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Review on the PhD thesis of Vincent Maicher

"Biodiversity patterns of butterflies and moths on Mount Cameroon"

The PhD thesis of Vincent Maicher consists of 8 papers, which are united by a common introductory chapter and a common summary chapter. Four of the papers have been published while four of the papers currently have the status of a manuscript (two of them submitted). In four of the papers, V. Maicher is the first author, and it appears that he has had substantial independent contribution to also to the rest of the studies. I can thus conclude that in terms of the quantity of science (amount of work done), this thesis safely exceeds the international average (my evaluation is primarily based on comparison with theses defended in Estonia, Finland and Sweden, which I know best), even if to consider that all papers have multiple authors.

The accepted papers have appeared in reasonably well ranked journals, and there is no doubt that the unpublished manuscripts will end up in at least similarly positioned periodicals. The work by Maicher thus meets the criteria of a PhD thesis also in terms of quality of the science.

As the third aspect, a PhD thesis is not just a piece of science – a PhD thesis is also a proof that the defendant has learned a lot, much enough to be able to work in science independently. This is definitely the case: apart from the certainly valuable experience obtained in the course of extensive field work in a logistically complicated area, the diversity of approaches and analyses used in the thesis is unusually high (from faunistics and taxonomy to community ecology and conservation related issues). The very high quality of writing provides the evidence that professional skills have been acquired in this aspect as well. In other words, the defendant must have learned a lot which certainly gives him an excellent starting point for his forthcoming academic career.

Summing up, I find that PhD thesis of V. Maicher meets all the criteria of a good PhD thesis and **I am happy to recommend the thesis to be defended**.

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The ecological papers (Chapters II, III, IV, V, IX) deal with differences between butterfly and moth communities both in space and time, and look for ecological factors explaining these differences. The amount of data accumulated is respectable and the conclusions reached appear therefore reliable, given the restrictions on justified interpretation (below).

The authors have found that there is strong seasonality in the composition of lepidopteran assemblages (II), and that there is a substantial interaction between seasonal and altitudinal gradients (V).

My main critical point – which I would like to discuss during the defence – is insufficient attention to distinguishing between patterns relying on life history phenomena and population dynamics. Let me explain. Here is the north where most insects are univoltine, it is clear that most of the observed seasonality is based on life history adaptations: each species typically has a distinct a-few-weeks-long period of adult flight. The fact that adults cannot be recorded outside of the flight period is obviously explained by the adaptive timing of the life cycle. However, in the tropics where insects are potentially polyvoltine, the story may be completely different: the temporal abundance patterns of particular life stages may not be adaptively related to the seasonal cycle. The differences in the number of adults between e.g. January and July may reflect actual changes in population densities which can well have occurred in the course of several generations separating July from January. In the (unlikely) extreme case, the differences which the defendant has interpreted as phenological differences may have no causal relationship with seasonality at all, the researchers may have simply hit different phases of the population cycles of particular species. In other words, do the seasonal patterns result from phenological adaptations of the involved species, or do we see just a mechanistic outcome of ecological interactions? How could we eliminate this ambiguity?

Another point to discuss is the relative role of different selective forces on the phenological patterns in Lepidoptera. I personally believe that (in our native temperate zone) the main drivers of seasonal patterns are 1) phenology of larval host plants and 2) seasonal dynamics in predation risk. The defendant seems to have a slightly (but not completely) different view, and the things may be different in the tropics indeed. Let's discuss! On page 32 resource partitioning is mentioned. Does this mean that lepidopterans compete over adult resources on Mount Cameroon?

The used diversity indices appear not to contain any phylogenetic information. I understand that phylogenetic relationships of the moths (but perhaps not of the butterflies) are not known well enough. However, I would like to know the opinion of the defendant on the utility of phylogenetically corrected diversity indices in this context (implying that two closely related species contribute less to the diversity index than two distantly related species).

Further, the authors have found that lepidopteran communities are affected by forest openness, plant diversity and, to lesser extent, by forest structure (III). These parameters of vegetation are in turn modified by the activity of forest elephants (IV). One may criticise these studies as being too descriptive with a limited logical role of general *a priori* hypotheses. It could also be said that the causal factors behind the detected patterns remain too obscure. However, I understand that, at the present stage of knowledge, these shortcomings are unavoidable and thus they are actually no shortcomings. We have to start with descriptive data.

One obvious source of potential criticism is related to potential systematic bias in trap efficiency. It can hardly be questioned that the efficiency of both light and bait traps can be affected by parameters of vegetation (both in space and time). How important may this bias be in the case of your study? How can we estimate and how could we avoid this bias?

I am happy to see that the defendant has also been involved in taxonomically oriented research (VI, VII, VIII).

In this context I would ask him to characterise the present state of taxonomic and faunistic knowledge about (West-)African lepidopteran fauna, and our knowledge about the knowledge. I mean that how easy is it to find enough information to be reasonably sure that a particular species is undescribed, or just new for Cameroon?

July 02, 2019

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Review PhD thesis Vincent Maicher

'Biodiversity patterns of butterflies and moths on Mount Cameroon'

The PhD thesis of Vincent Maicher consists of eight main chapters, a general introduction chapter and a chapter providing an overall conclusion and a summary of results. This summary, together with the so-called 'annotation', allows for an easy overview and understanding of the key aspects tackled, despite the indeed large and diverse amount of content within the PhD. The quality of the actual research, the novelty, as well as the clarity of writing throughout, further contribute to the high quality of this thesis.

The focus of the thesis is on understanding patterns of biodiversity across a complete elevational gradient of natural forest cover on Mount Cameroon. The study involved standardised sampling of species subsets of both butterflies ánd moths, which is indeed a strong aspect of this PhD. Sampling was done at seven altitudes, and this during three seasons between 2014 and 2017, which nicely allowed testing effects of seasonality, next to the effects of forest habitat variables, across the elevational gradient. The thesis also looks at the ecosystem value of forest elephants, via their effect on diversity levels. Furthermore, it includes three chapters with valuable faunistic records, and a final chapter on the biodiversity value of coastal forest, highlighting the need to better protect such unique ecosystems.

I here review the chapters, adding four questions:

The **General Introduction** gives a concise but good overview of the current state-of-the-art of the various topics touched upon by this PhD research. Apart from giving a literature review and background knowledge essential to position and frame the research, this chapter also nicely indicates where current knowledge is lacking and how this PhD helps to address such gaps. The introduction covers topics such as biogeography, Lepidoptera as model systems for biodiversity research, and diversity of tropical rainforest Lepidoptera along elevational gradients. It sufficiently introduces the Mount Cameroon study system. The chapter ends with a clear overview of the aims of the thesis.
(Minor mistake: p.2, 1st par. species richness and favourable climatic conditions are negatively correlated with increasing, not decreasing latitude, as latitude is 0 and 90 degrees at the equator and poles, resp.)

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Chapter two, which is published in *Ecology and Evolution* (2018), reports on an extensive and detailed study of several groups of butterflies and moths in the lower parts of Mount Cameroon. Sampling was done via both bait- and light trapping. This multi-taxon study investigates how seasonality affects diversity in an extremely wet environment, with GLMMs showing high seasonal specialization of several groups, while the multi-taxon aspect allowed showing that different groups reacted differently to seasonality. For instance, fruit-feeding butterflies show a different pattern than fruit-feeding moths. It is generally a strong aspect of this PhD that it tries to dig deeper than broad-brush generalisations for Lepidoptera as a whole, and this via ecological mechanisms linked to traits typical for separate subgroups. Also, the authors make a valuable link to global climatic change in their discussion, saying that the observed strong seasonal patterns could indicate a high sensitivity to disturbed climatic patterns, which in turn may affect the whole ecosystem as Lepidoptera are such important players within ecosystems.

Chapter three contrasts species richness and community composition of fruit-feeding butterflies with fruit-feeding moths in terms of effects of several habitat variables linked to forest openness, forest structure, and plant diversity in lowland forests, and this for both understorey and canopy strata, which is another strong characteristic of this PhD. Although the results are at times hard to follow, GLMMs show relatively similar responses of both butterflies and moths, with understorey Lepidoptera mainly sensitive to canopy openness, and to plant diversity too, while canopy Lepidoptera are mainly affected by forest structure. So, all three factors appear important in shaping Lepidoptera communities. The authors discuss several mechanisms that could explain spatial distribution of Lepidoptera, and they highlight that there is a need to sample both understorey and canopy.

- **QUESTION 1:** It appears you sampled four times as intensively in the understorey than in the canopy layer (within each plot four traps were installed at ground level and only one at 20 m height). Despite this unbalance, all analyses were first run for the pooled datasets. Did you correct for this unbalance? If not, are the results for the pooled groups not merely a reflection of the results for the understorey groups? (E.g. no variables significantly explain species richness of neither understorey butterflies, nor pooled butterflies; DTnb and MxTDF explain both understorey and pooled butterfly and moth community composition, resp.) Would it anyway not be better, clearer and more concise to only present the results for understorey versus canopy samples?
- **QUESTION 2:** Forests typically exhibit a diverse vertical structure, with several niches along the vertical gradient, especially so in tropical forests as they are generally characterised by a strong multi-layered structure. So, one could expect that this results in varying moth community assemblages along the gradient. For instance, recent research (De Smedt et al. 2018, *Insect Cons. Div.*) at ground level and at five different heights (7, 14, 21, 28 and 35 m) in a temperate forest showed strong vertical stratification, resulting in distinct moth communities in different strata. However, for tropical forests, vertical stratification is typically addressed by 'simply' comparing the canopy with the understorey layer (e.g. Ashton et al. 2015, *Glob. Ecol. Biogeogr.*), as you also did here. But sampling at only one height of 20 m does not cover the whole gradient. Do you believe the simplification of understorey versus canopy layer approaches reality, or is it indeed possible there are more than two communities?

Chapter four neatly contrasts Lepidoptera (and tree) diversity at mid-elevation (two altitudes) for a zone impacted by forest elephants versus an exclusion zone. This work provides evidence that these elephants are a key ecological engineer species, similarly to Savannah elephants, as they positively and strongly impact both vegetation and Lepidoptera communities.
(Mistakes: (i) p .88, 1st par., line 2-3: judging from Fig.6b this should read: "...with a steeper decline in the upland forest."); (ii) p. 85 at three occasions should 'Fig. 1' be replaced with 'Fig. 5'.)

- **QUESTION 3:** Elephant disturbance appears to significantly alter the mean distribution range of Lepidopteran communities, but in opposite directions for butterflies versus moths (here, sphingids and saturnids), at least in 'upland forest' (see p. 88). Range-restricted butterflies benefit from elephant disturbance, while the absence of elephant disturbance benefits range-restricted moths. How do you explain this intriguing result? And why would this effect be absent in montane forest?

Chapter five, which assuming from the abstract was submitted to *Global Ecology and Biogeography*, makes a strong case that seasonal aspects need to be included in studies on tropical biodiversity, especially for studies on elevational gradients, as this chapter is novel in demonstrating seasonal up- and downhill shifts for six out of nine tested Lepidopteran groups. This chapter is an exceptionally important contribution to the science on tropical biodiversity and altitudinal ranges, especially so within a context of assessing the impacts of global climatic change on elevational shifts.

- **QUESTION 4:** How could you with a future study disentangle the relative contribution to the described shifts (of species elevational range) of on the one hand phenologically delayed adult emergence versus on the other hand seasonal up/down slope migrations?

Chapters six till eight prove that the exceptional diversity of Lepidoptera on Mount Cameroon is still largely unexplored; the area appears to be a new hotspot for the *Alucita* genus of the many-plumed moths and a high amount of new country records of other Lepidoptera species is reported on.

Chapter nine, which is published as a short communication to the *African Journal of Ecology*, makes a strong case for inclusion of the last large patch of coastal forest within the national park.

Overall, all datasets appear large and sound, well-analysed using appropriate statistical techniques, while the interpretation of results is done cautiously.

Given the high quality of the work presented, I officially recommend the thesis to be defended, and I look forward to the actual defence, wishing the candidate the very best.

Dr. Thomas Merckx