



## A meta-analysis to infer generic predator functional response

[Samir Simon Suweis](#) based on reviews by [gyorgy barabas](#) and [Ludek Berec](#)

A recommendation of:

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Matthieu Barbier, Laurie Wojcik, Michel Loreau. **A macro-ecological approach to predators' functional response (2020)**, *bioRxiv*, 832220, ver. 4 peer-reviewed and recommended by Peer Community In Ecology. [10.1101/832220](https://doi.org/10.1101/832220)

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Species interactions are classically derived from the law of mass action: the probability that, for example, a predation event occurs is proportional to the product of the density of the prey and predator species. In order to describe how predator and prey species populations grow, is then necessary to introduce functional response, describing the intake rate of a consumer as a function of food (e.g. prey) density. Linear functional responses shapes are typically introduced in the ecological modeling of population dynamics for both predator-prey and mutualistic systems [1,2]. Recently some works have proposed alternatives to the classic approach for mutualistic systems [3,4], both because

cooperative interactions also model effect not directly related to mass action [3] and for analytical tractability [4,5]. In this work [6] the authors challenge the classic modeling of functional response also for predator-prey systems. In particular, they use a meta-analysis of several observational studies of predator-prey ecosystems to infer a generic predator functional response, fitting a phenomenological generalization of the mass-action law. Using advanced statistical analysis, they show that the functional response obtained from data is clearly different from the mass-action assumption. In fact, they found that it scales sub-linearly as the square root of the ratio between predator and prey biomass. They further argue that, from a macro-ecological point of view, using such a phenomenological relationship might be more valuable than relying on various mechanistic functional response formulations. The manuscript thus provides an interesting different perspective on how to approach predator-prey modelling and for this reason, I have recommended the work for PCI Ecology.

## References

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## Revision round #2

2020-02-17

Dear Authors,

thanks for the resubmission. After reading your revised manuscript and your response to reviewers comments, I think that the concerns have indeed been addressed very satisfactorily, and I would now like to suggest very minor revisions following some of the comments of one of the reviewers that I highlight here.

Once they are done, I will post my recommendation for the updated preprint.

Besides the typos highlighted at the end of the review, I think that the following points raised by the reviewer should be considered:

- 1) Please add a short paragraph at the introduction explicitly stating "why knowledge of an over-arching functional response is of an importance. What understanding it provides and what kind of predictions it can be used for"
- 2) Justification of eq. 6. Why it is reasonable to assume that the constant A is scale independent? I add a further comment on this point. In the text you write: We investigate a power-law dependence of predation losses (see discussion in Box 1). However, in Box 1 there is no an explicit connection between the power law functional shape and Eqs. (11). This is connected to the comment of the reviewer "nowhere explain why you have chosen the power-law functional form for your general..."
- 3) Answer to reviewers criticism on footnote 3
- 4) If it is possible, I think that it is worthwhile to investigate the reviewer suggestion: "I am wondering whether the scalings you derive in section 3.3 are actually supported by your simulations used to develop Figures 3 and 4. Could you extract data on  $P_i$ ,  $B_i$  and  $B_{(i+1)}$  at equilibrium from your simulations and show how they relate to your formulas (17) and (18)?"

Thanks

**Additional requirements of the managing board:** As indicated in the 'How does it work?' section and in the code of conduct, please make sure that: -Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.

-Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused. -Details on experimental procedures are available to readers in the text or as appendices.

-Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI XXX recommenders."

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Reviewed by [Ludek Berec](#), 2020-02-06 11:19

First of all, I would like to thank the authors for a substantial revision they have done. The revision adds much especially as regards clarification and improves the manuscript quite a lot. Following terminology used in this work, I admit I am rather a micro-ecologist than macro-ecologist and that is exactly why I was originally quite skeptical about this kind of work, but after reading it twice and thinking about it from different angles, I find some relevance in this work and am sure that many other macro-ecologists might love this study. Still, I have some concerns that other micro-ecologists could have, too, and therefore would like to ask the authors to consider them in preparing the final version of their manuscript. I admit my comments may appear a bit chaotic but this only underlines my still

sort of 'messy' state of thinking about the topic of this study (no offense meant here).

My major question, most likely trivial for macro-ecologists but perhaps quite valid for at least some micro-ecologists, is what is all this good for, why knowledge of an over-arching functional response is of an importance. What understanding it provides and what kind of predictions it can be used for? I would like the authors to devote a paragraph specifically to this, somewhere in the introduction, just for us micro-ecologists to disperse the mist that we might find on it.

I have long time thought that  $A$ , the parameter that scales the consumption rate in eq (6), is specific to each of the predator-prey pairs, but later got an impression that this might not be the case. Can you please clarify this somewhere around eq (6) and justify why not just the functional form and the scaling parameters  $\beta$  and  $\gamma$ , but also  $A$  should be system independent.

I have already touched that in my previous review yet I have to say that again, since I am still not quite convinced about this issue: In my opinion, the major reason for conducting short time experiments to standardly estimate functional responses (not necessarily all mechanistic) is that times scales of predation and much shorter than those of demography. On the other hand, your approach considers time scales of predation and demography as quite equivalent. Or maybe it does not, but in any case predation is integrated over long time scales. And this is not like integrating over space or age, since by integrating over the latter, space and age become only implicit, but in any dynamical model time is always explicit. What sense would an age-structure model have if its main processes would be aggregated over age? I do not want to say your approach is inherently wrong, but rather that there is still some friction that needs to be justified. Maybe this can be done in the paragraph I suggest above on this utility of this kind of macro-ecological functional response.

I quite disagree with your arguments in the footnote 3 on page 6. First of all, if  $r$  or  $K$  in the logistic model varies with  $B$ , then the model is not logistic any more. For example, if  $r(B) = r_0 (B-A)$  for some positive  $A < K$ , you get a model with Allee effect. Second, when  $r$  changes with  $B$  as you assume for your second bullet,

production rate is  $P = r(B) B$ , and if  $r(B)$  is not linear, why should  $P$  be quadratic? And if you argue that the system is at equilibrium, then also for the first bullet  $P = L = D(B) B^2$ , so then likewise depends on  $D(B)$  how would production scale with  $B$  (if  $D(B)$  is linear then it scales with  $B^3$ ).

You nowhere explain why you have chosen the power-law functional form for your general functional response. Given that virtually all observed functional responses saturate with prey density, why e.g. function (10) the form  $(B_1/(B_1+B_{1min}))^\beta$  is not used instead of  $(B_1/B_{1min})^\beta$ ?

Last paragraph on page 10: Including non-equilibrium dynamics would be relatively easy here. One may not look just at the equilibrium, but also whether a  $C_{12}$ - $B_1$ - $B_2$  triplet close to the observed ones is not encountered on the way to the equilibrium, and then use the corresponding pair beta-gamma as well. I understand your discussion about non-usefulness of using common functional responses for your purposes. But apart from the fact that there are other functional responses accounting for interference than the Beddington-DeAngelis one (I actually do not like this response too much) there is also other approach to getting a system-wide functional response. Some researchers take the Holling type II functional response, for example, but estimate their parameters not for each predator-prey pair, but rather estimate the attack rate and handling time as a function of masses of the two species, and do this estimating across taxa and even ecosystem. I regret you do not compare this approach anywhere to yours, and since I consider the just described procedure as a link between micro- and macro-ecology, please could you discuss this approach in the light of yours?

I am wondering whether the scalings you derive in section 3.3 are actually supported by your simulations used to develop Figures 3 and 4. Could you extract data on  $P_i$ ,  $B_i$  and  $B_{(i+1)}$  at equilibrium from your simulations and show how they relate to your formulas (17) and (18)? I think this is an ideal opportunity, as it would reinforce your expectations quite a lot (and of course also reveal problems if the fit would be poor).

The last paragraph of section 4.2: Maybe this is not possible, but if your data can be divided into several groups according to the spatial scales they correspond to

(small, large) you could apply your estimation procedure on each of them separately and see what happens. If they do, I strongly suggest doing that. Because otherwise people take your message too literally and would not care much later on that exceptions exist or things are a bit more complex. That happens, really.

Regarding your evolutionary considerations in section 4.3, finding the circumstance under which population density is maximized by evolution does not in my opinion mean that there is a selection for maximum density. There is always an evolutionary trait behind, mostly at the individual level, and often also traded off to some other trait, which in your case is a degree of non-consumptive competition, which is actually selected, and maximum density is just a consequence of having such an evolved trait. But your wording tends to suggest that density is what is primarily selected for. I may be wrong and perhaps some change of wording may clarify this.

Many researchers study food webs, not just food chains but quite complex food webs. Mostly they study static food webs, but some also aim to put dynamics on them and look for equilibria and stability of such food webs. The general problem with studying dynamics on food webs is how to set the equations. Holling type II functional responses are traditionally used and different researchers parameterize them differently. Some use the allometric relationships for attack rate and handling time as I mention above in this review. I am quite curious whether your approach can be useful in this respect. Can you please discuss it? And if yes, what part of the functional response will change with trophic level, for example?

Small things: 1. Line 4 in section 2.1: rate is by definition something per time, but your unit of rate here is W/kg which is weird.

- Line 6 in section 2.1: where -> were
- Line 6 in section 2.3: particularity -> particularly
- First line after eq (10) in Box 1:  $C \rightarrow C_i$
- Line 5 on page 6: What is ecosystem growth rate?

## Author's reply:

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## Revision round #1

2019-12-19

Dear Authors,

I invite you to revise the paper at the light of the reviewers' reports. I think that the manuscript will be improved if you take seriously and discuss reviewers' comments and suggestions.

Best regards

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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.

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.

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.

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

Reviewed by [Ludek Berec](#), 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.

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.

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. Moreover, as you measure biomass in kilograms per km<sup>2</sup> per year, why fall in biomass under 1 kilogram per km<sup>2</sup> per year means extinction? If various species have various weights why this is fixed? 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  $L_i \sim B_i^\delta$  follows from (6). Clearly, when  $L_i \sim P_i$  then equation reduces just to  $dB_i/dt = -C_i$  but what else. But what if not  $L_i \sim P_i$ ? How general is this assumption?

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.

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? By the way, why don't you model longer food

chains that just composed of two species do not demonstrate that the power-law 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. 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? 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?

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?

To me, there is a lot of things 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.

### **Author's reply:**

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