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Evaluation of the PhD Thesis by Nichola Plowman

Mechanisms structuring arboreal ant communities along ecological gradients in New Guinea rainforests

Understanding the environmental drivers of variation in the composition and biodiversity of species communities is a fundamental goal of ecology, and highly relevant both for our basic understanding of ecosystems and for applications such as conservation management of nature. The thesis submitted by Nichola Plowman focuses on variation of a highly diverse arboreal ant community in a tropical rainforest, where ants are known to play a key role in ecosystem functioning and in determining the composition of other arthropods. Her work distinguishes the potential effects of several drivers of ant communities, particularly elevation, succession (secondary and primary forest) and tree species composition, and other structuring mechanisms such as interspecific competition between ants are considered

The first chapter of Nichola Plowman's thesis focuses on the density and (very high) diversity of arboreal nests of ants in forests, a unique approach that is greatly facilitated by the rarely applied method of surveying larger forest areas in which trees have been felled. Many previous studies on rainforest canopy ants elsewhere, e.g. based on insecticide fogging, were unable to distinguish resident ant colonies from foragers or 'tourists', whereas the distribution of arboreal nests is much more stable and likely represents a more reliable response to environmental filtering and competition. Moreover, litter ants have been studied more intensively across forests, but are driven by different environmental conditions and revealed contrasting responses to elevation (see below). The study focuses on the comparison of three elevation levels, but also explores parameters of each tree to unravel the variation in nest density and composition, e.g. showing the increase of ant nest numbers with an increase in tree size and relatively low tree species-specificity. The proportional representation of types of nests, e.g. underneath epiphytes that are particularly common in mid-elevation forests, provides particularly valuable information. The main, unique message delivered by the chapter is that the forest at mid elevation (900 m. a.s.l.) has by far the highest density and diversity of resident ant colonies in the trees, and this mid-elevation peak contrasts with findings for leaf litter ants elsewhere that reported monotonous declines with elevation. While the pattern at plot and tree level is well analysed and presented in detail, I can imagine that further insights into the structuring mechanisms can be gained if future analyses are spatially more explicit, considering the position of trees, e.g. similarity between neighbouring trees where effects of ant-ant competition (ant mosaics) may be most severe.

Nichola Plowman's chapter 2 then unravels in greater detail the elevational gradient of a specific subset of arboreal ants and their interactions with plants, studied along transects: 10 ant species that inhabit 23 species of myrmecophytic plants, and their relationship as represented by ant – plant species interaction networks. In contrast to chapter 1 (but not including the lowland forest therein), this study showed a monotonous decline in ant and plant diversity and resulting network complexity with elevation (from 700 to 1500 m. a.s.l.). The network analysis in conjunction with null models was well conducted and appropriate, and the study very nicely controlled whether the change in network patterns can be attributed to changes in species diversity alone or not: several fundamental changes in interactions occurred on top of changes in diversity. These changes translated into variation in the ant's main protective function for plants: leaf patrolling declined, experimentally installed termites received fewer attacks and leaf damage increased in higher altitude forests. Therefore, important new insights into changes in interaction networks along gradients – but moreover into changes of ecosystem processes associated with these networks – have been gained from this study. Due to the importance, novelty and scientific quality, this chapter has been successfully published in the prestigious journal *Proceedings of the Royal Society B* with Nichola Plowman as first author.

In chapter 3, Nichola Plowman compares the phylogenetic and the phenotypic (functional) diversity of a primary and a secondary lowland forest, and whether these show consistent trends with species diversity. Differences between both forests in terms of these different types of diversities were similarly pronounced, but not when abundance-weighted indices were considered that showed only weak differences. Both the distribution of phylogenetic and functional traits potentially show effects of habitat filtering (stronger phylogenetic and functional clustering) or competition (overdispersion). However, the phylogenetic composition was not significantly different from random, and the functional diversity showed a slight clustering in the primary forest site. Relationships with species diversity and subsets of nesting species versus potential 'tourists' were explored. However, while this study is conceptionally interesting, it just compares two unreplicated sites, hampering statistical analyses and generalizations. This topic – the relationship between functional diversity, sampling and species' abundances, is explored conceptually and methodologically in greater detail in chapter 4. Here, Nichola Plowman functions as one of three leading authors in the article published in *PloS One* using one of the ant datasets in addition to plant and bird data. The authors showed how several relevant issues in practice, particularly missing data and transformation of abundance data, affected the reliability of the results across these datasets, which will help to make decisions in functional diversity studies.

The Introduction and the Summary provide a suitable framework of a very complete, thorough and scientifically valuable thesis. Methods have been sound, starting with the ant sampling and rigorous identification at species level where possible, supported by DNA barcodes, and including various levels of very appropriate, modern statistical analyses that are well justified, profound and state of the art. Some statistical analyses, particularly on functional diversity, have been explored critically for methodological limitations. Nichola Plowman's thesis is well written, and the findings are interpreted carefully and discussed in the context of the relevant literature, particularly within the framework of tropical ant communities but also beyond ant ecology. Altogether, her work provided very interesting, meaningful and novel insights into the variable structure of arboreal ant communities, some of the underlying drivers and its functional consequences.

Beyond any doubt, Nichola Plowman has proven sufficient proficiency in the independent practice of science to be admitted to the defense, and I have no hesitation to recommend acceptance of this very good thesis.

Best regards,

(Prof. Dr. Nico Blüthgen)

Questions:

(1) Ant mosaics: In chapter 1, you analysed the distribution (and C-score) of ant colonies at the level of tree individuals and sites, but not in a spatially explicit way, e.g. as ß-diversity between neighbouring trees or as stratification within a crown. Assuming that these nests are indeed mapped in space, can you formulate some predictions based on the 'ant mosaics' hypothesis, i.e. effects of interspecific competition, and how to test them?

(2) Networks versus ecosystem processes: In chapter 2, you show parallel elevational changes in network topology and functional consequences (protection of plants against herbivores). What are potentially underlying mechanisms of a positive relationship between diversity, network topology and functioning?

(3) Specialization: Why do myrmecophytic ants specialize on certain myrmecophytic plant species (e.g. high H_2'), whereas ants have a much more generalized distribution across non-myrmecophytic tree species (low H_2')? Which characteristics of the communities or traits of ants and plants may generally increase this specialization and thus host-plant partitioning in the ant community? Why are herbivorous insects usually much more specialized on host trees than ants?

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Ph.D. Thesis Review

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Mechanisms structuring arboreal ant communities along ecological gradients in New Guinea rainforests

Tropical rainforests comprise a huge part of terrestrial biodiversity, especially invertebrate species. Still we know little about the ecology of these species, although their habitat is critical endangered in most parts of the world. Ms. Nicola Plowman has focused her PhD study on the ecology of arboreal ant species in the rainforest of north-eastern Papua New Guinea, which she has studied in extensive fieldtrips since 2012. The study has been supervised by RNDr. Petr Klimeš (PhD), while Prof. RNDr. Votjtěch Novotný (CSc.) was consultant. The resulting thesis comprises 149 pages with an introduction, four chapters, and a summary as main parts. Each chapter is structured as a scientific paper with several authors and Ms. Plowman is first author in all of them.

In her thesis Ms. Plowman explored the taxonomic, functional and phylogenetic diversity of arboreal ant communities along gradients of elevation and succession, considering forest structure and plant distribution patterns, as well as nesting habits and mutualistic behavior of the ant species. Results are based on a unique destructive sampling of whole tree plots (>1600 trees) that were systematically sampled for ants and allowed also for the collection of cryptically nesting species, which have been formerly neglected.

In chapter I she studied the impact of nest microhabitat and tree size on the arboreal ant communities along an elevational gradient, thus demonstrating a mid-elevational peak in nest abundance and ant species diversity. Using co-occurrence patters of ant species on single trees of different size and at different elevation Plowman and co-workers investigated whether ant assemblages were structured randomly, clustered or overdispersed and reveal that the impact of competition on community structure changes with elevation. This is a very sound piece of work that leads to interesting insights in arboreal ant community patterns.

Chapter II was published 2017 in the Proceedings of the Royal Society B and investigates how communities of ants and ant-plants and their mutualistic interactions change along an elevational gradient. Due to reduced species richness at higher altitudes ant-plant interaction networks became less complex and less specified at higher altitude, resulting in lower benefits for both partners.

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Chapter III compares the functional and phylogenetic diversity of arboreal ants in primary and secondary rainforest. This manuscript reports on a huge sampling effort (852 trees with 1543 ant nests), a detailed DNA investigation and extensive measuring of morphometric traits of 127 taxa, the construction of ant community phylogeny and data exploration using multivariate statistics and null modeling approaches. The results show that succession has only little impact of phylogenetic diversity, while functional diversity differed stronger: primary forest hosted functional redundant species, whereas ant communities in secondary forest were randomly structured. This is a truly excellent up-to-date community ecology study that I enjoyed reading a lot!

In chapter IV authors evaluate the impact of missing trait data, species abundance structure and data transformation on the calculation of functional diversity indices, thus compiling basic statistical knowledge on the robustness of indices used in the earlier chapters. This paper has been already published in early 2016 in PLOS ONE.

Taken together Ms. Plowman conducted outstanding research that combined modern methods in molecular biology and biological statistics with extensive data collection in the rainforest of Papua New Guinea, a hot spot of biological diversity in a very remote area. Her focus is on arboreal ants - a group of extraordinary importance for diversity and functioning of the rainforest ecosystem, yet still hardly assessed. The outcome is a set of exceptional studies in the fields of functional and phylogenetic community ecology that can well stand for the present state-of-the-art. Two of the four manuscripts in her thesis have been already published in excellent scientific journals; I have no doubts that the two other articles will be readily accepted in similar or even higher ranked journals. It speaks for the scientific quality of Ms. Plowman that she not only applies a number of up-to-date methods, but takes a closer look to the applied methodology itself (Chapter IV). The hard conditions of field work in the primary rainforest and extra challenges within the multicultural team (Ms. Plowman learned Tok pisin language for communication) are also worth to mention. During her PhD she was able to publish altogether 6 scientific papers on related topics, attended a bunch of scientific conferences and applied for a number of grants, all of these points towards an outstanding scientist whom I wish to face a bright career. I cordially congratulate Ms. Plowman to her outstanding PhD thesis that I grade among the top 10 % of comparable studies. I fully recommend the thesis for defense.

M. Pfeiffer

Bayreuth, 11.11. 2018

PD Dr. Dr. h.c. Martin Pfeiffer

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Nichola Plowman PhD Thesis

Questions:

A. In Chapter I, Fig. 5 you use c-scores to assess the structure of ant communities in different tree size categories and at different elevation. Values represent "means", including dominant and subdominant species. According to ant mosaic theory (Leston, 1973) colonies of dominant ant species should be overdispersed, moreover they act like a habitat filter for certain groups of subdominant species that are clustered inside their territories. Pfeiffer et al. (2008) calculated SES of c-scores separately for dominant and subdominant ant species and could proof such a pattern in oil palm plantations.

   Can you identify dominant ant species for all trees or a certain group (e.g. large trees) in the low and/or mid elevation and check whether this subgroup is significantly overdispersed?

   Can you check –example wise-, whether the subdominants (this may include visitors) of a certain dominant species (e.g. *Crematogaster polita*) are significantly clustered?

   Are there any further hints for an ant-mosaic like pattern?

B. In Chapter III you have established a phylogeny and trait database of all ant species. Please check if subdominants of a certain dominant species (e.g. *Crematogaster polita*) are phylogenetically or functionally clustered or overdispersed.

Leston, D. (1973) The ant mosaic- tropical tree crops and the limiting of pests and diseases. Pest Articles and News Summaries, 19, 311-341.

Pfeiffer M, Tuck HC, Lay TC. (2008) Exploring arboreal ant community composition and co-occurrence patterns in plantations of oil palm *Elaeis guineensis* in Borneo and Peninsular Malaysia. Ecography 31:21–32.