Referee Report on *Mutualists construct the ecological conditions that trigger the transition from parasitism* by

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Summary

Here the authors investigate an evolutionary path from parasitism to mutualism using a host-symbiont simulation model. While previous work has investigated the transition to mutualism in systems where symbionts are vertically transmitted, the present work studies this transition when symbionts disperse freely. Analysis of simulated results demonstrates that, alongside spatial structure emerging via the evolution of local dispersal, host competition plays a key role on this evolutionary path to mutualism.

Evaluation

Overall, this is an interesting study that provides novel insight into the transition from parasitism to mutualism. The approach taken to simulation and analysis is, for the most part, nicely done. However, there are a few technical details that I found concerning and aspects of the writing that I think can be improved (see below). Assuming these issues and the writing will be ironed out, a revision of this preprint will make a nice contribution to the field.

Writing: I found the introduction section to be well-written, providing both a solid motivation for this study and a satisfying review of previous work on the subject. However, the quality of writing deteriorated towards the end of the introduction and throughout the rest of the manuscript. In particular, when listing the goals of the study, the authors left out the question on the effect of local competition. The sections on model description, results and appendix A1 lacked consistent notation (see below). Some details in the appendix, such as the model of mixed local and global competition, should be moved to the main text for clarity. In the results section, the effect of local competition on the transition to mutualism, while interesting, seemingly appeared out of nowhere. The description of competition earlier in the main text made no mention of local competition and there was no mention of investigating this phenomena in the introduction. There are smaller aspects of the paper that made it difficult to follow. For example, in the caption of Figure 5 panels a), b) and c) are described in order, but then more information on panels a) and b) followed. It seems like it would be easier to read this caption if the information on panels a) and b) were kept together, especially since panel c) is presenting a relatively different result.

Viability of parasitic system: My greatest technical concern is the value chosen for the maximum expected offspring number of solitary hosts (which appears in the three notations $f^{sh}_{\max}$, $f^{a}_{\max}$ and $f^{\max}_{a}$ throughout the main text and appendix). It seems like setting $f^{sh}_{\max} = 0.5$ is problematic for this study since the host population (and therefore the whole system) would be doomed to extinction. A population where individuals have at most 0.5 offspring on average is not viable. Under these conditions there is no so-called *parasitic system*. Hence, it seems that the conditions for mutualism to evolve coincide with persistence of the system whenever $f^{sh}_{\max} < 1$. I would be curious to understand how the results change when the solitary host population is (more) viable. In particular, what is the threshold maximum expected offspring number for solitary hosts at which mutualism does not evolve? At least a ballpark estimate would be interesting (e.g., greater than one). Alternatively, demonstrating that mutualism usually does not evolve when maximum expected offspring number of solitary hosts is fixed to 0.5, but some other important parameter has been modified, would be sufficient to demonstrate that simulations are not rigged to force mutualism to evolve.

Reproducibility: Another issue is with reproducibility. Although the description of the simulation seems to be thorough enough to reproduce this study, reproducibility can be improved by hosting the code for the simulation and subsequent analysis on a public repository such as github. This would also aid the reviewing process by allowing the reviewers to check the code directly.

General comments/suggestions

- The addition of line-numbers would aid the review process.
- In the case of sexual reproduction, recombination may relax the correlation between dispersal and interaction traits. Does this imply that sexual reproduction would inhibit the transition to mutualism under this model? Might be worth including in the discussion.
- Since the evolution of local dispersal in many systems can lead to the evolution of local competition, I am curious how the results of this study change when competition occurs on the same scale as dispersal and therefore evolves in response to dispersal ability. This differs from the model of local/global competition described in the appendix since there the scale of competition is a fixed parameter. In particular, could a system that begins with global competition/dispersal transition to mutualism via the evolution of local competition/dispersal or does the evolution of local competition prevent this transition? Also might be worth discussing this in the main text.

Line-by-line comments/suggestions

Main text

Introduction

- On page two, beginning of third paragraph: "With respect to altruism" should be "With respect to mutualism"?

Model description

- Second paragraph under the subsection titled *Fecundity rate and mutualism/parasitism*: Is "strong mutualism" something that has been defined elsewhere? If so, please cite that source.
- Third paragraph under the subsection titled *Fecundity rate and mutualism/parasitism*: "We note interaction traits of the host and symbiont. . . " should be "We **denote** interaction traits of the host and symbiont **by**. . . ".
- The section on mutation in the model description: What rates did you use in the exponential distribution for each trait and for each species? How are mutations accumulated? Is the exponential variable capturing a mutation simply added to the parental trait value? If so then mutations can only increase trait values, which is obviously problematic. Are the mutations actually added or subtracted depending on fair Bernoulli trials? This would be better since trait values can then decrease as well and mutation would not add bias to the evolutionary trajectories of each trait. If this is so, then the mutation model is better described by a mean-zero Laplace distribution than exponential. See `https://en.wikipedia.org/wiki/Laplace_distribution`

- Section on dispersal: The cost of global dispersal d has already been used as a parameter limiting the size of mutations. Please pick a different symbol to clarify notation.
- Section on competition: Since one of the results was the effect of local competition on the transition to mutualism, it would be best to include information on both models of competition (the purely global model and the mixture of global and local model) in the main text. Otherwise, the result on the effect of local competition

Results

- Beginning of fourth paragraph in results section: What is coevolving with dispersal? I believe you mean the interaction trait in coevolves with the dispersal trait in both species during the transition to mutualism.
- Subsection titled *Effect of competition*: The authors report results on the effect of local competition. This is interesting, but caught me off guard as the model of local competition had not been introduced or mentioned in the model description. From the outline of the competition model in the model description section, I understood that competition was always global. Looking in the appendix, I see there is a description of local competition. It would be best to mention this in the main text.

Discussion

- Subsection titled *The role of quasi-vertical transmission*: The statement on mutualistic phenotypes retaining their global dispersal ability is confusing. Something like, "a significant fraction of individuals with mutualistic phenotypes also dispersed globally, in contrast to the tendency for local dispersal and mutualism to coevolve" might communicate this point with more clarity.
- Subsection titled *Host dependency and irreversibility of the transition*: I understand that the transition to mutualism is reversible if the competition among hosts declines. Is this also true if competition among hosts becomes local?

Appendix

A1

- The term *fecundity rate* makes it sound like a continuous time model where offspring are produced at a specific rate. This confused me since the authors develop a discrete-time model. I think replacing the term *fecundity rate* with something like *offspring number* would be less confusing.
- What is the significance of γ_f? Why is it interesting to include in the model? Why is it only applied to host and not symbiont?
- There appears to be a typo in equations (2). In particular, setting $\alpha_i = 1$ for either $i = h$ or $i = s$ does not return $f_{I,\max}$. Instead, if the authors dropped the second $f^i_{I,\min}$ appearing between c^i_f and α_i, these equations would return $f_{I,\max}$. It's unclear whether this was a type and if so whether the simulations inherited it.
- Figure A1: From this figure it appears that symbionts do not disperse. However, it seems like they should disperse freely since they are not vertically transmitted.
- Caption for Figure A1: Instead of calling it a *numerical algorithm*, please refer to it as a simulation or, even better, an individual-based or agent-based simulation. Although it technically is a numerical algorithm, simulation is the more colloquial phrase.

- Sentence following Figure A1: This sentence is redundant and confusing. I think the point would be clarified without it.
- Eqn (5): Why should the host be affected by its mutualism cost when it is not engaged in the interaction? In the following paragraph the authors claim that the cost is a *developmental cost*. However, I'm not sure what this means. I would like to know some biological examples that motivate this reasoning. The motivation for the competition component of the model beneath Figure A2 is a good example of what I would hope to see for the developmental cost component of the model.
- Eqn (7): Just a small point on notation. The spatial scale parameter c_s looks like it should be affiliated with the symbiont. Something like ψ_h may be less confusing.