Report on

Positive fitness effects help explain the broad range of *Wolbachia* prevalences in natural populations

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The authors re-investigate and extend the qualitative dynamical behavior of *Wolbachia* prevalence in populations. Classical models of *Wolbachia* population dynamics assume a fitness disadvantage of infected host individuals. Together with a positive frequency-dependence caused by cytoplasmic incompatibility, this results in bistable dynamics. The two stable equilibria, separated by an instable equlibrium, are the *Wolbachia*-free state and a high frequency of *Wolbachia*-carrying host individuals. Here, the authors relax the assumption of negative fitness effects and show that positive fitness effects can change the model behavior substantially. Positive fitness effects have already been studied by Zug & Hammerstein (2018). However, the focus of that study was predominantly on invasion dynamics of cytoplasmic incompatibility and male-killing parasitic invasion behavior. In contrast, the present study focuses exclusively on cytoplasmic incompatibility in diplodiploid and haplodiploid populations and adds analytical justification to undermine the results.

First, the authors study the *Wolbachia* dynamics in diplodiploid populations. After reviewing the classical theory, they add a rigorous analysis of the case of positive fitness effects of a *Wolbachia* infection. This assumption may result in situations without an invasion threshold, which cannot be the case if infection comes with a fitness disadvantage for the host. The authors do a great job explaining the new findings both mathematically and biologically. Second, the authors apply the same methodology to *Wolbachia* dynamics in haplodioploids. Essentially the same conclusions as in the case of diplodiploidy hold. Unfortunately though, in the case of haplodiploidy the results cannot be shown completely analytically. Instead, the authors conduct a large numerical study that supports their claims.

Overall, the manuscript is well written. The authors have reviewed and acknowledged the vast existing theory very nicely. The new contribution of the manuscript is highlighting that stable intermediate and low frequency equilibria of *Wolbachia* prevalence in host populations can be explained by positive fitness effects of the infection. The rigorous analysis is, as far as I can say, correct, though I have a question regarding the haplodiploid case (see comment 12 below). Besides this, I only have a small number of minor comments that I list now.

Comments

1. *Terminology 'low frequency'* (first in line 29 and throughout the manuscript): I personally would prefer the term 'intermediate frequency' instead of 'low frequency'. To me, low frequencies are very close to the extinction boundaries, e.g. maintained by mutation-drift-balance. The manuscript, however, studies and emphasizes the possibility of frequencies far from the zero frequency boundary, which is why I would prefer the term 'intermediate'. (I am aware though that technically 'low' can be interpreted as closer to zero than to one, which is how the authors seem to use the term.)

2. Line 220: two → three

3. Lines 222ff.: I am not sure to understand that paragraph correctly. The authors first state that changing the parameter f may lower the equilibrium frequency of *Wolbachia*.

Then the authors state that increasing the value of f and all else remaining equal, the equilibrium frequency increases, which is in line with the biological intuition. This is in contradiction to the introductory sentence of the paragraph. I suggest to rephrase it or to clarify what exactly is counter-intuitive.

4. Fig. 1: I suggest to add a legend with the different values of L directly to the plots. Additionally, I think it would be helpful to zoom into the low frequency range of p_T in subfigure b) because the very low stable frequency mentioned in the main text (line 215) is barely visible.
5. Lines 361-363: My (very small) literature research also resulted in small evidence for *Wolbachia* evolution towards a mutualistic, hence positive fitness effect, lifestyle, e.g. Weeks et al. (2007), PLoS Biology, From Parasite to Mutualist: Rapid Evolution of Wolbachia in Natural Populations of *Drosophila*. It is maybe worth mentioning this biological possibility of parasite evolution that enable stable intermediate frequencies.
6. Line 317: I think in the Section 'CI infection dynamics' in the paper by Zug & Hammerstein they show (or claim?) that the invasion threshold vanishes if $ft > 1$ (even though I am not sure if they show this analytically or numerically).
7. Line 424: inequation $\rightarrow$ inequality
8. Line 437: I suggest to add a sentence about the purpose of the analysis, e.g. 'we show that $\hat{p}_F > 0.5$ whenever $f \leq 1$.
9. Line 440: I suggest to repeat that the case $f \leq 1$ is considered.
10. Line 457: I think the title should rather be Local stability analysis?
11. After Eq. (B.3): I suggest to give a reference, where an interested reader could look up the standard technique of local stability analysis, e.g. the book by Otto & Day.
12. *Matrix calculus and the analysis of the haplodiploid case*: First, I need to admit that I have not seen the framework of matrix calculus before. This might be the reason for my confusion. Basically, I was wondering why the authors take the detour of matrix calculus instead of conducting a 'standard' local stability analysis of the polymorphic equilibrium, i.e. studying the eigenvalues of the Jacobian of the model dynamics? Maybe this approach would yield analytical results? Or could the authors explain why they used the matrix calculus framework and how it is different from the 'standard' local stability analysis approach?