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REVIEW OF PH.D. THESIS IN ENTOMOLOGY AT THE UNIVERSITY OF SOUTH BOHEMIA

Thesis author: Mélanie Thierry

Thesis title: Mechanisms structuring host-parasitoid communities in a global warming perspective

Reviewer: George E. Heimpel

7 September 2021

This Ph.D. thesis investigates the effects of community structure on the outcome of species interactions within the framework of global climate change. Both direct and indirect interactions are studied empirically using a host-parasitoid system as a model to address general questions of community structure under scenarios of global warming. The host-parasitoid system consists of 3 *Drosophila* species and 3 of their parasitoids, all collected in tropical Australia and reared under laboratory conditions at the University of South Bohemia. In all I found the topic compelling, and the framework of the thesis to have been logically organized. The main questions posed were what affects elevated temperatures and shifting communities have on parasitism rates and host suppression, and how the structure of community modules (or 'motifs') themselves have on interaction outcomes. The results were interesting if a bit difficult to summarize, but some highlights included positive effects of temperature on parasitism rates, positive effects of parasitoid diversity on host suppression and a mixture of effects of community modules and species identity. My assessment of the thesis overall was that it represents a forward-looking set of questions, experiments and analyses and that it produced a number of novel results and insights. The approach of bringing the host-parasitoid system from Australia to a laboratory in Europe was courageous and reflective of a creative approach and a desire to break new ground. The experimental and analytical approaches were sophisticated and demonstrated high scientific maturity. It is my impression that Ms. Thierry has emerged from this process as a very well-trained experimental ecologist with a strong grasp of important and timely topics such as global climate change, community ecology and host-parasitoid interactions. Each of these disciplines has an extensive literature associated with it and I was impressed by the mastery of demonstrated for all three.

The overall writing is excellent although there are some slight errors in English grammar. I have noted some of the errors in English grammar on the pdf but not all. Despite these comments I would like to commend Ms. Thierry for writing so well in a second (or beyond) language. I have every sympathy for scientists that are forced to write in a language other than their native one and remain impressed with the quality of the writing in this thesis under these circumstances.

Beyond questions of grammar, I have a few questions that I would like Ms. Thierry to consider in making some minor revisions to the thesis, and these are listed below. In my view, a consideration of these questions and resulting minor adjustments will bring the thesis to its final version.

1. It is stated in the introduction (page 12 of the thesis; 22 of the pdf) that apparent competition is more important than resource competition among hosts of parasitoids. This statement is made without citing any references. The question is: What is this statement based on? Does it come from

the scientific literature or is a conclusion that you have formulated on your own? If the former, please cite the reference(s), and if the latter, please elaborate.

2. Chapters 2 and 4 use two interrelated indices to characterize the effect of the parasitoids on the hosts. One is the 'degree of infestation' (DI) and the other is 'successful parasitism' (SP). The former is described as the 'proportion of hosts attacked' and the latter the 'proportion of parasitoid adults emerging among the number of hosts attacked' (pg. 84 of pdf, 74 of thesis). From my reading of the methodology, I was having trouble understanding how these estimates could be extracted with only emergence data and no observations or dissections. Could you please explain how the methods used could account for resistant hosts (i.e., hosts that were attacked but survived and emerged as adult flies)? If 'attacked' is not the right word to use based on the methods, please consider another.

3. It is stressed in chapters 1 and 3 that global warming can have two classes of effects – (i) exposing species to higher temperatures, and (ii) causing geographical shifts. But if (ii) happens, (i) may not because presumably the geographical shifts are undertaken to minimize exposure to higher temperatures. The question is whether there is a need to consider these 2 effects of climate change together (and how one may cancel the other), and whether you would anticipate any interesting or important interactions.

As a follow-up to this question I would like to ask about one of your data sets. We learn in chapter 2 that *Drosophila birchii* seems to be very sensitive to high temperatures whereas the other 2 *Drosophila* species don't seem to be very affected (see Fig. 2 of chapter 3 – pg. 123 of the pdf). Does this suggest any hypotheses to you regarding movement of these species?

As a further follow-up, I would like to ask about the statement from chapter 1 that there is a trend for species to move poleward in response to global warming (pg. 8 of thesis, 18 of pdf). How would you apply this hypothesis to your host-parasitoid system in Tropical Australia?

4. The last question is relatively minor and is prompted by a statement in chapter 4 that 'Multiple predator effects on prey suppression are often assumed to be additive . . .' (pg. 141 thesis, 151 pdf). Two papers are cited to support this claim, one from 20+ years ago so maybe not relevant and one (Schmitz 2007) that to my reading does not make this point, but rather discusses additive designs in experiments (a different topic in my view). To get to the point, I worry that the statement may be a straw man argument. In my observations at least, aspects of synergism and antagonism among predator species have been hot topics for the last few decades, and additivity is not assumed at all. As an example, there have been many reviews (including at least one edited book by J. Brodeur & G. Boivin) on the topic of intraguild predation. One of these reviews was written by my Ph.D. advisor Jay Rosenheim (Rosenheim et al. 1995 Biological Control) and it is considered a classic and has been cited over 900 times. I would ask you to consider whether the statement above is still true or whether it is dated. If you think the problem of assumed additivity persists, perhaps you could cite some recent papers to that effect.

Sincerely and with best regards,

George Hempel

Written assessment of PhD thesis of Mélanie Thierry - 10th September 2021

Mélanie's thesis focuses on host-parasitoid communities in the context of global warming, and specifically investigates abiotic and biotic factors affecting host-parasitoid interactions and community structure. To do so Mélanie established and developed a model laboratory system of *Drosophila* and parasitoids she collected from Australian tropical rainforest. This is a huge feat in itself, and included seven months of field work and no doubt a similar amount of time setting it up in the laboratory before she could even start the experiments on which her thesis is based. Mélanie has demonstrated a variety of approaches to her research including fieldwork, laboratory experiments and mathematical modelling, not to mention expertise in experimental design. Given the disruptions over the past 18 months due to Covid, Mélanie has done exceptionally well to complete her PhD. Well done Mélanie!

Mélanie's model laboratory system notably enabled her to go beyond the usual pairwise host-parasitoid study systems and experiment on fully replicated parasitoid assemblages with different species compositions, all derived from the same natural community. This experimental approach has enabled her to separate the different structuring factors and therefore go beyond the patterns in parasitism and host-parasitoid community structure that have been previously observed, and investigate the mechanisms. In doing so she has contributed to the body of knowledge about the context-dependency of species interactions and the role of multiple predators and how these are altered by increasing temperature. Her results have relevance for community ecology, climate change ecology and their intersection. For example, they will enable better prediction of how host-parasitoid communities might respond to global warming and other environmental changes.

The thesis contains four data chapters, of which two are published with Mélanie as first author and a further two are in manuscript format, and likely to be submitted by the time of the thesis defence or soon after. Overall the thesis is comprehensive and gives a clear and concise account of the work conducted. The written English is generally very good, with just a few places where the clarity might be improved (for example page 16 the sentence beginning "In Chapter 4..."). Methods, including statistical analyses are well described and justified, and the results throughout are discussed and interpreted intelligently and detailed, in the context of the wider literature.

Mélanie's thesis introduction demonstrates an up-to-date and broad understanding of the impact of global warming on ecological communities, from the direct impacts on species due to their thermal breadths, to the impact on their interactions, and how this might play out at the community level. She highlights the gaps in knowledge relating to how these abiotic and biotic effects might interact. She then focuses in on host-parasitoid, and specifically *Drosophila*-parasitoid communities and how these are impacted by global warming. Mélanie could have expanded on her main aim (page 16) as I think this understates what she has done.

In Chapters 1, 3 and 4, the focus is on global warming. Chapter 1 is already published in *Ecological Entomology* and reviews the evidence of the effect of global warming on host-parasitoid networks, and the mechanisms behind the observed effects. The mixed evidence for changing patterns of parasitism with warming is revealed. The chapter particularly highlights the likely role for endosymbiotic bacteria, although this is not followed up on in the following chapters. Mélanie paves the way for the rest of her thesis by discussing the role of manipulative experiments and models in this research area. In Chapter 2, the only chapter not focusing on global warming, Mélanie uses laboratory experiments to investigate whether host-parasitoid assemblages are more affected by the structure of the community or the species identity. The results showed that multiple parasitoid species enhanced top down control, but that this was dependent on species identity. This is a novel and key result from a really well-designed experiment, as only with this sort of design, with replicate

assemblages, would it be possible to disentangle these effects. In Chapters 3 and 4 manipulative experiments are described that investigated the effects of warming on host-parasitoid assemblages. First, Chapter 3 (published in PLOS One) using simple assemblages of three hosts and three parasitoids, shows that direct effects of warming on species abundance are more important than effects via their biotic interactions (competition and predation). Then, an elegant combination of modelling and experimentation (Chapter 4) reveals the effect of warming on host suppression in assemblages of one host and three parasitoid species, finding that warming decreased host survival when multiple parasitoid species were present, but increased competition among the parasitoids. The results are logically interpreted and possible mechanisms are suggested from other relevant studies.

In the discussion Mélanie draws out several themes that have arisen from her thesis that will guide our broader understanding of ecological community responses to global warming. The future directions could have been developed further, as I am sure Melanie had many more ideas she could have included. Overall Mélanie's thesis provides original contributions to the ecological literature, specifically through her experiments that have manipulated a naturally occurring community to investigate mechanisms rather than simply patterns. Mélanie shows an excellent understanding of the relevant literature, and she draws on this to give insight into her own results, elucidating the mechanisms. I would particularly like to highlight her contribution to the understanding of the context-dependence of interactions, something that is often overlooked and this will contribute a welcome example to the literature.

Having read the thesis my overarching questions are as follows:

-A key finding from your thesis regards the context-dependency of species interactions. How does the context of small assemblages of 2-5 species in a laboratory affect the relevance of your results to natural communities in the field?

-Your laboratory experiments lasted one generation. How and why you might expect your experimental results to change should you have carried out experiments over multiple generations? For example, in Chapter 2, you mention that you might not have detected indirect interactions between prey species because you only studied one generation.

- Interactions are expected to be more susceptible to climate change than species, so why do your Chapter 3 results show that warming affected the *Drosophila* parasitoid community via species performance rather than by influencing species interactions?

- You discuss predators and parasitoids almost interchangeably in parts of your thesis (Chapter 4 and discussion). In the context of your work, when can we consider predators and parasitoids to be the same and when should we highlight differences, particularly in their response to global warming?

In my opinion the thesis represents a substantial and original contribution to science. My recommendation is therefore that the thesis is worthy of the award of PhD.



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