

Responses to Reviewers

August 5, 2024

We thank the Editor and the three reviewers for their careful consideration of our manuscript and constructive comments. Our point-by-point responses (in blue) follow. We have sequentially numbered all comments across reviewers to facilitate cross-referencing.

Reviewing Editor's Comments

1. Please clarify, and spell out in detail, what assumptions and approximations are made in calculations, and at what stages. In the presentation of the mean-field approximation, it should be explicitly said that extra have been made approximations (e.g. when computing the mean of the inverse). Moreover, given these approximations, it is important to clarify when they break down and when they work well, both with explanations and concrete examples.

We have made extensive revisions to the results section, significantly increasing the detail (and hopefully clarity) of the text. This includes stating the assumptions more explicitly when they are made. We have also corrected an error in the derivation of the mean field approximation, removing the need to make assumptions about the mean of the inverse. We have also included a sensitivity analysis to make clear the conditions under which the approximation does not work.

2. Please clarify the manuscript. In particular, please clearly define each notation and motivate parameter or function choices. Please address all of the reviewers' points to improve this.

As noted above we have rewritten most of the results and methods to make the derivation of the theory clearer. This includes explicitly defining parameters and the assumptions in the main text.

3. Please discuss why a consumer-resource model was not chosen and what it might change. Please also discuss the motivation of the temperature dependence of the interaction parameters.

We have included explicit discussion of the pros and cons of using a consumer-resource

type model in lines 337-346. In brief we chose the GLV because of the analytic tractability and existence of methods such as the mean field approximation for its analysis.

Though using a consumer-resource model would change the exact results, we expect the general effects of thermal physiology parameters (i.e variation and covariance determining the magnitude and location of peak richness) would remain and thus some of the broad results would be the same. This ultimately is a promising avenue for future research and we have included it explicitly in the discussion.

Reviewer 1's Comments

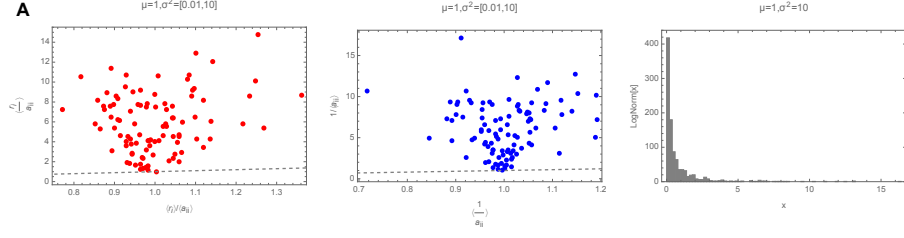
4. ...the central mathematical results are not clear in my view, some strong approximations are not discussed, but they hold only in very specific conditions. A lot of important details are missing or scattered here and there, the notation is a little sloppy, and in general, it has been difficult for me to reproduce their finding. The overall structure and flow of the manuscript can be remarkably improved.

We have significantly revised the manuscript hopefully making it easier to understand. In particular we have moved a lot of the detail in the methods and derivation of the model into the main text (see new results section). We also make state the assumptions clearer in ther main text (lines 118-120) and methods (388-397).

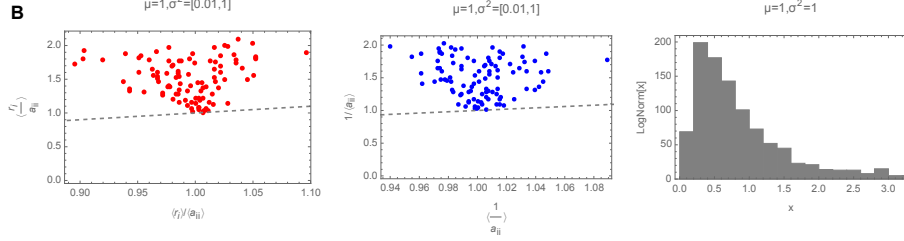
5. The derivation of the mean field result is not correct. It may hold in some specific conditions that are not properly discussed. The problem is after Eq. (8) of the Methods section. Tacking the average across the N populations does not lead to the following equation for the average stationary population. In fact, denoting by $\langle \cdot \rangle$ the average, then the mean field consistency equation should read:

$$\overline{x^*} = \left\langle \frac{r_i}{a_{ii}} \right\rangle + (N - 1) \overline{a_{ij}} \left\langle \frac{1}{a_{ii}} \right\rangle \overline{x^*} \quad (1)$$

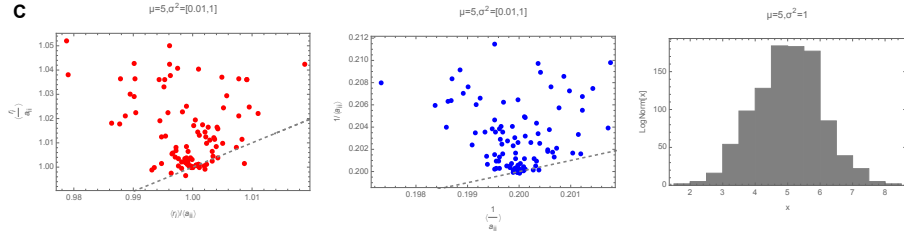
but $\left\langle \frac{r_i}{a_{ii}} \right\rangle \neq \frac{\langle r_i \rangle}{\langle a_{ii} \rangle}$ and $\left\langle \frac{1}{a_{ii}} \right\rangle \neq \frac{\langle 1 \rangle}{\langle a_{ii} \rangle}$. Therefore, the mean field result presented in the paper, in general are not correct. In some specific cases, e.g. the random variables is sharply peaked around its mean, then it may hold that $\left\langle \frac{r_i}{a_{ii}} \right\rangle \approx \frac{\langle r_i \rangle}{\langle a_{ii} \rangle}$ and $\left\langle \frac{1}{a_{ii}} \right\rangle \approx \frac{\langle 1 \rangle}{\langle a_{ii} \rangle}$. The figure below shows numerically the comparison of $\left\langle \frac{r_i}{a_{ii}} \right\rangle$ with $\frac{\langle r_i \rangle}{\langle a_{ii} \rangle}$ and of $\left\langle \frac{1}{a_{ii}} \right\rangle$ with $\frac{\langle 1 \rangle}{\langle a_{ii} \rangle}$ for three different cases (mean and variances highlighted as plot label:)



B) r_i and a_{ii} drawn from a Log Normal Distribution with “low” variance;



C) r_i and a_{ii} drawn from a Log Normal Distribution with “low” variance;



So it is clear that actually, in the log-normal case, that should be the actual distribution from where r_i and a_{ii} have been drawn, the average of the ratio of the two random variables cannot be substituted with the ratio of the averages.

We thank the reviewer for pointing out this error in the derivation of the mean field. We have amended the derivation which requires two new steps (lines 398-407):

(a) Specifically accounting for the mean of the reciprocal of intraspecific interactions $\langle a_{ii}^{-1} \rangle$. This means the effective interaction strength is redefined as $\langle a \rangle = \langle a_{ij} \rangle \langle a_{ii}^{-1} \rangle$. Note that the inverse of a log-normal variable still has a log-normal distribution allowing us to write an expression for the temperature dependence of the average.

(b) Assuming that growth rates and intraspecific interactions are independent $cov(r_i, a_{ii}) \approx 0$. This allows the average of the product to be written as: $\langle \frac{r}{a_{ii}} \rangle = \langle r \rangle \langle a_{ii}^{-1} \rangle$

with these two changes the derivation is more explicit in its assumptions. Whilst the structure of the equations changes slightly this does not affect the overall effect of the parameters on the behavior of the model. We have generated a new set of results with

this updated model including the numerical simulations.

6. Relatedly, given the above results, it is not clear to me, how it is possible that the approximation proposed by the authors work so well, for example in Figure 2. Moreover, it is not clear to me how r_i , a_{ij} and a_{ii} are chosen in the numerical simulation of the full GLV. Are they drawn from a LogNormal distribution? Just after Eq. 2 it seems that indeed they are lognormal distributed, but this should be specified better in the Figures and also it is necessary adding information about which parameters have been used. Moreover, how much the goodness of the analytical approximation depends on the specific choices of the parameters? I think that a sensitivity analysis and related discussion on the limitation of the analytical approximations are needed.

We have added a lot more detail on the methods in the main text which hopefully make the procedure for simulating and predicting patterns of richness across temperature more clear (lines 214-230). We have also added explicit discussion of the limitations of the assumptions in the model in lines (see response to comment 1)) as well as a new sensitivity analysis (see lines 232-245).

7. In general, I think that it should have been more appropriate to perform a more advanced mean field approximation, for example following the work “Collapse of resilience patterns in generalized Lotka-Volterra dynamics and beyond” (Tu, C., Grilli, J., Schuessler, F., & Suweis, S. (2017). *Physical Review E*, 95(6), 062307), from which a similar approximation of the effective average population could be derived. Moreover, using this approximation, it is possible to go beyond purely competitive ecosystems, as it holds also for communities with mutualistic interactions. In fact, the statement that GLV only works for competitive communities is not correct (there are many works using GLV with (also) positive interactions (e.g. Rohr, Rudolf P., Serguei Saavedra, and Jordi Bascompte. “On the structural stability of mutualistic systems.” *Science* 345.6195 (2014): 1253497; Suweis, S., Simini, F., Banavar, J. R., & Maritan, A. (2013). Emergence of structural and dynamical properties of ecological mutualistic networks. *Nature*, 500(7463), 449-452.)).

Whilst it is of course always possible to use a more complex approximation we have chosen to use the simplest form of the mean field approximation (sometimes called a “naive mean field”). We argue that this approximation is adequate to demonstrate the effect of variation in the thermal physiology parameters as a mechanism for community level richness.

In the paper mentioned Tu et al. (2017) demonstrate the conditions under which a similar mean field type approximation works for Lotka-Volterra systems. They show that the approximation becomes less accurate as variation in interaction rates increase. This result makes sense and is related to the assumption that interactions are relatively uncorrelated with abundances in the mean field derivation. It is easy to show that all else being equal, increasing variation in interactions increases the magnitude of the covariance term, breaking the assumptions of the mean field approximation. This

assumption and the link to variation in interactions is explicitly discussed in lines 382-393.

We have also amended the language with respect to the cooperative interactions, we acknowledge that they can be considered in the GLV model and have altered the text (lines 346-360).

8. While it is quite clear the physiological dependence of the growth rate on temperature, it is not quite evident why also the interactions strengths should depend on the interactions strengths a_{ij} . How the works conclusions would change if only r_i depends on time (see also Abreu, C. I., Dal Bello, M., Bunse, C., Pinhassi, J., & Gore, J. (2022). Warmer temperatures favor slower-growing bacteria in natural marine communities. bioRxiv).

We argue that exponential-like temperature dependence of interactions is likely due to their dependence on metabolic rates of interacting populations. In the case of microbes the strength of competition will primarily be determined by uptake rates which are known to depend on metabolism and thus be described by biochemical kinetics. Indeed expressions for the strength of interactions derived from more mechanistic consumer resource models such as marshall et. al. (2020; Scientific Reports, 10) demonstrate this dependence well. We have updated the manuscript in lines 147-159 to include this reasoning.

9. The section The theory holds in dynamically-assembled communities is hard to read, as it lacks of the definition of what is a dynamically-assembled community, how it is mathematically defined and why you also want to explore such a case. Some information must be available in the main text, some other you can refer (but please explicitly put the link) to the Methods section.

We agree with the reviewer here, the section was unclear and added little to the readers understanding of the main focus of the effects of variation in thermal physiology. As such we have chosen to remove this section of the paper. The topic of community assembly with immigration-extinction dynamics adds a lot of additional complexity and the mean field approximation we apply does not extend well to such situations.

Minor Comments

- In the Abstract there is a blank missing word after “thermal”
- The reference (von 30 Humboldt and Bonpland, 2013) does not exist, or it is not possible to find in the internet.
- Remove “in particular” line 33
- Line 61 multi-trophic instead of muti-trophic
- Notation: I would prefer S instead of N for the number of species.

- The average interaction strength defined in Eq. 6 should depend only on i , not on both i and j !
- After Eq. (15) there is a prime missing in $\log(r_i(T)) \rightarrow \log(r_i'(T))$
- In the introduction it is stated that “the temperature responses of microbial richness or diversity are “consistently inconsistent”, with no single pattern in terms of shape (monotonic or unimodal) or direction (positive or negative) dominating. But then Figure 4 seems to provide a quite consistent behavior obtained from the data of Smith et al., 2021 and Smith et al., 2019.

We thank the reviewer for their careful reading of the manuscript; we have fixed all these issues

Reviewer 2

10. I feel like the manuscript is too terse and hard to follow. For example, the parameter E is not defined explicitly anywhere in the main text. I would suggest that the incorporating thermal responses of traits (including Equations 13 and 14) be moved to the main text and this discussion greatly expanded. I could not follow what was going on.

We agree with the reviewer that the clarity of the manuscript needed improvement. As noted in our reply to comment 4 we have made significant changes (such as including additional equations in the main text) which we hope make the manuscript flow better.

11. I do not understand the physical/ecological motivation for $\log B_0$ and E are anti-correlated. Does this follow from theory or empirical fits? How do we know that the experiments from Smith et al hold more generally?

We have now clarified this on lines 164-179 of the manuscript. In short, the anti-correlation arises from the trade-off between thermal specialists (species that perform high at a narrow temperature range have high sensitivity E and low baseline performance B_0) and generalists (species perform at a lower level but across a wider range high performance B_0 and low sensitivity E). This trade off arises as species cannot perform highly across all temperatures and must either invest in either strategy.

12. Currently, parameters are drawn from a log-normal distribution. This means that it is long-tailed. Do the general trends they hold for non-long tailed distributions. I understand that the r_i must be positive, but this can be done by for example, using a truncated Gaussian. If the long tails are essential, could you please explain why the tails matter? The form of \bar{r} below Eq. 15 would suggest that the results here may depend very strongly on the long tailed distribution assumption. It would be nice to understand how the phenomenology changes if this is not the case.

In general long-tailed distributions are not required and the relationship between the parameter distributions and richness are not affected. The only way the specific shape of the distribution would matter is if long tails resulted in the violation of the small covariance assumption, that long tails in interaction strengths meant that some individual interactions had a disproportionate effect on biomass. This is a limitation of the mean field approximation and is clearly discussed in the main text (lines 387-393).

It is important to note that the specific distribution of the traits arises mechanistically from the exponential-like temperature dependence at the individual population level. Given this we are confident in the appropriateness of the distribution describe community-level trait distributions.

13. I feel like the averages below equation 7 are done sloppily. The agreements with numerics suggest these are small effects but in reality we have that ...[The remaining comment is qualitatively identical to Rev 1's comment 5]

Please see our response to comment 5

Reviewer 3

14. *Conditions on growth and interaction rates for feasibility and stability.* The authors approach this using a mean field approximation, and it is important to note that there is no particular temperature dependence assumed here: as far as it goes, this analysis is completely general for arbitrary Lotka-Volterra interactions.

However, the starting point for the authors' mean field analysis is the statement that "it is not possible to meaningfully link the structure of species interactions to the exact closed-form analytical solution for [equilibria] x_i^* in the Lotka-Volterra model.

I may be misunderstanding, but I don't agree with this statement. The time-independent equilibrium solution with all species present (i.e. at non-zero abundances) takes the form

$$x^* = A^{-1}r \tag{2}$$

where A is the inverse of the community matrix, and r is the vector of growth rates. The exceptions to this would be when one or more species has abundance = 0, or A is not invertible. I don't think the authors intended to tackle either of these cases, but maybe I am misunderstanding that.

So to me, the difficulty here is not in writing a closed-form solution for the equilibrium x^* , it is in writing the inverse matrix as a nice function of the entries of the matrix A itself, which is where the authors want to get to. In this light, it looks to me like the condition for feasibility (i.e. that all x^* are positive, which is necessary for an ecologically-interpretable solution) is maybe an approximation for the inverse of

A—perhaps valid when off-diagonal entries are small. A weakness then for me was in understanding the range of validity of this approximation, and whether it still holds when off-diagonal entries of A (i.e. inter-specific interactions) are arbitrarily large. I could not tell from the simulation runs whether this full range of off-diagonal values was tested.

We thank the reviewer for pointing this out and we agree that the language used is imprecise. The GLV model is solvable using the matrix inversion method but as they note, this does not give an interpretable expression in terms of the system parameters. This is important as we aim to build understanding of how these parameters (which in turn depend on temperature) affect the richness in communities. We have made this clearer in lines 372-379.

In regards to the validity of the approximation we have significantly increased the detail of the method in the manuscript, including the assumptions it makes (lines 384-393). In general the method assumes that any individual interaction has a weak effect on abundance. This will fail when the variation in interactions becomes too strong but should be robust to changes in the average interaction strength across the community.

15. As a secondary issue here, it would have been helpful to understand whether the authors' feasible solutions are always stable to small perturbations. In general, I would expect this to be an additional criterion needed to understand diversity, though as the authors point out there are certain broad classes of solutions where feasibility implies stability.

As the reviewer notes previous work using the GLV model by ? has shown that stability almost surely implies stability in the GLV. Thus we expect that our richness estimates derived from feasibility will closely resemble those from stability. We have amended the maintext to make this argument clear on lines 321-335.

16. I did not follow the precise rationale for selecting the temperature dependence of growth rate and interaction rates, or how the latter could be tested with empirical data, though I do think that in principle this could be a valuable way to understand the role of temperature dependence in the Lotka-Volterra equations.

First, as the authors note, “the temperature dependence of resource supply will undoubtedly be an important factor in microbial communities”

Even though resources aren't explicitly modeled here, this suggests to me that at some temperatures, resource supply will be sufficiently low for some species that their growth rates will become negative. For example, if temperature dependence is such that the limiting resource for a given species becomes too low to balance its maintenance costs (and hence mortality rate), it seems that the net growth rate will be negative. The alternative would be that temperature affects resource availability, but never such that a limiting resource leads to a negative growth rate when a taxon

is rare.

On the other hand, the functional form for the distribution of growth rates (eq 3) seems to imply that growth rates are always positive. I could imagine that this is a good description of microbial populations in a setting where the resource supply rate is controlled independently of temperature, but it wasn't clear how generally this would hold.

We thank the reviewer for their comment. The assumption of positive growth rates is indeed a feature of the Boltzmann-Arrhenius model of temperature dependence. We use the Boltzmann-Arrhenius model due to the dependence of growth on metabolic rate. As metabolic rate is ultimately determined by biochemical kinetics its temperature dependence is well described by the Boltzmann-Arrhenius. In addition to this reasoning there is a wealth of empirical evidence supporting the use of the Boltzmann-Arrhenius to describe the temperature dependence of growth rate in microbes.

Ultimately the temperature dependence of resource supply is not something we can directly consider in our model. As such we have to assume that resource supply is sufficient to maintain positive growth rates in the community. Note that this assumption only requires resource supply is sufficient to maintain positive growth rates (i.e. the maximal growth rate of species in isolation) not that resource supply is sufficient to maintain growth in the presence of intra- and interspecific competition. We have updated the manuscript in lines 156-159 to make these assumptions more clear.

17. Secondly, while I understand that the growth rate in the exponential phase for a single population can be measured to high precision in the lab as a function of temperature, the assumption for the form of the interaction rates' dependence on temperature seems very hard to test using empirical data. In the section starting L193, the authors seem to fit the model parameters using growth rate dependence on temperature, but then assume that it is reasonable to "use the same thermal response for growth rates and interactions". I did not follow this, and I think a weakness here is in not providing clear evidence that the functional form assumed in Equation (4) actually holds.

The reviewer is correct, it is very difficult to measure interaction coefficients experimentally and to our knowledge there is little to no data available on their empirical temperature responses. We as a best guess use the observed variation in thermal physiology parameters for growth rate as a proxy assuming that interactions must also depend on metabolic rates of the interacting species (see also response to comment 8).

18. To what extent is the mean-field approximation for x^* (which I think can be interpreted as an approximation for the inverse of a matrix with entries a_{ij}) valid for the full range of values of a_{ij} .

Please see response to comment 14 above.

19. There is also a long literature on feasibility analyses, going back at least to the ‘70s (e.g. Goh and Jennings, 1977, Ecological Modeling), and some of this is pertinent e.g. in relating to the authors’ results for the probability of feasibility and how this depends on the number of species present. It would be helpful to engage with this literature.

[We thank the reviewer and have added the reference to the maintext \(lines 323-327\)\)](#)

20. In general, I do not fully understand the justification for the functional forms of growth rate and interaction rate on temperature. The latter (the way the a_{ij} are assumed to depend on the temperature) seems particularly difficult to pin down. Is there any clear justification for this form?

[Please see the response to comments 8, 16 and 17.](#)

21. Whatever the temperature dependence, in Lotka-Volterra it seems inevitable that this will be a phenomenological assumption. The way the authors build up in the introduction, I thought they were headed towards a consumer-resource model, maybe even with intracellular dynamics determining the temperature dependence of interactions. This would be the approach e.g. of the Droop model (also going back to the 70s), or e.g. work from a couple of years ago (Muscarella O’Dwyer, 2020). I am not claiming that we can’t drop explicit resources, reduce to Lotka-Volterra, and make progress. But it makes it hard to understand how robust the results are to the authors’ assumptions about the way Lotka-Volterra parameters change with environmental context.

[Please see response to comment 3.](#)