suggestion; again, it is clear that our original description was not sufficiently specific. We have included the precise model specifications used for each analysis in the main text (lines 160-62, 168-69, 173-174), expanded the details on model fitting and selection in the supplement (S1, S2, S3), and encourage interested readers to consult the online repositories for fully annotated code.

We apologize for the lack of clarity regarding the model for *C. baileyi* proportional energy use. We initially fit the model using the full set of terms:

treatment + time period + treatment:time period.

We note that the interaction term (treatment:time period) has no qualitative effect on the results, and does not improve model fit over including separate, non-interacting effects for treatment and time period (AIC for the full set of terms = 237; AIC with separate, non-interacting terms = 231; see Appendix S2 for a full account of model comparison). We initially left this term in the model, because

it is biologically relevant (i.e. *a priori* we believed that the effect of time period could vary between exclosures and controls). In this revision we have removed the interaction term, resulting in the model:

treatment + time period (lines 173-174).

We detail this decision making process in the supplement (S2).

COMMENT

1.10 - L159 and L164: "quasibinomial". Explain why a quasibinomial link model was used instead of the more traditional binomial model... or any other model for that matter.

Response:

We have reverted to the use of binomial GLMs, with no qualitative effect on the results (lines 168, 173; Appendices S1, S2, S3).

RESPONSE TO REVIEWER 2

COMMENT

2.1 - This manuscript provides important updates to the long-term results from a rigorous experiment that excluded functionally-important rodents, kangaroo rats. First, it finds that the previously reported functional compensation by the pocket mouse has substantially decreased in the past decade, after a community reorganization event. Second, it finds that the kangaroo rat energy use has also decreased in the past two decades. Together, these results demonstrate the importance of long-term experiments, and how species colonization and fluctuations can alter ecosystem functioning and the ability of remaining or colonizing species to functionally compensate for lost species. I agree with the authors that 'this type of temporary, context-dependent compensation may be common.' I have only one main suggestion, as well as many specific suggestions that I hope will help further improve this manuscript, which is already strong.

Response:

Thank you!

COMMENT

2.2 - To help compare with other studies, I recommend including a figure, even if only in the supplement, presenting raw rodent body mass in grams. Although I am not questioning the importance of these metabolic and energetic calculations, many other theoretical and experimental studies considering biodiversity and ecosystem functioning have reported the biomass of various trophic levels and functional groups of species. In addition to these metabolic rate and energetic estimates, which are a nonlinear function of measured body mass (as shown on L131) and which depend on the combinations of body mass and numbers of individuals, a broad readership would also be interested in the raw body mass results for the treatments and key species. How does rodent biomass compare between treatments and change over time? This question seems relevant to the framing of the paper.

Response:

We agree that it is natural to look at biomass, in addition to energy use, as a currency of community function in this context. We have added an appendix (S3) with a full analysis and figure using biomass instead of energy use (referenced in the main text at lines 92-95, 142-143, 182-184).

The results for biomass and energy use are nearly identical, because the quantities in our analyses are all proportions of some form (and a step removed from the original units of measure), and there is not a pronounced decoupling in the dynamics of energy use and biomass across treatment types or over time. We were therefore comfortable including these results in the appendix.

COMMENT

2.3 - L23-24: The main results statements would be stronger if the words 'changed' and 'changes' are avoided and replaced by directional statements. For example, rather than stating that the degree of functional redundancy changed on L24, it is much clearer to state that there was decreased functional overlap, as nicely stated on L27.

Response:

We appreciate the importance of being specific about the types and direction of change. In the first instance, we intentionally used the more inclusive "changes" to refer to the full arc of changes over time, which were then detailed in the following sentence (i.e. increases in compensation due to the colonization of *C. baileyi*, and the subsequent breakdown of compensation associated with *C. baileyi*'s decline). To help signal that there have been multiple changes, in different directions, in this system, we have changed the phrasing to "…has changed *repeatedly* and dramatically over time", from "…has changed dramatically over time". In the second instance, we have replaced "changes in species composition and in the degree of functional redundancy among the same set of species" with "1) the addition of new species to the community and 2) a reduction in functional redundancy among the same set of species" (lines 23-24).

COMMENT

2.4 - L32: I recommend removing 'zero-sum constraints' from this sentence in the abstract because the results do not support this assumption, as explained in the discussion. Including this here, without further explanation, might suggest the opposite to readers.

Response:

We agree, and have made this change as part of implementing the suggestion in 2.15 (lines 31-34).

COMMENT

2.5 - L42: I believe 'have similar functional traits' is too specific here, given that ecosystem functioning depends not only on functional composition and traits, but also on species interactions, the latter of which are often poorly predicted by functional traits. The results of hundreds of randomized biodiversity experiments tend to show large effects of species richness on ecosystem functioning, even when all the same species and traits are present at different levels of species richness (i.e., to study effects of richness independent of changes in composition). Thus, when a species is lost from a community, two things change: species composition (which species and traits are present) and species richness (how many species and what variation in traits are present). Perhaps you are focused on the special case, though, where the lost species is replaced, and thus composition and traits shift, without a change in richness? How did rodent richness change between treatments and over time?

Response:

We have revised our language to avoid making a specific statement about functional traits and to instead focus on the functions species perform in the context of a community (i.e. taking into account species interactions) (lines 42-46, 54-56).

We agree that species richness effects are relevant to the wider study of relationships between community change and community function. Here, we do not engage directly with species richness effects *per se*, because the experimental design of our study is structured around the removal of keystone species (kangaroo rats) selected because of their specific functional role in this community, and so the effects of changing species richness are intertwined with strong effects on species and functional composition. Expanding beyond the scope of this experiment, richness effects (and how they manifest at metacommunity and evolutionary scales) are an important dimension of this area of

research, and we have added a specific reference to the importance of species diversity in this context (lines 281-282, in addition to lines 286-289).

COMMENT

2.6 - L58: Perhaps begin a new paragraph with the sentence beginning 'Even without...' because you make two very important points in this paragraph (shifts in composition and shifts in functional redundancy).

Response:

Done! (line 59)

COMMENT

2.7 - L110: Somewhere in the methods, it would be good to describe the measurements. For example, how and how often were body mass measurements made?

Response:

We have added this detail (lines 117-118).

COMMENT

2.8 - L115: I appreciate the land acknowledgement.

Response:

Thank you.

COMMENT

2.9 - L122, L136: Given the small and unbalanced sample sizes (4 controls and 5 exclosures), it makes me uncomfortable that the data were combined across all plots within treatments. Note that there may be effects of the number of fluctuating variables (plots in this case) on the temporal mean and variance (Yachi and Loreau 1999 PNAS). I recommend randomly choosing 4 of the 5 exclosures to ensure a balanced design and that any treatment differences are not due to differences in sample sizes.

Response:

We have made this change (lines 123-125; Appendices S1, S2, S3). With a random subset of 4 (of 5) exclosure plots, results are qualitatively unchanged.

Throughout our analyses, we were also concerned about the trade-off between combining data across plots within treatments and the need for consolidated baseline (control) values for calculating compensation and the total energy ratio. To explore whether between-plot, within-treatment variability would impact our results, we repeated our analyses using plot-level values for exclosure plots (but using the treatment-wide means for control plots, in order to make the necessary calculations), and including plot as a random effect. The results were qualitatively the same (see Appendix S1). We elected to use the treatment-level means in the main analysis, because this allowed us to treat control and exclosure plots consistently throughout the analysis.

COMMENT

2.10 - L151-154: Given that results for all variables were combined across plots within treatments (as stated on L136), was there any replication for these repeated measures analyses? What sources of variation are included or excluded in the 95% confidence and credible intervals in Fig. 1? It would help to clarify this in the Methods.

Response:

Where possible, we accounted for repeated sampling of the same plots over time by including temporal autocorrelation structures in the statistical models (lines 162-164; Appendices S1, S2, S3). In all instances, the 95% intervals represent model estimates for the time period (or, in the case of *C. baileyi*, time period-by-treatment) level means for the quantity of interest. For compensation and the total energy ratio, these models account for temporal autocorrelation between censuses within time periods. We have added these details to the main text (lines 174-177).

As we explain in our response to 2.9, we also explored the consequences of consolidating values across plots within treatments, and found no qualitative effect on the results (Appendix S1).

COMMENT

2.11 - L173: It would help to add a few words clarifying what 19% and 55% are in reference to. If I understand correctly, then these are the percentages of KR energy use in control plots during these respective periods. Is this correct?

Response:

This is the correct interpretation, and we have added language to clarify this point (lines 186-188).

COMMENT

2.12 - L206: I recommend changing 'substantially' to 'partly' or 'incompletely' because the energetic compensation shown in Fig. 1B is very far from complete, even during the middle period of time.

Response:

We agree. We have changed this to "substantially, but incompletely" (line 220) to capture the two points that 1) *C. baileyi* far from fully compensated for kangaroo rats, but that 2) *C. baileyi* greatly increased compensation from that which was achieved by the other small granivores.

COMMENT

2.13 - L208: As noted in the preceding comment, the results in Fig. 1B do not suggest that C. baileyi was able to fully compensate for KR. Thus, it seems overstated to refer to C. baileyi as a 'functional replacement' for KR.

Response:

We agree, and have modified this to "partial functional replacement" (line 222).

COMMENT

2.14 - L267-270: Yes, and there is considerable evidence that different sets of plant species promote an ecosystem function at different times and places, and under different global changes (Isbell et al. 2011 Nature). This is consistent with your results and suggests that we should not think of species' contributions to ecosystem functioning in a static sense.

Response:

We appreciate this resonance, and have incorporated this reference into the text (lines 275-277).

COMMENT

2.15 - L271-272: This is a strong statement, which is fully-supported by the results: 'this type of temporary, context- dependent compensation may be common.' It might help to include a clear statement such as this one in the Abstract.

Response:

We appreciate this observation! We have incorporated this statement into the Abstract (lines 31-32).