UCL GEOGRAPHY
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ASSOCIATE PROFESSOR
BIODIVERSITY CONSERVATION AND
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Re: Reviewer's statement, PhD thesis of Carlo L. Seifert

To the
School of Doctoral Studies in Biological Sciences
Faculty of Science
University of South Bohemia in České Budějovice

Dear Sir or Madam,

As Thesis Reviewer appointed by the Faculty, I wish to submit the following evaluation of the PhD thesis 'Ecological factors affecting the structure, diversity, and specialisation of caterpillar communities in forest ecosystems', submitted by PhD Candidate Carlo L. Seifert.

The thesis contains four main chapters, along with a general introduction and concluding summary. All main chapters represent joint work with multiple co-authors, and the candidate is first author on three of the associated manuscripts. The thesis furthermore contains a summary of the candidate's independent contribution, and written confirmation by the supervisors of the candidate's major contribution. Based on this documentation, I believe that the thesis and the candidate's contribution both clearly meet the requirements for a PhD dissertation.

Three of the thesis chapters have already been published in good international journals. One of the chapters (II) is yet to be published, but is included in the thesis in the form of an advanced manuscript draft that in my view already represents a 'submittable' standard, and it is likely only a matter of time before this last manuscript will be accepted for publication. As can be expected, in particular the published manuscripts (I, III and IV), but also chapter II, are more polished than the unpublished introductory and summary sections of the thesis, and some sections of the introduction could also have been slightly more up-to-date with regards to most recent developments in the published literature, but the thesis in its entirety is in my view clearly of high international quality.

With regards to its scope, the thesis reflects an extremely impressive amount of fieldwork and associated data that allows for a highly robust analysis and meaningful interpretations of the emerging trends from the data, and it in my view greatly contributes towards advancements in our understanding of forest caterpillar communities and their structuring both in tropical and

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temperate regions. The thesis combines two individual case studies from the US and Ecuador, both addressing highly relevant and novel topics with regards to the vertical stratification of caterpillar forest communities (Chapter I) and the composition of feeding guilds, using bamboo of the genus Chusquea as target host plant (Chapter III). While past work on lepidopteran vertical structuring in forest ecosystems has been strongly limited to adult assemblages, Chapter I represents to my knowledge the first detailed plot-based analysis of the stratification of their caterpillars, and it presents results of both great novelty and importance. Equally, the high prevalence of 'non-herbivore' caterpillars associated with Chusquea clearly pushes the boundary of our understanding of caterpillar communities and their functioning in tropical mountain rainforest environments. Chapter II does not only combine data from three different temperate forest sites around the world, but also links data on the caterpillar communities with phylogenetic information of their respective host tree species at these sites. Again, this results in clearly novel, extremely interesting findings that strongly advance our understanding of links between host plants and their herbivore communities from a phylogenetic perspective. Chapter IV finally reflects the results from a large initiative of forest canopy-researchers across the globe, resulting in a methods-focused study comparing different plot-based canopy-dwelling arthropod recording approaches with other methods used to record such communities. Again, this paper does not only provide an up-to-date overview of forest canopy arthropod research methods, but also represents novelty in proposing a clear sampling protocol and calls for a network of sites across the globe where this protocol is to be implemented. Again, this chapter makes a significant contribution to current debates on canopy arthropod research, while also moving beyond the strong focus on caterpillars towards a broader view encompassing generally non-flying canopy arthropod assemblages.

Overall, I was very impressed both by the broad scope and novelty of the thesis. The methods chosen are widely appropriate, very well applied and the results are clearly presented and skilfully analysed throughout. I hence like to congratulate the candidate for their impressive work.

Reviewers are asked to formulate a few questions for which the candidate is then given time to prepare answers. In this context, I would like to ask the candidate to prepare for the following questions:

1. Generally, the focus of the thesis is on arboreal caterpillar assemblages. In the introduction, it is argued that these represent a large proportion of caterpillars found in forest ecosystems. Nonetheless, at least in many temperate forest ecosystems, the bulk of diversity in the vegetation will be represented by the herbaceous (and to a lesser degree shrub) vegetation in the undergrowth of these forests. What can in your view explain this discrepancy, and can you elaborate what proportions of the local caterpillar fauna (e.g. looking at local faunal records

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for the respective forests and/or known food-plant records) you will likely have accounted for with your exclusive focus on trees – looking both at temperate and tropical forest ecosystems?

2. Chapter I: In the methods, it is stated that the forest type chosen is typical for the region and similar to other well-studied forest plots in the wider vicinity. Nonetheless, there is no information about the actual age and structure of the forest, nor on the question if this is an old-growth, mature forest or a secondary/younger forest ecosystem.

2a) Would you expect this to matter, and what do you think could potential differences be in the caterpillar assemblages and canopy assemblages between secondary and mature forest ecosystems?

2b) Crucially, you then continue to define 3 strata, each 10m in height, for the classification of different forest strata. Looking at the actual distribution of tree species across these three strata, it nonetheless appears that the uppermost stratum, defined here as "canopy", only contains a very small number of tree species that additionally also all have the vast majority of their leaf / crown volume contained in lower strata. Given this structure, please explain how an alternative approach, treating the few trees >20m as "emergent", and with the main canopy layer defined by the actual height of the uppermost continuous layer of leaves covering the entire forest plot area (excluding any gaps - e.g. derived from aerial photography or remote sensing), could have altered the results. In your answer, please also take account of the ecological patterns you mention here and in the introduction, i.e. the morphological differences between sun-exposed and shade leaves in the crowns of canopy-forming tree species, and how the approach taken here might partly explain the lack of any canopy-specialist species in this study.

2c) Finally, given that caterpillars in the "canopy" layer were only encountered on trees representing 3 species, how can you differentiate the caterpillar community effects relating to a distinctly established "canopy" assemblage from simple 'host plant richness'-effects, given that you are comparing assemblages/networks containing 14 ("understory"), and 12 ("midstory") versus only 3 ("canopy") tree species? Please, also consider the relative herbivore diversity and ecology variations between the different tree species, reflecting e.g. on the well-established high diversity of herbivores particularly on *Quercus* spp.

3. Chapter II: This study contains the statement "Altogether, the patterns observed across our three study sites lead to the conclusion that species diversity of arboreal caterpillar assemblages in temperate forest ecosystems is primarily driven by those tree species that are common and have close relatives (e.g. congeners) in the plant community." Elsewhere, a clear indication is given that the similarity in the communities between individual host tree species is overall very low. Can you in this context please elaborate on the relative importance of a) the most common host tree species, b) groups of congeners and c) overall diversity of host tree species for the diversity of caterpillars in the investigated forest systems?

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Also, just for clarification regarding the methods in this chapter: the study uses Jaccard and Bray-Curtis as well as Morisita-Horn (M-H) as dissimilarity measures – the former two in my view requiring that the compared samples were sampled completely (with regards to the species pools they represent) – or were at least of equal size in terms of individuals and reflecting equal sampling effort to make even the relative dissimilarity values comparable between pairs. Was this the case here, and how was this established/tested? For M-H, this index does focus strongly (almost exclusively) on the similarity of two communities with regards to the most dominant species, only – how could the results be expected to change if other members of the NESS family were used to calculate dissimilarities for larger sample size values?

4. Chapter IV: Felling is proposed as one approach to sample canopy-dwelling arthropods (and is indeed used as a technique elsewhere in the thesis, e.g. in Chapter I). This method is proposed and used in a temperate forest context, while this chapter also highlights the need to sample over different seasons to reflect the seasonal differentiation in arboreal arthropod assemblages. Looking at a plot-based approach, does this mean that small sections / subplots of a study plot are to be felled at different times throughout the year (which will likely damage the vegetation of the remaining plot, and crucially also strongly alter the microclimatic conditions in the interior of the remaining forest plot, in turn likely leading to a strong shift in the arthropod assemblages)? Or is it rather suggested that at different times of year, entirely different, spatially separated plots within an otherwise continuous forest area are logged? Will this in turn lead to very specific requirements for the practical implementation of activities that potentially limit the use of this approach in cases where they are to accompany planned logging activities?

Huntingdon, 28/05/2020

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Carlo Seifert dissertation: Ecological factors affecting the structure, diversity, and specialisation of caterpillar communities in forest ecosystems

Assessment and questions

Robert J. Marquis
University of Missouri-St. Louis
7 June 2020

This dissertation presents the results of sampling caterpillars, mostly in the canopies of temperate forests. It breaks new ground through very thorough sampling of entire canopies of trees on three continents, followed by very creative statistical analyses. Unless I am missing a study, this is the first three-continent comparison of insect herbivore communities, which is a major logistical feat in itself. Such geographical in sampling helps us understand the generality of results, and is to be commended. The team of researchers overcomes a host of sampling issues, and problems with identifying the caterpillars encountered. The results, presented in Ch. 1, tell us about the degree to which canopy insects are stratified on a vertical gradient (they are!), a hypothesis that has not been tested very thoroughly until now. The results also reveal the impact that relatedness of the sampled trees has on the structure of the insect community as a whole (Ch. 2). There is much focus today on the impact that plant phylogeny has on structuring insect communities, their impact on the plant, and the consequences for plant evolution. Now we have some temperate data to compare to the tropical studies that are coming out. The results presented in Ch. 2 are also very relevant to current questions ecologists are asking about how communities "are put together". The *Chusquea* study (Ch. 3) is relevant to all those who will sample unstudied herbivore faunas in unexplored regions of the world, highlighting the difficulty of knowing who exactly are the herbivores. Finally, Ch. 4 is a wonderful review of the methods used to sample insect communities of tree canopies, comparison of the suitability of those methods to answer particular questions, and specific details employed by the study team. There are myriad sampling questions to answer and hurdles to overcome in order to make a convincing case that results obtained truly answer the questions asked. In being so thorough in explaining the possible methodologies, the authors provide a pathway to a research program encompassing a series of sample sites across the globe.

All four studies are solid contributions to our understanding of the canopy ecology of caterpillar faunas. "Weaknesses" fall in regards to what the researcher did not do, rather than faults in the sampling design for the hypotheses tested. But one could say this is true of every study. The very best research leads to new questions and more research. The one weakness of the temperate canopy study is that the sampling/analysis did not explicitly quantify seasonal

turnover in caterpillar composition. It appears that at least on *Quercus* in Missouri USA, there is almost no overlap between the faunas on young leaves and mature leaves. If the researchers had stratified their sampling, they would essentially be able to test the hypotheses presented in Ch. 1 and Ch. 2 two times, once for the spring fauna and once for the summer fauna. There is the possibility they could analyze their current data this way if they are able to assign caterpillar species to either spring or summer faunas.

I would like to complement Carlo on one thing in particular. He does an excellent job of reviewing the literature in his introduction. And in his chapters, he places his studies in the context of what has been done previously. I think this is very important, and is often missing in many studies being published these days. This leads me to ask whether he has thought about publishing this written introduction to his dissertation.

Here are my questions:

1. My first question has to do with the generality of the analysis and results presented in Ch. 2. If you had sampled the caterpillar faunas of the herbaceous layer (much cheaper and much less labor intensive, of course!) instead of the tree canopies, how different would your results be, and why? And if you were to sample the tree canopies of species rich conifer forests, how similar or different would your results be? In other words, how generalizable are your results to other plant strata and biomes? What general principles can be derived by the fact that your results are fairly similar for all three locations? Is this the result of sampling mostly shared tree genera and related insect faunas across the three sites? Or instead do you think sampling anywhere in north temperate forests would give similar results?
2. You found that shelter-building caterpillars appear to be more specialized than free-feeding caterpillars. How might this conclusion be affected by the fact that shelter-building is more common in some caterpillar families than others? The alter ego of this of course is that free-feeding is more common in other caterpillar families. What factors might be driving higher specialization in shelter-building caterpillars compared to free-feeding caterpillars? Can these be tested?
3. You do not tell us much about the factors that are driving stratification of caterpillars with canopy height, especially the role of the third trophic level. What do think the impact of natural enemies of caterpillars is on caterpillar stratification, and how would you verify this? In particular, no doubt your team has sampled hundreds of thousands of spiders and ants, and scared away many birds. Are these spiders and ants eating caterpillars? The role of parasitoids? One of my favorite papers in this regard is: Brown, J., Vargo, S., Connor, E., & Nuckols, M. (1997). Causes of vertical stratification in the density of *Cameraria hamadryadella*. *Ecological Entomology*, *22*(1), 16-25.
4. How do you think forest age might influence the results found in Ch. 1 and Ch. 2? What processes might be important? What are the conservation implications?
5. Please discuss a bit more about the taxonomic isolation hypothesis and its implications for overall caterpillar species richness in a forest. I agree that adding more closely related tree species to a forest might increase the resource base for specialist herbivores on those tree species, but adding phylogenetically distant species should bring in unrelated, specialist herbivores. I would think that both would be working simultaneously to increase overall caterpillar diversity. And, would not the abundance of the phylogenetically distant tree species make a difference? Your study

suggests that there might be two axes that are important: degree of phylogenetic isolation and abundance of the host plant species.

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