

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

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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.

Associate editor Dr. Christopher Klausmeier and two anonymous reviewers believed the topic higher order interactions was both important and of great 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.

1. We have reorganized the material. In the introduction, we motivate the paper by describing the important implications of higher order interactions for ecological theory. We then move immediately to introducing our new definition of higher order interactions. This addresses the concerns of Dr. Klausmeier and the second reviewer that the definition of higher order interactions be introduced much earlier and more clearly.
2. We provide a more detailed discussion of what higher order interactions are and how they have been historically defined. Here we are more pointedly critical of older definitions and recent work that we believe has introduced confusing ad-hoc definitions of higher order interactions into the literature.
3. We provide a new definition of higher order interactions based upon the concept of functional decomposition and path dependency diagrams, tools developed for understanding complex systems in engineering.
4. In addition, we describe a simple mathematical method for rigorously applying our definition to any model (line new definition we provide a rigorous tools used in complex systems and engineering.

Ecologists are increasingly aware of the potential for higher order interactions to shape communities of more than two species1,2,3. However, recent papers provide inconsistent definitions of higher order interactions and offer few explanations for how higher order interactions might emerge in the first place. In our manuscript we address both of these issues.

First, we develop a general definition of higher order interactions that focuses on multispecies competition and distinguishes higher order interactions from non-linear density dependence. Our definition leads to a practical set of procedures for detecting higher order interactions in empirical data. Next, we build a simple mechanistic model of resource competition among three annual plant species and simulate competition in two and three species communities. We then attempt to detect higher order interactions in the per capita growth data generated by the simulations. This example shows how the right experimental data can be used to detect higher order interactions and sheds light on the traits and environments that are likely to generate them. We believe our work will be widely cited as more ecologist work to detect higher order interactions in natural communities.

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

Grilli, J., G. Barabás, M. J. Michalska-Smith, and S. Allesina. 2017. Higher-order interactions stabilize dynamics in competitive network models. Nature 548:210–213.

2 Levine, J. M., J. Bascompte, P. B. Adler, and S. Allesina. 2017. Beyond pairwise mechanisms of species coexistence in complex communities. Nature 546:56–64.

3 Mayfield, M. M., and D. B. Stouffer. 2017. Higher-order interactions capture unexplained complexity in diverse communities. Nature Ecology & Evolution 1:0062.