

## Comments to the Author

The manuscript "On multiple infections by parasites with complex life cycles" presents a model to investigate the consequences of infection with multiple parasites for the persistence of the predator-prey systems on which these parasites rely, and hence their own persistence. Given the departures with previous models, the authors include that it is essential to consider the reality of multiple parasites in the theory of parasite ecology. This covers an important topic. While I am not qualified to evaluate the model, I see the value of the study, but I also feel that the current presentation of the work is inadequate:

- it is not well explained what sets apart the model from previous models;
- the different parameters in the model are poorly explained;
- there is not always enough guidance for the readers to understand the figures.

These shortcomings don't invalidate the importance of the work, but hamper the understanding of the study and its importance. Below I give some pointers of how the presentation could be improved.

We thank the reviewers for the overall positive assessment of our manuscript. In the following, we provide a point-by-point reply to the comments and suggestions.

## Abstract

L5: is suppress the right word choice? Predators can be suppressed by the parasite or parasites might become less efficient in host manipulation, which in both cases can lower predation rates.

We thank the reviewer for catching this right in the abstract. Now, we use "reduced" instead of the overloaded term "suppressed".

## Introduction

L38: "the assumption on" should be deleted? Does manipulation affect the fertility or the assumption on the fertility?

The cited literature shows the effect of host manipulation on the predation response function and the hampered reproduction of the infected definitive host. Now we state it simply so without a reference to the fertility assumption in line 38-39.

L42: "These models, however, lack a crucial aspect of parasite dynamics, multiple infections (Kalbe et al., 2002)." This is now the last sentence of this paragraph, but it would be better to use it for the start of the next paragraph and then elaborate on it. Please change "lack" into "have not explicitly considered", as further down you write that some studies have considered multiple infections. At first mention, please explain what exactly you mean with "multiple infections". This information is available further down, but should be moved up.

We thank the reviewer for suggesting to restructure the introduction to multiple infections. We have now rearranged the text appropriately where we start with introducing the concept and only then delve into the details of it connecting to manipulation and the specific example of copepods. The modified text is in line 44-46.

L63-L76: While the text is well-structured and relatively easy to follow until L63, from L63 until the end of the paragraph (L76) the text reads like an unstructured list of statements/ideas about the shortcomings of previous studies, without clear specifications. I suggest to revise the whole section

to better summarize what attention modeling work has been given to host manipulation, multiple infection, and predator-prey dynamics, or combinations of these factors (maybe a table is useful too to provide such overview, where you could also indicate how many intermediate hosts have been considered). Overall, the flow of ideas should be better structured to better formulate the key message and to facilitate the understanding of what theoretical work has or has not achieved.

We thank the reviewer for the comment. The restructured paragraph now highlights the connection between the studies on infectious parasite (which involve virulence) and trophically transmitted parasites (which involve host manipulation). While we mention the similarities between the two approaches, we now specifically highlight where the models differ (direct contact models), thus motivating the need to use the free-living environmental pool stage we introduce in our study. We hope the reworked paragraph adds clarity to our arguments. Lines 55- 72

L63: Please specify why studies pay less or insufficient attention, and point out which studies did pay attention.

L65: Please specify what you mean with "there are differences"

L65: "Host manipulation influences the predation rate in trophically transmitted parasites, predominantly affecting predator-prey dynamics." This sentence seems lost here, probably fits better in the 1st or 2nd paragraph.

L67-69: Consider to write: "The few theoretical studies on host manipulation in trophically transmitted parasites that consider multiple infections (Parker et al., 2003; Vickery and Poulin, 2009) do not consider predator-prey dynamics, which will likely have an important feedback on the evolution of host manipulation".

L72: "Most importantly": it is unclear why this is considered more important than the shortcomings mentioned previously

The above issues were addressed when we rewrote the text from Lines 55-72

L86: Unclear which of the abovementioned examples you refer to - better cite them here.

Thank you. We have now rewritten the paragraph as this part is no longer necessary. Lines 73-88

L87 (and elsewhere where this could be confusing): replace "host" by "host species". Note that the statement here might fit better in the discussion where you discuss the pros and cons or strengths/weaknesses of your model and compare them with other models.

Thank you for this idea. We have implemented it as recommended.

## Models and Results

L95: It is unclear where the model explanation stops and where the results start. Both should be clearly separated.

Indeed, in theoretical studies, the model itself is often the result. We followed this strategy at the beginning. However, to make our model accessible to the broader readership of

Oikos, we follow your suggestion. Now the Model and Results sections are provided separately (Page 6 and Page 8).

L112, L125 and anywhere else: all parameters (like I and D) and subscripts (s, w, ss) should be explained in the main text

Yes indeed this was our oversight. It has now been corrected in Line 97-99

L120: unclear what is meant by "the force of infection". Power, strength, intensity?

We added the explanation of the term "force of infection" in line 116. We initially did not provide a detailed explanation as this term is standard in epidemiology and has been defined and used in many previous references such as in the book Infectious diseases of humans by May and Anderson, Alizon and van Baalen, 2008, Alizon and Lion 2011, and so on. Again, to appeal to the broad readership we understand the need for reiteration.

L131: Unclear what is meant by the based line predation.

This is, in fact, a typo in our writing; it should be baseline predation, as mentioned in the previous sentence. We also added an explanation for this term in line 126.

L133: Table S1 should be in the main text

Thank you for the suggestion! We have moved the table into the main text in the model description now.

L136: Sentence ends abruptly and sounds incomplete

We fixed this issue.

Figure 2: Caption should explain the symbols I and D and w and ww. Is it possible to add other parameters to this visualisation?

Thank you for this comment. We have now added the symbols in the caption and also added the description of the processes that the arrows denote. We hope this makes the schematic more intuitive. We refrain from adding additional parameters to the visualisation so as not to overload the readers with the symbols that are now also included in the table in the main text.

L196: "significantly" is a statistical term. I suggest to drop it.

We fixed this issue.

L211: Reference to Figure 3A, 3C, 3D is missing in the text

This issue is fixed. The reference to Figure 3A, 3C, and 3D is now added in line 210, and 212.

Figure 3: Unclear what the X and Y axis in panel B and D represent, and in which unit

We have now added more information for the X and Y axes. They are the densities of the susceptible intermediate and definitive host. In theoretical models, the unit for density is often not provided. Without loss of generality, it usually is units of animals per unit area.

L218: depressed = suppressed?

Yes we now use suppressed.

L221: unclear which parameters you are comparing with parasite production. Why should they be comparable? See also L287.

We thank the reviewer for pointing out this issue. We now added more details about the comparison in line 221-224.

L243: depressed = suppressed?

Yes we now use suppressed.

L251-263: What exactly is meant by the newly introduced term here, "coordination" in reproduction and manipulation. Is it the right term? It has not been introduced that parasites coordinate their actions, neither this level of coordination seems part of the model. I understand it is a possible biological mechanism, but in terms of the model it is just a combination of parameter values. I think the term "coordination" should be reserved for the discussion"

We thank the reviewer for pointing out this issue. We now explain the meaning of coordination. It is indeed, as you mention, a combination of parameter values. We wish to introduce the term coordination here in the result section as we want to describe the model results and also link these mathematical results with their biological meaning. That is why we will not delay it until the discussion. The explanation of different combinations of parameter is now in line 252-259, and also in the caption of Figure 5.

Figure 5 and Figure caption 5:

- Unclear what is the hatched area in panel A. The purple region?
- indifference in English does not mean "not different". Replace by "equal"? Indifference is used twice in this caption
- Please explain why the parameter space indicates sabotage, cooperation, enhancement and depression (depression is probably the wrong word choice again). This also applies to figure 6.

We have redone Figure 5, where all the above issues have been addressed. Especially we also removed the word depressed. The bistability area is now clearly marked and explicitly labelled. The caption now also describes the sabotage vs cooperation regions in the right panel.

Discussion and conclusion

L276: The discussion and conclusions only contain relatively few citations. That is fine, but this opens the scope for an additional table where you can clearly show how the various models differ from the model in the present study, which can be used in the introduction to justify the need for such model. This will also make it easier to follow the discussion.

We now elaborated more on the comparison with two previous models of the same topic. We do not think a table is necessary as there are only two models on trophically transmitted parasites, to our best knowledge.

L322: While the evolutionary aspect deserves a mention in the discussion and is also already mentioned in the introduction, I am surprised that the entire conclusion is about the evolutionary aspects, which was not the focus of the study. I think the conclusion should primarily address the present model, how it improved current theoretical knowledge, what are the potential weaknesses, and what would be the way forward to e.g. include more reality/complexity, of which the evolutionary dynamics could be one aspect.

We agree with the reviewer and now reduced the part with the evolution. We were so eager to discuss evolution because our ecological result will serve as a baseline to further explore the evolutionary processes of our system. The introduction of the free-living pool has the potential to qualitatively change the eco-evolutionary feedback of the system leading to some rich dynamics.

We thank the reviewer again for the time and effort in evaluating this manuscript and hope that it is now in a better readable shape than before and a fit for the Oikos readership.