Reviewed by gyorgy barabas, 2019-12-18 11:35

The manuscript presents a meta-analysis of 32 observational studies of predator consuming prey, and uses the data to fit a generic predator functional response. The Authors argue that, despite the large uncertainty in the fit (due to limited data), the functional response f is clearly sublinear, and that it is close to f = sqrt(N / P), where P is the predator and N the prey biomass. They further argue that, from a macroecological point of view, using such a phenomenological relationship might be more valuable than relying on various mechanistic functional response formulations.

The manuscript is generally well-written, and provides an interesting new perspective on how to think about larger-scale predator-prey interactions. However, there is one potentially important concern I have, which I believe should be addressed.

Thank you very much for your comments. We hope that our reply below and edits in the manuscript will be satisfactory.

Any valid functional response form should satisfy certain basic logical requirements (Morozov & Petrovskii 2013 PLoS ONE, Rossberg 2013 "Food webs and biodiversity: foundations, models, data"). The most basic one of these concerns the problem of consuming multiple prey species at once - an issue currently not considered in the manuscript. Briefly: for logical consistency, it must be true that arbitrarily splitting a prey species into two identical "species" and summing the consumption rates should give the same result as the total consumption over all prey. Say, a predator population consumes individuals of one prey species. We then tie blue ribbons on one half of the prey population and red ribbons on the other half, and start calling them the "blue" and "red" species. Then, the summed consumption over the blue and red species must be the same as the consumption over their sum. Indeed, since the prey are in fact identical, the predators cannot differentiate between them, and so it should make no difference whether and how we decide to arbitrarily subdivide the prey into distinct categories.

That much is clear - however, the functional response $f = \sqrt{N / P}$ does not satisfy this requirement, because $\sqrt{(N1 + N2) / P} \neq (\sqrt{N1} + \sqrt{N2}) / \sqrt{P}$ (the same holds for any exponent beta that is not equal to 1, not just beta = 1/2 as above). It is therefore unclear how well it can really serve as a tool for modeling e.g. large food webs, where each species has potentially many prey and also many predators. As this is a logical requirement and not one of modeling choice, it should apply independently of whether a proposed functional response form is mechanistic or macroecological.

This logical requirement only holds if we assume a form of extensivity, i.e. that consumption of the red and blue 'species' happen independently of each other and can therefore be summed, without interaction. In fact, many functional response forms do not satisfy this requirement, including the classic Beddington-DeAngelis expression (as noted by Morozov & Petrovskii). Of course, any non-extensive functional response must be a phenomenological result derived from underlying hidden structures and interactions (e.g. spatial structure, behavioral states, etc.). It does not tell us directly about mechanisms, so we cannot make easy intuitive arguments about it.

This requirement is also problematic in the way that it is strictly predator-centered: by saying that consumption is P * f and asking some properties of f, we assume that it is a given that consumption scales with predator density, i.e. that we can take the perspective of a single predator and ask how its consumption is happening.

We wonder whether a more balanced view of how both predator and prey control consumption (through all sorts of mechanisms and strategies) would do a better job at connecting approaches that are very predator-centered (e.g. functional response) and very resource-centered (e.g. trophic transfer efficiency, prey vulnerability, etc. as used in Ecopath models and the like).

In light of the problem of consuming multiple prey, I am also wondering if this has influenced at least some of the data compiled by the Authors. It is mentioned that there were datasets containing multiple predator-prey pairs. What is not clear is whether there were any datasets where one predator preyed on multiple species at once. I can easily imagine that such multiple consumption might have been ubiquitous, even in the studies where only one predator and one

prey happened to have been recorded. But then the kill rates inferred from these data are not the "pure" kill rates, but instead the kill rates given that the predators have also killed individuals of various other prey species. I wonder if this may, in part, be also responsible for explaining the sublinear relationship found by the Authors.

We have some information about when the predator-prey relationship is specialized or there are other prey, but for too few studies to make a clear statement; a more extensive meta-analysis should certainly include this as an explanatory feature. And indeed, this might very well be one of the factors contributing to the observed sublinearity, if we assume for instance that species diversity increases concurrently with density of predator and prey.

The main question, from our perspective, is not so much whether we can understand the precise causes of this sublinearity, but whether it makes sense to take this observed result and use it to make predictions, e.g. plug it into an equation (see also our reply to reviewer 2). Here for instance, the question would be: can we say something relevant about the effective interaction between one predator and one prey species, even though they both have other interactions. We hope to address this question in future work.

In summary: a discussion of the implications of the Authors' findings for food web ecology in general, as well a discussion of their potential limitations, would greatly benefit the manuscript by clarifying when the Authors' results should and should not be used.

Sincerely, Gyuri Barabás

We hope that the revision better states the limitations of these findings – that ultimately, only a true dynamical test can tell us whether our proposed law is informative, and nothing else can replace it in our opinion.

Reviewed by anonymous reviewer, 2019-12-09 15:33

This article is about revealing, if possible, a functional response formulation that would (approximately) hold at a macro-ecological level, that is, across many ecosystems, time scales and spatial scales. It is obviously sexy these days to promote the idea of universal laws of ecology that can describe an infinite variety of nature by just a few simple formulas. Do we really strip off all complexity of nature and what remains are some overarching, universally valid, even though largely phenomenological descriptions? Do we really start to see the proverbial forest and not just the individual trees? Or is it just a clever way of playing with data followed by an effort to build verbal arguments in favor of our results? I do not know, as also my comments will clearly demonstrate.

Thank you for your comments and constructive criticism, which have helped us clarify many points in the manuscript.

We hope that our revisions and replies below will convince you that, rather than arguing in favor of our results, we are only trying to explore what they might mean. We do not claim that our interpretation represents the truth of this complex question, but that it is a novel direction worth studying.

Our message in one sentence could be: we have no proof of a universal law, but some hints that we should really think about saturation and interference at all scales (rather than only at the classic individual behavioral scale), and that we should ask whether these phenomena could be explained by their positive consequences on stability and abundance.

> The main thing that strikes me is that we can estimate functional responses over such long time intervals as one year and still seriously think of plugging them into differential equations. To me, there could probably be no gap larger than this. Of course I may be wrong but then please fill this gap for me. Estimating functional response from annual counts of predators and victims provides just an average consumption rate over a year, if at all, with multitude of effects and processes causing the actual consumption rate to vary from day to day. Numbers of predators vary, numbers of prey vary, predation and anti-predation strategies need not be constant over such time spans, etc. On the other hand, what really matters for differential equations in ecology is the instantaneous rates of processes that affect density or biomass of the involved species. We all know the difference between average and instantaneous from our everyday driving experience. This is exactly the reason why some classical experiments on functional responses used short term experiments, and why some even replaced the consumed prey items by new ones – to correctly estimate instantaneous consumption rates as functions of prey and predator density or biomass. Some discussion of this point somewhere in the introduction and how the average and instantaneous consumption rates can be reconciled is more than necessary. Especially because you do exactly this: plug your functional response into differential equations and built all your next arguments on solutions of these differential equations.

We see two points to disentangle here: one is a technical one concerning differential equations specifically; another is whether we can plug the statistical "functional response" into any dynamical model at all.

From a purely technical point of view, there is no absolute problem in using differential equations as a formalism to represent the dynamics of population and consumption averaged over years. Aggregating over time is not so different from aggregating over space: predation is also discrete and heterogeneous in space, so we could truthfully make the same argument that the average density over space is not the density where interactions are taking place. Likewise for any other kind of hidden structure over which we average: sizes, ages, phenotypes, etc. There are conditions in which one can still write an effective model for the averaged quantities (although perhaps with different coefficients and nonlinearities), as has been shown in multiple works that we cite (see e.g. Pascual and Levin 1999). Sometimes we truly cannot write such a simplified model, but when in doubt, it seems like a reasonable starting point. The choice of differential rather than discrete time (or lagged) equations is purely technical anddoes not affect our equilibrium conclusions, and the two options converge when demographic changes are not very large over a year, as suggested by the fact that, most often, $C \ll B1$.

Concerning the more general issue, we have hopefully made it much clearer in the revised manuscript that the idea of using any statistical relationship to make dynamical predictions (e.g. by plugging it into a differential equation) is very exploratory in many ways. We do it by assumption to see what it predicts, but we do not claim that this is correct or "proven" by the data in any way.

> Even if I buy the above, I still have some questions and comments:

> Page 8, 2nd paragraph: I admit I am lost here. You say that without self-regulation an equilibrium is unstable, whereas in the stable equilibrium something will be determined by self-regulation. Are you speaking of one or two systems? Do you what to say that you need to consider self-regulation to make the originally unstable equilibrium stable? But you show in Figure 2c that there are actually two predator equilibria in the stock-limited system. Is that true? Why the blue line ends? Does it mean predator extinction and are any limit cycles implicated in this? This panel (c) is quite confusing to me.

Our apologies if this part was confusing. There is only one stable equilibrium throughout the parameter space (though there can be another unstable one, due to the nonlinearities). We ask whether self-regulation is important to determine that stable equilibrium, so we first compute the solution of the equations without self-regulation, and see if indeed that solution can be reached, or if the terms that we neglected in the equations are in fact important. This is not a crucial point, but that solution is convenient for illustrating the role of the different parameters. Hopefully this is now clearer.

> Moreover, as you measure biomass in kilograms per km2 per year, why fall in biomass under 1 kilogram per km2 per year means extinction? If various species have various weights why this is fixed?

In the model exploration we are not aiming at realistic extinction thresholds, since we assume that all situations considered remain well above the threshold.
As noted in Box 1 and now in the main text, we should really be using an expression such as (B1 / B1min)^beta (B2/B2min)^gamma with B1min and B2min some minimum level of biomass. We have now added a discussion of the fact that B1min and B2min are probably roughly constant across species, since minimal biomass density appears to be broadly independent of body size (Stephens 2019, Hatton 2015). Hence we have simply integrated these constants into the prefactor A, but they would need to remain explicit if we wanted to study extinction precisely, which is where our power-law function breaks down.

> While the formula (22) trivially holds, the text just above it remains a mystery to me. There is many if-s here and I do not see how Li ~ Bi^delta follows from (6). Clearly, when Li ~ Pi then equation reduces just to dBi/dt = -Ci but what else. But want if not Li ~ Pi? How general is this assumption?

Sorry that this paragraph was unclear. Li ~ Bi^delta is another assumption, and our argument is based on the idea that Li ~ Ci ~ Pi i.e. all have the same order of magnitude, but perhaps with different constants (e.g. Li = 0.3 Pi and Ci = 0.7 Pi if losses from predation are a bit larger than self regulation).

We must still have that Pi-Ci-Li =0 at equilibrium, we simply require that the contributions of Ci and Li both be non-negligible.

> The last formula of Section 3 follows from assuming delta = 1, but you need delta > 1 to get and defend some of your earlier results. Similarly, towards the end of Section 4.4, you defend one of your results by pointing out that your exponent estimates satisfy beta + gamma < 1, but most of your previous results you emphasize the importance of having nearly beta + gamma = 1 and try to justify several times that it is actually this equality that your study reveals. Such an inconsistency is quite weird to me, using what supports my observations and theories more.

In Section 4.4 we note that we cannot, given the error bars, judge whether beta+gamma = 1 (allowing delta=1 as is often assumed) or beta+gamma <1 (allowing delta<1 as in Hatton et al's review), but that both results are within the range of possibilities.
We do not mean give the impression that our model "fits everything", just that evidence points to beta+gamma being close to 1 but needs to be refined before we can make a stronger statement.

> Returning back to the previous paragraph, I really do not know why matters so much to know how the functional response scales up across several orders of magnitude in abundance, body size and area. What sense this has for modeling, for example, food chain dynamics?

It is important if we wish to predict macroecological scaling laws in predator-prey relations, such as studied by Hatton et al 2015. Proving that this macroscopic viewpoint can be useful would require predictive success on dynamics, which we do not have.

> By the way, why don't you model longer food chains that just composed of two species a do not demonstrate that the power-low relationships on ecosystem functions just from these simulations. This would be much more convincing and at the same time it could show some important deviations from the anticipated formulas.

A longer food chain is modelled in Appendix, our apologies if we are not understanding your recommendation.

> Also, why don't you compare your two-species simulations with a system with the Beddington-DeAngelis functional response? Under what conditions the dynamics coincide and when they differ? And why?

We do not wish to put too much weight on the Beddington-DeAngelis response, especially in the theoretical analysis, as it is only one possible choice among a great number of other functional responses, but we gree that this could be the topic of an interesting theoretical paper.

> Only in the very last paragraph on page 14, after trying to convince the reader how the derived functional response is novel and revealing you admit that there may be problems in comparing such dynamics. But isn't dynamics at least as important as statics. What if the proposed functional response does not truly apply to the dynamics of an ecosystem?

We now discuss much more and earlier the question of when a statistical relationship can be used to make dynamical predictions. As noted above, we do not believe that this is an easy question or that one can automatically do it, we are only exploring what would happen if it were the case, to get some possible ecological interpretation, which we note as hypothetical.

A real proof that this is the true dynamically-valid functional response would require completely different types of data, for instance predator removal experiments, and even then, it is known that deducing the correct functional response from dynamics is very difficult (e.g. Barraquand 2014)

Hence, we have no claim that this is truly how ecosystems work, but we wish to entertain it as a possibility. We are not sure that any more convincing statement can actually be achieved using existing data, but we will keep working toward it.

> The thing that I miss in the article, of no less importance than the above, is an effort to estimate functional response of the proposed type for more clearly selected data sets, such as short-term vs. long term, over small vs. large spatial scales, etc. And then the global one, as suggested here. This would certainly provide an important insight on many speculations made in the article. Is this possible?

We agree that this is just a first step. We think that a detailed meta-analysis covering many types of datasets would be extremely important, but it is a whole other endeavor, and would greatly increase the length of the article. One option would be splitting our results into a longer data paper and a pure theory paper, but it feels unfortunate to lose the interconnection between the two, since we are still at a very exploratory phase where theoretical and empirical understanding enhance each other a lot.

> To me, there is a lot of thinks that require clarification. The most important information I find in this article is that likely most of the predator-prey interactions in nature involve predator interference. But going beyond this and propose a unified form of a functional response many more arguments and more balanced treatment of the topic, as I partially suggest above.

We appreciate your concerns, and have toned down the writing whenever we think it seemed to claim more generality than what we are actually trying to achieve.