

Response to reviewers Round 2: Mutualists construct the ecological conditions that trigger the transition from parasitism

Ledru et al.

We would like to thank the reviewers for this second round of review, including the minor comments (typos, unclear sentences) which enabled us to improve the overall quality. Naturally, we also took into account the important issues regarding (1) Appendix A2 and (2) the use of the beta distribution. Below, you will find the reviewers' comments in black, and our responses in blue. The line numbers in our responses refer to the revised manuscript.

1 Reviewer 1, François Massol

1.1 Appendix A2

Personally, I had the same reading as E. Kisdi regarding Appendix A2 – it seems that the "probability of getting a symbiont" have been lost and replaced by fecundities instead. I don't think doing the calculation with the right quantities is going to be much more difficult, so I encourage you to reiterate the exercise of obtaining some mathematical insights in this Appendix.

We followed your comments and we modified the appendix A2 to take into account the colonization probability and the density dependence. Please look at our responses to Eva Kisdi for more details about our changes on the appendix A2.

1.2 Beta distribution

Regarding the mutation distribution, I am afraid I was misunderstood (and thus I deeply apologize for being too obscure in my description of the beta distribution). What I was thinking of as a perfect distribution for mutation was not to add a beta-distributed noise, but rather to draw the value of the new trait from a beta distribution centered on the value of the parent trait. In this way, there cannot be any problem of overshooting 0 or 1 (beta distributions are constrained between 0 and 1). The technical point is just to use the parameterization of the beta that uses mean and precision, rather than the usual (a,b) parameters that is the natural parameterization of the distribution, such that mean = $a/(a+b)$. With such a distribution of mutations, the mean of mutant traits is always the value of the parent's trait. The variance will vary depending on the localization of the parent trait value, but it will be less brutal than the doubly truncated exponential.

Sorry for the misunderstanding. It is clearer for us now. We could have drawn the offspring trait from a beta distribution with a mean equals to the parent trait. On the one hand, we agree that this option is simpler and does not involve any truncation of the distribution because the random variable which follows Beta distribution always lie between 0 and 1. On the other hand, the variance depends on the parents' trait, as mentioned by the reviewer. And when the trait of the parent α is close to the boundaries either 0 or 1, the variance vanishes ($Var(X) = \alpha(1 - \alpha)/(1 + \phi)$ if the variance X follows a Beta distribution with mean α and precision $\phi > 0$). This last point is a critical issue because it prevents the parasitic system from evolution. Indeed, in the parasitic system $\alpha_s = \alpha_h = 0$. Thus the probability to create a symbiont with a trait greater than 0 is 0.

As a result, we think that the Beta distribution seems interesting to deal with mutations occurring on offspring from parents with intermediate trait. Moreover, in this situation we can fix the variance to a constant value. However, when the trait becomes close to the boundaries, this model is not appropriate and we need to use different mutation kernel as the one used in our paper. Consequently, we kept the doubly truncated exponential mutation kernel because the shape of the mutation kernel remains the same for any parents' trait and it solves the issues on the boundaries.

2 Reviewer 2, anonymous

(No new comments)

3 Reviewer 3, Eva Kisdi

3.1 Appendix A2

The new mathematical analysis in Appendix A2 is based on incorrect equations of the population dynamics. In equation (17), the authors assume that a fraction $f^s(\alpha_h, \alpha_s) * \rho_{hs}$ of the surviving hosts will acquire the symbiont. This quantity is however not a fraction (and therefore 1 minus this quantity can well be negative, possibly rendering the density of symbiont-free hosts negative). The simulation model assumes that the symbiont propagules disperse at random and therefore the number of propagules arriving into one cell is Poisson distributed; if more than one propagule arrives, then one survives with the host and the rest die. These assumptions are not reflected in equation 17. Instead of the quantity $f^s(\alpha_h, \alpha_s) * \rho_{hs}$, there should be the Poisson probability of having at least one propagule, which is $1 - \exp(-f^s(\alpha_h, \alpha_s) * \rho_{hs})$. In addition, a factor $1 - m$ should multiply ρ_{hs} because only the surviving symbionts reproduce (it appears that census is before mortality).

We totally agree with the reviewer about the Poisson probability and the $(1 - m)$ (the last term were actually present in our numerical simulations). In fact our previous model is an approximation of the Poisson probability when the density is low, that is $\rho_{hs} \ll 1$, which is the case when the traits α_s or α_h are close to 0. However, when the density becomes large our model is wrong and we should use the full Poisson probability.

Thus, we modified our model so that the dynamics of the proportion of sites occupied by the host alone ρ_{ha} or host with symbionts ρ_{hs} is now given by

$$\begin{aligned}
 \rho_{ha}(t+1) &= (1-m)\rho_{ha}(t) \exp\left(- (1-m)^2 f^s(\alpha_h, \alpha_s) \rho_{hs}(t)\right) \\
 &\quad + \left[1 - \exp\left(- (1-m)(f^{ha}(\alpha_h)\rho_{ha}(t) + f^h(\alpha_h, \alpha_s)\rho_{hs}(t))\right)\right] (1 - (1-m)\rho_h(t)) \left(1 - ((1-m)\rho_h(t))^{\gamma_c}\right) \\
 &\quad + m(1-m)\rho_{hs}(t) \\
 \rho_{hs}(t+1) &= (1-m)^2 \rho_{hs}(t) + (1-m)\rho_{ha}(t) \left(1 - \exp\left(- (1-m)^2 f^s(\alpha_h, \alpha_s) \rho_{hs}(t)\right)\right)
 \end{aligned} \tag{1}$$

where $\rho_h = \rho_{ha} + \rho_{hs}$ is the total proportion of hosts and α_h and α_s are interactions trait of host and symbionts respectively. In this model, all the terms are positive which guarantees the positivity of our density ρ_{hs} and ρ_{ha} whether symbionts are parasitic $\alpha_s < \alpha_s^*$ or mutualistic $\alpha_s \geq \alpha_s^*$.

In this new model, the term $\exp(- (1-m)f^s(\alpha_h, \alpha_s)\rho_{hs}(t))$ corresponds to the Poisson probability that no symbionts' offsprings arrive in an available host, whose density is $(1-m)\rho_{ha}$ after survival. The term $m(1-m)\rho_{hs}(t)$ corresponds to hosts that lose their symbiont due to the death of the symbiont. Finally, the term $\left[1 - \exp\left(- (1-m)(f^{ha}(\alpha_h)\rho_{ha}(t) + f^h(\alpha_h, \alpha_s)\rho_{hs}(t))\right)\right] (1 - (1-m)\rho_h(t))$ corresponds to the Poisson probability that at least a host propagule arrives in an unoccupied cell. This term takes into account the space density dependence through the free cell proportion $(1 - (1-m)\rho_h(t))$. The last term $\left(1 - ((1-m)\rho_h(t))^{\gamma_c}\right)$ is the probability of establishment of a host propagule.

The extinction equilibrium $(0, 0)$ of this model has the same characteristics as the previous one. Indeed, the R_0 is still the same $R_0 = (1-m)(1 + f^{ha}(\alpha_h))$. Thus the parasitic system starting with a large population won't go extinct, if $R_0 > 1$, which is fulfilled by our parameter ranges.

Moreover, we can check that the equilibrium without symbiont $(\rho_h, 0)$ is also unstable in the case with the full Poisson probability and the space dependence. Indeed, one of the eigenvalue of the Jacobian around this equilibrium is $\lambda = (1-m)^2(1 + \rho_h^* f^s)$. This eigenvalue is positive and is greater than 1 for our parameter ranges (see Fig. 1). Thus, the stochastic system of hosts and parasitic symbionts will survive with probability 1 if the initial size of the population is large.

In addition, we can extend our model to the situation with two types of symbionts. The model

becomes

$$\begin{aligned}
\rho_{ha}(t+1) &= (1-m)\rho_{ha}(t) \exp\left(- (1-m)^2(f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right) \\
&\quad + \left[1 - \exp\left(- (1-m)(f^{ha}(\alpha_h)\rho_{ha}(t) + f^h(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^h(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right)\right] \\
&\quad (1 - (1-m)\rho_h(t))\left(1 - ((1-m)\rho_h(t))^{\gamma_C}\right) \\
&\quad + m(1-m)\rho_{hs}(t) \\
\rho_{hs}(t+1) &= (1-m)^2\rho_{hs}(t) + (1-m)\rho_{ha}(t) \left(1 - \exp\left(- (1-m)^2(f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right)\right) \\
\rho_{sp}(t+1) &= (1-m)^2\rho_{sp}(t) + (1-m)\rho_{ha}(t) \left(1 - \exp\left(- (1-m)^2 f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t)\right)\right) \\
&\quad \left[\exp\left(- (1-m)^2 f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)\right)\right. \\
&\quad \left. + \left(1 - \exp\left(- (1-m)^2(f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right)\right) \frac{f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t)}{f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)}\right] \\
\rho_{sm}(t+1) &= (1-m)^2\rho_{sm}(t) + (1-m)\rho_{ha}(t) \left(1 - \exp\left(- (1-m)^2 f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)\right)\right) \\
&\quad \left[\exp\left(- (1-m)^2 f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t)\right)\right. \\
&\quad \left. + \left(1 - \exp\left(- (1-m)^2(f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t))\right)\right) \frac{f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)}{f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)}\right]
\end{aligned} \tag{2}$$

This model always exhibits competitive exclusion of the symbionts. The parasitic symbionts always wins the competition excepted when its relative proportion with the mutualistic symbionts is extremely low (≈ 0.01). Thus in absence of mutations, the parasitic system remains free of mutualistic symbionts.

Now, let us include mutations within symbionts. The model becomes

$$\begin{aligned}
\rho_{ha}(t+1) &= (1-m)\rho_{ha}(t) \exp\left(- (1-m)^2(f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right) \\
&\quad + \left[1 - \exp\left(- (1-m)(f^{ha}(\alpha_h)\rho_{ha}(t) + f^h(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^h(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right)\right] \\
&\quad (1 - (1-m)\rho_h(t))\left(1 - ((1-m)\rho_h(t))^{\gamma_C}\right) \\
&\quad + m(1-m)\rho_{hs}(t) \\
\rho_{hs}(t+1) &= (1-m)^2\rho_{hs}(t) + (1-m)\rho_{ha}(t) \left(1 - \exp\left(- (1-m)^2(f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right)\right) \\
\rho_{sp}(t+1) &= (1-m)^2\rho_{sp}(t) + (1-m)\rho_{ha}(t) \left(1 - \exp\left(- (1-m)^2((1-U)f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + Uf^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right)\right) \\
&\quad \left[\exp\left(- (1-m)^2((1-U)f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t) + Uf^s(\alpha_h, \alpha_{sp})\rho_{sp}(t))\right)\right. \\
&\quad \left. + \left(1 - \exp\left(- (1-m)^2((1-U)f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t) + Uf^s(\alpha_h, \alpha_{sp})\rho_{sp}(t))\right)\right) \frac{((1-U)f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + Uf^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))}{f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)}\right] \\
\rho_{sm}(t+1) &= (1-m)^2\rho_{sm}(t) + (1-m)\rho_{ha}(t) \left(1 - \exp\left(- (1-m)^2(Uf^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + (1-U)f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))\right)\right) \\
&\quad \left[\exp\left(- (1-m)^2(Uf^s(\alpha_h, \alpha_{sm})\rho_{sm}(t) + (1-U)f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t))\right)\right. \\
&\quad \left. + \left(1 - \exp\left(- (1-m)^2(Uf^s(\alpha_h, \alpha_{sm})\rho_{sm}(t) + (1-U)f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t))\right)\right) \frac{(Uf^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + (1-U)f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t))}{f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)}\right]
\end{aligned} \tag{3}$$

With a mutation rate of 0.08, which corresponds to the probability to mutate from a parasitic symbiont to a mutualistic symbiont in our stochastic model, we obtain a relative proportion of mutualistic symbiont around 0.02 which is in agreement with our stochastic model.

We modified the appendix A2 according to those comments: *see line 708-762 page 22-24.*

Further, host competition for space is missing in equation (17) (the factor with γ_C is resource competition).

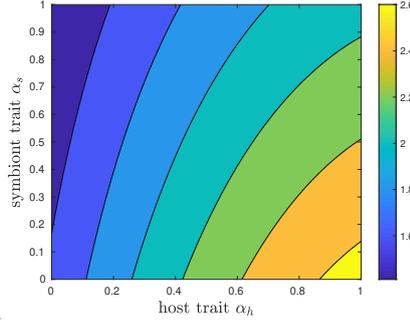


Figure 1: Evolution of the eigenvalue $\lambda = (1 - m)^2(1 + \rho_h^* f^s)$ of the jacobian associated to the free symbionts equilibrium $(\rho_h, 0)$, with respect to the interaction traits of the symbionts α_s and hosts α_h .

You are right the term $(1 - \rho_h^{\gamma^C})$ is the establishment probability when the competition is global. However this term does not take into account the fact that only 1 host occupies each cell. Thus we add the following terms in our model to include this space dependency:

$$\left[1 - \exp \left(- (1 - m)(f^{ha}(\alpha_h)\rho_{ha}(t) + f^h(\alpha_h, \alpha_s)\rho_{hs}(t)) \right) \right] (1 - (1 - m)\rho_h(t)) \left(1 - ((1 - m)\rho_h(t))^{\gamma^C} \right)$$

(see previous comments for more details on this term).

In equation (20), I don't understand why the unweighted sum of parasite densities appears in the denominator.

When fixing the previous issues, we have modified the equations. Now, a new parasitic or mutualistic symbiont can colonize an host without symbiont, in two ways. First only offspring symbiont of the same type arrive in the cell. Thus they colonize with probability

$$(1 - m)\rho_{ha}(t) \left(1 - \exp \left(- (1 - m)^2 f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) \right) \right) \exp \left(- (1 - m)^2 f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t) \right) \quad (4)$$

The first exponential term is the probability that at least a parasitic symbiont arrives in a host alive, while the second exponential term is the probability that no mutualistic host arrives in this host.

Otherwise, symbionts of different types (mutualistic with trait α_{sm} or parasitic with trait α_{sp}) can arrive in the same host. Then the probability that a parasitic symbiont of trait α_{sp} colonizes the host is

$$(1 - m)\rho_{ha}(t) \left(1 - \exp \left(- (1 - m)^2 f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) \right) \right) \frac{f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t)}{f^s(\alpha_h, \alpha_{sp})\rho_{sp}(t) + f^s(\alpha_h, \alpha_{sm})\rho_{sm}(t)} \quad (5)$$

The first two exponential terms are the probability that at least a parasitic and a mutualistic host arrive in the host. And the fraction term is the uniform probability that a parasitic symbiont actually colonize the host.

– While I agree that a mathematical analysis would valuably complement the lattice simulations, at this point it seems to me that it is better to abandon this and focus on the simulations alone to publish this paper in a reasonable time.

We have modified our mathematical approximations of the stochastic model to fix the issues raised by the reviewer. We agree that a deep analysis of the link between our approximations and our stochastic model would take time and it is challenging. As a result, we remove the last section of the appendix A2 "Transition from parasitic system to mutualistic/parasitic system". However, we think that the above mathematical analysis would help the reader to understand our simulations. In addition, it gives some a priori behaviours of our simulations and justifies the parameter ranges chosen for our simulations.

Other comments

1. The formula given in line 198 is not with the parasitic symbiont but for the host without any symbiont. More importantly, this is the inverse of R_0 and not the probability of extinction. For (infinitely)

large populations, the probability of extinction is 0 when $R_0 > 1$ and 1 when $R_0 < 1$, with no values inbetween. For initially small populations, the formula is more complicated.

We have clarified this point. We agree that our formula $(1 - m)(1 + f^h a)$ is the R_0 of our parasitic system. Thus if $R_0 > 1$ the parasitic system won't go extinct. In addition we have shown that the parasitic symbionts always persists in the parasitic system (see previous comments on model (1)). Thus the parasitic system is viable. We clarify this point

line 205 page 5

"To tackle the issue of transition to mutualism, we assume that the system is viable without mutualism (see appendix A2 for details). More precisely, in the absence of mutation, the per capita growth rate at low densities of hosts is $R_0 = (1 - m)(1 + f^a)$. In our study, we have chosen parameters (see Table 1) for which R_0 is greater than 1 so that if we start with a large density of hosts initially, the probability of extinction is 0. "

2. It is unclear why the strength of selection would be given by γ_f (line 166) or why competition would be "strong" or "weak" depending on γ_C smaller or greater than 1 (line 194). In line 231, it is unclear why density is high when competition is strong. This is important to understand because the ms discusses the effect of competition strength but it is more likely the effect of density. In line 262, the % mutualistic symbionts decreases and not increases with γ_C . At this point, I was lost.

The fecundity is optimal when $\alpha = 1$. And the gradient of fecundity with respect to the trait α at the optimum $\alpha = 1$ is proportional to the coefficient γ_f . Thus we interpret this coefficient as a measure of the selection around the trait $\alpha = 1$. Since we are interested in the selection of mutualism, we said that γ_f is the selection strength. We clarify this point by adding some comments

line 173 page 4

" The parameter γ_f scales the fecundity gradient with respect to the trait α_s around the optimal trait $\alpha_s = 1$. Since we are interested in the emergence of mutualism, $\alpha_s = 1$, this parameter γ_f describes the selection strength on the trait α_s - the selection strength on α_h is set to $\gamma_s = 1$. "

The parameter γ_C corresponds actually to the **inverse of the competition strength** for resources, we apologize for this mistake. That is why competition is strong when $\gamma_C < 1$ and weak when $\gamma_C > 1$. Indeed, the establishment probability is increasing with respect to γ_C , that is for a given density of host ρ , the establishment probability of an offspring goes to 0 when $\gamma_C \rightarrow 0$, while it increases to 1 when γ_C goes to ∞ . Moreover, when $\gamma_C > 1$ the probability establishment decreases sub-linearly with the host density. Thus a slight increase in density reduces strongly the establishment probability. Inversely, when $\gamma_C < 1$, the relation is super-linear. Thus an increase in density induces a slight reduction of the establishment probability. In Fig.5(a), the % of mutualistic symbiont actually increases with the competition strength $1/\gamma_C$. We add some sentences to clarify this point and modify the Fig.5.

line 202 page 5

"The parameter γ_C corresponds to the inverse of the competition strength. Indeed, the establishment probability is increasing with respect to γ_C . Thus, the competition is strong when $\gamma_C < 1$ (sub-linear function), while it is weak when $\gamma_C \geq 1$ (super-linear function)."

3. The authors declare that "the higher fecundity of mutualists is not advantageous enough to compensate for the ability of parasites to invade mutualistic clusters". How do we know that this is true in general, not only for the parameters used in the simulations?

This sentence comes from the concluding paragraph, which is rather short by nature. However, this issue has been detailed in the section "The key role of intraspecific competition". Within the limits of the general assumptions of our model, which have been discussed in the Discussion section "Assumptions, limitations and generality of the model", this assertion is true whatever the parameter values: competition between host is always necessary for the evolution of mutualism (in the absence of dispersal costs).

3.2 Minor remarks

line 200, " In this case," -ç with the parameters in Table 1 / with the parameters used (otherwise it reads as if for ALL parameters satisfying the viability condition you would get the same densities)

Response: Done

In line 416, it is unclear what kin selection refers to

Response: This section now reads:

line 421 page 12: "The retention of some degree of global dispersal in both hosts and symbionts in order to colonize remote suitable places has another advantage; it indeed tempers local overpopulation generated by mutualism. Since overpopulation due to local dispersal increases kin competition, this reminds the evolution of altruism, which can be limited by kin competition..."

line 419, competition between groups is local -; between individuals is local?

Response: Akdeniz and Van Veelen [2020] showed that the evolution of cooperation is less likely when competition between *groups* is local. We therefore kept the sentence as it was.

line 463, speciation theory shows that recombination can prevent rather than only delay a transition like this The language could be improved.

Response: This is indeed what we had in mind. We rewrote the corresponding sentence in order to improve language and clarity:

line 473 page 13: "In the present case, we speculate that sexual reproduction would not prevent the transition in the long term, but would only delay it".

4 Reviewer 4, anonymous

Line 31: eucaryotic cell should be eukaryotic cell Line 32: eucaryote should be eukaryote

Response: Done

Line 156-158 and figure A1: In the text, it is written that individuals reproduce, potentially undergo mutation, and then disperse. In contrast, in the figure it is depicted that individuals reproduce, disperse, and only then undergo mutation. Whereas the order is unlikely to have a strong effect, it could affect the dispersal behaviour somewhat depending on whether mutation occurs before or after dispersal. To clarify this point, the representation in the text/figure should probably correspond, to make sure there is no confusion on the part of the reader, on the exact used approach.

Response: Figure A1 is the exact approach. We changed the text accordingly, moving mutations towards the end of the process. It now reads:

line 158 page 3:

- The host and symbiont die with fixed probability m .
- They produce offspring. The average offspring number of a parent depends on its traits and on its interactions with their cell-sharing partner, if any.
- The offspring are dispersed according to the parental trait ε . For instance, the dispersal abilities of akenes depend on the parental genotype.
- The host offspring may establish only in empty cells, while the symbiont offspring can only establish in cells already occupied by a solitary host. If several organisms come to implant in the same cell, a uniform lottery determines which one will implant, while the others die.
- The offspring traits mutate with a given probability, which will affect their own interaction with hosts/symbionts and the dispersal of their future offspring. In nature mutations occur as soon as offspring are produced, instead in the model only the surviving offspring mutate, which saves computation time.

Caption of figure 5, figure A6, figure A7: confident intervals should be confidence intervals

Response: Done

Caption of figure 5: You note here that the dashed red line is the 10 % transition threshold. This is indeed the case in panels A and B, but not so for panel C, where you use it to denote the transition/reversal. This should probably be clarified in the caption.

Response: We specified in the caption that the dashed red line is the 10 % transition threshold in panels (a) and (b) only.

5 Reviewer 5, anonymous

5.1 Blockyness

Aside from specific comments below, I would just state the structure of the paper comes off a bit blocky. It would be nice to make the writing more fluid, especially between subsectioned content that appears to just be different paragraphs of the same section. Although I found the structure of this paper abnormal, it was still digestible. In the pace of modern science it seems higher priority to communicate basic results than to finesse a literary achievement. Hence, I'm content with the blockyness.

Response: We chose to keep the structure of the paper as it was since we believe that blockyness, despite its drawbacks, improves the clarity of the text. We apologize for that.

5.2 Introduction

I have just one suggestion: Since not everyone is familiar with the book Major transitions in evolution (particularly myself), beginning with this reference in the first sentence may only resonate with a fraction of the audience I believe would be interested in reading this paper. Perhaps discussing major transitions in biology more generally, without such an explicit reference to a specific book or paper, would be a more inclusive way to motivate this paper.

Response: We completely agree with this suggestion, and have modified the text accordingly (please refer to the first sentences in the main text, line 25 page 1).

5.3 Discussion

line 313: The sentence “Mutualistic symbionts, which help globally dispersing hosts, would be counter-selected” seems to imply all mutualistic symbionts specifically help globally dispersing hosts. To clarify the point, perhaps something more like “Mutualistic symbionts (which help all hosts, globally dispersing hosts in particular), would be counter-selected”.

Response: We changed this sentence into:

line 321 page 10: “If mutualistic symbionts would help globally dispersing hosts, they would be counter-selected.”

line 337: The sentence beginning with “The transition needs some time to occur. . . .” feels both abrupt and like it's starting a new paragraph.

Response: This sentence now reads:

line 351 page 11: “Several obstacles must be overcome (simultaneity of the mutations, demographic stochasticity, possible invasions by parasites) before the mutualists are numerous enough to induce the shift in host competition, which explains why the transition needs some time to occur”.

We also reorganized the corresponding paragraph a little bit (please refer to the main text).

line 424: Can you please expand on this sentence a bit? Just give us a taste of what we're about to get into.

Response: This sentence now reads:

line 434 page 13: “Our results rely on several hypothesis which have, if violated, either positive (vertical transmission, plastic costs) or negative (antagonistic coevolution, sexual reproduction, superinfections) effects on the likelihood of the transition to mutualism.”

5.4 Word “Methods” absent

I searched for the word “Methods” in the revised manuscript and found no match. Where is the Methods section?

Response: We changed the section “Model description” into “Methods”

6 Other changes

- We included a citation of Eldakar et al. [2010], who found in natural conditions that water striders males that behave aggressively with females are more mobile than less aggressive males, and that spatial structure is key to the evolution of low aggressivity.

- Inspired by comment 5.2, in the discussion we extended the sentence (line 540 page 14) starting with

”The re-production of pairs constitutes a another mechanism of inheritance, different from the one occurring during organismic reproduction” by the following:

”and fits with the idea that major evolutionary transition involve the evolution of informational systems [Szathmáry, 2015, Szathmáry and Smith, 1995]”.

This small addition is important because it strengthens the link between the present work and the original framework of evolutionary transitions.

References

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