Yale SCHOOL OF THE ENVIRONMENT

Liza Comita, Ph.D.
195 Prospect Street
New Haven, CT 06511
Phone: 203-432-5100
Email: liza.comita@yale.edu

July 10, 2021

Department of Zoology
Faculty of Science
University of South Bohemia

Subject: Review of the PhD thesis of **Piotr Szefer**

Summary:

In the PhD thesis entitled *Fungi, Herbivores and Predators as Determinants of Secondary Succession in Tropical Rainforest*, Piotr Szefer presents novel results from experimental studies conducted in secondary forests in Papua New Guinea. The first chapter focuses on the role of fungal pathogens vs insect herbivores, as well as the impact of predators, in driving vegetation dynamics during the early stages of forest succession and finds that insect herbivores enhance plant diversity, while fungal pathogens and predators have little effect on the plant community. The second chapter provides a deeper examination of the effect of predators on insect herbivores and plant-herbivore interactions and finds that herbivorous insect communities in this system are structured by bottom-up rather than top-down controls. The third chapter shifts focus to examining site- and species-level drivers of leaf litter composition and finds that leaf nitrogen content and, to a lesser degree, forest successional stage were significant drivers of decomposition rates. Finally, the fourth chapter is a software note that describes a new software package for the analysis of ecological networks.

Overall assessment:

I found the thesis to be novel with well-designed experiments and interesting findings. It is impressive that three of the four chapters have already been published in highly ranked journals in the field of Ecology. I believe that the thesis can be accepted without hesitation. Below I summarize the main strengths and weaknesses of the thesis, and include some questions to be answered during the defence.

Main Strengths:

The thesis is highly novel in that it is one of the first studies to examine the role of plant enemies in shaping secondary succession in tropical forests. Previous studies of tropical forest secondary succession have looked almost exclusively at the role of abiotic factors, particularly light availability, in driving plant dynamics over time. In contrast, this study tested whether biotic interactions play a role in driving ecological succession. Rather than look only at one class of interactions, the thesis examined effects of both insect herbivores and pathogenic fungi, as well as tri-trophic interactions, specifically the effect of predators of insect herbivores. Together, Chapters 1 and 2 provide novel insights into how bottom-up vs top-down processes structure ecological communities during early secondary succession. Another strength was the use of an experimental approach in Chapters 1 to 3, which was critical for teasing apart the different potential drivers and identifying causality, rather than simply relying on correlations. This was

particularly clear in Chapter 3, where the experimental design allowed for the independent assessment of the role of forest age and species-specific leaf traits on decomposition rates. Inclusion of plant functional trait data in Chapters 1-3 was also a strength, since the functional trait approach allows for more general conclusions about how plant species' ecological strategies influence plant-enemy interactions, and for better predictions about how other plant species at other sites will be effected. Finally, Chapter 4 provides a useful tool that will motivate and permit future studies of ecological networks, and thus is likely to have a large impact on the field of ecology.

Main Weakness:

The main weakness of the work is that the short duration of the study and the focus on initial forest recovery following disturbance restricts conclusions to the earliest stages of succession (in the case of Chapters 1 and 2) and to the initial stages of decomposition (for Chapter 3). (However, I acknowledge that long-term studies are not feasible for a thesis.) In addition, the conclusions from Chapters 1 and 2 may not be generalizable to other tropical forest landscapes where larger areas of forest are disturbed and thus dispersal limitation may play a larger role in determining the composition of both plant and insect communities due to a lack of nearby forest remnants. Because the study only looked at vegetation dynamics in disturbed areas, it is also unclear whether the patterns found (ie the importance of insect herbivores, the lack of effect of pathogens and predators) are specific to early successional conditions or reflect what is going on in intact mature forest in this area. For example, it is not clear whether the lack of pathogen impacts on plant diversity is due to the fact that pathogens are unimportant during early secondary succession or because pathogens are overall less important in forests in this region of Papua New Guinea compared to in the Neotropics (where most of the tropical plant-pathogen studies have been conducted).

Questions to be addressed at the defence:

What types of fungi were eliminated by the fungicide used? Might it have failed to eliminate some pathogens that have been shown to be important in driving tropical tree seedling mortality (eg Oomycetes) or also affect rates of decomposition, and therefore nutrient availability?

How can you explain the significant effect of insecticide treatment on Shannon diversity, but not on species richness or evenness, when those are the two aspects of diversity that are jointly accounted for via the Shannon index?

How specialized are insect herbivores in this forest and does specialization differ between secondary and mature forests? For both insect herbivores and their predators, to what extent do 'generalists' show host/prey preferences, and how do you expect that to influence plant and insect community composition and diversity?

Have there been any studies evaluating the importance of insect herbivores and fungal pathogens in promoting plant diversity in mature forests in this region?

Sincerely,

Liza S Comita

Dr. Liza S. Comita
Professor of Tropical Forest Ecology
School of the Environment
Yale University

Written assessment of PhD thesis: Fungi, herbivores, and predators as determinants of secondary succession in tropical rainforest
Candidate: Piotr Szefer
Reviewer: Dr Sofia Gripenberg

Background and wider context:
The overarching theme of the thesis is biotic interactions in the context of tropical forest succession. The explicit focus on secondary forests is highly relevant: A large proportion of tropical forest systems are in relatively early successional stages, yet many of the longstanding 'truths' about how tropical forests function are based on studies conducted in primary forests. The fact that the focal study system is located in a part of the world in which the dynamics of plant communities have not yet been studied in detail makes the work even more novel and important.

Overview and structure of the thesis:
The thesis is comprehensive and well written. It consists of four data chapters plus a general introduction and discussion. Three of the chapters (1, 3 and 4) have already been published in reputable ecology journals (*Journal of Ecology*, *Oikos*, *Ecography*) and, at the time of thesis submission, Chapter 2 had been submitted for publication. Although all data chapters are co-authored, it is clear that the candidate's contributions to the work have been substantial: he is the lead author on three of the chapters.

Specific chapters:
Chapters 1 and 2 make up the core of the thesis. These chapters are based on data from an ambitious field experiment in which plant enemies (insect herbivores, fungal pathogens) and higher trophic levels (vertebrate predators and ants) were manipulated and the responses of the plant community (Chapter 1) and plant-associated arthropod communities (Chapter 2) investigated one year later. The ambition of the experiment is admirable, and the key results of Chapter 1 – that top-down control on vegetation can indeed be an important process alongside the more commonly studied abiotic environmental filtering processes – is interesting, especially since the results on the impacts of specific enemy guilds contrast with some previous studies. By analysing a data set on ~5000 arthropod individuals and their host plant associations, Chapter 2 goes much further in attempting to understand the potential routes through which predators affect arthropods (and indirectly plants) than most other studies have done. The results in this chapter are a bit less conclusive/more open to interpretation than those of Chapter 1, but it will make a valuable contribution to the ecological literature once published.

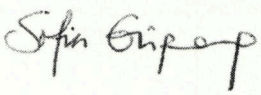
The remaining chapters (Chapters 3 and 4) are more loosely linked to the central theme of the thesis. Chapter 3 assesses decomposition rates in relation to the successional status of plant species and the environmental setting (primary versus secondary forest). This is a well-written paper and although based on an old (previously unpublished) data set collected by others, the candidate's contributions have been substantial as he has been leading the analyses and write-up. The final chapter (a software note introducing a new tool for analysing ecological networks) presents work that was largely led by others. Nevertheless, through his participation in this project, the candidate has demonstrated an ability to contribute to developing tools for data analysis and to conduct research in settings outside the host institution.

Writing an overall introduction and discussion that connects such a diverse set of chapters will inevitably be challenging, and it is not surprising that the candidate has opted to frame the general introduction and discussion mainly around the first two data chapters (Chapters 1 and 2). Some links are made between these chapters and Chapter 3 (for example, the candidate highlights the need for ecologists to better integrate above- and below-ground processes when studying succession and other phenomena), but these connections could perhaps have been developed a little bit further.

Summary and recommendation:
In summary, the thesis is ambitious, novel, and of high quality. Through the thesis work, the candidate has demonstrated that he masters a wide range of research skills, including field-based research in challenging environments, quantitative analyses of large and complex data sets, and communicating the results through high-quality publications. The thesis also provides ample evidence for critical thinking as well as a strong understanding of the wider ecological research field.

I recommend that the thesis is accepted and that Piotr Szefer is awarded a PhD.

Oxford, 9th July 2021



Dr Sofia Gripenberg
University of Reading, UK

As a reviewer I have been asked to present the candidate with 3-4 questions prior to the defence ceremony. My questions are as follows:

1) Results from ecological studies are often context-dependent. How widely are you prepared to extrapolate your results from Chapter 1 to other systems/sites/contexts?
2) Throughout the thesis you highlight the need to study species interaction networks (e.g. fungi-plant-insect interaction networks). What additional insights can a network approach provide into the impacts of natural enemies on plant communities compared to the more commonly used approach of assessing the net impact of different enemy guilds?
3) In Chapter 3, you argue for the need to move from community-weighted mean trait values to species-specific trait values. Could/should this argument be taken one step further, to include variation *within* species?
4) In Chapter 4, you present a new tool for analysis of ecological interaction networks. How do you convince researchers who feel comfortable and happy using R based packages like *bipartite* about the need to switch to *EcologicalNetworks*? Or should they?!