Response to editors and reviewers

Dear Editor,

please find attached our revised manuscript “Neutral competition boosts chaos in food webs” (original submission id: #58706).

We thank the editors for their useful suggestions. In this revision we now relate our results directly to biodiversity, which was indeed missing in the previous version. We now show that not only the probability of chaos but also the biodiversity peaks if prey are close to neutrality. Additionally we show that cyclic dynamics also leads to a strong increase in the number of species although this effect was consistently lower than for similar chaotic solutions.

We also considered all other minor suggestions, see details below.

We believe that the revised manuscript has improved significantly and hope that it is now suitable for the American Naturalist.

Best regards,

Pablo Rodríguez-Sánchez, Egbert van Nes and Marten Scheffer

## Editor’s comments

Dear Author:

The Editorial Board of The American Naturalist has reached a decision regarding your article, “Neutral competition boosts chaos in food webs.” Your manuscript has been evaluated by Dr. Christopher A. Klausmeier, one of our Associate Editors. After reading the manuscript and Dr. Klausmeier’s comments (below), I find myself in agreement with the Associate Editor’s recommendation. Consequently, I regret to inform you that I cannot accept your manuscript for publication in The American Naturalist. However, we believe that, if the concerns outlined below can be addressed, your paper could move forward successfully here. Therefore, I have assigned Decline Without Prejudice, a decision that allows you to resubmit this manuscript at some point in the future.

I was interested to read about your work attacking the longstanding question of how so many species coexist in natural communities. By constructing an analyzing a model that integrates the effects of two factors thought to promote coexistence independently, you show that conditions of near neutrality coincide with an increased likelihood of chaotic dynamics. This result could suggest a novel mechanism by which near neutrality promotes species diversity. Along with Dr. Klausmeier, I find this result intriguing, but I also share his concern that showing that near neutrality promotes chaotic dynamics falls short of a demonstration of effects on species coexistence. I think relating the conditions in the model directly to increased species diversity would be necessary to make a convincing case that would be relevant for a broad audience. In addition, from the perspective of an empirical biologist, I found the strong emphasis of the discussion on technical aspects of the modeling to suggest that as currently composed, the paper is aimed at an audience with a stronger focus on theory than ours. I do agree that with further development your modeling along the lines suggested by Dr. Klausmeier, an expanded biological interpretation of the results, and a clearer and more focused text, this work could support a contribution of interest to our readers. Thus, I agree entirely with the recommendation to decline the paper without prejudice, which offers the option to resubmit after substantial further revision that fully addresses of all of the input from the Associate Editor.

In light of these significant concerns, but in recognition of the strengths of the paper, I have assigned a decision of Decline Without Prejudice. This means that we find promise in your paper, but have found it to have substantial weaknesses that prevent us from clearly evaluating its merit. This decision does mean that if you feel you can successfully address our concerns, we would be willing to consider submission of a greatly revised manuscript. Such a manuscript would be considered a new submission, subject to full review.

Please upload a detailed cover letter explaining your responses to the comments. This letter will be available to any subsequent reviewers, so do avoid identifying yourselves if you wish to maintain double blind anonymity.

Our journal is under extreme competition for space among many excellent articles, so we are forced to consider the value of a paper relative to the number of pages it requires. Therefore, please be careful in your revision not to add to the length, and any ability to condense a bit here and there would be appreciated.

To some extent, we are suggesting that you submit a revision quite different from the present paper. I fully realize that is something that you may not wish to do. Regardless of whether or not you choose to re-submit, we thank you for considering The American Naturalist as an outlet for your manuscript, and wish you the best with your continued research.

Sincerely,

Alice A. Winn Editor American Naturalist

## Associate editor’s comments

Dear Alice,

I’ve given the manuscript “Neutral competition boosts chaos in food webs” by Pablo Rodríguez-Sánchez & colleagues a careful reading. The authors use a multi-prey, multi-predator model where prey compete according to a Lotka-Volterra model with random competition coefficients and predators have random diets with type-II functional responses. Varying the average strength of interspecific to intraspecific competition from stabilized to neutral to destabilized, the authors show that the likelihood of chaos is maximal when competition is on average neutral. They conclude that neutrality can enhance coexistence by promoting chaos, because other studies have shown that chaotic dynamics can allow species to coexist that otherwise couldn’t.

The idea is certainly intriguing, but it needs much more development. The authors’ argument, summarized in Fig. 5, is that average neutrality of competitors promotes coexistence because 1) other models have shown that chaos is associated with supersaturated species coexistence and 2) average neutrality promotes chaos in this model. However, just because some other models show that chaos is associated with (and perhaps causes) increased diversity, it doesn’t necessarily follow that it is the case here. Despite framing the paper as one of maintenance of diversity, the authors do not actually investigate coexistence / diversity in their model, only likelihood of chaos. It will take more to make a convincing argument that chaotic dynamics enhances species coexistence here.

>> Although the competition itself has clear effects on biodiversity, we now show that the chaotic solutions consistently had a higher biodiversity. We think that this is clearly shown in figure 4, which summarizes the key ideas and is clearly the main figure in this new version

The text of the manuscript could also use work. Many paragraphs are quite short (1-2 sentences), which makes for choppy reading. Large parts of the appendix do not appear relevant to the main points of the paper and could be removed. Appendix 1 derives four different predator-prey models, only one of which is studied in the paper. Appendix 3 is well known and not actually relevant, because the competitors are not truly neutral, only neutral on average. Both could be removed.

>> We revised all texts and removed large sections dealing with too general and/or basic topics from the appendix.

I would suggest that epsilon=0 does not really represent neutrality, since the individual competition coefficients aren’t all 1. “Neutral on average” seems like a more accurate descriptor.

>> We used near-neutrality instead. It seems to be more commonly used in the literature.

Also, the variation away from neutrality studied here is only along the stabilizing/destabilizing axis, since all species have equal carrying capacity K. What about “fitness differences” sensu Chesson, which would be variation in species-specific K’s?

>> Thank you for this interesting suggestion. Variation of species specific K’s will clearly lead to more competitive exclusion and an optimum biodiversity at a near neutrality seems not so surprising. The interaction of variation in K and the competition parameter seems interesting but we think this is beyond the scope of this manuscript.

Based on these issues, I think we should decline the manuscript. I suggest we decline without prejudice, so that the authors could resubmit a paper on the same topic, but it would need to be totally rethought so that it directly investigates the problem of diversity.

### Other comments

### Comments to the main body

l.36 - Ref. 3 (Hutchinson 1961) is about phytoplankton, not animals

>> Fixed reference

l.45 - “created quite a stir” - this phrase might be a bit informal

>> Substituted by “created some controversy”

l.56 - Armstrong & McGehee’s 1980 example of coexistence due to fluctuations was also internally driven

>> Added citation

l.72 & elsewhere - use concrete references to material in the appendix (e.g. Fig. A1) not just “see figure in the Online Appendix”

>> Done

l.74 - there are no resources explicitly in the model

>> True. We improved the explanation.

l.79 - prey grow according to the Lotka-Volterra competition model, not logistically

>> Done

l.81-82 - this is probably so obvious it doesn’t need to be stated

>> Removed

eq.1 - define P as the vector of P\_i’s

>> Done

l.88 & elsewhere - don’t indent after display equations

>> Done

table 1 - H isn’t exactly a half-saturation value in this formulation, since sH/(sH+H)!=1/2

>> Renamed to saturation constant

table 1 - put the description of how S\_ij are chosen in the text, not just table legend  
>> Done

l.102 - you don’t really look at “different degrees of heterogeneity” since w is fixed  
>> Used “competition strengths” instead

l.120 - what about heteroclinic orbits?

>> Heteroclinic orbits are very unlikely to happen in this model. The immigration term was included to avoid the chances of finding this kind of orbits (van Nes and Scheffer, 2004).

fig. 3 - explain why you stop at epsilon=-0.8

>> An explanation of our choice has been added to the Methods/Numerical experiment section.

l.163 - how do we know these are the asymptotic dynamics? complex systems can have long transients

>> This is indeed a fundamental problem. As far as we know, there is no robust way of distinguishing transient chaos from a chaotic attractor in such highly dimensional model. In our approach we tried first to find a typical timescale of transient dynamics by very long simulations. After that, we made sure that our stabilization time was longer than the typical timescales of those clearly identified transients. However we cannot exclude that we have misinterpreted some transients, but we think that these slow transients are not so common that it would have a significant effect on our results.

l.168 - the CEP isn’t really relevant here, because the Lotka-Volterra competition formulation implies more than 1 resource, and the predators are limiting factors too (Holt 1977, Chesson & Kuang 2008)

>> True. The reference to CEP has been removed.

l.182-189 - even without the predators, the model here isn’t neutral, it’s neutral on average (see above)

>> True. This is now clarified in our text

### Comments to the appendices

Appendices - restart labeling figures and equations at A.1  
>> Done

references - please reformat according to journal format  
>> Done

l.208-210 - if the different measures of chaos give different results, how do we know which is correct?  
>> This whole section was removed. We expanded the explanation about why we chose the Gottwald-Melbourne test above others in the discussion section.

Appendix A.2 doesn’t give enough info to really understand the chaos test used. It wasn’t clear to me the advantage over computing Lyapunov exponents.  
>> This whole section was removed. We expanded the explanation about why we chose the Gottwald-Melbourne test above others in the discussion section.

l.310 - how were the Lyapunov exponents in fig. 7 calculated?  
>> This whole section was removed as suggested by the associate editor.

fig. 7 - label x-axis and describe what is plotted in legend – “Performing the same analysis with different chaos detection algorithms…” isn’t informative, particularly when a reader jumps to the appendix when it is first cited in the main text.  
>> This whole section was removed as suggested by the associate editor.

l.346 - how did you decide if the square displacement is bounded or not?  
>> This whole section was removed as suggested by the associate editor.

eq. 20 - also assumes equal r and K  
>> This whole section was removed as suggested by the associate editor.

fig. 10 - label axes. what are x and y? what are the blue lines?  
>> This whole section was removed as suggested by the associate editor.