



Prague, June the 2nd, 2020

The thesis "*The effect of tropical land use change on soil-dwelling ants and termites, their interaction and on ecosystem processes they affect*" submitted by Ph.D. candidate Jiří Tůma at School of Doctoral Studies in Biological Sciences, FS, USB ČB is meeting the formal criteria. The thesis spans over 131 pages including 11 pages of introductory text, three chapters made of two published papers and a late MS draft, and four pages of summary. The standard of the thesis preparation is very high, and I could find just a few marginal issues.

The core of the thesis is formed by three scientific contributions as follows:

Tůma J., Eggleton P. & Fayle T.M. 2020: Ant-termite interactions: an important but under-explored ecological linkage. *Biological Reviews* **95**: 555-572.

This paper represents a review on ant-termite interactions, published already in a very good journal. I find it well-written survey of an important relationship in the tropics. Authors prepared a sound overview of a particular phenomenon playing important role in the tropical soil biology. Although the text covers many interesting phenomena, it is not exhausting, and many additional observations could have been included. I don't mean this as a critique but rather as a simple statement – the focus at broader readership is probably required for such kind of review, which could be written in another way to satisfy few experts in the field, and would then become publishable in a specialised journal of much smaller impact.

Tůma J., Luke S.H., Davies R.G., Eggleton P., Klimeš P., Jones D.T., Konvičková H., Maraví P.M., Segar S.T. & Fayle T.M.: How does rainforest logging and conversion to oil palm affect soil-living ants and termites and ant-termite predation rate?

Quite well-written piece of work, publishable in a good journal. The methodological approaches are sound and novel. The text still contains some imperfections here and there including formal issues, however, these can be easily improved and I tend to believe they already were during the thesis processing. Missing explanations in the figure headings sometimes disallow full understanding. I generally find the text a bit too wordy, or the form of presentation a bit old-fashioned: I believe the paper can be raised a level up if significantly shortened by cutting off the parts weakly connected to the take-home message.



Tůma J., Fleiss S., Eggleton P., Frouz J., Klimeš P., Lewis O.T., Yusah K.M. & Fayle T.M. 2019: Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation. *Applied Soil Ecology* **144**: 123–133.

This chapter is published article represents a nice and novel piece of work. The methodology is pioneering, and, although it allows quantification of a minor fraction of bioturbation only, it represents a very important contribution to the existing knowledge.

To conclude, the candidate participated at important and truly novel research, which was, among other outcomes, summarised in three scientific works summed up in this thesis. The candidate is the first author of all contributions what shows that his input to these papers was very high. He thus proved his ability to conduct an interesting field research and to publish the outcomes in leading journals, what is the main expectation from the Ph.D. studies. I am happy to say that this thesis is high above the average, I fully recommend defending the thesis, and granting to the candidate scientific degree Ph.D.

Some minor points and questions are as follows:

Annotation

Studying ant-termite interactions in the tropics in natural and disturbed habitats makes a good sense to me, however, the switch between the topics is too abrupt here: „some ant species have developed sophisticated methods that enable them to specialise on termite predation. My field sampling demonstrated that soil ants and termites are susceptible to habitat degradation, with logging having minimal...”

Introduction

The Introduction provides important insights into the natural habitat losses in the tropics due to expansion of oil palm plantations. Although the text is clear and sound, the statements often sketch the future prospects (“Recently...”, “... in the near future”), while they are supported by papers 10 or more years old. What is the current situation? What changed in the last few years? Do the negative trends continue, do they slow down or accelerate?

Ants have undoubtedly multiple crucial functions in the tropical habitats, however, concerning the soil, it is termites who are responsible for most of the soil-formation processes (grinding the dead plant matter, soil organic matter decomposition, transport of enormous amounts of materials, creating the soil heterogeneity etc.), while ants are rather inhabitants of this environment. The impact of ants on soil aeration, soil watering or soil properties is indeed rather negligible compared to termites, and I would thus find more logical to start from termites and their impact on the tropical soils... Among other issues of this part (P5-7), most of the



examples of ant impact on the soil come from higher latitudes, and have thus a little in common with the situation in tropics.

The text on termite decomposition abilities is somewhat superficial and lacks a clear structure. The part on nitrogen-fixation abilities is misleading: Although all termites studied so far contain symbiotic microorganisms carrying nitrogen-fixing genes (Nif family), this pathway is active predominantly in wood-feeding termites that cannot access other sources of organic nitrogen (typically *Kalotermitidae*). Most of termites satisfy their nitrogen needs by digesting microorganisms from their food, and some soil-feeding termites reveal in their gut amounts of ammonia comparable to carnivores (Ngugi & Brune 2012, *Environmental Microbiology* **14**: 860–871).

P5: "Ants and termites are both highly developed, eusocial insects." Or "... advanced behaviour ..." I don't like such expressions much, as they impose a feeling that "lowly developed" or "retrograde behaviour" belong to less successful lineages. However, there is nothing like that, there are just different ecological strategies of competition over limited resources during the evolutionary times...

P8: "Since the main breakdown processes take place in the nest and the collected food items are stored there, the nest represents a nutrient-rich hotspot in the environment" This is not true! Firstly, the digestion takes place mostly in the gut (fungus combs in *Macrotermitinae* only) of workers and soldiers that may but don't have to live in a discreet nest. Secondly, there are relatively few termites storing food within their nests, and all these are grass-feeders living in savannahs. (The same might be true for certain soil-feeders, however, the only paper dealing with this topic is Hellemans et al. 2019, *Oecologia* **191**: 541–553)

Chapter 1

P31: "... dehiscence that mostly occurs in soldierless termite workers (Sands, 1982), although it has been found in soldiers of the genera *Glossotermes*, *Serritermes* and *Apilitermes* (Deligne & DeConinck, 2006; Šobotník et al., 2010a)." Not true: Soldiers of all these three genera release defensive secretion originated from the frontal gland, as described in original papers (source for *Serritermes* is not cited - Costa-Leonardo & Kitayama 1991, *Sociobiology* **19**: 333–338). This behaviour should thus be called autothysis.

Assoc. Prof. Jan Šobotník, Ph.D.



Reviewer Report - Jiří Tůma thesis. The effect of tropical land use change on soil-dwelling ants and termites, their interaction and on ecosystem processes they affect.

This interesting thesis investigates interactions between ants and termites and the impact of tropical land-use change on these groups and their functioning in ecosystems. The work includes a detailed literature review, field-based studies of diversity and abundance across a land-use change gradient, and novel measures of ant and termite-mediated bioturbation. Overall, this is a scholarly piece of novel research. I look forward to discussing the project in detail and include my notes on the chapters below.

Introduction. This section provides an overview of land-use change in the tropics and Southeast Asia in particular, the impact of oil palm expansion, the role that ants and termites play in ecosystems, and the interaction between ants and termites. Overall, this places the thesis in context well. However, I did think that some sections were quite sparsely referenced and I would recommend going through and making sure that each statement is properly supported. I also felt that it was missing a section specifically discussing the role of ants and termites in agricultural systems, especially given the large focus on oil palm in this thesis. As ants and termites are heavily impacted by microclimate, I think that there could also be more of a discussion of the interacting impacts of climate change (or events like El Nino) and habitat disturbance on ant and termite communities.

Specific comments:

Page 2 – “Concerningly, the tropics are among the most strongly affected regions by human-caused habitat change while also being global biodiversity hotspots (Brooks and Spencer, 1997; Myers et al., 2000).” Presumably this is referring to contemporary change? I think this should be qualified.

“Pesticides and herbicides are used regularly on plantations to suppress pests and undergrowth” Like other statements, I think this needs some backing up. I’m also not convinced that this is true for pesticides, which tend to be quite sparsely used in oil palm compared to many other crops – I think this statement needs qualifying.

Page 3, Where certification schemes are mentioned, I think it is worth making the distinction between new plantation establishment and management within established plantations. New plantations lead to a loss of forest habitat and biodiversity. Choice of where to establish new plantations and limiting their spread is key to combating this. Recommendations of management within plantations will not help this, but could be useful to support important ecosystem functioning in established plantations.

Page 3 “There are low densities of deadwood, leaf litter and understory vegetation. The only organic materials left are palm fronds (leaves) piled in rows between the palm trees and patches of scattered used oil palm fruit bunches.” There are quite a few studies measuring this – it would be good to reference them here. I also think this is very variable between plantations and what this describes is the plantations where this study was based in. I think the variability that can be found in existing plantations should be discussed more clearly here.

Page 3 – Resilience in ecosystem functions is mentioned, but only briefly: “Species diversity is vital for ecosystem functioning (Schmidt et al., 2009). An ecosystem that is reliant on only a small number of species to provide ecosystem services is more susceptible to failing to provide these in altered conditions”. It would be good to discuss this in a little more detail. I would also like to talk about this in relation to the findings of this thesis during the viva.

Page 9 - “Affected plants can also cope better with herbivory, as termite mounds provide sufficient amounts of nutrients to regenerate leaf area and survive” Suggest rewording to “Affected plants can also cope better with herbivory, as termite mounds provide sufficient amounts of nutrients to facilitate regeneration of leaf area and increase plant survival.”

Chapter 1. This published paper represents a useful review of the literature and does an excellent job of describing the ecological importance of ants and termites worldwide, their likely interactions, and key knowledge gaps. Overall, this was engaging and well written and Figure 2 was innovative in specifically flagging the global distribution of ants and termites and their overlap. I would have liked to hear more about how the literature was screened to identify the studies included in this paper. There are some details of this in the additional material (S1), but I would like to discuss this in the viva. In particular, was there any scope in using some of the methods from systematic literature reviews (snowballing, screening other author publication, benchmark papers etc)? Do the search terms preclude any of the literature being located? I also felt that the number of studies actually identified was quite small – certainly less than I would have thought. I think this is interesting in its own right. I was also expecting to see a bit more about potential secondary interactions between the two groups, mediated by changes in the environment and influences on other biota.

Specific comments:

Figure 1 – This is very interesting. It would be nice to show how this varies between temperate and tropical regions.

Page 26 – “It is unclear whether any of these ant–termite interactions have progressed beyond being ‘by-product’ mutualisms (De Jaegher, 2017) to a stage where there is reciprocal altruism between partners.” I would like to hear a bit more about this and also to discuss what conditions are necessary to progress to reciprocal altruism.

Page 30 - “If termites are an important prey group for ants, then we would expect correlations at the community level in terms of numbers of species of the two groups.” I am not sure this is necessarily the case. I’d like to discuss this in the viva.

Chapter 2. This is the first of the fieldwork chapters and investigates how ant and termite abundance, species richness, diversity and composition vary between primary forest, logged forest and oil palm plantation. The study is the first to do this systematically at the species level and includes a wealth of useful information. Importantly, it also uses DNA barcoding approaches to investigate the degree of termite predation by ants across habitats. The study finds some clear differences in abundances and composition, but also some surprises – for example termite abundance does not change across habitats. I did wonder whether more could be made of a comparison with the Luke et al 2014 paper, which found some consistent but also some contrasting patterns to this study. Although only identified to genus level, this essentially used the same methods and was from exactly the same area. It would therefore make a very interesting way of checking consistency of results over time. The finding of relatively high levels of termite predation across habitats is important and very novel. I wasn’t quite

sure why only a constrained ordination was chosen for the community analyses – I would like to discuss this in the viva. The importance of identifying to species level is mentioned a lot in this chapter – this could be specifically tested by analyzing at both the genus and species level and comparing results. This would lend considerable weight to the argument. I wasn't sure from the methods what proportion of the data were collected in the two field seasons, or whether all sites were sampled at both time periods? I think this needs clarification. I also wasn't sure how (or if) this was taken into account in the analyses? For example, this could be driving things like the observed impacts of soil temperature on ant community composition. I think that the impact of the El Nino event on the results should be more clearly discussed. For example we might expect the impacts of habitat degradation to be more pronounced in an El Nino Year. I was also interested to see the much higher variability in ant individuals per plot in logged forest than primary forest – again, I felt this could be discussed and would like to hear more about why this could be. Finally, as this is just one oil palm site and management varies quite a bit between plantations, I think some of the results need qualifying a bit.

Specific comments.

Abstract - "This deforestation is caused by expanding oil palm plantations throughout the region with serious impacts on biodiversity." This sounds like oil palm is the only driver – this needs rewording.

Abstract - "Furthermore, 32% of analysed ants contained termite DNA and this rate differed between ant taxa, but was similar across habitats" – I think this is a take-home message and it would be good to include the specific percentages for each habitat here.

Introduction – As with the introductory chapter, I think this slightly conflates the impacts of new plantations on biodiversity and management for functions within existing plantations. I think this would benefit from some additional clarification.

There are some minor inconsistencies in capitalization and spelling here and throughout the thesis – the 'project' in SAFE Project is sometimes capitalized and sometimes not. Southeast Asia is sometimes SE Asia, sometimes Southeast Asia, and sometimes South-East Asia. I would recommend sticking to one.

Figure 3 – it would be good to have the individual sites plotted, as in the supplementary material.

Without this, it isn't possible to see the variation in the data.

Figure 4 could be removed – it is redundant if Table 2 is included.

Page 60 "The soil temperature was negatively correlated with litter depth and positively correlated with soil cover (note the opposing direction of the arrows representing these variables, Fig. 3B)." As this is a constrained ordination, I don't think it is possible to conclude this from the figure - you would need to do a PCA or something based purely on the environmental data to demonstrate this.

Page 64 "Furthermore, our sampling sites in oil palm were of a young age (10 years), so the effect of terracing (soil scraping and levelling prior to oil palm planting)" - 10 years isn't that young for oil palm and it already has a closed canopy. Suggest tweak to the wording to clarify this.

Chapter 3. This is the most innovative chapter of the thesis and introduces novel methodology to investigate the impact of habitat change on soil perturbation and the changing roles of different taxa in supporting this. The chapter finds that termites are responsible for a very high proportion of standing bioturbated soil across habitats, but that shorter term and smaller scale bioturbation was mainly related to earthworm activity. Significantly, *Macrotermes gilvus* was overwhelmingly responsible for standing soil in oil palm plantations. I was interested to see the very high variability in measures within habitats that often meant there was no significant difference between habitats. I would like to discuss whether any other environmental variables were measured and whether these

could be included in models to address this variability? Are there any issues with apparency being higher in oil palm (with reduced leaf litter etc), meaning there is a bias in recording across habitats?

Specific comments

Methods – I'm not completely clear what data fed into the "a bioturbator diversity index" and would like some additional details on this.

Discussion – as with the previous chapter, I felt that the impact of the El Nino could have been discussed more, particularly the potentially heightened impact of this dry period in more degraded and open habitats. For example, presumably the higher death rates of *Dicuspidermes* spp. mounds in logged forests could be related to the El Nino event interacting with the hotter and more variable conditions in logged versus primary forest?

Thesis summary. This is an accurate summary of the thesis as a whole and its implications. I did feel that more could be made of the implications of the findings for oil palm management. For example, the results highlight the vulnerability of oil palm soil perturbation owing to reliance on one species, but I think I would also highlight that this process is, as yet, maintained. I also think that many of these effects could feed into specific Principles and Criteria of the Roundtable on Sustainable Palm Oil, a number of which are related to the maintenance of sustainable soil practices. I think these could be specifically referenced here.

I have enjoyed reading this interesting thesis and look forward to discussing it further at the viva.

Yours faithfully,



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