

Review of the PhD thesis by Pavel Matos Maravi

Michael Balke, Munich

Chapter 1 - Phylogeny and population genetic structure of the ant genus *Acropyga* (Hymenoptera : Formicidae) in Papua New Guinea

This paper is a phylogenetic and population level study of one genus of ants across PNG. With strategic sampling across different geological elements of PNG as well as different habitat types it is contribution to biogeography and community ecology in more general terms. The study design and then methods employed are robust and highly adequate.

The results reveal that there is one very widespread species present in almost all 13 sampling spots, and another one present in 4 sites, both of them also with presence north and south of the major highland chain. Most species were more localized, yet some also have records from both sides of the highland spine of PNG. Thus, it seems that such major geographic barriers had little impact on species level distributional patterns. On the other hand, on the population level, the widespread *Acropyga acutiventris* shows geographic structure. This is according to geological history, but with the deep division also according to habitat type (dry seasonal *versus* more humid climates). This study therefore not only significantly adds to New Guinea biogeography but also challenges the assumption that there is little structuring in species of tropical lowland forest. This might or might not be so, but clearly more studies are needed and this is another step forward.

Chapter 2 - Investigating the timing of origin and evolutionary processes shaping regional species diversity: Insights from simulated data and Neotropical butterfly diversification rates

This paper addresses issues with oversimplified meta analyses of diversification processes which often do not account for incomplete taxon sampling and equally important the possibly significant uncertainties with node age estimates. The author uses tree simulations as well as empirical data from Neotropical butterflies to show that using species divergence ranks in meta analysis might be misleading and urges for a more integrative approach which, ultimately, would need to consider not only abiotic factors but also possibly changes of biotic interactions and preferences. Such an approach has to be developed yet and is certainly difficult to base on empirical data for the majority of

highly understudied organisms, but awareness for the problem would be the starting point for research needed here.

The paper is very well designed and written and I can only say it was a great pleasure reading, especially as it addresses diversification in the Neotropics, one of the more hotly debated themes in ecology and evolution. A very timely paper.

Chapter III - An ant genus-group (*Prenolepis*) illuminates the drivers of insect diversification in the Indo-Pacific

This paper uses a comprehensively sampled molecular phylogeny of an ant clade to shed more light on the evolution of Melanesia / Tropical South Pacific (TSP) species diversity. In fact, this is one of the most extensive such studies in invertebrates to date. The authors present evidence of early to middle Miocene colonization of Melanesia / TSP via the Wallacea. This is older than generally thought possible based on geological evidence or suggested for other invertebrate taxa recently (Tänzler et al. 2015). However, previous studies might have suffered from node age underestimation, and indeed geologists will agree that the timing of land formation in Wallacea and land configuration *per se* remain ambiguous to some degree. Thus, biological evidence such the one presented here can help to illuminate the early colonization history of and across the Wallacea.

The analyses of “ecological shifts, geographic range expansion, and phylogenetic diversification of insular arthropods ecological shifts, geographic range expansion, and phylogenetic diversification of insular arthropods” presented in this paper is excellent, and marks hopefully the beginning of a new era in Melanesian / Pacific biogeography.

Suggested additional references which address these issues:

Toussaint EFA, Hendrich L, Hajek J, Michat M, Panjaitan R, Short AEZ, Balke M (2016) Evolution of Pacific Rim diving beetles sheds light on Amphi-Pacific biogeography *Ecography* 10.1111/ecog.02195

Tänzler R, VanDan M, Toussaint EFA, Suhardjono YR, Balke M, Riedel A (2016) Macroevolution of hyperdiverse flightless beetles reflects the complex geological history of the Sunda Arc. *Scientific Reports* 6:18793 | DOI: 10.1038/srep18793



Toussaint EFA, Hendrich L, Shaverdo H, Balke M (2015) Mosaic patterns of diversification dynamics following the colonization of Melanesian islands. *Scientific Reports*. 5, 16016; doi: 10.1038/srep16016 (2015).

Questions

Q1. I would be very interested in a discussion / comparison of the Taxon Cycle and the Taxon Pulse hypotheses. Does the Taxon Cycle indeed imply that specialisation is reversible, e.g. – in short, out of narrow endemism comes a dispersalist? In terms of ants or e.g. butterflies, which properties need to be “invented” (unscientifically spoken, evolved, or activated). How does this relate to the Taxon Pulse? And would this not also relate to the Supertramp concept to some degree? What is a marginal habitat?

Q2. In BioGeoBEARS you use “incorporation of paleogeographical reconstructions as relative dispersal rates across areas over time periods”. How can we assign confidence in the timing and extend of emergence of proto areas? As we speak of geological / evolutionary time, might ancestral species not evolve very different dispersal capabilities over such time?

Q3. A question with regard to sampling – in paper 1, presence in a surveyed locality can be highly unpredictable – stochastic, so how confident can we be with the data at hand? *Pallida* and *acutiventris* are sister species and syntopic at least in Weam (S PNG), are others also like that?

Michael Balke, 12.October 2016

Posudek doktorské disertační práce

Matos Maraví, P. F. (2016). Biogeography and evolution of Melanesian and South Pacific ants

Overall:

In my opinion this is an excellent PhD thesis, the best in its field that I have seen at our department. Both the published papers and the manuscripts are of very high quality. The author additionally has a much larger publication record than only those papers included in the thesis.

I have a rather long list of questions, which however reveal not a poor quality of the thesis but on the contrary its analytical complexity and the complexity of the studied group and the area.

Introduction:

The Introduction to the thesis is well structured and well written with an appropriate length. All subchapters contained the most relevant information and literature. The Results chapter of the Introduction provides a well written overview of own results and published information embedded within the present knowledge of the historical biogeography of the studied area.

1) Most of the focus in the biogeographical chapter is given to paleobiogeographical possibilities of colonization and its reflection in the phylogenies of the studied ant groups (which is perfectly correct) but *I have missed some general information on the biology of ants in the studied area relevant to the posed biogeographical questions* * (apart from the classical taxon-cycle associated proposed colonization associated mechanisms). I would be happy just for the sake of my curiosity *to hear some discussion of ant biology as pertaining to biogeography and colonization potential and mechanisms during the defense. I would in this context also very much welcome comparisons between ant endemism ranges and e.g. mammal or bird endemism (sorry if you do not like this choice, but these are the groups from the area I know best leaving aside fishes which are not comparable) to give one the idea about indirect evidence for dispersal capabilities. A combination of observation of patterns and deduction leads me to conclude that ants are better dispersers than even the birds among the vertebrates. What is your opinion on this?*

General note on supplements:

It would have been nice to have the thesis including also the supplements of the published papers and especially the manuscripts because even today one can read the thesis without access to the internet (as I initially tried to do). Supplements to the papers are quite considerable; for Chapter III supplement 2 is 40 pages long and contains virtually all the needed information for the review process.

Chapter I (published paper):

- 1) How does the author substantiate the use of different models of evolution between the BI and ML analyses and at the same time the use of the same model for the various markers within each analytical approach (BI vs. ML)? (pp. 43/44 of thesis)
- 2) Why was in BEAST used the birth-death speciation process and not a coalescent model? (p. 44) See your own comments related to this in the first half of the last paragraph of the paper before Conclusions (p. 50).
- 3) There is no mention regarding congruence of the mtDNA COI with the nDNA markers (pp. 45-47). What was the degree of congruence?
- 4) Why was only one individual per colony analyzed in the population analysis? How many queens do these ants have per colony? Always just one? Has it been proven that also genetically the colonies are always derived from just one queen in this genus of ants?

Chapter II (published paper):

- 1) I really liked this paper for a number of reasons. Since I am always interested predominantly in particular histories of concrete taxa my question is to which extent can these or similar (simulation) studies reveal group-specific extinction events (which is relatively easy also with other approaches) but also group-specific past diversity patterns?

Chapter III (manuscript):

- 1) Why have you not used coalescent models for species boundaries delimitation (as in your Paper I)? Solely relying on branch lengths is to me unrealistic. More generally, how about “paraphyletic species”? What is your stand on these entities?
- 2) **Have you also attempted a completely unconstrained biogeographical analysis? It is hardly surprising that under the used models the biogeography of the studied group closely matches palaeogeographical reconstructions. What if your ants do not match palaeogeography(ies) (see next question) and you are forcing this explanation onto the data through your models? This concern is even more obvious in another paper by you on Caribbean butterflies – there it is clearly evident that the biogeography of the group is forced onto the palaeogeographical reconstruction. If you model your results using a wrong paleobiogeography (and there always are competing paleobiogeographies) than your results are wrong. All paleobiogeographies out there today can be wrong. This approach also virtually dismisses group-specific biogeographies of the given clades that need to have no or little connection with paleobiogeography. In my view one should first always pay attention only to the biogeographical patterns within the data, then proceed to modeling, and if the modeling is not in agreement with the raw biogeographic patterns than start asking questions. The first step is in my view indispensable.****
- 3) How did your models deal with probabilities of dispersal based on geographical distance? More specifically is it realistic to have all long distance dispersal drastically reduced in probability in this group of animals?

- 4) Have you tried also other value settings for your translations of palaeogeographical reconstructions into dispersal rates? If yes, how much did the results differ? If not, what was the rationale for using these exact values?
- 5) Was there any indication that the absence of possible vicariance in the BAYAREALIKE analyses was the reason they were outperformed by the DEC models? If not what do you think was the reason for the better DEC performance?
- 6) Am I correct to interpret the absence of "subset" sympatry in the BAYAREALIKE models as prohibition of the possibility of sympatric radiations? If yes, is it not that rather inappropriate? Is there no possibility for sympatric radiations in ants?
- 7) I think that models with zero extinction rates are as unrealistic. How do you argue that a diversification model containing this assumption is your best resulting model? Were there really no extinctions? Is there any other explanation? Would the absence of extinctions not violate the hypothesis of the taxon cycle?
- 8) Fig. 5 legend is the same as Fig. 4 legend. But Fig. 5 is well understandable to me even with this error .-) Can you include the correct legend or explanation of the figure into your presentation? (thanks)

Chapter IV (manuscript):

Several of the questions to Chapter III also apply to Chapter IV.

- 1) Why did you use the Yule model in the species delimitation?
- 2) Should not only probabilities above 0.95 be taken as evidence for species boundaries (Fig. 2)?
- 3) Dispersal from the New World to Melanesia (and most other sampled areas) at this time interval (ca. 20 Mya; Fig. 4). I do not think that the 2 explanations in the middle paragraph on p. 145 are relevant or at the least sufficient. To me it very much looks like long-distance dispersals which is also supported by the majority of your analyses. Your own results within Melanesia following colonization from the New World seem to support east-west colonization. See my comments 3 and 4 on Chapter III stressing concern about long-distance dispersal in your groups.
- 4) How did you include the missing species into the diversification analysis (Fig. 5)?
- 5) To me based on your results the increase in diversification in the clade including both New World and Melanesian groups appears to have happened in the New World? Do you agree?
- 6) The title and introduction of the manuscript are all about the taxon cycle hypothesis, yet most of the results and discussion do not mention it and do not appear to be particularly relevant. In general Chapter III is text-wise in a better shape than Chapter IV (I think the author is aware of this and the order of the chapters also suggests this).

I have raised only one in my opinion serious concern (points 2-4 on Chapter III; this group of concerns is however contained in most papers by the author) the ignorance of which however does not seem to bother the biogeographical community as this type of analysis now becomes prevalent. There is simply these days too much modeling and too little independent interpretation of ones own data and patterns.

I fully recommend the thesis.

V Českých Budějovicích

13. 10. 2016

Mgr. Oldřich Říčan Ph.D.

A handwritten signature in blue ink, consisting of several loops and a long horizontal stroke, positioned below the printed name.

Presented PhD thesis "Biogeography and evolution of Melanesian and South Pacific ants" written by Pável Fortunato Matos Maraví consist of 36 pages of introductory essay and four articles. However, two of them are unpublished and one is primarily neither about ants, nor Melanesia and South Pacific region. Thus only one paper is published and on the right topic. When I considered this content, I afraid that all the thesis will be problematic. I have found that my first view prejudice were mostly unjustified. However, number of published papers is quite small for a PhD thesis in my opinion.

Followed reading if introductory part makes me positively tuned. The texts were fluently written, nearly without type mistakes. I really like such analyses about history of animals based on DNA and morphological datasets, which seems to be comprehensively analysed. This always bring some interesting "stories based on real events", of course as our knowledge about reality can allow. I was also satisfied with inclusion of chapter II (the test of diversification models on Neotropical butterfly datasets) to the ant context of dissertation thesis.

During the reading of chapter I (*Acropyga* study), I found that methods described in an introductory part (pages 13-17) are not general enough and does not cover methods in this chapter. It rather corresponds to unpublished manuscripts (chapters III and IV). Article about Papuan *Acropyga* seems to be well conducted. I just have not found Australian haplotype(s) in the haplotype network on the figure 3C. Why it was not included? In general, I would prefer much shorter discussion about the pattern of *A. acutiventris* distribution. It is overly long and the data insufficient for such discussion. There is very likely a strong bias in molecular dating and the sampling should be denser, especially from Australia, but also south of Central Cordillera. I acknowledge that authors note such likely result bias and insufficient sampling in their results. Accordingly, I expected that the author should be more careful in branch support reliability in manuscripts III and IV. I disagree that $PP > 0.95$ is strong support. I am used to accept 0.99 or 1.00 PP, everything lower is not worth of discussion, because it cannot be called reliable. In the case of figure 3 in chapter IV the stare scale for Maximum likelihood bootstrap is missing, so I cannot make a comparison of branch support for your results in PP and ML. In other way, I have to say that I like both manuscript chapters III and IV. I know that we always working with data that we are able to make and we can reach. I acknowledge, how comprehensively acquired data are analysed and I am quite certain that both manuscripts will be published in good journals and will be accepted soon.

Chapter II (test of diversification models) is very interesting and valuable article. The problem is that the results depend on quality of phylogenetic tree resolution and taxon sampling. Of course, this is problem well known also to the author. Because I do not have a good knowledge about mentioned methods, I would be very glad when the author can explain how it can be used in standard phylogenetic-biogeographic studies.

Firstly I have afraid that the quality of the PhD thesis will be problematic, but after reading it I am certain that Pável Matos Maraví deserves PhD title without any doubt.

In Prague, 13.10.2016


Mgr. Jakub Straka, PhD