

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

621 CHARLES E. YOUNG DRIVE SOUTH

BOX 951606

LOS ANGELES, CALIFORNIA 90095-1606

Nov 27, 2019

Daniel Bolnick, Editor in Chief

*The American Naturalist*

Dear Dr. Bolnick,

Please consider our submission of a regular article to *American Naturalist* titled, **“Mechanisms underlying higher order interactions: from quantitative definitions to ecological processes”.** It is a complete rewrite of an earlier manuscript (MS #58934) that was returned with a decision of Decline Without Prejudice.

Dr. Christopher Klausmeier and two anonymous reviewers believed our previous manuscript covered an important question of high interest to readers of the *American Naturalist*. However, they expressed concerns about the organization of the manuscript and our definition of higher order interactions. We have addressed their concerns in this complete rewriting of the manuscript and more specifically made the following changes:

1. We have reorganized the material. In the introduction we motivate the paper by describing the implications of higher order interactions for ecological theory. We then move immediately to introducing our new definition of higher order interactions. This addresses the critique of Dr. Klausmeier and the reviewers that the definition of higher order interactions needed to be introduced earlier.
2. We provide a more detailed discussion of what higher order interactions are and how they have been defined in the literature. We are pointedly more critical of previous definitions and recent papers that have introduced confusing ad-hoc definitions of higher order interactions.
3. We provide a new more rigorous definition for higher order interactions (Line 119-121). The defining feature of models with higher order interactions is that they include parameters that are not present among the set of single competitor models. This is agrees with earlier verbal definitions of HOIs (Pomerantz 1981) and sets HOIs apart from other issues that they are often confused with such as indirect effects, non-linear density dependence and higher order *terms* from a Taylor expansion. By “single competitor” models we mean models where densities of a single competitor species affect the performance of a single individual of a focal species (Line 112).
4. In addition, we provide a less technical heuristic that will help empirical ecologists determine whether a model has higher order interactions or not (Line 130-139).
5. We use a new simulation model in the manuscript. The underlying mechanistic model we use here produces more realistic growth dynamics than in the previous paper.
6. We use simpler phenomenological models to fit the results of the simulated experiment. In the previous manuscript, none of the phenomenological models fit the underlying simulation experiment very well. This admittedly made it difficult to determine whether the inadequate fit was due to HOIs or to some other problem in the model structure. In the new manuscript, we can accurately describe pairwise competition between all pairs of species with a simple Hassel-Comins competition model. Moreover, we are able to fit HOI coefficients in the new model and these provide a clean way to quantify and compare the strength of HOIs between competitors.

We respond to all the comments on the previous manuscript in the following pages. Since the manuscript is completely re-written many of the comments will no longer be relevant for this draft.

We have no competing interests to declare, and none of the data or results reported in the manuscript have been published or submitted elsewhere.

Sincerely,

Andrew Kleinhesselink on behalf of co-authors

**References:**

Pomerantz, M. J. 1981. Do “Higher Order Interactions” in Competition Systems Really Exist? The American Naturalist 117:583–591.

**Here we have provided the full decision letter and reviewer comments on our earlier submission below. We respond to each of the major comments, but since we have re-written the manuscript many of the line-by-line comments are no longer relevant.**

*“MS #58934  
  
Dear Author:  
  
The Editorial Board of The American Naturalist has reached a decision regarding your article, "Mechanisms underlying higher order interactions: from quantitative definitions to ecological processes."  Your manuscript has been evaluated by two reviewers and by Dr. Christopher Klausmeier, one of our Associate Editors. After reading the manuscript, the reviews, 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, it 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.  
  
Incorporating the role of non-additivity in multispecies interactions into our understanding of community dynamics is an important and challenging goal, and I was interested to read about your ideas on this subject. Along with Dr. Klausmeier and the reviewers, I sense promise in your general approach to this problem, but the elements of that approach are not well supported by a systematic presentation of clear logic in the paper. Most importantly, we all struggled to understand your definition of higher order interactions (HOI) and how it relates to previous uses of this term. I agree with the consensus that mathematical definitions will be more effective than verbal descriptions for achieving clarity and identifying equivalence (or not) among existing uses of the term. Confusion on this point was sufficient to lead one reviewer to give up on the paper before fully working through the modeling. This is a clear indication that a substantial rethink of the presentation of your ideas is needed.*

*Although comments focus on the definition of HOI, there is also input to improve the structure, interpretation, and presentation of the modeling. Collectively, the comments on your paper reflect both strong enthusiasm for the potential in the work and deep frustration that the presentation does not do it justice. Given the scope of the problems identified, the paper is not suitable for publication in its present form, but I think the work has the potential to support a valuable contribution to the literature after very substantial revision. It is difficult to suggest exactly what is needed for the paper to move forward here, but Dr. Klausmeier does offer some promising ideas. Given the potential for your ideas to support a valuable advance on a tough and important problem, I hope you are willing to take on the challenge of developing them in a way that makes their contribution to clarifying the meaning and measurement of HOI clear and compelling.  
  
In light of some 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 all the criticisms outlined in the comments below, 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.  
  
Note that there is no deadline for resubmission. If you do choose to resubmit, please upload a detailed explanation of your responses to reviewers’ comments. Your responses will be available to any subsequent reviewers, so to maintain double blind review (unless you opt out), please do not write the responses as a cover letter with identifying information.  
  
Please make every effort in your revision not to add to the length of the paper, and any ability to condense a bit here and there would be appreciated. The American Naturalist believes in principle that a paper should 'be as long as it needs to be'. However, because of a high rate of submission of excellent papers, there is extreme competition for space.  
  
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  
  
xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx  
Associate Editor Dr. Christopher A. Klausmeier 's Recommendation  
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Dear Alice --  
  
We've received two reviews of the manuscript "Mechanisms underlying higher order interactions: from quantitative definitions to ecological processes" and I've given it a careful reading myself.  This manuscript seeks to enhance our understanding of higher order interactions (HOIs) by giving a new definition of HOIs and a new way to detect them, then examining how they arise in a seasonal model of plant competition for pulsed water supply.  I haven't thought about HOIs much, so I was looking forward to learning more from this manuscript.  
  
Both reviewers and I found the manuscript somewhat confusingly written.  In fact, Reviewer 2 was obviously so frustrated that they couldn't make it to the end of the manuscript.  While some of their comments might not have been the most constructive, they make the valid point that the authors should give their definition of HOIs much earlier and much more clearly, well before discussing its properties and benefits in the introduction.  Reviewer 1 also suggests "getting deeper into the weeds of the mathematics in prior works", which I also agree with.  The introduction is completely verbal, which contributes to some of the confusion.  It'd be best to state the various historical and new definitions of HOIs in crisp mathematical terms as soon as possible.*

**>> Response: We have re-written the introduction to make it more concise. We present our revised, more technically rigorous definition earlier in the manuscript (Line 109-123).**

*Having dug into the relevant literature from the 1980s and 1990s cited by the authors, I tend to agree with Reviewer 1 that it isn't clear how the new definition of HOIs given here differs from the one given by Billick & Case (1994).  B&C explicitly state that their general definition of non-HOI interactions (their eqns 1-3) "may involve any sort of nonlinearity", which contradicts the statement "one advantage of our definition of HOIs over earlier definitions (e.g. Billick and Case 1994) is that it does not require that each species’ growth depend linearly on density" (lines 172-174 here). Shuffling these interactions into a competition term C is the main difference, but it seems merely cosmetic to me.*

**>> Response: We have revised our definition considerably and this should help. We no longer use the “C” term. We add a more thorough discussion of the higher order interaction literature and clarify our argument that higher order interactions must be viewed as distinct from non-linear density dependence and we explain why previous definitions have failed in this regard (Line 152-218).**

*Also, the authors say that the HOIs of Grilli et al. (2017) "are essentially indirect effects or interaction chains" (line 116).  I would say the same about the HOIs that emerge at the inter-annual scale in the resource-competition model studied here: "large changes in resource availability and plant biomass in our simulation contribute to the magnitude of HOIs." (lines 393-394).*

**>> Response: We agree that the line between higher order interactions and indirect effects can sometimes be blurry. However, we believe there is an important difference between (see Lines 391-402).**

*I appreciated the seasonal resource-competition model, which seems like a useful addition to the plant competition literature.  Perhaps a more thorough exploration of it could stand as a paper on its own?*

**>> Response: The principle aim of this paper is to describe and define higher order interactions for a broad audience of readers including theoretical ecologists and ecologists that mainly work with empirical data. We use the simulation model in the second half of the paper to simulate the kind of field experiment that would be needed to rigorously demonstrate two-species higher order interactions among a set of three competitors. We hope that this illustration of the process makes the question of higher order interactions more tangible to empirical ecologists. While our model generates some interesting results, an exhaustive exploration of how resource competition generates higher order interactions is beyond the scope of this paper.**

*The approach to detecting HOIs in the resource-competition model is to simulate it within a year, then fit the results to a phenomenological discrete-time inter-annual model.  The discrepancies between this fit and the mechanistic model are taken to indicate HOIs.  I'm not sure about this approach but am concerned that the conclusion depends so heavily on the choice of the phenomenological model (lines 308-309).*

**>> Response: We agree that our previous approach was problematic. We use a new mechanistic simulation in this manuscript that we believe generates more realistic seasonal growth dynamics. After this change, we were able to find some phenomenological models that fit pairwise competition nearly perfectly (Fig. 4). In addition, we found that a single higher order interaction parameter added to the pairwise model fit the dynamics reasonably well (Fig. 5). This makes defining HOIs in this paper and quantifying their strength much more straightforward than in the previous version.**

*In summary, the manuscript has enough shortcomings that I suggest we decline it, but was thought-provoking enough that I suggest decline without prejudice.  Dealing with the issues will require a major reframing of the manuscript but I can't say which direction would be best.  Possible ideas: 1) focus more on the mechanistic model, 2) explore more carefully the emergence of HOIs from indirect effects or interaction chains over different time scales.  In any case, such a manuscript would be sent back for review by a potentially new set of reviewers and may not be successful.  The authors should respond to both reviewers' comments, but do not need to follow all of the suggestions if they have a reasonable disagreement.*

**>> Response: We appreciate suggestions 1) and 2) above and agree that they are good directions for future papers. However, it is our contention that any work on either of these requires first and foremost a good definition for higher order interactions, which is precisely what we endeavor to provide here.**

---------- RESPONSE

*Other comments:  
  
As the reviewers note, the word "phenomenological" is overused.  I'd stick with using it as an adjective for "model".*

**>> Response: Hopefully this will not be a problem in the new manuscript. However repetitive it may be, the distinction between phenomenological and mechanistic models is critical to defining higher order interactions and so we often make this explicit when discussing a model. See section on “Phenomenological nature of HOIs” (Line 409).**

*l. 21-24 It's not clear that these first two sentences are contradictory.  I'd just delete the first.*

**>> Response: This text is not in the new manuscript.**

*l. 38-39 This might also be true without HOIs.*

**>> Response: This text is not in the new manuscript.**

*l. 52 "original emphasis on interaction modification" where?*

**>> Response: This text is not in the new manuscript.**

*l. 133 Density-dependence in any discrete-time model should be a nonlinear function, otherwise the model would project negative densities of n\_{t+1} for some values of n\_t.  To align with continuous-time models, wouldn't the right thing be to take logs of both sides, which would render the multi-species Ricker model the same as Lotka-Volterra?*

**>> Response: This is a good point about discrete time models and is a reason why previous theory focused on HOIs in the context of continuous time models is incomplete.**

l. 142-143 "single species competition"?

**>> Response: We try to be clearer in the new manuscript. In order to discuss HOIs it is critical to distinguish between “multi-competitor” models (Line 62 and Line 108, Eq. [1]) and “single-competitor” models (Line 112 to 116). The competition models in our text define how the performance of one individual of a focal species responds to densities of competitor species. If there is only one competitor species, regardless of whether this is the same species as the focal species, then the model is a “single-competitor” model. This reflects the fact that the focal individual, does not count as part of the competitor densities, i.e. it doesn’t compete with itself. If there is more than one competitor species in the model then it is a multi-competitor (or multi-species) model. We hope that makes sense but realize it can be confusing.**

l. 150 I'd like to see this connection with continuous-time models worked out explicitly, particularly since most of the existing literature on HOIs assumes continuous time.

**>> Response: This is an important issue but beyond the scope of the current manuscript. Our definition for HOIs should work for both continuous and discrete time models.**

l. 160-163 This is unclear.

**>> Response: This text is not in the new manuscript.**

l. 165 C\_i became C here.

**>> Response: The new manuscript does not use the “C\_i” definition.**

l. 167 The phrase "for any function g(n\_j)" is ambiguous -- does that mean there is no such function or that it's not true for any function.

**>> Response: This text is not in the new manuscript.**

Consider citing: Grover, J.P. 1990. Resource competition in a variable environment: phytoplankton growing according to Monod's model. American Naturalist 136: 771-789.  It's not quite the same, but has a lot of similarities to the mechanistic model studied here.

**>> Response: We’ve changed the mechanistic model considerably and there is no longer quite the same analogy with this paper. Let us know if still feel this should be cited.**

l. 202 Maybe specify that u is "time within a season"

**>> Response: Added (Line 266).**

l. 214 with conversion factor c -- I'd introduce the inter-annual part of the model (eqns 5) here anyhow

**>> Response: We re-organized our description of the model—and it’s a new simulation model too. Hopefully this fixes the issue.**

l. 224-225 Miller & Klausmeier isn't the best reference for a type-II functional response

**>> Response: This is no longer cited because we changed the underlying model.**

l. 233 can delete "empirically"

**>> Response: This text is not in the new manuscript.**

eqns 6 & 7 what is competition C\_i in these models?

**>> Response: The new manuscript does not use the C\_i term.**

l. 272-273 lambda is defined not just with no competitors, but also at low density of the focal species

**>> Response: This text is not in the new manuscript, and hopefully we define lambda more carefully on line 157 in the new manuscript.**

*l. 299 these HOIs are deemed "stronger" than others, but can we tell if they're "strong" in some absolute sense?*

**>> Response: Good point. A big improvement in this manuscript over the previous submission is that here we were able to much more closely approximate the mechanistic simulation using phenomenological models. The HOI model uses a single parameter, , to capture the two-competitor HOIs in the simulation. Examining this parameter provides a transparent way to evaluate the strength of HOIs (Figure 6).**

Chris Klausmeier  
Associate Editor  
  
xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx  
  
*Reviewer #1:  
  
This manuscript's authors propose/advocate a formal definition of HOIs in competitive systems.  They then simulate competition among each combination of 3 species using a mechanistic model with pulsed provision of resources, use the results of simulations in which each focal species is impacted only by a single competitor to parameterize phenomenological models, and then quantify HOIs by comparing the results of simulations in which focal species are impacted by multiple competitors to what the parameterized phenomenological models would predict.  My comments below are roughly organized according to the manuscript's suggested contributions of: 1) a new quantitative definition of HOIs, 2) examination of whether HOIs arise in this specific model scenario, and 3) elucidation of mechanistic basis of any HOIs in their model.  (I'll use the shorthand R = resource, E = early species, M = middle species, and L = late species where applicable for brevity).     
  
The manuscript presents the value of the newly proposed HOI definition as being that it: "distinguishes [HOIs] from non-linear density dependence and emphasizes their consequences for multi-species competition (lines 6-8)".  One paragraph in the Introduction also implies that the new formal HOI definition will help resolve inconsistencies in the way the term HOI is used (lines 41-42: "the field still lacks a common quantitative definition of HOIs"; line 51: "The lack of an agreed upon definition for HOIs is apparent... ").  I was not convinced of either of these claims, and think that each gives a potentially misleading impression of the relevant literature (which is well covered by the works cited).  For example, the paragraph in lines 130-138 seems to describe the type of "non-linear density dependence" being excluded, but most of the works cited already adopt this perspective.     
  
My take on the qualitative use of the term HOI is that it is not as complicated or problematic as this manuscript's discussion of the relevant literature suggests.  I think it is widely appreciated that: 1) the term HOIs has generally been used in roughly two ways, to either encompass a wider set of phenomena that include non-linear density dependence, or a narrower set of phenomena that cause effects of one species on another to depend on additional species, 2) most recent papers adopt the latter use, and 3) the latter set of phenomena can be further subdivided, with many papers specifically choosing to focus on interaction modifications.  (as an aside, I think Wootton 1993 Am Nat might be a good reference to add to this literature review for the directness with which it addresses these points... see its 4th paragraph for example).  Even if these points aren't as widely appreciated as I'm assuming, I don't think that the multiple uses are a major issue given how prevalent  
the latter usage is among recent papers.  The definition put forward in this manuscript would be another recent adoption of that qualitative use.*

**>> Response: We appreciate the reviewers knowledge of the literature and we agree there is an important distinction between non-linear density dependence and interaction modification more strictly. However, we disagree that this distinction is well understood or that there is a consistent and clear definition for HOIs in the literature. A clear and generally applicable definition for HOIs as distinct from indirect effects and non-linear density dependence cannot be found in the literature. It is our hope to provide such a clear definition, which we believe we do in the current manuscript.**

**The introductory paragraphs of Letten and Stouffer (2019) illustrates some of the confusion among ecologists about HOIs. Namely: 1) Confusion of HOIs with indirect effects—Letten and Stouffer describe HOIs as a type of indirect effect, however, we agree with previous authors that the distinction between the two phenomena is important (see (Billick and Case 1994, Levine et al. 2017)). While there can be some cases where the line between HOIs and indirect effects is blurry (Grilli et al. 2017), in the context of widely used models, there is a clear difference, which we explain in the section from Line 391 to 408. Our discussions with colleagues working at many different institutions confirms that confusion on this issue is widespread. 2) Equating higher-order *terms* with HOIs. Two recent papers, Letten and Stouffer (2019) and Mayfield and Stouffer (2018), equate higher order interactions with higher order *terms*. This definition faces several major problems. First, it only applies to a narrow range of models in which higher order terms are literally added to a series of first order terms. If the pairwise interactions between competitors take another functional form this definition is problematic (see the light competition example in (Adler and Morris 1994)). There is a significant conceptual problem as well: HOIs occur when “the nature of density-dependent competition between two species is influenced by *additional* species” (Morin et al. 1988)[emphasis ours]. The presence of higher order terms only indicates interaction modification when a continuous time LV model is used as the baseline (discussed on Line 210 to Line 218). Moreover, this definition includes as HOIs higher order terms involving a single species. This is counter to most verbal definitions which emphasize *interspecific* interaction modification (see Morin quote above).**

**We believe that Adler and Morris (1994) come closest to capturing the true nature of HOIs with a technical definition, unfortunately they mostly use the term ‘interaction modification’ which can obscure their contribution. Moreover, their definition is not quite as general as ours, is not focused on competition and the derivation of their definition is not obvious. There is also some inconsistency in their specific definition because it does not count as an HOI an interaction modification between an intraspecific and interspecific competitor.**

**In short, we believe our paper is a critical and timely addition to the literature. Several recent papers (Mayfield and Stouffer 2017, Grilli et al. 2017, Letten and Stouffer 2019) discuss HOIs but either do not clearly define them, or define them in ways that disagree with longstanding verbal definitions, or define them in ways that can only be applied narrowly to the models in their own papers.**

*Quantitatively, the HOI definition put forward in lines 164-173 amounts to advocating that HOIs be defined by non-additivity of separate species' effects on a competition term within a population growth equation, rather than on per capita population growth itself.  I did take some time to revisit several of the papers cited within the manuscript to try to fully appreciate the contribution this represents.  It seemed to me that it represented one further level of sophistication and flexibility in combining multiple species' effects than the framework outlined by Billick & Case 1994, but in some ways a step backward from that presented by Adler & Morris 1994 (which allows non-linear combination of species' effects).  I can imagine how the method proposed in the manuscript might be made more useful by the practical need to quantify competitive effects as parameters in a phenomenological model, but I think a more detailed case needs to be made which will involve getting deeper  
into the weeds of the mathematics in prior works.  Another thought is that perhaps comparing the HOIs estimated by the method used here to those estimated by one or more prior methods might help illustrate and clarify this approach's utility.*

**>> Response: We have revised our definition greatly and hope that this solves some of the issues above. The definition presented here is perhaps more abstract mathematically but hopefully it is straightforward conceptually. We believe the clearest way to determine if there are HOIs in a model is to ask whether additional parameters are required to model the effects of competition on focal individual when more than one competitor species is present (Line 119 and Line 134). This definition hews closely to one of the first verbal definitions provided by Pomerantz (1981) who defined higher order interactions as requiring “additional competition parameters [be] added to the [pairwise] equations”.**

*After getting through the Discussion, I also did not come away with a clear understanding of the degree to which the proposed framework resolved the issues highlighted in prior methods.  For example, the paragraph immediately preceding the Conclusions section (lines 417-428) clearly describes why HOIs as defined within the manuscript must be present within a certain class of models.  This seems very similar to the issue with prior methods discussed in lines 47-50: "Billick and Case (1994) attempted to define HOIs more generally as the presence of non-additive effects between species, but this definition was itself viewed as problematic (Adler and Morris 1994) because such non-additivity automatically arises in any model with non-linear density dependence"*

**>> Response: We believe the new manuscript avoids these issues.**

*A related issue is that the HOIs detected in the manuscript could have arisen either from 'real' IMs (or interaction chains involving R) within the mechanistic model, artifacts inherent in the ways in which species effects are combined in the phenomenological models, or limits in how well the phenomenological models could be fit to the data.  I appreciate that the manuscript presents illustrating the presence of the latter two as a valuable result, but I felt that the lack of clarity regarding the relative contribution of biological mechanisms related to species' trait (parameter) differences to the HOIs undercut the goal of better understanding the mechanistic basis of HOIs.*

**>> Response: We used a new mechanistic simulation in the current manuscript. The results of the simulation are much more neatly fit by the phenomenological models and indeed we fit “beta” coefficients to capture the HOIs. This hopefully avoids some of the problems discussed above. We argue that HOIs are inherently phenomenological (section starting on Line 409). By their very nature we believe that it will often be difficult to determine if HOIs are “real”. It seems likely to us likely that only in very simple mechanistic models will we be able to derive HOIs from mechanistic models of competition (see discussions in (Abrams 1983, O’Dwyer 2018). The problem here is that for the vast majority of communities and species, there are no strictly mechanistic models of competition that capture dynamics or predict multispecies coexistence. It is our belief that in anything other than toy models, HOIs will likely remain phenomenological.**

*I found the focus on R uptake curves, overlap in timing of R uptake by competitors, and average R uptake rates when explaining competitive effects to be confusing.  Some of this might be improved by more clearly emphasizing which particular competitive effects and responses each observation regarding these metrics is meant to illuminate.  Even so, I think a discussion based on the fact that preemptability of resources means that (for both competitive effect and response) earlier species will tend to have much stronger effects on later species than vice-versa would be easier to follow.  The following points elaborate on specific ways in which I think they are non-intuitive, misleading, or uninformative in some specific locations:*

**>> Response: We agree that our description of how HOIs came about in the previous manuscript was unclear and confusing. In the current manuscript we try to explain the HOIs in our results briefly (Line 380 to Line 390). However, because we cannot derive competition coefficients or HOIs from the mechanistic simulation model, the exact cause of the HOIs in this case (and in most realistic communities) will always be somewhat difficult to interpret.**

*\* lines 321-324: "For instance, the early species has the most rapid growth and resource uptake rate early in the season. This shifts the resource uptake rates of the mid and late season species towards the left along their resource uptake curves (Figure 6a)".  This could misleadingly suggest that M and L take up more R earlier (=left) in response to E.  I think it would be clearer to say that R taken up by E (or any other species) at any given moment reduces the R available from that point forward, which reduces any active species' growth and R uptake.*

**>> Response: This text is not in the new manuscript.**

*\* lines 324-325: "Because the mid and late season species resource uptake curves are shaped differently"... Since R uptake curves are somewhat complex metric that is a level removed from the biology, I did not think this represented a proximal or intuitive mechanism.*

**>> Response: This text is not in the new manuscript.**

*\* lines 326-327: "during the period of time when both species are active"... As currently written I think this could be misconstrued as suggesting that R uptake during this window is of unique significance to L (that's how I initially interpreted it).*

**>> Response: This text is not in the new manuscript.**

*\* lines 321-330 as a whole: line 320 suggests that this section will illustrate how one species affects interactions between two others, but it actually seems to stop at describing M and L's differing responses to E.*

**>> Response: This text is not in the new manuscript.**

*\* lines 341-342: "In principle, resource uptake by the late season species should reduce the early season species' average resource uptake rate more than it does the mid-season species" - This did not make sense to me, and I suspect that it is incorrect: my reasoning is that M is impacted by more of L's R uptake than E is, because E ceases to grow sooner.  (I later saw that the next sentence suggests this... maybe the issue was what "in principle" was intended to mean?)*

**>> Response: This text is not in the new manuscript.**

*\* lines 345-348: "the mid season species does not significantly change the resource uptake rate of the late season species because the late species' resource uptake curve is flat over the range of resource availabilities that the early species is active (Figure 2)".  This also didn't make sense to me: I don't see how M failing to substantially affect R uptake by L would be a consequence of L having taken up little R early in the season when E was growing.  Also I think this illustrates some shortcomings of focusing on R uptake curves: M takes up R, which leads to the R concentrations at which L's growth and R uptake rapidly decline (and then cease) being reached earlier, which yields lower seed production by L.  The flatness of L's uptake curve over any early or intermediate span of the simulation will not necessarily reflect this in any striking way, so I don't think it's a good tool for understanding competitive effects in this model.*

**>> Response: This text is not in the new manuscript.**

*\* Fig 6 B: Assuming the data for L here are correct, I think the lack of any effect of E on L's average R uptake rate here illustrates the limitations of using this as a metric (since E does have a competitive effect on L that isn't reflected).  If average R uptake rate is intended purely as an indicator of competitive effect rather than response, I think that could be more prominently explained in the text and Fig caption... also, should the averages in that case not be taken over windows during which particular competitors are active?*

**>> Response: This text is not in the new manuscript.**

*Finally, I thought that the manuscript could use a stronger motivation for interest in the specific competitive tradeoff/scenario modeled (i.e. how wide its relevance is), particularly given the presentation of mechanistic insight into HOIs as one main goal of the work.  Other tradeoffs involving pre-emption (such as the digger/grazer tradeoff) might be relevant to this.*

**>> Response: We make the purpose of our mechanistic simulation clear at several points in the new manuscript: (Line 11, Line 57, Line 227, Line 242). In summary, our goal in presenting the mechanistic simulation is to illustrate how one could go from raw data describing the per capita performance of a focal species in a range of competitor densities, to actually detecting and measuring HOIs. This simulates exactly the kind of experiment most empiricists will actually need to do to measure HOIs in nature. Using a mechanistic model in our simulation is critical in that it does not beg the question—that is HOIs are not baked into it by design. This model is just complex enough to generate some interesting dynamics and generate fairly realistic growth curves, but we try to make it as simple as possible otherwise. Moreover, this particular model is intended to simulate a community of annual plants we are familiar with for which pairwise competition has been thoroughly characterized (Kraft et al. 2015). There are undoubtedly an almost infinite number of ways HOIs could arise in other systems and categorizing these is beyond the scope of the current manuscript. Hopefully with our definition as a guide some progress on that can be made in the future.**

*Overall, I thought that in each of the areas that the manuscript sought to address it presented interesting food for thought, but also either left a great deal unclear or underexplored, or gave a potentially misleading characterization of the contribution.  I think that the revisions needed to address these issues are extensive and should include new analyses and more mathematically detailed comparison to prior approaches for quantifying HOIs, with the ultimate outcome of those changes not being clear (potentially including a more nuanced and narrowly focused description of goals).  I do think that a manuscript that presents a more fleshed out exploration of some or all of the points raised here would be interesting and valuable.*

**>> Response: We hope that the new version of the manuscript lives up to some of the potential the reviewer saw in the first version.**

*More minor/editorial comments:  
  
(One recurring point below is that I was often unclear as to the rationale behind specifying 'phenomenological' as opposed to mechanistic in: I think there's something general there that needs to be explained/unpacked).*

**>> Response: This is a good point. We try to unpack this in section “The phenomenological nature of HOIs” (Line 409 – 435).**

*lines 58-60: I did not follow the point here as written (why the presence of HOIs in mechanistic models would suggest they're artifacts in phenomenological models).*

**>> Response: See section described above. We argue that HOIs cannot be present in mechanistic models by definition.**

*lines 60-63: "However, the question of whether perfect knowledge of pairwise interactions is sufficient to predict the dynamics of more complex systems is fundamentally phenomenological and thus can only be investigated in the context of phenomenological interactions"... I don't get what's meant by "phenomenological" here: prior sentences seemed to contrast it to "mechanistic", but there are certainly many specific mechanisms that can cause species interactions to be more than pairwise.  Put another way, the presence of certain types of IMs would mean that empirical data from experiments containing only two species at a time could never allow dynamics of the full system to be predicted: I do not think that is appropriately characterized as a phenomenological issue.*

**>> Response: We hope our discussion of phenomenological vs. mechanistic models will clarify this. However, the reviewer is hinting here at perhaps a deeper philosophical issue. Essentially, they question whether one can have a perfectly adequate mechanistic model for the growth of *m* species but that nonetheless does not predict dynamics when all *m* species are growing together? If so then something like HOIs could occur in mechanistic models. However, we do not see quite how this would be possible while preserving the usual meaning of ‘mechanistic’. Of course this may depend on how mechanistic is defined which is admittedly not always straightforward (McGill and Nekola 2010). Nevertheless, we believe the current paper and discussion lays out a clearer description of how these issues are related.**

*lines 67-70: "understanding of the mechanistic basis of HOIs would help ecologists predict when and where HOIs are most likely to emerge—and may help explain why phenomenological models without HOIs have been successfully applied in many communities."  
I think this, particularly as concluding sentence to its paragraph, contributed to muddling the goals for me (between better understanding mechanisms behind HOIs that this particular mechanistic competition scenario introduces, vs. better understanding ways in which HOIs can arise or be detected as artifacts of model formulation).*

**>> Response: This text is not in the new manuscript. Hopefully we resolve clarify the purpose of the manuscript and the issue of mechanism vs “artifact” in the new manuscript.**

*line 74: I think there's a flow issue here with "To illustrate our definition" sentence coming before any statement indicating that a definition will be suggested.*

**>> Response: This text is not in the new manuscript.**

*lines 80-81: "Our virtual experiment demonstrates that HOIs may indeed be common even in relatively simple mechanistic models of competition." (As the authors point out, this is not new)*

**>> Response: True. However, nearly all previous demonstrations of HOIs arising from resource competition have been in the context of very simple LV models. Beyond studies of microorganisms, most ecologists work on organisms in which population density is measured at discrete time intervals and for which the mechanistic basis for negative density dependence is unknown. Indeed much of the empirical literature on modern coexistence theory is built upon such systems e.g. (Kraft et al. 2015). Our simulations show how HOIs are defined in these widely used and empirically relevant models.**

*lines 81-83: "Importantly, we suggest that systems in which competitors vary in timing of resource uptake are likely to show HOIs, and that HOIs will likely be stronger for species maturing later in the growing season."  I think emphasizing preemptability of resources might help convey key aspects of the nature of the models.*

**>> Response: This text is not in the new manuscript and we think it avoid this issue.**

*lines 83-85: "Our example also shows how the strength and even the direction of HOIs are dependent on the structure of the phenomenological model being fit to the data."*

**>> Response: This sentence is not in the new manuscript.**

*line 87: "Exploitative competition" or something similar would be more precise*

**>> Response: This text is not in the new manuscript.**

*line 105: I did not understand the significance of "phenomenologically" here (i.e. why the same statement wouldn't work including "mechanistically").*

**>> Response: This text is not in the new manuscript and hopefully the section on Line 409 resolves this issue.**

*line 127: I thought "inconsistent with" was imprecise here*

**>> Response: This text is not in the new manuscript.**

*line 139: "Defining Higher Order Interactions" I think this sub-heading should come earlier... much of what appears from line 102 to here deals with this topic.*

**>> Response: In the new version of the manuscript we bring the definition up earlier.**

*line 161: typo: superfluous "the"*

**>> Response: This text is not in the new manuscript.**

*lines 180-183: Could this effect not be 'folded into' the effect of the latter species on the former for conceptual simplicity?  (Maybe not, or maybe only with certain models?)*

**>> Response: This text is not in the new manuscript.**

*lines 185-190: "To illustrate how we might detect HOIs in empirical data on species interactions, we simulate competition among annual plants for a single shared resource using a mechanistic resource competition model. We then fit species' responses to interspecific competition using a simple phenomenological competition model. By considering the cases in which higher order interactions emerge in this phenomenological description of the system, we can address the processes causing these interactions to develop"  
This currently appears immediately under the sub-heading: "HOIs in a mechanistic resource competition model"... I think the flow would be easier to follow if it were expanded into a separate sub-section laying out & justifying & explaining the value of the approach.*

**>> Response: This text is not in the new manuscript and re-organization should help with this issue.**

*lines 223-226: Imprecise phrasing... tradeoff is achieved by parameter choice within the function, not by assigning the function... also, Miller & Klausmeier reference does not seem to give or elaborate on saturating resource uptake function... finally, assuming R' is a typo & should just be R?*

**>> Response: This text is not in the new manuscript. We refer to the resource dynamics as “Michaelis-Menton” kinetics in the new manuscript (Line 285).**

*line 230: I think it could help to state here that E had highest r & K and L had lowest r & K.*

**>> Response: This text is not in the new manuscript.**

*line 260: is "model" the right word (as opposed to something like "quantify" or "estimate")?*

**>> Response: This text is not in the new manuscript.**

*line 298: extra apostrophe after "species", and weak HOIs "on" might be clearer than "for"*

**>> Response: This text is not in the new manuscript.**

*lines 310-312: this is shown in references cited, and lines 417-428 explain that it must be the case as a result of phenomenological model structure, so seems a stretch to characterize as an insight gained from the simulations*

**>> Response: We do not use this model in the new manuscript and hopefully we avoid this issue.**

*line 313: typo: "effect" should be plural*

**>> Response: This text is not in the new manuscript.**

*lines 312-314: I wasn't sure what other methods of detecting HOIs this was being compared to.  Comparing species' effects in isolation vs. in multispecies combinations seems like the obvious, and maybe the only way to detect HOIs?  Or put another way it seems almost definitional.  Maybe explicitly describing and contrasting other approaches that are used would help clarify.*

**>> Response: This text is not in the new manuscript.**

*line 318: I thought this statement seemed overly obvious as written.  Rephrasing slightly to highlight that R uptake, which depends on R, determines both a species' growth and its effects on competitors might work better?  
  
I initially thought Fig 2A was showing a curve only for E present and was missing curves for M and L, and so was puzzled as to why R would keep dropping past the point at which E had stopped growing if only E were present.  Using a different line style or color for that panel might help prevent other readers from making the same mistake.   
  
Why not swap in Figs S1 and S2 for Figs 3 & 5?  Comparison between the two alternate phenomenological models is fairly central to the manuscript's main conclusions, and the supplementary versions of these Figs don't seem to have a problematic density of information.*

**>> Response: The figures and text are different in the new manuscript.**

*lines 358-371: I think there would be some benefit to having much of this paragraph's content appear in the Intro to help justify & clarify the goals & approach.*  
**>> Response: Our reorganization of the content should address this.**

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Reviewer #2:  
  
*This paper purports to be about "higher order interactions" (HOIs) in species interactions, and purports to give a definition of them.  Unfortunately it falls short of doing this, frequently contradicts itself, and steadfastly refuses to be clear.  The opening pages contain a description of previous work that is superficial at best, and plain wrong at worst. The authors seem to settle on a definition of HOIs that mean "quadratic terms" inside equations.  However, the authors use a mechanistic competition model which is itself additive and contains no quadratic terms (eqn 2). That they then statistically fit some quadratic functions (eqn 6 and 7) to the output of the non-quadratic model in order to argue that the quadratic terms were critical to understand the result is hardly evidence of anything.  If quadratic terms were important for the output of the model then eqn 2 would have contained quadratic terms.  Indeed, everything the authors needed to understand their model is  
already in their mechanistic resource model. Thus, the paper repudiates itself.*

**>> Response: We are sorry our previous manuscript was so unclear to the reviewer. In the current manuscript we hope that our definition for higher order interactions and our contribution will be much clearer.**

*I have a personal rule to write positive and constructive reviews, and I will do my best in what follows.  But I strongly encourage the authors to think more carefully about approaches in mathematical biology.*

*Numerical packages like deSolve are wonderful tools, but they are no substitute for a clear mathematical description of a phenomena, and analytical treatment of a series of equations.*

**>> Response: We agree. In the new version of the manuscript we provide a cleaner mathematical definition for HOIs. We also hope that our contribution can be useful not just to theoretical ecologists (who may seek further understanding of HOIs the analytical route) but also to empirical ecologists who will necessarily need to explore HOIs using simple phenomenological models.**

*In addition, I would invite the authors to take a deeper dive into the literature.  The oldest paper cited here is from 1976, but much of the subject of the paper addresses things that were being worked out in the 1920s and 30s, and fairly fully formed by the 1960s.  I'm not sure why ecologists do this, but rediscovering and renaming things that we have understood for almost 100 years is - in my opinion - why ecology has been so slow to make progress as a field. Below I expand on these thoughts.*

**>> Response: In the new manuscript we provide a more thorough discussion of the literature. One issue is that older theoretically motivated papers on this subject are largely focused on Lotka-Volterra competition models which, while analytically tractable, do not describe the population dynamics of the vast majority of real multispecies communities in nature. A more sophisticated definition of HOIs is clearly needed for ecologists today who are investigating multispecies competition with empirical data.**

*General comments:  
What is the definition of HOIs?  By line 42 I was asking myself "are HOIs just non-additive terms?". There was some discussion of linearity (Though what about Allee effects?) which seemed to support this.  However, by line 102 the authors seem to suggest that HOIs had something to do with pairwise interactions versus triad interactions, and so maybe they only meant that HOIs meant something like  3>2. By line 116 they are discussing indirect effects, but no these are not HOIs. And by line 120 they are back to non-additive terms. Except by 131, they suggest that non-linear (i.e. non-additive) was not HOIs. We are now 6 pages into the manuscript and I'm still not sure what the paper is going to be about and what the main topic of the paper will be. Fast forward to line 165, and we learn that HOIs are indeed just non additive quadratic terms. I realise I have taken a while to get to my point, but in many ways that is my point. If HOIs are just quadratic terms in models, readers  
would be helped by learning this much earlier. The authors could define HOis this way in the very beginning, and then spend the introduction describing what they imagine these quadratic terms represent biologically speaking. This would be a much clearer paper.*

**>> Response: In the current manuscript we provide a cleaner definition for HOIs which distinguishes them from other phenomena discussed above. We also provide this definition earlier in the manuscript to head-off some of the confusion.**

*If HOIs are just quadratic terms, then the authors should also address how this is useful beyond a good fit of data.  I can always get a better fit to any data, concerning any phenomena by just shovelling in more quadratic terms. Of course if I had a million quadratic terms I might get an almost perfect fit to almost any data by almost any equation. Better yet a 3 parameter sin wave can usually be tuned such that it touches almost every data point in almost any bivariate plot thus achieving a nearly perfect fit to the data! (One could do the same with cos or tan depending on the angles of a triangle one prefers.) Of course this is not really evidence of anything.*

**>> Response: The reviewer missed our point. We do not equate HOIs with quadratic terms, and this is clarified in the new version.**

*There are a large number of issues with the math.  For example, f is defined as two different things.  As a mathematical biologist, this is very confusing. In equation 1, the authors say that f is a function of C\_i, but that C\_i is also a function of f.  The definition of a function means that this cannot be true, and mathematically this is nonsense. Similarly, there is some mention of non-linearity, but then two log-linear models are given as examples. This is after HOIs are described as quadratic terms, and so I found it confusing that two linear, and non-quadratic models were given as examples. Lastly, the authors give a very simple differential equation model which they only solve numerically. I would have liked to see some attempt at approaching this model analytically. My guess is that things like equilibrium points, or isoclines or even basic flow field diagrams would be very illuminating.  I would refer them to some of Alfred Lotka's papers from the 1920s and 30s for  
examples of the sorts of analytical approaches that might be useful.*

**>> Response: We’ve tried a number of these approaches. One of the issues with HOIs is that they are necessarily occurring in at least three dimensions, two for the densities of the two separate competitors, and one for the focal species response. This makes visualization with the traditional methods very difficult.**

*My last general comment is that it is an absolute sin to use statistics to fit a model to the output of a mathematical model.  There are myriad references the authors can look up on why this is a problem.  The main reasons are: 1) if you have made a mathematical model then you know the mechanisms and why in the world do you need statistics to discern the mechanisms?  2) Your sample size can be anything you want in a mathematical model and so you can prove, or disprove whatever you want using statistics on the output.*

**>> Response: The reviewer (understandably) missed the intent of our simulation experiment. In the new manuscript we try to make it much clearer why we simulate dynamics using a mechanistic model and then fit that model with a statistical phenomenological model. There are two main reasons: first we want to illustrate how an empirical ecologist, operating with real data but without a mechanistic description of competition, would proceed in using our definition and measure HOIs. Second, even though we know exactly how species compete mechanistically in our simulation, we were not able to derive pairwise competition coefficients, let alone HOIs parameters, analytically. This will often be the case for many mechanistic competition models (O’Dwyer 2018). An efficient way to proceed and recover competition coefficients and HOI parameters then is to use a statistical/phenomenological model to approximate simulated data. Note that we do not make any claims about statistical significance so the comment about sample size is irrelevant.**

*Specific comments:  
  
Line 23: "… pairwise fashion …" This is wrong.  For example Lotka-Volterra models from almost 100 years ago are additive, but they are not simply pairwise.*

**>> Response: What is the reviewer’s definition of pairwise? We provide a definition for pairwise on Line 74 and Line 118.**

*Line 35-37: How are HOIs a challenge for coexistence? I fail to see how this is true.*

**>> Response: We elaborate on Line 34-37. See also (Levine et al. 2017, Grilli et al. 2017)**

*Line 108-109: This is also wrong. The per-capita interactions between species are NOT independent of density in L-V models. In fact this is precisely how these models work.*

**>> Response: We believe per-capita interactions in LV are independent of density. That is each individual depresses the population growth rate of each species in the community the same way regardless of how many individuals there are. Maybe we are missing something here.**

*Eqn 1: Surely C\_i should be some function too?  That integrates the abundance and traits of other species? If populations grow according to fecundity and competition, this seems to just be a sort of LV model.*

**>> Response: We no longer use the the C\_i definition, so this should not be relevant to the new manuscript.**

*Line 159-160: As I said in my general comments these are both log-linear, which is a form of linearity.*

**>> Response: This text is not in the new manuscript.**

*Line 168: What do the authors imagine these non-additive terms to mechanistically represent? I found myself having a hard time connecting these ideas to reality.  Quadratic terms are fun, but I can always get a better fit to data by adding more and more quadratic  
terms to any model.*

**>> Response: This reflects a misunderstanding of our definition and should not be relevant to the new manuscript. Our new definition is much clearer.**

*Eqn 2: Why is time represented by u and not t?  This isn't really a problem, but by convention time is usually t …*

**>> Response: This was by design, there are two timescales in the paper. “*u*” is chosen for the growing season timescale—i.e. plant biomass and resources change continuously over a period of 200 days. “*t*” is used for the annual timestep over which population abundances change. This is the standard timescale for most theoretical work on coexistence and competition. We fit a phenomenological competition model based on population density at time *t* to the results of a simulated experiment occurring on the timescale of days “*u*” during a single growing season. Contrast be “t” and “u” is described on Line 266 and Line 287.**

*Line 211: a second definition for f.*

**>> Response: We’ve changed the notation to *h*() to avoid confusion with previous functions (Line 272).**

*Line 224-225: this is the sort of superficial treatment of previous work that I mean. The authors call eqn 4 a "monad" function and cite a paper from 2017.  Yet most people would know this as Michaelis-Menton kinetics from 1913.*

**>> Response: Apologies for the imprecision. We’ve removed the citation to the 2017 paper and refer to the function as Michaelis-Menton kinetics (Line 285).**

*Line 264: The authors cite Kraft 2015 for equations 6 and 7, but these are not derived in this paper.  Where do these models come from?*

**>> Response: These are Beverton-Holt or Hassel-Comins models. We cite Hassel and Comins (1976) in the new manuscript as well as Kraft et al. 2015.**

*I stopped reading at this point, I'm sorry.*

**>> Response: We apologize for submitting such a confusing paper. We believe the new version makes an important contribution and is much clearer.**

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Please submit your revision file with comments and track changes turned off.  
If you wish to ALSO include a track changes version, attach it as file type "Other."  
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