THE UNIVERSITY of York

DEPARTMENT OF BIOLOGY
Wentworth Way, York YO10 5DD U K

Prof Jane K. Hill
Direct Telephone: +44 (0)1904 328642
Direct Facsimile: +44 (0)1904 328505
E-Mail: jane.hill@york.ac.uk

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External examiner pre-viva report - Martin Libra PhD thesis
University of South Bohemia in České Budějovice Faculty of Science

Thesis title: **Community structure of caterpillar parasitoids from tropical rainforest.**

The thesis examines the community structure of tropical forest parasitoids and their interactions with their caterpillar hosts in Papua New Guinea. The study focuses on investigating patterns of beta diversity spatially and with altitude. The main conclusions from the study are that:

- parasitoid beta diversity is higher than that of their caterpillar hosts (Chapter 1);
- there are altitudinal patterns in parasitoid diversity, with Ichneumonidae more diverse at high elevation, which is unlike elevation patterns seen in most other insects (Chapter 2);
- caterpillars experience higher predation at low elevation, but there are no differences in parasitism rates with elevation (Chapter 3).

The final chapter of the thesis (Chapter 4) describes three new species of Tachinidae that are hosts of lepidopteran larvae in Japan.

The thesis comprises 4 data chapters, plus a general Introduction and concluding summary. Chapter 3 is published in *Entomologia Experimentalis & Applicata (2019) 167: 922-931: Elevational contrast in predation and parasitism risk to caterpillars in a tropical rainforest.*

The thesis tackles an important ecological question about the role of species interactions, particularly host-parasitoid interactions, in the context of tropical rainforests. The research is novel and important, as evidenced by the fact that one paper is currently published. The thesis tackles big questions about the factors determining tropical biodiversity, and why some parasitoid groups show very different macroecological patterns with respect to altitude and elevation to most other species. The thesis is very carefully written, with a clear narrative and very concise presentation of a vast quality of ecological information. The thesis analyses a vast amount of field data from hand-reared lepidoptera sampled from different combinations of sites and sample periods in Papua New Guinea (e.g. >40k caterpillars and >4k parasitoids reared and identified in Chapter 2).

Q1 I will be interested to find out what the motivation was for selecting beta diversity as a focus for the thesis, and get a little bit more background information on the source of the data. Also what other questions the field data could be used to tackle, and what Martin's next analyses would have been.

Chapter 1 examines beta diversity at 8 sites up to ~500km apart. It analyses data for plants, caterpillars and parasitoids, and finds that beta diversity is higher for parasitoids

than caterpillars or plants. Analyses also consider interactions between caterpillars and parasitoids, and between caterpillars and host plants. The analyses are very careful to consider different beta diversity indices (analysing presence/absence, rare species, or based on abundances) and includes a repeat sample from one site, and also sub-setting the data to explore implications of analysing rare or common parasitoids. The conclusion about higher beta diversity in parasitoids is linked to assumptions about greater forest heterogeneity and dispersal limitation of parasitoids.

Q2 I am interested in the ideas about whether rainforest is 'homogeneous' or 'heterogeneous' at different trophic levels, as suggested, and discussing how greater heterogeneity leads to higher parasitoid beta diversity among sites, due to greater species turnover.

Chapter 2 examines parasitoid diversity at high and low elevation sites, and finds that Ichneumonidae are more diverse at higher elevation, mirroring patterns seen with latitude, and opposite to patterns seen in most other species. It tests 4 hypotheses about which factors could be driving these patterns in Ichneumonids (predation, fragmentation, nasty host, temperature). Results were not able to identify the ecological mechanism responsible for higher diversity in Ichneumonids at high elevation.

Q3 I'd like to explore whether elevation transects are analogous to latitude, and when/if they are not. It will be interesting to discuss what the next hypotheses to test might be, to better understand Ichneumonid diversity patterns with elevation and latitude.

Chapter 3 is a field experiment, testing for difference in predation and parasitism at high and low elevation sites. From experimentally manipulating 800 caterpillars, it finds much higher invertebrate predation at low elevation sites, but no differences in parasitism between low and high elevation sites. Chapter 4 describes three new species of Tachinidae from temperate forests in Japan. This chapter 4 seems to be carefully written, but it is not my area of expertise.

The thesis shows broad knowledge and understanding of the discipline and its associated research techniques by the candidate, and I think the candidate has applied appropriate research techniques and analyses of existing data in their thesis to tackle the questions they have posed. A substantial data set is analysed for parasitoids, caterpillars and plants.

Q4 It will be interesting to discuss with the candidate why they chose this specific study system to focus on, and to explore their choice of research questions and hypotheses to tackle.

Overall this is a very good thesis, tackling interesting and fundamental ecological questions. The thesis is generally very well written and presented, with one chapter already published. It will be interesting to hear plans for publishing the other chapters, and whether it is possible to convert findings from the study into policy recommendations and conservation management of tropical forest biodiversity.

Yours,

Jane Hill

Prof Jane K. Hill, Professor of Ecology

University of Nevada, Reno

Review of Martin Libra dissertation

by M L Forister, University of Nevada Reno

Below I have provided general comments and chapter-specific comments, as well as questions that I will ask during the dissertation defense. In the chapter-specific comments, you will see that (for the most part) I offer thoughts or suggestions that can be incorporated or not into the final, submitted draft of your dissertation (I hope you find the suggestions useful to consider, even if you decide not to use them in the final product). Finally, note that I have focused most of my efforts on chapters 1 and 2, and less on 3 (because it's already published) and also not so much on chapter 4 (given the taxonomic nature of that work).

General comments

It was a pleasure to read the dissertation by Martin Libra, and I have no reservations in recommending that the dissertation be submitted for completion of the degree. In general, Martin and his advisor should be commended for the diversity of methods and questions being addressed in this dissertation, and also on various aspects that are especially ambitious and labor intensive (e.g., the large number of caterpillars reared from the wild, and the use of live caterpillars to study top-down pressure in a tropical forest at different elevations). I also appreciate the way that the work is successfully placed into a broad context (e.g., latitudinal gradients) that is relevant to ecologists working anywhere in the world; the dissertation also benefits in many places from being explicitly hypothesis-driven.

Chapter 1

This is an important chapter and will be a valuable contribution to the tropical ecology literature. The work falls squarely in the tradition of other products from Dr. Novotny's research group in being ambitious, rigorous, and building on previous findings to advance our understanding of tropical plant-insect-enemy interactions. The most important finding here is of beta diversity at the highest trophic level that is driven by species turnover rather than "rewiring" of host-parasitoid interactions. If I understand correctly, you are suggesting that this pattern is driven not necessarily by rigidity of host preference but by dispersal limitation as a function of resource heterogeneity that amplifies up the food chain. That does seem like a plausible (and interesting) explanation, but I encourage you to make that interpretation as clear as possible in your Discussion (and Abstract) when you submit for publication.

One thing that I will suggest is that this chapter (and the conclusions in particular) would be strengthened by a more straightforward quantification of diet breadth (host range) in the parasitoids and in the caterpillars. As it is, the reader is a bit confused to see some superficially-contrasting statements. For example, in one place (p.35) you refer to the inability of parasitoids to switch hosts (which could be associated with extreme specificity) while in another place (p.37) you refer to the "wider host range of parasitoids." Unless I'm mistaken, you don't actually report a distribution of host ranges for either caterpillars or parasitoids. Doing so would strengthen this chapter, and this is probably the only point that I might suggest you consider including before you submit your dissertation (but that's up to you and your advisor, and I don't mind if you consider it later, for publication, or not at all).

From a methodological perspective, I appreciated your use of rarefaction and repeated subsampling to compare caterpillar and parasitoid datasets. The analysis of spatial turnover could have been a bit more modern, as the rank-based Mantel tests are not necessarily the most powerful approach. In future efforts, you might look into Moran's eigenvector maps as a strategy for quantifying and examining spatial patterns are arbitrarily-fine and crude geographic scales (that approach also generates covariates for spatial autocorrelation that can be readily incorporated into linear models).

Chapter 2

Overall, the use of an elevational gradient to complement and address questions associated with a latitudinal gradient is particularly well done in this chapter; such a comparison (elevation to latitude) is often implied but not often stated as clearly as you have done here. I also appreciate the range of hypotheses that you have laid out, although I admit that one aspect of that presentation confused me. I didn't see anything in those hypotheses (Nasty Hosts, Fragmentation, etc.) that would be likely to apply to Ichneumonids any more than any other parasitoid group. That fact made it unlikely to me (a priori) that they would be successful hypotheses for the elevation patterns examined in this chapter. You might consider making that a bit more clear (why you expect these hypotheses to be relevant to Ichneumonids in particular) as you prepare for publication, but it's not a crucial point.

The finding that the Ichneumonids do something different (relative to other groups) along the elevational gradient is fascinating and encouraging (with respect to the robustness of the latitudinal pattern for this group). Similarly, the finding that they do not have the same elevational pattern in body size as other groups is important and will be (as you suggest) a solid jumping-off point for future work.

A few methodological points that you might or might not consider useful at this time:

(1) In general, the presentation of Results in this chapter relies a lot on "significance." There is a gradual and important shift in the field away from reliance on arbitrary significance cutoffs (e.g., alpha = 0.05). Whether or not you are able to reject a null of no effect is more about power and less about biological importance. Rather than only discussing "significance" you should consider at times discussing the magnitude of a coefficient (e.g., slope from a linear model) and uncertainty around that coefficient (e.g., standard errors). This approach makes it more natural to discuss biological importance and frees you from arbitrary alpha cutoffs.

(2) I'm not sure how (or why) a Poisson model would be used on size as a continuous (non-integer) dependent variable. Please check that.

(3) Unless I've misunderstood, here and in other chapters you have used traditional diversity entropies rather than species equivalents that are easier to interpret. You might look into that literature which starts from Jost but is readily accessible in a variety of resources including R packages.

University of Nevada, Reno

Chapters 3 and 4

As mentioned, I have not focused on these chapters in the same way as the previous two, because the third chapter is of course published, and the fourth chapter is taxonomy (which is not my area of expertise, so I can't comment in detail on the methods used). However, I congratulate you on chapter three which will be an important citation for the field of tropical ecology (and natural enemy ecology in general), and I also appreciate your taxonomic approach that includes solid natural history data in the final chapter.

Questions to prepare for defense

(1) Although your dissertation is focused on interactions, I believe it is important for all ecologists to have an answer to the question: *why is there a latitudinal gradient in species diversity?* As a part of your answer, review a few of the classic ideas for the latitudinal diversity gradient and tell me about the explanation (or explanations) that are most powerful from your perspective.

(2) You mention (on pages 6 and 7) a diversity of latitudinal patterns among major lineages. Do you think it is profitable to seek an explanation for all of those differences, or should we consider them stochastic variation around a central pattern?

(3) For the most part, you seem to assume that parasitoid beta diversity is only a function of interactions with hosts (e.g., page 25 where your expectations for parasitoid beta diversity are explicitly tied to host specificity). What are other factors (perhaps not quantified by your work) that might drive beta diversity?

Matthew Forister
Biology Department
University of Nevada, Reno, USA