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).

We thank you very much for your comments and for having spent time rereading and thinking carefully about this work! We wish that even our own thinking about macro-ecology were absolutely non-messy.

> 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.

This question was also asked of us a few times as we presented this work, and thus was clearly not trivial. The new second paragraph of the introduction attempts to address this question.

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.

The idea is not so much that A is system-independent, but that it represents a random effect, contributing only variance to the fitted relationship log C ~ log A + beta logB1 + gamma log B2 (in other words, in this regression y~x, we assume that all values of y may not fall exactly on the line a*x, but that variations around the trend are independent, so that the slope with x can be captured no matter what).
Of course, estimation problems appear when the "intercept" log A is correlated with the variables log B1 and log B2, as we discuss in our subsection 2.5

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 oved 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 id its main processes would be aggregated over age? I do not want to say you 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.

We would argue that any continuous-time equation representing an underlying discrete process (such as demography itself) does just that: it writes the dynamics over long times of a quantity integrated over short times. For instance we can try to write a demographic equation
    dB/dt = f(B)
to represent yearly measurements of a population B of bacteria, even though individual demographic events happen on a scale of days, so the change that we are representing by the smooth function f(B) is in fact the integration of a large number of small jumps. In some sense, our continuous-looking equation is secretely a discrete integral equation

B(yr+1) - B(yr) = integral(f(B) from yr to yr+1)
in which we have in fact approximated the integral by f(B (yr)) * 1yr

There are certainly cases in which the approximation will not work! Perhaps things happening within a year are so complex that it makes no sense to try to predict B(01/01/2020) from B(01/01/2019) only; we may need the full daily trajectory to know where we end up.

But this problem does not feel specific to our approach: anyone writing a Lotka-Volterra-like model is making the same assumption that one can, somehow, define a function f(B) that does not represent specific events, but their integrated effect at the relevant time scale for our observations. We try to convey this idea in the new paragraph.

> 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) = r0 (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).

We have rewritten the footnote to be hopefully clearer here, as this is the crucial point of trying to infer a dynamical law from a purely statistical relationship.

Dynamically, we always assume that P= r B with r a constant for any given ecosystem. But if you have many distinct ecosystems at equilbirium, each made of a single species k following a logistic growth with a rate r_k and an equilibrium B_k, there *will* be a correlation between r_k and B_k when you look across all those species. This is the problem of looking at a statistical law across systems (where r_k and B_k are correlated) and trying from it to infer a dynamical law P=r B within an ecosystem, where r is constant and thus independent of the dynamical variable B!

> 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 (B1/(B1+B1min))^beta is not used instead of (B1/B1min)^beta?

We try to explain this a bit better now in the text. It is true that, at small scales, we tend to see classic saturation (e.g. for mechanistic reasons that are easy to understand). But if we go across all scales we do not seem to see saturation: it does not appear that consumption becomes truly independent of B1 when B1 is much larger some threshold.

It can be explained like this (as we now do in the manuscript): Intuitively, if we run a day-long experiment in a box, we can for instance measure saturation with prey density due to predator satiety.

But over a month in an open landscape, a different saturating effect may appear due to the existence of prey refuges, for instance. If we measure multiple systems at different scales, each will have a different saturation constant, and we cannot fit them all together with a saturating function with a fixed threshold (or even one that depends only on body size for instance, as noted below)

What we need instead is a functional response that keeps varying consistently at all scales. This "scale-free" property is found in power-laws, but not in saturating functions, or exponentials, or many other expressions. This is the main reason why we generally resort to power-laws for any kind of phenomenon which can happen at many different scales, rather than being relevant only at small (or large) scales and completely saturating/vanishing beyond some threhsold.

> 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 C12-B1-B2 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?

We already tried that unsuccessfully, using scaling laws such as reported by Pawar Dell and Savage 2012 among others. The issue is that this captures the variation between systems that is due to individual properties (body size), but not at all the fact that here, our variables B1 and B2 are densities of entire populations at a large spatial scale – there is much more happening and distinguishing systems than just the body size of the species. The parameters of (say) a Holling type II response are not really invariant when aggregating over more than one individual, as noted above, and we have found no good way to account for that.

> 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 Pi, Bi 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 you expectations quite a lot (and of course also reveal problems if the fit would be poor).

Thank you for this very good idea. We have added a figure showing this result. Doing so indeed allowed us to clarify our reasoning and find under which conditions our result holds or not (and to suggest how different calculations could be performed in settings where this result does not hold)

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

You are certainly right that we want to be careful there. Unfortunately all our sources are at relatively large scales compared to individual organisms, and in our data, spatial scale did not seem to have an identifiable effect. It may be that its effect is drowned in noise (and we do not trust that the data is sufficiently unbiased to believe in a pure statistical test).

Regarding your evolutionary considerations in section 4.3, finding 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.

We try to suggest that, no matter whether density is what is primarily selected for, or just a side-effect, there are simple reasons to expect that strategies leading to higher densities will dominate in our data.

But it does not feel absurd to us that an individual trait could be selected precisely as a consequence of the fact that it leads to maximum density. This would indeed be selection for population density, even if the underlying trait exists of course at the individual level.

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?

That is a very good question for which we are afraid that we have no answer or expectation at this stage. Our data is for carnivore-herbivore pairs (or a few omnivore-omnivore cases such as chimpanzees eating small monkeys), because of the practicalities of gathering field kill rate data, so we do not know if our finding generalizes with the same exponents to other trophic levels.

All we can say for now is, as noted above, that we were not successful in using allometric parameterizations to fit our data, but finding other data for species that differ much more taxonomically and in size could help us in the future (if for instance allometric size-based relationships become more prominent and less drowned in other sources of variation thanks to having many more orders of magnitude in size)

> 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.

We would tend to agree with you there, but it is a common way of reporting mass-specific metabolic rates (and most other commonly used units are even worse, dimensionally)

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

Thanks, we corrected all that.