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Dr. James Harwood

Editor, Food Webs

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Dear Dr. Harwood,

This paper was previously submitted to Food Webs as Ms. Ref. No.:  FOOWEB-D-14-00006. We have revised our manuscript according to the useful suggestions of the editor and two reviewers. A more detailed description of our response to the comments on the previous version of the manuscript is included.

Our paper revives and revises an old hypothesis to answer the standing question of why trophic chains are so short. Understanding the determinants of food chain length has been of interest to ecologists for over 40 years. Yet, there has been no single answer that explains the observed pattern. We have revised the hypothesis of dynamic constraints and provide a novel test to determine whether it can explain the trend towards short food chains.    
  
We have distinguished our study from past analyses of food chain length and dynamic constraints by testing food chains that are made more reticulate with omnivory rather than chains that are linear. Like previous studies we analyze the Jacobian matrix, but rather than focus on return time to equilibrium we measure quasi sign-stability. Quasi sign-stability (QSS) is a measure of the probability that a food web will be stable given randomized coefficients. (QSS) has never been the primary focus of tests of dynamic constraints on food chain length.   
  
A recent paper by Ulanowicz, Holt, and Barfield examined the limits to ecosystem trophic complexity. They found that the number of effective trophic levels in an ecosystem is typically around 3, and while more trophic levels may be present the amount of biomass flowing along transfers to higher levels is typically low. In their paper, Ulanowicz et al. allude to the idea that such a pattern could arise from the loss of unstable configurations during community assembly.   
  
The hypothesis outlined in our paper complements the Ulanowicz et al. study. Our results provide strong support for dynamic constraints on food chain length. Chains with more trophic levels are less likely to be stable. We also discuss how our hypothesis may be modified by two leading alternative hypotheses explaining food chain length. While several studies testing the two leading alternative hypotheses, productivity and ecosystem size, have found directly conflicting evidence, we suggest that our revised dynamic constraints hypothesis may be modified by productivity or ecosystem size to produce the conflicting results.

Sincerely,

Jonathan Borrelli