

Ecology Letters

Decision Letter (ELE-01100-2023)

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Subject: Ecology Letters - ELE-01100-2023

Body: Dr. Joshua Fowler University of Miami 1320 S Dixie Hwy
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United States
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Millbrook, 21-Dec-2023

Dear Dr. Fowler,

Manuscript number: ELE-01100-2023 Title: Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity Author(s): Fowler, Joshua; Ziegler, Shaun; Whitney, Kenneth; Rudgers, Jennifer; Miller, Tom

We have now received the referees' reports on your manuscript. You will find them below. As you will see, the referees make a number of comments with the aim of improving the manuscript.

I invite you to revise and resubmit your contribution (see instructions below), and the subsequent publication decision will be based in part upon your point-by-point responses to the referees' comments. It is possible that in making this decision, we will refer back to the original referees or have additional referees examine the paper.

Your revision should include a point-by-point list of replies to all of the comments. We strongly suggest that you carefully lay-out your point-by-point replies (each referring to page and line numbers in the revised manuscript), since they will be provided verbatim to the reviewers on your submission.

It is important to note that this letter does not pre-judge the issue of whether your paper will be finally accepted: a consensus of novelty and generality must be obtained after reassessment if your revision is to be published in our journal.

It is the policy of Ecology Letters that revised manuscripts be resubmitted within 6 weeks of the date of receipt of this letter. Please contact the Editorial Office if you are unable to submit your revision before the option expires.

It is our expectation that revisions will not make the manuscript exceed the permitted maximum number of words. Authors should use concise writing, avoid giving several duplicate citations to support the same statement, and consider moving to Supplementary Information materials that are beyond the interest of most general readers who wish to understand what was done in general terms.

Please upload a tracked-changes version of your manuscript as a supporting document, in addition to the clean version uploaded as the main body (required).

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Yours sincerely,

Barbara A. Han, PhD
Senior editor, Ecology Letters
Staff Scientist, Cary Institute of Ecosystem Studies

Referees' comments to the author(s):

Referee: 1

Comments for the Authors

It was a real pleasure to read this document. The analysis of the importance of the effects of variance on population dynamics and its relative role in relation to mean effects is critical and innovative. I am positive that this type of approach will influence future analysis in demographic studies. The document is extremely well written, the study design is robust, and the analysis carefully explained. While the level of involvedness of the modeling and statistical approaches is impressive, the details of the procedures are easy to follow and convincing. This is an extremely valuable document because provides a superb example of the value of long-term data from a well-designed work to address significant academic questions. I have only two minor concerns. The first is a suggestion to temper their conclusions because the study still does not address the role of spatial variation and habitat heterogeneity, which may change these results in unpredictable ways. The study was done in relatively controlled (fenced, similar soils in a research station) and homogeneous environments in a very small portion of the distribution of the study species. The second is an observation that the model of *P. sylvestris* of Spikes/Infl. in page 25 does not fit well the data in the left portion of the abscissa range. This is particularly concerning because while it has the larger sample size it appears the be the farther from its model distribution.

Pedro F Quintana Ascencio

Referee: 2

Comments for the Authors

The authors use long-term demographic data on seven grass species to investigate the role of microbial symbionts on host performance. As endophytes were removed in half of the plants, the authors could test for the effects of endophytes on various vital rates, by fitting generalized linear mixed models. The authors specifically tested the hypothesis that the symbionts buffer against inter-annual variability in demographic rates, benefiting long-term host fitness. To do so, they use the vital rate models to construct stochastic matrix population models, and decompose the endophyte effect into contributions from effects on the means, variances and their interaction. In general, I enjoyed reading this manuscript.

The idea that a symbiont may buffer against fitness variance across years is interesting, and the authors use a great dataset to test this. When reading the manuscript, I kept on pondering about how this idea relates to the idea that microbes may sometimes also benefit hosts by increasing phenotypic variance, for example enabling hosts to faster explore the fitness landscape (Henry et al., Nat. Comm., 2021) or conferring phenotypic plasticity (Lange et al., ISME, 2023). In this study, does the symbiont affect the within-year variance? Also, associating with variable microbes may help hosts to express a diversified bet hedging strategy (Bruijning et al., Nat. Ecol. Evol., 2021), maximizing the chances that some hosts can cope with any environment they may encounter, also reducing fitness variance across generations. Further, demographic buffering may be seen as a form of conservative bet hedging, if the decrease in variance comes at the cost of arithmetic mean fitness (Childs et al., Proc. Roy. Soc. B., 2010). This doesn't seem to be the case in this study, as the presence of the symbiont not only decreases the variance, but at the same time increases the expected fitness for the majority of species. I am missing some discussion on such points, that put the results of this study in a broader context and that include other recent ideas on how symbionts may benefit hosts under changing environments. In general, I find that there is little discussion of the results in a

broader (evolutionary) context. I hope that the authors can add such as discussion, reflecting for instance on the above points.

Further, the authors mention that they test for a context-dependency in the benefits of the symbionts. I am not convinced that this is what is actually tested (but maybe I'm missing something). It seems that the endophyte generally has a positive effect on host performance across years, so I don't understand how these results indicate a context-dependence, where the symbiont is beneficial in some environments, but harmful in others? Even in the absence of a context-dependence, the symbiont could still benefit hosts both by effects through the mean and variance, correct? Could the authors elaborate a bit more on this in the text? Related to this, it would be helpful to illustrate their hypothesis (L134) in a conceptual figure early on in the manuscript, and perhaps even adding a schematic overview of the study design and approach.

I have no major comments on the methodology and the presentation (I really like the figures!). My main suggestion here is to improve clarity, as I found it not always easy to follow the text, in particular the link between the methods and results sections. If I understand it correctly, $\sigma_{\tau_{e,h}}$ is one of the core parameters, quantifying the inter-annual variance, estimated per endophyte treatment, per host species and per vital rate. Then, β_{2h} is a second crucial parameter, denoting the mean effect of the endophyte, for each host-vital rate combination. This is what is shown in Fig. 1 (after standardization), correct? It took me a while to get this, and I suggest to make this clearer throughout the text (for instance adding to the legend of Fig. 1 how these are calculated in terms of tau etc, explicitly linking Eq. 2 to the presented results).

Related to this, I believe that the coefficient estimates are nowhere provided, except for the appendix figures showing the posterior distributions for one parameter. It would be useful to compare different effects, for instance the effect of the symbiont compared to the 'origin' parameter. I would also like to see the how the inter-annual variance compares to e.g., the plot variance or residual variance. Please provide all coefficients, credible intervals, and variance components (either in the main text or in an appendix). Similarly, I can only find the differences in mean lambda between symbiont + and - host populations. But what are the actual lambda estimates? (are they anywhere realistic?)

I appreciate the attempt to show the amount of variation between years in Fig. 1D-E, but these graphs are difficult to interpret (the same applies to the similar appendix figures). Would there be another way to visualize the effects of the endophyte presence on the inter-annual variance?

I really like Fig. 2C. Is the bottom left corner where the symbionts lead to conservative bet hedging?

Fig. 4 shows the results of a decomposition analysis, quantifying the effects of the symbiont on long-term fitness through its effects on the mean and/or variance. Could this analysis be extended, further decomposing it into the contributions through each of the different vital rates? This would highlight through which vital rates the symbiont affects fitness the most, whether this is through effects on the mean of variance, and how the importance of different vital rates may change under future (more extreme) climates.

For the fitted vital rates, there are a few cases where the mean predictions seem to be quite off, not following the data so well, even though my understanding from Eq. 2 is that most parameters are estimated per host species, so they should be flexible enough to capture the observations (indeed, in most other cases, mean predictions do match the averaged observations nicely). For instance, in the case of adult growth of *P. sylvestris* and *P. alsodes* (Fig. S2), or the flowering probability of *L. arundinacea* (Fig. S2). What is causing this?

L382: How strong was the phylogenetic signal in each of the life history traits?

L374: Should this be Table S2?

Referee: 3

Comments for the Authors

Here, the authors use an experimental set-up combined with long-term demographic data to test for biotic mechanisms of demographic buffering. Overall, the manuscript is well written. Furthermore, the manuscript makes a timely contribution to the area of stochastic demography and includes 14 years of hard-fought demographic data across multiple grass species (very impressive).

I found the paper very interesting as, admittedly, this is an area of the literature in which I am deeply interested. However, there are a couple of points that I think would be beneficial to address to improve clarity (especially around the methods).

Points for consideration:

Keywords: I would recommend using keywords not already in the title.

L96: GCC is not increasing environmental variability everywhere. See Bathiany et al. (2018) Science Advances. You could approach it from the point of view that it is increasing in areas hosting the highest biodiversity.

L98: This final sentence needs some citations for this sort of claim. I'd recommend citing the initial Tuljapurkar papers as well as Doak et al (2005) American Naturalist.

Equation 1: Right now, log is being rendered looking like three separate variables. Perhaps remove the italics and make normal text.

L116: Negative correlations among vital rates

L123: The shift to this paragraph is quite abrupt. The introduction starts with a very concise journey through the fundamental ideas of stochastic demography that support the paper, and then, out of nowhere, a first-time reader is told about the roles of symbiotic microbes. I think this could be made a bit simpler and easier for the reader. I would recommend starting the paragraph talking about a variety of biological factors that can act as a buffering mechanism in a variable environment (e.g., maternal effects (bird literature), social network connectivity (deer), etc.). And then introduce the idea of symbiotic microbes. Currently the introduction is slightly on the lean side (especially with regard to the stochastic demography literature) – a little more fleshing and smoothing out would very much help the pitch.

L118: Just a heads up, throughout the introduction, many terms such as variance and stochasticity have been stated. I would highly recommend adding the word temporal before quite a few of them. As you will likely know, there are quite a lot of people from the stochastic demography side that will read "environmental stochasticity" and think about it in terms of temporal stochasticity (as I do). However, there are a lot of people in meta-population theory, community ecology and anthropogenic stressors researchers who may think about this in terms of "spatial stochasticity." The one word that tipped me off to write this comment was "autocorrelation" for which there is a vast literature in both camps. This comment is really because the paper is being pitched for a general audience – the clarification is important.

L135: This ("buffer hosts against variability") is too vague to the non-buffering indoctrinated reader. I would recommend being explicit. What is buffered? Is this an attribute attributed to an individual or a population (host seems to implicate individual – heads up)? What is the variability? I apologize for being pedantic about definitions and language, but this is quite important.

L141: Inverting this sentence: "To test the hypothesis that, we used a combination...." Would make the transition to the new paragraph a little smoother.

L157: Throughout the introduction, "variance buffering" has been used. This is the first introduction of "demographic buffering." Personally, I was happy to see it, I would recommend standardizing across the manuscript.

L194: Any estimate of the size?

L329: Apologies if I am misreading the methods, but (as I understand it) isn't the model a generalized integral projection model with two states? If this is the case, I don't see why this is not stated. The entire methods section reads like the methods of an IPM without ever saying it. Honestly, a little puzzled. Slightly separate to this point..... I think the methods would greatly benefit from a life cycle graph. Even if this is only added in the supplementary materials, a life cycle graph would greatly aid the reader in how the model is constructed. There are plenty of examples of how to do this for IPMs (simple example of pre-breeding census in Ellner IPM textbook).

More about the methods: From my reading, it seems as though the authors use a matrix/kernel stochastic approach by selecting certain matrices for their variance treatments. Not saying that this is the wrong way to do it (as there is no right way), I think this needs more support. Is

there are reason the methods includes a matrix stochastic approach instead of parameter stochastic approach (i.e., terms of regressions for example)? Also, I do not know why λ -s has not been standardized across variance treatments. This is very easy to do and seems like a more elegant way to mitigate the issue of the expected asymptotic properties of the treatments. This may not make it to the hall-of-fame that is the manuscript but I think is worth consideration.

L.377: What is meant by reference condition?

L.439: Saying average is a bit loaded, λ -s is also an average. I would recommend thinking of standardizing terminology to the arithmetic and geometric means. That way there is no confusion.

L.443: This is a very tricky sentence to read and understand.

Fig 3: Why isn't longevity used as it is throughout the manuscript? Also, longevity is just one part of the pace-of-life syndrome. To show the impact of life history, I would recommend showing the impacts of other components of POLS (e.g., generation time, Keyfitz entropy). Furthermore, to show POLS is the axis of interest and not reproductive schedule, I would highly recommend also running this analysis for R_0 and Demetrius' entropy. Following your writing, you would hypothesize positive relationship for POLS components and minimal covariance with reproductive schedule (although see Tuljapurkar et al. 2009 Proc B and their description of demographic dispersion in variable environments). Right now, seven points is not the most convincing..... broadening the pool of life history traits may aid with this.

Fig 4: I am a big fan of this plot. Thank you. Out of curiosity though, does the increased positive effect of symbiosis on λ -s rescue the populations? Buffering has a positive effect but has its limits. You cite Rodriguez-Caro et al 2021 which discusses this with tortoises..... it may be worth a look to show how meaningful buffering across the scenarios. Do they all persist or do some of them more than others?

I hope the authors find the above comments constructive.

Samuel Gascoigne

Referee: 4

Comments for the Authors

This paper highlights the important issue of demographic rate variance and its effects on long-term stochastic population growth rates. Because variance in vital rates decreases population growth, all else equal, incorporating stochasticity into demographic analyses provides a more accurate representation of population dynamics. The authors use a multi-species dataset to address the potential for variance-buffering effects of endosymbionts by modeling long-term dynamics estimated from data collected from an 14-year symbiont removal experiment to compare the effects of variance-buffering relative to those of improved mean vital rates, among populations with endosymbionts removed vs. those with endosymbionts present.

The authors provide simulations that demonstrate what has long been known – that decreasing variance in vital rates (and thus in annual population growth rates) increases long-term stochastic population growth rates. Their endosymbiont removal experiment provides relevant data and demonstrates not just that lower variance increases population growth, but that protecting or increasing the prevalence of endemic endosymbionts would likely improve population performance, which could have valuable applications in conservation settings.

A few important issues were overlooked, however. One important caveat is that long term population growth rates depend not just on the variability (or noise) in population vital rates, but also upon the correlations between these vital rates and upon the importance of the vital rates for population growth (reflected in vital rate sensitivities or elasticities). While Eq(1) uses a version of the stochastic growth rate (λ_S) that depreciates the mean population growth rate by the scaled variance in annual population growth rates, there is a more accurate formula that also incorporates the effects of vital rate correlations and elasticities - the small noise approximation of the stochastic population growth rate (Tuljapurkar 2013). Positive correlations compound the negative effects of variance, whereas negative vital rate correlations can buffer long term population growth rates against fluctuations in annual growth rates. Considering that the authors are interested in buffering effects, these negative (compensatory) correlations and

positive correlations (knock-on effects) could be important for their analysis and they would provide a more complete and nuanced view of the role that endosymbionts play in buffering population growth rates against annual fluctuations in vital rates. In particular, it would be interesting to know if endosymbionts promote more negative correlations (which would further buffer against stochastic fluctuations) or whether they increase positive correlations (improving multiple vital rates simultaneously but likewise hurting multiple rates during "bad" years). Although it could be merely noted (with some preliminary predictions about the effects of correlations), addressing the full range of stochastic effects would make their findings more robust and allow for more context in interpreting their findings.

These observations are included in comments annotating the draft pdf, which also include some questions about the methodology. In all, I think this paper uses an appropriate study system and relevant experimental approach to study the variance-buffering potential of endosymbionts, and could be a welcome contribution to our understanding of stochastic effects that could help advance theoretical understanding of population dynamics and provide the motivation for further studies highlighting the conservation potential of symbiotic relationships. However, they overlook other important elements of stochastic population dynamics in addition to variance-buffering and could benefit from additional analysis that examined the effect of endosymbionts on vital rate correlations and population-level differences in the force of selection that could be identified through differences in vital rate sensitivities or elasticities.

Editor's comments to the author(s):

Editor

Editors Comments for the Author(s):

The paper has received four reviews that each provide substantive comments for improving the manuscript, which was generally very positively received. I hope the authors find these comments to be constructive for improving the manuscript. I'm looking forward to seeing a revised version.

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