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Review of the thesis "Stability and dynamics of size-structured freshwater communities along environmental gradients" by Samuel Dijoux

It was a pleasure to read this thesis. It covers a range of very timely, important and intellectually challenging questions that have been addressed through the conception and analysis of dynamical models of ecological communities. The thesis explores the influence of two ubiquitously acting environmental factors - temperature and habitat productivity - on food web interactions and the resulting community composition, with a special emphasis on the role of organismal body size. With respect to the latter, a more traditional approach was used in chapter 1 that treats body size as a fixed organismal trait, whereas chapters 2 and 3 include the often more realistic, but also more challenging, assumption that individuals start as small newborns and grow in body size over their lifetime.

Below I comment briefly on each of the chapters. Before I do this, I want to acknowledge that I have been impressed by the comprehensive approach taken throughout the entire thesis. Each chapter explores its specific questions through numerical simulation, yielding a risk that results are limited to specific choices of parameter values and potentially lack generality. While this potential criticism can never be entirely ruled out in numerical work, Samuel Dijoux went through great efforts to explore a diverse set of the most relevant factor combinations. This is demonstrated by numerous multi-parameter bifurcation plots and analyses comparing model outputs in which specific factors of interest have been turned on or off to assess their influence on the results.

Chapter 1

To be up front, I found this chapter much more difficult to penetrate than the other ones, in part because it tries to condense the results from a very large set of numerical analyses into a limited space, and in part because the methods have not been as clearly described as I would have needed to fully understand what has bee done. This said, the manuscript addresses a very ambitious task, i.e. it investigates how the success and consequences of species invasions depends on the combined influence of temperature, environmental productivity, and the trophic niche of the invader in the invaded community. This niche was defined by the invader's trophic position in any of four theoretically possible 3-species food web modules. I very much like this approach of boiling down the question to a few fundamental food web modules. Still, not surprisingly, possible outcomes differ among food web modules in ways that are not easy to summarize in a few general statements. Yet, an outcome that was consistent across all food web modules is that invasions are more likely to be successful if the invader is of relatively small body size, regardless of its trophic niche.

In my experience, understanding the consequences of changes in both temperature and organismal body size for food web dynamics is a daunting task, largely because these factors affect very many processes simultaneously, making it difficult to tease out the dominating mechanisms. Unfortunately, chapter 1 lacks clear descriptions of how each of the relevant processes and rate constants, taken separately, changes along gradients in body size and temperature. I therefore tried to plot the temperature and body size dependence of important parameters and rates based on the information in the supplementary material, which was only successful for the body size dependence. I believe there must be one or more typos in the equations and/or parameter values concerning the temperature dependence. Yet, if I got it right, the rate constants were parameterized in a way that makes smaller invaders always competitively superior (regardless of their trophic niche). While this could explain the higher success of smaller invaders in the numerical simulations, I would argue that comptitive superiority of smaller individuals is not a general rule in real food webs. Indeed, in chapter 2 of the thesis, the critical resource density at which a species can exist (which is the relevant measure of its competitiveness) was shown to be independent of body size. I could, of course, be wrong in my interpretation, but I believe this aspect should be clarified to explore the generality of the prediction that smaller invaders should be more successful.

During the defense, I will probably ask about the previous point. Two other potential points/questions I might address concern an improved understanding of the drivers of the patterns in Fig. 1f-j. First, I find it confusing to apply the concepts of resistance and rescue to regions in parameter space where the resident community is either a fully extinct one or one that only contains the basal resources. Currently, Fig. 1 does not show the regions where the ‚resident' community is extinct of truncated. In comparison, I found Figs. S5 and S6 much more informative. Second, I was a bit surprised to notice that the two main environmental drivers, temperature and enrichment, are confounded by the fact that the carrying capacity of the basal resource (which is the measure of enrichment) is temperature dependent. Honestly, I do not think this is a good idea and it may be the (trivial) explanation for the rounded upper left corners in all panels of Fig. 1.

Chapter 2

This chapter has already been published in a very prestigeous journal. I will therefore only give a short summary of some highlights and then list a few questions. It is, again, a very ambitious and comprehensive numerical investigation of the influence of several important drivers of community dynamics. The paper is a spatial extension of a tri-trophic food chain model with a size-structured intermediate consumer that has previously been shown to exhibit a so-called emergent Allee effect in the top predator that is driven by size-dependent growth and mortality rates of the intermediate consumer. The important novel aspect here is the existence of a second habitat with a second food chain that has an independent resource base, and the possibility that the two habitats can be linked through a shared top predator. This opens up for the possibility of apparent competition (and apparent mutualism) between members of the two food chains, but also for multiple stable states that can be driven by very complex Allee effects. The authors explored primarily two aspects of this system, i.e. the consequences of productivity asymmetries between the two habitats and the role of relative body size differences in the two food webs. Very nice work.

As my questions I would like to stimulate a couple of speculations about alternative assumptions. For example, I would argue that the assumption that benthic and pelagic productivity are independent from each other and can be treated as fixed fractions of overall productivity should be frequently violated. After all, the basic resource in the benthic habitat (detritus) depends on continuous supply from the pelagic habitat that stems originally from pelagic primary production. Second, it seems highly likely that the top predator does not feed indicriminantly on prey from the two habitats. It seems more plausible that the top predator cannot feed simultaneously in both habitats and will make behavioral decisions (for example based on optimal foraging) on how to distribute its foraging efforts among the two habitats. How could these alternative assumptions be integrated into the model, and can we speculate about the consequences?

Chapter 3

This chapter uses the same tri-trophic food chain model with a size-structured intermediate consumer as the previous chapter but without the second habitat. Instead, the model is used to explore how the integration of hump-shaped temperature-performance curves affects the temperature and productivity dependence of food web composition, and how these effects compare with more indirect effects of temperature as manifested in the so-called temperature-size rule (which postulates that organismal body size declines with increasing temperature). I really enjoyed this chapter, which also has one very clear message: The dynamic temperature dependence of ingestion, growth and birth rates completely overwhelms the influence of the temperature-size rule on community composition and dynamics.

Again, I would want to jump right to a few questions/comments. First, I have a hard time believing that a change in temperature will lead to instantaneous jumps from a 1- to a 3-trophic level system and back, as for example in Fig. 2a at high resource productivities? Is there really no (so ever small) region of resource-consumer persistence inbetween? If so, what would explain this phenomenon? In this context, I am confused by panel (b) in Fig. S1, which seems to indicate the exstence of alternative stable states in the dark brown region (which is supposed to have none). Second, I am wondering why the effect of adding temperature dependence to the predator traits has an asymmetrical effect to the left and right of the optimal temperature (e.g. panel 2d). The explanations in the text do not convince me, because I got the impression that the temperature effects on the predator's rates are approximately symmetrical around the optimal temperature. Finally, I wonder why the authors have chosen to use different functional forms for the description of the temperature dependence of rates in the consumer vs. the top predator.

I have probably emphasized my questions more than the well-deserved praise of this thesis. But I have no doubts that the thesis would – with a good margin - meet the requirements of a PhD thesis at my own home institution. I am more than happy to recommend Samuel Dijoux for the award of a PhD based on this thesis

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