

Response to Samraat Pawar

I enjoyed reading this paper. It was concisely written, in reasonably accessible language (but some suggestions below to improve this further). My overall assessment is that this is a technically correct study which provides valuable (heuristic, qualitative) insights that will facilitate further investigation of the p-p power law. My most substantive comments are that ecological metabolic theory (AKA MTE) could be used to better parameterize the modelling and obtain deeper insights. My specific comments follow.

We are grateful for the feedback and for the suggestions. We address the specific comments below, including considerations on the role of MTE.

1. End of Abstract could have somewhat more specific conclusions perhaps.

We are now more specific in stating the three classes of mechanisms considered in the paper in the conclusion of Abstract.

2. Not so sure about the first sentence of the Introduction - biological scaling laws are common!

Fair! We modified that sentence.

3. I found the Introduction to be somewhat difficult to follow. In particular, the logic and arguments presented in the 2 middle paragraphs on p2 were hard to follow. Need more precise descriptions of the links between environmental variation, species' differences, and species interactions. Yes, understood that Hatton et al did not consider these very rigorously, but how exactly does the environment impact or relate the the "top-down" vs "bottom-up" mechanisms that are the main focus? The gedankenexperiment in Fig 3 does sufficiently clarify things for me at least. There are also little things, like the usage of the acronym ABM without definition.

We have now modified the introduction and added a new conceptual figure (with an extensive caption) to summarize the potential explanation of the predator prey power-law and to clarify the relation between what is the driver of different biomasses between sites and the "top-down" vs. "bottom-up" mechanisms.

We now define the acronym ABM on first appearance.

4. I really don't understand the flow of logic that leads to the statement at the end of the Introduction. If precipitation were a significant co-factor, determining the p-p abundance scaling law, why not include it directly in the allometric analysis? And how does this lead to the conclusion that only top-down explanations are feasible? Also, top-down vs bottom-up need to be defined more clearly up front.

Precipitation appears mainly as a proxy of primary productivity for which we have data. It seems to capture the right trend overall, but the R^2 is quite low, especially for the predator-prey ratio, suggesting that it may only be a correlate of the important environmental factor(s) causing this variation. We are not sure how it could directly be included into the allometric analysis.

Our new figure clarifies what we mean by top-down versus bottom-up and how that relates to NPP being the main driver in the variation of species biomasses: roughly speaking, given the various processes contained in the equilibrium equations for prey and predator, the most parsimonious way to explain a 1D scaling law is that a single parameter (or combination of parameters) is varying to create the gradient of biomass, therefore one process is "responsible" for variation in biomasses, while other processes must exhibit constant features (parameters and functional form) that impose the power-law relationship between the two biomasses.

We call an explanation bottom-up if the processes that impose the power-law relationship (not those that create the gradient) are mainly about the prey and its own resources, and top-down if they are mainly about the predator and its effect on the prey.

If the prey equation contains the varying parameter (NPP), then the predator equation is typically the one imposing the scaling law, and so the explanation is top-down. This is of course a slight oversimplification, as details of both equations matter, but it captures the core intuition behind how we apply the bottom-up and top-down labels.

5. Then first para of section 2: what class of phenotypic traits are we talking about here?

We have now removed the phenotypic-environmental dichotomy.

6. Eqn 2 - shouldn't there be a gain term here?

The gain term is P_2 , which depends on \vec{B} , therefore on both species. In this general formulation we are assuming that it can differ in functional form from the predation loss C .

7. C/B_1 - please elaborate a bit on how this is a functional response.

We have removed that definition as it was not clear and not useful for the rest of the work.

8. Not clear what the purpose of the qualifications in the paragraph about ρ in the paragraph following Eqns 1-2 is.

We have now shortened and reshaped that paragraph.

9. Eqn 4 - q should be search not catch rate (units of area or volume / time).

We agree that "catch rate" is not the most appropriate definition of the parameter q . Since we are considering biomass densities, the dimensionality of q is [area / (time · mass)] and is, indeed, the "search rate" over the predator's body mass. To make the discussion more general, we decided to refer to q as "interaction strength," consistent with Hatton et al. 2015.

10. Eqns 5-6: OK, but not all the elements in σ would be independent of environmental parameters. This is a slightly pedantic point, but, a in particular, depends on the euclidean (and in principle, also fractal) dimension of the environment for example (DeLong and Vasseur, 2013; Pawar et al., 2012). The point about covariance / non-independence of q , r and q is an interesting and I think correct one. But you can clarify that these are metabolically inter-linked. Indeed, a is also linked to the other rate parameters in this way.

The crucial point here, as we now hopefully clarify in the text, is that we are assuming that elements in σ are roughly constant across the gradient, and therefore are not driving the variation in biomasses between the various sites. In particular, anything that has to do with individual body size and mass, including metabolism, is presumed constant across the gradient since there is no significant change in the size structure between communities (as shown in Hatton 2015). Thus, while there may be relationships between these parameters in theory, there will not be covariance between these parameters in the gradient here – something that is not about individual-level metabolism has to be driving the variation of the one parameter (or parameter combination) that creates the gradient.

11. Following Eqn 7-8: The exponent k merits clearer rationale / derivation.

The model presented in the bottom-up section is widely discussed in Hatton et al. 2015, we are only reporting it in this work for completeness. We agree that a mechanistic derivation for the sublinear exponent in the dynamical equations would be valuable. That is, however, beyond the scope of this manuscript. We now explicitly defer to Hatton et al. 2015 and Hatton et al. 2024 in the main text for a complete analysis of the model and a discussion of the hypothesis behind the origin of the exponent.

12. One could argue that the ABM was a bit unnecessary as the preceding analytical model do already provide sufficient insights and demonstrate the potential importance of a combination of top-down and bottom-up regulation. I think using underlying metabolic scaling laws for p-p growth and interaction rates (see citations above) to bound the parameterisations in the ODE models would be more insightful. However, Fig 6 makes for some interesting viewing, and also highlights the fact that convergence to the power law is only expected at higher prey densities. I suggest that the authors elaborate a bit more on this

issue.

We agree with the referee that using available independent data to parametrize the ODE model is a good idea. We now added a paragraph in the main text and a section in the Supplemental Material in which we compare the fitted coefficient of the p-p scaling with the prediction we obtain upon parametrizing the model with estimations of the parameters from the literature, including using MTE.

We find that, under one assumption on the value of α , the estimated coefficient falls in the confidence interval of the fitted one. We don't explore the robustness of this prediction as we consider it a proof of concept and test to check if the estimated coefficient results are wildly different from the fitted one. We added some considerations for the scaling exponents stemming from this exercise.

Regarding the ABM, as suggested, we now point out that it shows that, even with the right ingredient the scaling law may break. We added a paragraph in the supplementary material in which we give an example of how this is a common phenomenology in predatory-prey models with explicit resource dynamics.

Response to Reviewer 1

The piece is well written, with clear and informative figures and easily accessible code (though it appears the data was removed from the current repository at some point). Overall, I enjoyed reading this work, but was left with several areas of confusion that could be ameliorated by improved explanations in the text.

We thank the reviewer for the overall positive feedback. We removed the .xsl file from the repository because it was an exact copy of the file accessible from Hatton et al. 2015. It was temporarily in our repository for practical purposes. The data needed to reproduce all the results in our work can be found in data.jl and data-reduced.jl. We address the remaining comments point by point below.

One source of confusion when reading the text was the authors' implicit conceptions of "top-down" vs. "bottom-up". These terms could use a more explicit treatment in the text. For instance, it makes sense to me that sublinear prey production is "bottom-up," that is, the consequences for the predator densities derive from prey dynamics (independent of the predator-prey interaction) (though see my next point for some further confusion on this topic). Likewise, density-dependent self-regulation of the predator and predation interference seem fairly intuitively "top-down," that is, the effect on predator densities is driven by the dynamics of the predators themselves, either explicitly in the context of the predator-prey interaction or not. Yet, prey saturation seems more like the former than the latter (despite being listed as a "top-down" effect. Finally, the authors state they are working from the assumption of "prey productivity as the primary driver for the biomass density gradient across ecosystems" (p 10), this assumption seems explicitly "bottom-up".

With respect to "sublinear prey production" in particular, the discussion in section 3 suggests two pathways for this: changes in r (prey growth rates; what I envisioned when discussing prey production) or changes in q (predator consumption rates; something that feels like it could also be described as a "top-down" effect). Moreover, as the authors point out, when r is the parameter of interest, it actually has no effect on equilibrium prey densities, raising the question of whether "sublinear prey production" is actually even an accurate description of this situation.

To clarify our "top-down" vs. "bottom-up" definitions, we have now modified the introduction and added a new explanatory figure that also summarize potential explanation for the predator-prey power law. In particular, in the caption of the new figure, we included the following sentence:

"[...] We focus here on explanations in which the $3/4$ exponent stems from the functional form (density-dependence) of population dynamics, and choose to call them "bottom-up" when prey consumption and growth control the exponent, and "top-down" when predator consumption and mortality control it. Typically, the source of variation between sites must then lie in the other equa-

tion, meaning that the variation in biomasses is expected to arise from 'bottom-up' factors, i.e. prey growth, if the exponent of the scaling law is driven by 'top-down' factors, i.e. predator consumption, and conversely. [...]"

On this topic, the figure depicting this case is confusing to me: are the little blue dots meant to represent reproduction? If so, I guess the "sub-linearity" is that not all four blue dots have offspring in the right subplot? I think it would make more sense if from the beginning not all points reproduced. And how is this functionally different from prey saturation, where there is also a depiction of slower prey growth? Regardless, the legend or caption needs to explain all symbols/colors used in this figure.

We have now modified the figure, including prey offspring in the legend, and added a full explanation of symbols and colors in the caption.

We kept both prey reproducing in the first subplot but we changed colors and number of offspring per prey to make clear that in the bottom-up scenario predators are sustained by offspring, and in a denser environment less offspring are produced.

We now make clear in the caption of the figure that the prey saturation cartoon does not involve reproduction but is meant to represent the situation in which one prey is shielded by the others.

By the end of the piece, I was left confused what the take-home message was. It seems the authors want to demonstrate the existence of alternative dynamical explanations for an observed phenomenon (a fair and admirable goal). And I particularly appreciated the second-to-last paragraph, in which the biological implications were explored. Yet, they also write that the previous explanation is "realistic and parsimonious" (p 6) and "more appropriate to capture the general dynamics" (p 11), and that, of the "range of [possible] explanations ... they are all top-down" (p 3).

One of our purposes is to expose possible alternative explanations for the phenomenon, and this is why we explicitly mention whether some explanations have advantages over others. Regarding the sentence at p.3, we mean that all the possible explanations are top-down *within the assumption of primary productivity as the most relevant driver*. We have now improved the sentence to make this more clear.

Finally, while I understand the authors' arguments for the consideration of single-parameter explanations for the empirical pattern, I think they could do more to explain why they might think this to be the case biologically outside of the argument for parsimoniousness. It seems that one of the primary explanations for a sublinear relationship is a discrepancy between two growth rates, which need not be governed by the same underlying parameter. For instance, on p 4, the authors state "We want to explore how dynamical, density-dependent effects can be relevant for the scaling. Therefore, we use as a working assump-

tion that only one environmental parameter, possibly different in other datasets, is responsible for the gradient.” Yet, this second sentence is a non sequitur. As I said, I think the authors do a good job in the introduction talking about this, but I would have liked them to be more comprehensive in other sections and, in particular, to come back to this possibility in the discussion as well, as it is a strong assumption underlying the work.

We thank the referee for this opportunity to clarify our argument. There are two points that we have tried to stress in our revision:

The first point, leaving parsimony aside, is that we focus on a gradient of primary productivity as the main varying factor simply because it is a classic and ecologically-plausible explanation of biomass variation between these sites, for which we have some empirical support from precipitation data. This is now stressed more clearly in the introduction.

The second point comes back to parsimony, and is now put forward with our new Fig. 2. We can indeed imagine that the densities or growth rates of the two trophic levels are controlled by different parameters (say shade, temperature, water availability...) as they vary between sites, but we would then need to explain why these different parameters co-vary in a way that creates a robust unidimensional power-law relationship between the two densities. This is shifting the burden of explanation onto some covariance structure in the environment (or in physiology, etc.).

If we believe that the core of the explanation lies only in the population dynamics, then the way to obtain a unidimensional power-law is if a single factor is varying between sites while everything else is constant. Now, that single factor might not be precisely one of our parameters, e.g. r or q – it could be some combination of them (for instance $r \times q$ could vary while r/q is constant). Hence only ecology, not parsimony, can tell us if it is reasonable to assume that this defining factor is e.g. r , which brings us back to the first point above.

Finally, our choice parallels the approach adopted in Hatton 2015 for the bottom-up explanation, to which we want to offer plausible alternatives in this paper. We have now rephrased the introduction to hopefully make this narrative more transparent.

Minor Points

Please add line numbers to facilitate revision in the future.

We now added line numbers.

p 3 – the emphasis on ”phenotypic” for sigma feels strange here since rho can likewise be a phenotypic difference

We thank the referee for pointing this out. We have now removed the dichotomy ”phenotypic” - ”environmental”.

There are several cases of the authors introducing a term with specific biological relevance to a system and without definition. This is particularly striking when most of the text is system agnostic. Examples: "catch" (p 4), "grass" (p 8)

We have now substituted expressions such as "catch rate" with more general ones such as "interaction strength." In the ABM section, we substituted "grass" with the more generic "resource."

Figure 5 (and the ABM in general)

– the parameter δ does not appear in the model explanation, only in the parameter list

We have now included a full explanation of the ABM in the text, including the definition of δ .

– why is there no energy change listed under "engages pred." or "engages prey"?

We made the modeling choice of including all an agent's energy expenditure (including metabolism and actions) at the beginning of the step when the agent moves. However, we can always reabsorb an eventual cost of engagement in the cost of moving with no consequences for the result.

– why is the model run on such a small grid?

All the phenomenology is already present at this scale, which makes the simulations lighter and enables easy and quick reproducibility of results.

– did the authors do any sensitivity analysis considering the other parameters of the ABM (i.e. $\xi, \omega_1, \omega_2, \delta, \eta, \mu$)?

The parameters ξ, ω_2, δ , and ν are combined in the coefficient that gives the intercept of the predator-prey scaling

$$(\xi^\nu \omega_2 \delta)^{1/(\nu+1)}.$$

Therefore, we know the effects of their change on the system in the regime where predator density follows the scaling. We have now added to the Supplementary Material a numerical analysis of the effects on the distribution of prey and predator density of changes of the parameters which do not enter in the scaling expression ω_1, η , and μ .