Review of the dissertation thesis of Jan Hrček „Caterpillar-parasitoid food webs in New Guinea rainforest"

This dissertation is focused on the analysis of complex food webs in tropical rainforest, namely the links between plants, insect herbivores, and their parasitoids. It comprises an introduction and four chapters which represent individual manuscripts or papers (to be more specific, two published papers, one manuscript in revision, and one unsubmitted manuscript). As such, the thesis clearly fulfills all the criteria on Ph.D. dissertation, and is acceptable without any substantial problem. Moreover, I really enjoyed reading it, and I think the presented material is interesting and important. Hereafter I will comment on it chapter by chapter (particular questions and queries are numbered).

The introduction is well and clearly written, albeit a bit short. I miss a little bit a more general overview of why it is important to study such system, i.e. why to study quantitative aspects of plant-herbivore-parasitoid wood webs and what is a general purpose/direction of this research. Note that the study is, after all, more or less descriptive, i.e. its main aim is just to quantitatively describe the structure of the food webs. My first (and indeed most general) question therefore is:

1. Why is it so important to know who eats who in the tropical rainforest?

Chapter 1 comprises the description of host parasitoid-food web in terms of host specificity and parasitism rate. It is very well written, and all analyses are sophisticated and sound. Although many results are presented, the overall picture is quite simple, and to a large extent intuitive (which means that the authors convincingly and reasonably interpret them). Here I have relatively minor questions:

2. The authors operate on several places with the usefulness of the results for potential biological control. However, they study tropical forest, and it does not seem to me that biological control should be applied in this environment. Are the results applicable and translatable to other environments, i.e. is there any chance that the results will be useful for real biological control somewhere?

3. The authors (also in the Introduction) highlight the „enormous diversity of herbivore-parazitoid food webs". What is it? Obviously, tropical forest is species-rich, so that all the possible networks of interactions is also complex and diverse, but is there anything special (in terms of diversity) of these food webs?

4. The authors operate on several places with „intraguild predation", but it seems to me that they have in mind something different from the usual meaning of this term (i.e. the situation when a member of a guild predates on another member of the same guild). What exactly is meant here?

5. On page 17 (bottom) the authors argue that the level of parasitism can be both underestimated and overestimated using rearing survey. However, it seems to me that the arguments for overestimation are stronger than those for underestimation. For instance, I do not understand why the fact that rearing removes the hosts from other natural enemies would lead to underestimating of parasitism level. Could you explain this?

6. Relatively low ichneumonid diversity in the tropics has been by some researchers attributed to their host specificity and inability to find suitable hosts in diverse host communities (similarly as in aphids). However, the results of the authors indicate that ichneumonids are generalists (and they have good flying abilities). Does it mean that the mentioned explanation is wrong? Or perhaps that they must be generalist to overcome the problems with finding a host, and this level of generalism constrains their diversity?

Chapter 2 represents, in my opinion, the very core of the whole work, and is apparently the most ambitious. The topic – comparison of the structure of plant-herbivore food webs with the herbivore-parasitoid food webs – is extremely interesting. The problem is that the manuscript (not yet submitted) is still very premature,

important concepts are not (or are very poorly) explained and some parts of the text are not understandable at all. This is most pronounced in the Abstract and Introduction. It is written in a languague which may be perhaps clear for specialists in this particular field, and although a reader can understand what is going on in the end (after reading the whole manuscript), the beginning of the manuscript is really incomprehensible. For instance, it is not clear how can food web structure (which is certainly not a quantitative variable) correlate with intimacy (see the Abstract), what is „herbivore species degree", what does it mean „We also report inconsistent results of compartmentalization and modularity with their relative versions..." (although later it is well explained) etc. I worry rewriting this part is necessary before submiting this otherwise extremely interesting text. I have following questions:

7. What is a food web? The authors often speak about multiple food webs (i.e. host plant-herbivore web or herbivore-parazitoid web), but I have always thought that food web is just the whole network. To which extent we can speak about individual parts of a food web as about separate webs?

8. Why should be less nested webs more stable (see first paragraph of Introduction)?

9. What does exactly mean that „phylogeny influences the structure of the food web"? I would think that the structure is given (by the revealed links between species), but it can reveal some phylogenetic signal – but this does not mean that structure is determined by phylogeny - or does it? Generally, the description of what has been calculated in this respect is not very clear, and should thus be clarified. In a related vein, why singleton lack phylogenetic signal (page 63)?

10. Why was Shannon diversity (concerning number of compartments?) computed (page 54 in the middle), and how was this measure later used?

11. Please explain following sentence (page 54 bottom): „We evaluated how the way in which are herbivory and parasitism level connected through the herbivores affects food web structure by correlating generalism degrees of herbivores in plant and herbivory webs using GLM with poisson distribution". I guess this sentence is perhaps even correct, but it is really complicated.

12. Please explain how it is possible that the null models provided results which were different from rarefaction results. I would, perhaps naïvely, assume that the null models do something similar to rarefaction, i.e. that they randomize the web with keeping some constraints on its structure.

Chapter 3 comprises the description of molecular tools to detect insect host-parasitoid relationships. It is clear, convincing, comprehensive and useful. I have no comments.

Similarly, I have no comments to Chapter 4 which describes a new genus and three new species of parasitoid wasp. I am not a taxonomist and this is a regular taxonomic description, which looks OK.

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Review of the PhD thesis of Jan Hrček 'Caterpillar-parasitoid food webs in New Guinea rainforest'

This thesis investigates interactions between caterpillars and their parasitoids, focusing on a highly diverse and uniquely well-studied community from tropical rainforest in Papua New Guinea. The thesis comprises a general Introduction and four data chapters, each in the form of a paper that has been published, or will be published in the international peer-reviewed scientific literature.

The general Introduction puts the work described in the thesis in the context of the wider ecological literature and existing research in the narrower field of study. The candidate makes a strong and convincing case that the thesis represents a novel contribution. The chapter is clearly written and the quality of the English is good.

I have some minor comments and queries for the candidate on the Introduction

1. (Page 1) The implication that insect communities may be structured by apparent competition while plant communities will be structured by competition seems like an over-simplification. How in practice can we distinguish the relative importance of these processes?
2. Regarding latitudinal diversity gradients in the Ichneumonidae, the candidate may be aware that a very recent paper (Veijalainen *et al.* (2012) Proceedings of the Royal Society B: Biological Science 279, 4694-4698) suggests that species richness of Ichneumonidae is markedly underestimated in tropical areas.

The four data chapters are as follows:

I. Parasitism rate and host specificity in a caterpillar - parasitoid food web from a tropical rainforest

This chapter presents data on parasitism rates and parasitoid host specificity in a complex caterpillar - parasitoid food web from lowland rainforest in New Guinea. Levels of parasitism are shown to differ among host guilds, and the degree of host-specificity varies significantly (and contrary to expectation) among parasitoid taxa. The chapter is novel and interesting and is unusual in allowing such analyses across a large number of co-occurring taxa occupying a diversity of feeding guilds. Another strength is the appropriate use of a phylogenetic framework. This chapter has been submitted for publication to the highly-ranked international ecology journal *Oecologia*. A revised manuscript has been requested, indicating that the manuscript is likely to be ultimately accepted for publication by this journal.

Comments and queries:

1. The methods do not explain the timescale over which sampling took place. To inform future workers it would be informative to give an indication of the amount of effort (in terms of person-days) required, and the duration of the data collection.

2. P.17. Can you elaborate on the assumption that the different biases affecting measures of parasitism rates 'cancel out'? Might your barcoded interaction data – or simpler data on parasitism rates within dissected hosts - be used to estimate the magnitude of the biases and the extent to which they can be ignored as cancelling each other out?
3. P.21. How were hyperparasitoids recognised as such?
4. P.21. To control for sampling effort did you consider using an asymptotic estimator (e.g. Chao) to extrapolate, as an alternative to interpolating using rarefaction?
5. For measuring specificity, did you consider using quantitative food web measures of specificity (e.g. *d'*) rather than the qualitative measures described here?
6. P.23. There are statements about the distinctive nature of the parasitoid communities on different categories of host, but little in terms of analysis or graphical presentation to justify this statement. Did you consider doing some multivariate analyses e.g. ordination?
7. P.26. Tachinidae do parasitise leafminers (e.g. in Memmott's (1994) Costa Rican web they are abundant but are parasitizing hispine Coleoptera absent from the Papua New Guinea networks).
8. P.28. Why should higher mobility of parasitoids lead to higher specificity? Might the opposite also be true?
9. P.28. Do higher rates of parasitism necessarily mean more effective control of host populations?

II. Interaction intimacy drives the structure of plant - herbivore - parasitoid foods webs

'Interaction intimacy' is the physical closeness with which interacting species are linked. This chapter shows that interaction intimacy influences food web structure, with low intimacy of herbivore interactions with their host plants (typical of external feeding Lepidoptera) leading to high intimacy of interactions with their parasitoids, and vice versa (typical of internal feeding leaf miners). This is a unique dataset and analysis for externally-feeding insects (as opposed to concealed feeders such as leafminers, which are a simpler focal system for this sort of study). As such, it provides for extremely valuable comparisons with other published networks.

This chapter has not yet been submitted for publication, but would be suitable for a leading international ecology journal such as *Ecology* or *Journal of Animal Ecology*.

Comments and queries:

1. The chapter mixes conventional binary food web metrics (e.g. for connectance) with some quantitative metrics. Did you consider using quantitative measures of e.g. connectance?
2. P.56. 'PII' measured as a percentage is I think a novel metric introduced in your study; I think it needs to be explained a bit better.
3. P.62. Similarly, I think the logic and practicalities of the phylogenetic approach need to be explained in more detail and more clearly.
4. P.63, second paragraph. I can think of situations where apparent

competition may be very important in plant communities too (e.g. for rainforest seedlings which have been shown not to compete strongly among themselves). This could be mediated by shared herbivores.

5. I find the use of 'weakly connected' and 'strongly connected' confusing. For food web biologists these phrases might be taken to refer to the (dynamic) strength of individual interactions. What you actually mean I think is 'low level of connectance' and 'high level of connectance'.
6. P.77, etc. Why do species coded as (for example) Geometridae appear within the Noctuidae? Are these samples that were tentatively assigned to those (wrong) families as larvae?

II. Molecular detection of trophic links in a complex insect host - parasitoid food web

This chapter describes the development of DNA barcoding methods for detection of herbivore - parasitoid interactions in complex communities. The datset is large and impressive and the methods are shown to work impressively Such approaches are likely to be game-changing in this field. It has been published in the leading journal Molecular Ecology Resources (Impact Factor: 3.062). I note that despite being published very recently (2011), the manuscript has already at the time of writing accumulated 13 citations, indicative that it is already highly influential and is likely to be widely and extensive cited.
I have no particular comments or criticisms of this chapter.

IV. A new genus and three new species of parasitoid wasp from Papua New Guinea and redescription of *Trigonophatnus* Cameron (Hymenoptera, Braconidae, Rogadinae)

This chapter (published in *Journal of Natural History* with the candidate as the senior author) describes parasitoid taxa new to science including a new genus (*Vojtechirogas*) of parasitoid and three new species. The rare genus *Trigonophatnus* is also re-described. The chapter represents valuable fundamental taxonomy and I have no particular comments or crticisms.

Overall summary and recommendation:

The thesis is of overall high quality and is comparable to some of the best PhD theses that I have examined at universities in the United Kingdom. The candidate has demonstrated mastery of a wide range of skills including quantitative analyses of large datasets, modern molecular methods, phylogenetics, taxonomy, and statistical analysis of large datasets. The candidate also clearly has a strong understanding of wider issues in ecology and evolution. Furthermore, the thesis summarizes a considerable volume of work; although the thesis may seem short in length, the effort (in the field, laboratory and at the computer) involved in generating and analyzing the data presented should not be underestimated.

My recommendation is that the thesis is worthy of the award of PhD.

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