

Report on a thesis submitted for the degree of PhD at the PhD thesis submitted at the Faculty of Science of University of South Bohemia:

Mgr. Richard Čtvrtečka: Host specificity and species diversity in communities of frugivorous insect in lowland rain forest of Papua New Guinea

General points

1. The thesis is based on a great deal of work under challenging conditions. Carrying out any quantified study in the tropics is fraught with difficulties, and the volume of fruit sampled in this project, and the observations made, are very impressive. The data will undoubtedly continue to be of significant value, and the analyses are of great interest.
2. A major focus of the project is whether density-dependant mortality due to pre-dispersal seed / fruit predation can drive plant diversity (Janzen-Connell effect), explored particularly in Chapters 1 and 2. A review of the extensive literature on the Janzen-Connell Hypothesis, especially as it relates to pre-dispersal seed predation, would have been helpful and is an unexpected omission. Why was this not included?
3. It would have been helpful to have had some formal hypotheses arising from the Janzen-Connell hypothesis that could have been tested. For post-dispersal seed predation this is comparatively simple. For pre-dispersal seed predation, testable predictions are more challenging; they might, for example, include a positive relationship between level of seed / fruit attack compared to stand density of potential hosts (noting that that negative effects of pre-dispersal seed predation in high conspecific stand densities could be outweighed by positive effects on pollination and hence fruit numbers (Jones & Comita, 2010)). No information about stand density is provided; was this considered? Were any hypotheses formulated?
4. In chapters I, II and III the assertion is made that the observed low levels of seed predation observed made it unlikely that the insects have a role in maintaining plant diversity as proposed in the Janzen Connell hypothesis (pp 29, 50, 77). This may be correct, but what level of seed-loss would be required for the Janzen-Connell effect to apply?
5. Tropical forests are notoriously heterogeneous for fruit production and, even though New Guinea is not in the major South-East Asian synchronous fruiting zone there are both synchronous and asynchronous fruiting species there (Wright, 2005¹). Were synchronous and non-synchronous species addressed separately? Given the fieldwork took place over a 12 month period and consequently no year-on-year comparison was possible, were fruiting volumes from other years sought to see if the study year was 'typical'? How was temporal heterogeneity addressed?
6. The logic of the argument for rarity rests, as noted in the paper, on the sampling being effective. There are several variables that are not addressed in the paper which may have an effect, and it would be helpful to know whether these were considered.

¹ Wright, D.B., 2005, Diet, Keystone Resources and Altitudinal Movement of Dwarf Cassowaries in Relation to Fruiting Phenology in a Papua New Guinean Rainforest. Pp. 205-236 in *Tropical Fruits and Frugivores*

- a. Phenology. Toy *et al* (1992) found in the phenological study of a Nanophyine on *Shorea* sp that there is a massive mortality early in development caused by the tree aborting its fruit (89.1% - 100% of the original infestation was lost at this stage). Was such an early impact considered? Because sampling was apparently restricted to mature and nearly-mature fruits any early seed predator, such as Nanophyinae, may have been omitted from consideration (there are none listed in the Appendix to Chapter 1).
- b. Were fruit sampled from all of the tree canopy, or only that which was reachable from the ground? Density of weevil attack may not be uniform on the tree. Studies on orchard fruit have shown the effect of tree architecture and local conditions on distribution of insects and attack (e.g. Chouinard *et al*, 1994²; Piñero & Prokopy, 2005³; Simon *et al*, 2007⁴). Silva *et al* (2007)⁵ even found a different within inflorescences on *Mimosa* by a bruchid. How was this issue addressed?

More specific points

Introduction

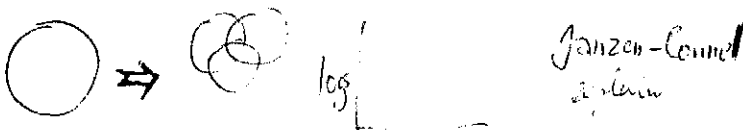
7. P. 2, para 3. While scolytines (note, Scolytinae not Scolytidae) may kill seeds pre-dispersal many are post-dispersal; Moore (2001) discussed both. He also noted that, like some bruchids (but by no means all) some scolytines will attack the seed only when the flesh is removed by vertebrates. The implication that these habits are taxon-related is a little misleading.
8. There seems to be a focus on fleshy fruits rather than dry fruits, and an assumption of vertebrate dispersal (e.g. page 3 half way down). Why is this?
9. P. 3 para 2. “chemicals deter frugivores or reduce their fitness due to lower fruit palatability”. Reducing the frugivores’ fitness through lower palatability seems a little surprising. I could not find the origin of this assertion in Moore (2001).
10. Chapter 1, p. 20. Reference was made to rearing, but this can provide an underestimate due to (i) larval mortality due at least in part to adverse conditions in the collected fruit and (ii) parasitoid attack. What attempt was made to sample actual numbers of larvae? In cases where no larvae were found (e.g. Lamiaceae) were the results based only on rearing or were fruit dissected as well (a faster methodology for presence/absence and recovery of samples for COI testing)?

² Gérald Chouinard¹, Stuart B. Hill & Charles Vincent, 1994, Spatial distribution and movements of plum curculio adults within caged apple trees. *Entomologia Experimentalis et Applicata*, 70 (20), 129–142.

³ Piñero JC, Prokopy RJ, 2005, Spatial and temporal within-canopy distribution of egg-laying by plum curculios (Coleoptera: Curculionidae) on apples in relation to tree size. *Journal of Entomological Science* 40, 1-9.

⁴ Simon, s., Sauphanor, B & Lauri, P-E, 2007, Control of Fruit Tree Pests through Manipulation of Tree Architecture. *Pest technology*. http://www.globalsciencebooks.info/JournalsSup/images/0706/PT_1%281%2933-37o.pdf

⁵ Laura A. Silva; Rita C.S. Maimoni-Rodella; Marcelo N. Rossi, 2007, A preliminary investigation of pre-dispersal seed predation by *Acanthoscelides schrankiae* Horn (Coleoptera: Bruchidae) in *Mimosa bimucronata* (DC.) Kuntze Trees. *Neotrop. Entomol.* vol.36 no.2 <http://dx.doi.org/10.1590/S1519-566X2007000200005>



Chapter 1: Frugivorous weevils are too rare to cause Janzen–Connell effects in New Guinea lowland rain forest.

11. Chapter 1, p. 27. The monophagy of congeneric polyphagy distinction may not be as clear as implied. In the Alcidodes-Dipterocarpaceae association an unpublished dataset suggests that there is a preference in apparently polyphagous species for one or two host species, other associations being from very low numbers of alternate hosts. Was any observation of preferences within polyphagous species made?
12. Chapter 1 p. 28. “The low diversity of frugivorous assemblages documented here could possibly be explained by the fact that interspecific competition in weevils is known to be high (Alves-Costa & Knogge 2005).” The competition examined by Alves-Costa & Knogge is intra-specific rather than inter-specific. However, there may be similar inter-specific competition. Whether such competition is a limiting factor on diversity is another question. I do wonder if ‘density’ was intended rather than ‘diversity’ here. If the low level of infestation recorded reflects reality then this suggests that competition, if it exists, may be of limited significance to either diversity or density. How could it be assessed whether competition is truly taking place? How would such competition affect diversity? Are there other possible limiting factors on diversity in operation?

Chapter II: Low host specificity and abundance of frugivorous Lepidoptera in lowland rain forest of Papua New Guinea.

13. Spelling of ‘specificity’ in ‘Contents’
14. P. 49, para 2 – delete ‘of’ in first line
15. P. 50, para 2 line 6 – there is an “xxx” in brackets – what should this be?

Chapter III Fruit morphology and the structure of frugivorous communities in a New Guinea lowland rain forest.

16. Some typos and grammatical errors to correct:
 - p. 64, para 2 line 7: comma after ‘color’ to be deleted, add comma after ‘morphology’; line 8: add comma after ‘genera’; line 11: add space after ‘Herrera’
 - p. 65, para 1 line 4: replace ‘requiring’ with ‘which require’
17. p. 65 “A general scenario is that older larvae kill those that enter later (Janzen 1975).” What Janzen actually wrote, on the observation that he only found one larva per fruit in the association between *Guazuma ulmifolia* and the bruchid *Cisteminus* was “I suspect that, as with the bruchids in *Scheelea* palm seeds (Janzen 1971b, Wilson and Janzen 1972), when there is more than one egg laid on a fruit, the larger (older) larva eats the smaller larva along with the seeds.” This is hardly a statement setting out a general scenario. It is also contradicted at the end of the same paragraph on p. 65 of the thesis, when reference is made to the mandibles of the first instar larva of the weevil *Revena rubiginosa* which may facilitate it killing older larvae, which have non-falcate mandibles. Souza de Medeiros et al (2014) for the weevil *Ancylorhynchus eriospathae* suggest that first-instar larvae fight with and kill other first instar larvae. Currently there seems too little work to propose any generalisations.

18. p. 68, second line from end, refers to 'weevils per fruit' but I assume should refer to 'insects per fruit' since this section is about all insects recovered.
19. Although no differences are found between fruit attacked by different Orders, were there differences between the fruit that was not attacked and that which was (either at species or individual level)? Were there differences in attack levels between fruit collected from the tree and that collected from the ground?

I recommend this thesis for defence for obtaining the degree of PhD.



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Review of PhD Thesis

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Title: Host specificity and species diversity in communities of frugivorous insect in lowland rain forest of Papua New Guinea

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The PhD thesis (97 pages) consists of results of scientific work performed in the Department of Zoology, Faculty of Science, University of South Bohemia and Institute of Entomology, Biology Centre, Czech Academy of Sciences, České Budějovice. Thesis contains results of research stay at New Guinea Binatang Research Center. The PhD candidate intensively studied predation of tropical fleshy fruits by insect predators. I would like to appreciate impressive amount of work performed under difficult conditions of tropical rain forest. I further stress the fact that during his one year i.e. relatively short stay the author accumulated data large enough to be published and interesting for wide scientific public. The thesis first includes Introduction (7 pages + c. 100 references) which is a literature review that covers the wide range of problems: abundance and diversity of tropical woody plants with fleshy fruits, biology of seed and fruit predators, predation and dispersal of seeds and ecological relations between plant and its seed predators. The Introduction is well written and its style is accessible to wide public; I would suggest transformation of this text to an article for public. The main results consist of three studies one of which is already published (*J Trop Ecol* 30: 521-535 (2014) $if=1.222$), the other two are still at the stage of a manuscript prepared for submission. In all papers is the candidate the first author among a small collective. His role in preparation of manuscript – important in all stages of research, data elaboration and text writing – is described in chapter „List of papers...“.

The leading motive of the work was testing „Janzen-Connell hypothesis“ which predicts a positive relationship between abundance of a host plant species in tropical rainforest and number of seed predator species associated with this species of plant, provided existence of a high trophic specialization of seed predators. This hypothesis was formulated and tested in Central America tropic rainforests. The candidate collected large samples of fruits of all tree species accessible in the surroundings of Binatang Research Center in Papua New Guinea. Using a standard method, he stored collected fruits until hatching of adults of all predator species present in the fruits at the time of sampling. He also measured and analysed morphological characteristics of sampled fruits. This and further data retrieved from literature and concerning both plants and their seed predators were used in the three studies of predation presented in the PhD thesis.

All studies are well written and the whole corpus of PhD thesis thus has high formal and content level. To my opinion the candidate made the most of what may be done using the available data. The already published work (*J Trop Ecol*) is a study of distribution and abundance of weevils in fruits. In the studied sample of fruit species the abundance of curculionids was low and hardly may affect population dynamics of host plants. The second work (MS not yet published) deals with species of Lepidoptera reared from the fruits. Here the candidate came to conclusion that frequency of parasitised fruits in most tree species is low and the Lepidoptera species living in fruits are not monophagous but mostly eating fruits

of several plant genera or families. The third work studies the relationship between fruit morphology of particular species of trees and occurrence of particular insect consumers. The candidate studied the effect of fruit morphology on the frequency of insect presence in fruits. Chapter Conclusions is a brief recapitulation of results of three previous works.

I have few general questions or, better to say, points for discussion: (1) On p. 7 the candidate writes: „mechanism ... known as the Janzen-Connell hypothesis ... is a leading explanation for high plant diversity in tropics“. Taking into account all his in principle negative results – what is candidates opinion on the status of this proposition? (2) I am interested in candidates opinion on possible effects of annual variation in abundance of predator species. May it have important or small effect on composition of fruit predator community and rates of fruit predation. (3) Are there – in Papua New Guinea rainforest - any species of seed/fruit predators that leave fruits after completing larval stage and then pupate in soil? Was the method used for collecting predators also convenient to capture such species? (4) Provided that a part of collected insects was identified using a parataxonomic method: could this method influence the results, e.g. change the estimated diversity of predator community?

I highly appreciate candidates field work and consider high significance and formal quality of presented PhD thesis. The preseted thesis „Host specificity and species diversity in communities of frugivorous insect in lowland rain forest of Papua New Guinea“ has all qualities necessary to bestow PhD title to its author. After successful defending of the thesis I recommend bestow this title to Mgr. Richard Čtvrtečka.



doc. RNDr. Alois Honěk, CSc

Prague, 14 January 2015

