Dec 11, 2017

Below are the reviewer’s comments and our answers, in italics and bold, respectively. L is short for line number.

Reviewer #1

*1. The figures are often too small. Some (e.g., Fig 1) might be larger enough if they utilized all the space given over to them, by reducing the white space around the actual figure.*

**We reduced the space around all figures.**

*Fig 4 is just way too small.*

**We changed Fig 4. It now contains only 3 panels for results with w=0.5. Results with w=0.1 and 0.9 are now in the SI, and a reference to the SI was added in the legend.**

*It could also be improved by having dotted lines drawn across the top of the insets to connect the corresponding dotted vertical lines.`*

**Following your suggestion, we tried drawing the lines across the panels top, but we feel that it makes the figures more cluttered.**

*2. The legend to Fig 4 says that the mean fitness decreases with each invasion; it seems to me to increase. Am I missing something (in which case maybe some further explanation should be given), or is this just a slip?*

**This was a slip, now corrected in the legend of Fig 4 to say “the mean fitness increases slightly with each invasion”.**

*This issue is related to lines 801-802, where it seems to me it should say "Figure 4 illustrates the increase over time of the geometric mean fitness with decreasing ρ at a polymorphic equilibrium ..."*

**Thank you, we corrected this in two places in the paragraph just before Section 4. It now says “the increase over time of the geometric mean fitness with decreasing ρ” (L739) and “…for small values of w, the mean fitness increases as ρ decreases.” (L744)**

*3. At the bottom of the LHS of page 6, there seems to be something missing. We have yet to meet ρ\*, which should be defined before the next column.*

**The first appearance of ρ\* now says: “Values of the evolutionary stable vertical transmission rate, ρ \*” (L678).**

*4. In Table 1, I would reorganize the table title (and footnotes) so that ρ\* is before ρ-hat, since that is how the columns are organized.*

**We reorganized the columns of Table 1 so that ρ\* is before ρ-hat to match the title and footnotes.**

*5. The function u(x) needs to be defined when it is introduced at line 940, not later on (at line 956).*

**Changed in L806: “… allows us to compute u(x), the probability that phenotype A goes to fixation when it's initial frequency is x, namely”**

Reviewer #2

*It is a long paper, and a different way to present the results would be to compress the text into 6 pages and put more details of the derivation into the Supplementary Material. I assume a deliberate decision was made to include most of the details in the main body of the paper, but you might consider preparing a shorter version with more emphasis on some of the unexpected results and the biological significance of these (see comments below on Section 3).*

**Thank you for your suggestion. After deliberation, we feel that a six-page manuscript cannot do justice to the material we present in this manuscript.**

*Abstract: The abstract launches straight into what this paper does. It would help to have a sentence or two introducing the topic and problem to be solved.*

**The beginning of the abstract has been modified. We replaced the first sentence with the following two sentences: “The evolution and maintenance of social learning, in competition with individual learning, under fluctuating selection, have been well-studied in the theory of cultural evolution.**

**Here we study competition between vertical and oblique cultural transmission of a dichotomous phenotype under constant, periodically cycling, and randomly fluctuating selection.”**  
*L55-59 "In these cases, inheritance of a phenotype may combine vertical transmission from the parent cell, and oblique transmission from other cells, even if the latter did not originally evolve for that purpose [17]."  
"did not originally evolve for that purpose" could be reworded to make it clearer and less teleological.*

**We have deleted that sentence (L61).**

*Line 335: "The local stability properties of the two fixations depend only on the fact that in a cycle of (k + l) generations A is favored k times and B is favored l times, and not their order in the cycle." This seems intuitively plausible. But to show this, do you need to show that F\_A and F\_B commute? Or it might suffice to point out that the linear approximation does not depend on the order (Eqn 11).*

**Now starting the line with “The linear approximation of F(x) near x\*=0 (Eq. 11) does not depend on the order phenotypes A and B are favored within a cycle of k+l generations.” (L337)**

*Figure 1. the axis labels in this figure and some of the other figures give the name of the parameter and the parameter symbol. It is useful to supply both, but separating them with a hyphen is sometimes confusing. E.g. in Figure 2, "Probability of environment favoring A - p". It might be better to use a comma (,) as the separator.*

**All axes labels and titles changed accordingly so that we have “parameter name, parameter symbol”**  
*Line 558 A constant environment ...*

**Added “A” to beginning of the sentence (L605).**

*Line 598 Symbols T\_1 and T\_2 are defined implicitly but could be made more explicit. Are they matrices and are they functions of x?*

**Added “non-linear transformation” to the descriptions of x’ and x’’ below eq. 34 (L617-619).**  
  
*Figure 4. The panels are too small and the labels are tiny and illegible. I would either reduce the number of panels (maybe w=0.5 instead of 0.1, 0.5 and 0.9, and put the other two into the Supplementary Material) or let the figure occupy two columns and reduce the text elsewhere.*

**We changed Fig 4. It now contains only 3 panels for results with w=0.5. Results with w=0.1 and 0.9 are now in the SI, and a reference to the SI was added in the legend.**

*Figure 4: The vertical inserts in panels C,F,I seem to show that the mean fitness INCREASES slightly after each invasion (the caption says DECREASES). Which is it?*

**The legend contained a typo and is now corrected to say that the mean fitness INCREASES.**

*Line 734: question mark (?) at the end of the sentence.*

**Done.**

*Figure 5 is interesting and raises questions. Is there a reason the simulation kept running after 10^6 generations (that is, after fixation of the rho=0.001 allele)?*

*Was it that a rho=0.0001 allele introduced but took too long to rise in frequency?*

**That is correct. We fixed the figure so that (a) the x-axis stops at 107 when the simulation stopped, and (b) the last invader (P=0.0001 allele) is plotted in red (it stays very close to 0 so it is hard to see) and described in the figure legend. We also changed Fig 4 accordingly.**

*Another issue is "accidental" loss of the invader. I would expect the invader to drop to frequency zero often. In the figure, the fluctuations near the zero boundary seem to show this. Did you continually reintroduce the invader or set a reflecting boundary at 1/N?*

**Indeed, we used a reflecting boundary such that when the invader frequency dropped below 0.0001 it is re-introduced at frequency 0.0001. The following was added to the captions of Figures 4 and 5: “Invading alleles are introduced at frequency 0.01%; whenever their frequency drops below 0.01% they are re-introduced.”**

*I am a bit confused by the text which points to Figure 4 showing a decrease in fitness (which I don't see, as remarked above) in the A1B1 regime. Based on Table 1, I would have thought that for A1B1, rho would decrease over time with increasing mean fitness.*

**Indeed, ρ decreases with increasing mean fitness. We fixed the mistakes in the text (L739, L744) and in the legend of Fig 4.**

*I was looking for an illustration of the dynamics for the A1B2 case where rho might increase over time while the geometric mean fitness decreases with successive fixation events.*

**We have replaced Fig S10 with a clearer and more elaborate exploration of the invasion dynamics. The new figure shows the sensitivity of the leading eigenvalue of the external stability matrix, λ1, to changes in the invader rate P for different values of the resident rate ρ. The figure demonstrates that for A1Bl, where 1 ≤ l ≤5, the only rate that is both stable and allows protected phenotype polymorphism is ρ=0. We corrected the mistake in Table 1 and in the text (L683, L767) which listed the stable rate ρ\* at 0.821, and it is now in agreement with the value for ρ-hat.**

*This mismatch between rho\* and rho-hat is interesting and could be explored more in the Discussion. Could you give biological reasons for this result?*

**We added a paragraph (L1124-1135) that provides an intuitive explanation for the change in ρ\* when k = l > 2: “To explain the marked difference in the value of the stable vertical transmission rate consider the probability q that offspring receive phenotype A when it is about to be the favored phenotype, and for simplicity, assume strong selection, such that parents are likely to be of the phenotype favored in the parental generation, a periodically changing environment AkBk, and a population at equilibrium.**

**With oblique transmission, q roughly equals the frequency of the favored phenotype in the parental generation. With vertical transmission, q=(k-1)/k = 0, 1/2, 2/3, 3/4, … for k=1, 2, 3, 4, …. Therefore, for large k, q is likely to increase with the vertical transmission rate.”**

*L945 frequency of x is given by [remove one "is"]*

**Done.**

*L971 maybe "orange traces" or "orange lines" or "orange series" instead of "orange diagram"*

**Changed to “orange traces”.**

Other changes:

* Fig. 3 legend is now inside the axes instead of outside and the x-axis range is fixed to the range of the actual values, removing unused space.
* Table 1 had a typo, ρ\* for w=0.9, k=l=30 is 0.99136 rather than 0.
* The stable rates ρ\* for w=0.1 k=3 k=10 and k=5 l=30 are any ρ values that lead to fixation of phenotype B (see Figure S10 and L685).
* We added a paragraph to the discussion (L1049) about the relationship of our model to the *storage effect* mechanism from community ecology.
* To accommodate a page-limit of 10 pages, we removed the derivation of the external stability matrix **L** to SI Appendix D and the derivation of the diffusion equation coefficients to SI Appendix H. This change required some minor changes to the text in L723 and L845.