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# Ecology of ants along elevational rainforest gradients in the tropics

Ph.D. Thesis

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## Annotation

The thesis investigates the community ecology and species diversity of tropical ants on tropical mountains. The primary focus is on the changes in the ground-dwelling ant communities along elevational rainforest gradients, and how their elevational patterns are influenced by various biotic and abiotic factors. First, we investigated how elevation, leaf litter depth and their interaction affect the abundance, species richness and composition of ground-dwelling ants on Mt. Wilhelm (Papua New Guinea). Next, we investigated how ant communities change with forest succession in time along an extensive tropical elevational gradient in Southern Papua New Guinea. The aim was to assess both spatial and temporal trends in the ant communities and whether these changes could serve as indicators towards ecological recovery after human-induced forest disturbance. Finally, we assessed the relationships of ant species richness and activity, and their relative use of six nutrients, with elevation and season in three different tropical mountain regions (New Guinea, Tanzania and Ecuador).

## Declaration

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

České Budějovice, 6th of May, 2021

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Jimmy Moses

This thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Entomology, Biology Centre CAS, supporting doctoral studies in the Entomology study programme.

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Finally, I wish to thank my family for their long-standing support during my PhD study.

## List of papers, manuscripts and author's contribution

The thesis is based on the following papers and manuscripts:

**Chapter I**

**Moses, J.**, Fayle, T. M., Novotny, V. & Klimes, P. (2021). Elevation and leaf litter interact in determining the structure of ant communities on a tropical mountain. *Biotropica* (impact factor: 2.090). https://doi.org/10.1111/btp.12914

*Personal contribution: Field work (50%); Conceptualization (50%); Data analysis (100%); Species identifications (70%); Literature survey (70%); Preparation of figures and tables (100%); Writing the manuscript (50%).*

**Chapter II**

**Moses J.**, Mogina J., Mosby A., Ilave R., Mogia M, Manumbor M., […] Novotny, V. & Klimes P. (Manuscript) Ant succession along a tropical forest elevational gradient in Papua New Guinea.

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**Chapter III**

**Moses J.**, Peters M.K., Tiede Y., Mottl O., Donoso D.A., Farwig N., […] & Klimes P. (Manuscript) Nutrient use by tropical ant communities varies among three extensive elevational gradients: a cross-continental comparison.

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## Co-author agreement

Petr Klimeš, the supervisor of this Ph. D. thesis and senior author in chapters I, II & III, fully acknowledges the major contribution of Jimmy Moses to these manuscripts.

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RNDr. Petr Klimeš, PhD

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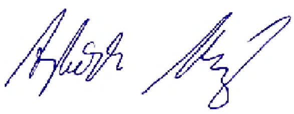

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prof. RNDr. Vojtěch Novotný, CSc.

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# GENERAL INTRODUCTION

## Ecology of ants along elevational rainforest gradients in the tropics

### *Overview*

Tropical rainforest ecosystems host a relatively high diversity of insect species (Hamilton *et al.* 2013) and support a high number of plant species compared to temperate regions (Novotny *et al.* 2006; Schuldt *et al.* 2018; Cámara-Leret *et al.* 2020). Recent global estimates of insect diversity ranges from 2.4 to 20 million species (~ 6.1 million) (Hamilton *et al.* 2013) making insects the most dominant group of organisms on the planet in terms of their richness, abundance and biomass (Mora 2011; Andrew *et al.* 2013). The highest insect diversity and endemism is harbored by tropical mountain ranges (Rahbek *et al.* 2019). However, the insect patterns in species richness and abundance along tropical mountain slopes vary greatly among mountain regions, as well as among individual taxa, and drivers of these differences are still not well understood (McCain & Grytnes 2010; Rahbek *et al.* 2019). Further, tropical primary forests contain higher arthropod diversity than secondary forests (Novotny *et al.* 2006; Basset *et al.* 2008; Klimes *et al.* 2012). As these primary forests are being increasingly cleared and degraded over the past several decades including the unique mountain forests(Schonberg, Longino, Nadkarni, Yanoviak & Gering 2004; Shearman 2010; Shearman & Bryan 2011), we need to improve our understanding of changes in the remaining natural systems, and how successional and elevational changes interact together. Habitat conversion apart from other abiotic and biotic factors, alters responses of arthropod communities including other animal and plant taxa (Dunn 2004; Boyle *et al.* 2020). Coupled with the adverse effect of global warming, both may facilitate rapid decline in insect populations or their species extinction, which may further impair important ecosystem functions and processes (Fayle *et al.* 2010; Peters *et al.* 2019; Tuma *et al.* 2019; Boyle *et al.* 2020; Hallmann, Ssymank, Sorg, de Kroon & Jongejans 2021). Perhaps surprisingly, while the forest disturbance changes attracted most of the recent tropical research (Ewers *et al.* 2015; Peters *et al.* 2016), we lack a good knowledge of the drivers of insect community structure along wide pristine rainforest elevational gradients, as a few such gradients are available and those are challenging to access. Further, the studies typically focus on a single mountain range, which makes a generalization of findings difficult (but see Colwell *et al.* (2016)).

This thesis focus primarily on tropical ground-dwelling ant communities of tropical mountain ranges, and how their abundance, species richness, occurrences and composition change in relation to elevational and successional gradients. Additionally, other aspects of environmental drivers of ground-dwelling ant communities in tropical undisturbed rainforests are considered, in particular leaf-litter, nutrient availability and climate. First, the thesis explores how elevation and leaf litter and their interaction affect the structure of ant communities in pristine primary forests of a tropical mountain (Moses, Fayle, Novotny & Klimes 2021). Next, the effect of elevation and forest succession on the spatial and temporal distributions of ant communities are assessed along an extensive (315 km long) gradient from lowlands to highlands. Finally, ant community elevational patterns and their relative nutrient preferences are explored for the first time to disentangle the effects of elevation and seasonality across three tropical mountain ranges, each situated in a different continent.

### *Alpha, beta and gamma diversity*

The different components of biodiversity measures, often used in community ecology and biological conservation studies focusing on taxonomic diversity (and more recently also on phylogenetic and/or functional diversity) include alpha, beta, and gamma components of community diversity across different spatial scales (Arnan, Cerdá & Retana 2017). These are three of the fundamental descriptive variables of ecology and conservation biology. However, their quantitative definitions remain a source of controversy (Jost 2007; Colwell 2009).

The richness of taxa in a local community or habitat is referred to as the alpha diversity, where assemblages of species are potentially involved in ecological interactions such as competition, herbivory or predation. Gamma diversity involves larger species pool size over wide spatial scales, and as such is thought to be shaped rather by the species (and their populations) speciation and dispersal (Ricklefs 1989). The beta diversity, in contrast to alpha and gamma, refers to the differences in species diversity associated with habitats or spatial scales among the samples, or the sites (e.g., diversity turnover). This measure has received less attention than the alpha and gamma diversity components in the past, but it is increasingly of the interest in last two decades (Novotny & Weiblen 2005). Considering these different measures of the (species) diversity, it is critical to understand their contribution to the elevational community patterns.

### *Geographical distribution ranges and theoretical background*

Species geographic distribution ranges have been used to explain diversity patterns along elevational gradients i.e., monotonic decline was observed in < 20 per cent of studies and the elevational mid-peak predominantly accounted for 70% in all studies of species richness patterns (Colwell *et al.* 2016). One of the first global patterns in the species ranges described became known as the Rapoport's Rule (Stevens 1989). The rule asserts that species at higher latitudes have wider latitudinal ranges than those species at lower latitudes (Stevens 1989). This rule was further extended to explain wider distributional ranges of species at high altitudes (Stevens 1992). Furthermore, a theorem - Rapoport's Rescue Effect, was developed from Rapoport's rule to explain the decrease in species richness with increasing altitude and latitudinal gradients (Stevens 1992). This "rescue" effect theory posits that the proximity of range margins of potentially interacting species strongly influence local species richness and that some species only persist through continued immigration from more suitable areas nearby (Stevens 1992).

However, apart from Rapoport's rescue effect, the Mid-Domain Effect (Colwell & Coddington 1994) was unexpectedly found (mid-peak of species richness on elevations) when Colwell and Hurtt (1994) tried to explain the latter theory from a one-dimensional species stochastic model, which they developed. This theory when applied to latitudinal gradients explains why there is high diversity at the equator but gradually declines to the poles assuming that it is not influenced by any biotic or abiotic factors (Colwell & Coddington 1994). Hence the Mid-domain effect, usually called the Geometric Constraints Null Models (GCMs), described the patterns of random overlaps in species ranges within geometric constraints (bounded domains) (Colwell & Coddington 1994; Colwell, Rahbek & Gotelli 2004).

Though the geometric constraint model may reasonably explain the pattern of diversity across latitudinal gradients and on mountains, it does not integrate biological, climatic and historical processes that are not independent, but also interact and affect species diversity and distributional patterns. This has recently been examined in Colwell *et al.* (2016) where they showed that combining midpoint attractor models with geometric constraints using a Bayesian framework generally produce similar empirical spatial patterns of species richness and range midpoints from tropical mountains for various animal and plant taxa. However, the midpoint attractor model is an abstract representing environmental favorability gradients (it represents neither a mechanism nor process) and other biological mechanisms may thus still influence the concentrations of taxon-specific ranges on certain regions of the mountains (Colwell *et al*. 2016). While the models are useful for theory, we need to explicitly assess the effects of various abiotic and biotic drivers (except the elevation itself) to improve our understanding of the elevational patterns of the communities.

### *The Ants: why they are important*

Ants constitute a large proportion of biomass in rainforest ecosystem (Davidson, Cook, Snelling & Chua 2003). Their species belong to multiple trophic levels, such as true herbivores which feed on plant resources (nectar, seeds), indirect herbivores that consume honeydew from hemipterans, primary predators which feed upon other ants and other prey, secondary predators that feed on predatory arthropods, and omnivores that feed on more than one trophic level (Mooney 2010). Ecological studies of ants (Hymenoptera: Formicidae) as biological indicators of ecosystem health have shown this insect group to be excellent bio-indicators because of their sensitivity to environmental changes (Groc *et al.* 2009; Axmacher, Liu, Wang, Li & Yu 2011), high (but not unmanageable) taxonomic diversity, their functional importance and ease of sampling (Andersen & Majer 2004). Three examples of broad ecosystem services that ants provide include: 1) scavenging and predation including biological pest control agents in agriculture, agroforestry and forestry systems (Philpott & Armbrecht 2006), 2), seed dispersal (Wall., B., Kuhn & Beck 2005) and 3) soil nutrient recycling (Frouz & Jílková 2008).

### *Distribution patterns of ants along elevational gradients*

The global biogeographic patterns in ants are neither randomly nor uniformly distributed on earth due to geographical, geological and climatic factors influencing the spread of lineages and diversification (Lach, Parr & Abbott 2010). Latitudinal gradients in ants show low species diversity at temperate latitudes and its increase towards the equatorial tropics (Hawkins 1999; Lomolino 2001). Hence elevational gradients have been seen as analogous to latitudinal gradients since they mimic some aspects of latitudinal gradients (such as decreasing temperature), but at relatively smaller geographic scale. The elevational gradient are thus useful natural systems to study macro-ecological and macro-evolutionary processes (Lach *et al.* 2010; Sanders & Rahbek 2012).

The spatial distribution patterns in ants, as of ectotherms, have been observed to show similar trend of decreasing species richness towards mountain peaks due decreased temperatures, but rather variable patterns at the lower part of the gradients, and across the different regions (Sanders, Lessard, Fitzpatrick & Dunn 2007; Machac, Janda, Dunn & Sanders 2011; Yusah, Turner, Yahya & Fayle 2012; Peters, Mayr, Roder, Sanders & Steffan-Dewenter 2014). These variations in abundance and species diversity patterns along tropical mountain slopes, as well as among animal and plant taxa is of broad interest to ecologists (McCain & Grytnes 2010; Rahbek *et al.* 2019). The three most common patterns found are monotonic decrease, low-elevational plateau and mid-elevational peak (McCain & Grytnes 2010). Several drivers or mechanisms responsible for driving these patterns include temperature, primary productivity, the classical species-area relationship, mid-domain effect, speciation and extinction rates and niche conservatism. However, these drivers are mostly correlative and it is difficult to disentangle their effects (Stevens 1992; Colwell *et al.* 2004; Sanders *et al.* 2007; Lach *et al.* 2010; McCain & Grytnes 2010; Wiens *et al.* 2010).

### *Effects of leaf-litter on ground-dwelling ant communities in tropical elevational gradients*

The top humus layer of the soil in tropical rainforest is mostly composed of leaf litter. Litter volume (i.e., depth/ mass) varies across time and space because of the differences in litter fall and decomposition rates driven by several factors; for example: weather, seasonality, topography, soil condition, soil fauna (decomposers) and plant species distribution (Röderstein, Hertel & Leuschner 2005; Goma-Tchimbakala & Bernhard-Reversat 2006; Sayer 2006). This litter is an important resource for ground-dwelling invertebrates as it provides both food and microhabitat.

The invertebrates including bacteria and fungi in turn facilitate nutrient cycling and litter decomposition (Hättenschwiler, Tiunov & Scheu 2005; Kattan, Correa, Escobar & Medina 2006; Shik & Kaspari 2010). Experimental removal and addition of a proportion of litter affect soil fauna. In particular, litter removal had a negative effect on the soil fauna, while litter addition effect was more difficult to predict, indicating that other factors may be limiting in these communities (Ashford *et al.* 2013). Further, litter availability on the ground in tropical mountains is affected by the interplay of multiple factors, including litter fall dynamics, decomposition rates, species composition of plants, fungi, bacteria and invertebrates, moisture changes across the seasons, and climate (Röderstein *et al.* 2005). Perhaps because of these differences in the litter availability and dynamics, the distribution of leaf litter invertebrates including ants varies greatly along tropical elevational gradients and between different regions. For instance, leaf litter invertebrate richness and biomass showed a decrease in Puerto Rico (Richardson, Richardson & Soto-Adames 2005) while in western Panama a mid-elevation peak was observed in the number of species for the majority of invertebrate groups (Olson 1994). However, we lack the studies that would explore the simultaneous effects of elevation and leaf-litter depth not only on the ants, but on the litter arthropods as such, along extensive elevational gradients. This is surprising, as measuring of the leaf-litter depth is relatively simple.

### *Diversity patterns and community structure of ants along elevational and successional gradients*

Plant and animal communities on mountain slopes are among classical study systems for ecologists (Lomolino 2001; McCain & Grytnes 2010; Rahbek *et al.* 2019). Elevation gradients comprise large climatic variation on a small geographic scale and as such are suitable for the study of underlying causes of spatial and temporal variations in diversity, as well as the mechanisms driving patterns in biodiversity and ecosystem functions (Lach *et al.* 2010; Sanders & Rahbek 2012). Many studies of various animal taxa have shown that although species richness recovers relatively rapidly, often within 20 – 40 years since disturbance (Dunn 2004). However, in secondary forests species composition can take substantially longer time (often >100 years) to resemble those of the original assemblage (Dunn 2004; Wilkie, Mertl & Traniello 2009).

The interaction of two key ecological gradients, elevational and successional, remains little understood. This is especially true for natural regeneration of the tropical forests after a complete clearance, as most studies focus on comparisons of different successional stages at one particular elevation (Whitfeld, Kress, Erickson & Weiblen 2012; Redmond *et al.* 2018; Rocha-Ortega *et al.* 2018; Mottl *et al.* 2019) or include comparisons of agricultural to natural habitats (Karp *et al.* 2012; Rocha-Ortega & Favila 2013; Peters *et al.* 2019). To our knowledge, only two studies conducted along an extensive tropical elevational gradient included both the effects of elevation and forest succession on the ants (Tiede *et al.* 2017; Hethcoat *et al.* 2019), both in the Neotropics. Both those studies found a rather steady decrease in ant species richness with elevation. However, another study by Peters *et al.* (2019) found such a linear pattern in the species diversity along a tropical rainforest elevational gradient only in the pristine habitats, but a unimodal pattern when land-use effect was considered. This indicates that the patterns may still change among different vegetation systems. Investigating how forest succession, in particular regeneration of vegetation affects the abundance, species richness and composition of ground-foraging ants along an extensive rainforest elevation gradient is needed, as there are not many such studies (only the two above that we know off), and those did not sample early-successional stage.

***Feeding preferences of ants along elevational gradients in the tropics***

The study of communities along climatic gradients (i.e., latitudinal and elevational) remains a central topic connecting biogeography and ecology (Rahbek 2005; Sanders & Rahbek 2012; Pontarp *et al.* 2019). Past studies on the distribution patterns of these communities have demonstrated varying trends, which are driven by factors associated with these climatic gradients. One such factor is the availability and utilization of macronutrients, which also changes across environmental and climatic gradients (Kaspari & Yanoviak 2001; Remonti, Balestrieri & Prigioni 2011; Kaspari 2020). However, the role of nutrients in shaping elevational patterns of individual abundance and species richness, via e.g. their effects on the foraging activity and nutrient preferences, is relatively less understood than that of the climate and geometric constrains (Peters *et al.* 2014).

One of the suitable insects to study the activity and diversity patterns along elevational gradients and the nutrient preferences, are ants (Peters *et al.* 2014; Lasmar *et al.* 2021). Apart from being a good biological indicator of environmental change, ants exhibit relatively complex nutrition ecology (Bluthgen & Fiedler 2004; Csata & Dussutour 2019). For example ants belong to multiple trophic levels (Mooney 2010) (see above). Further, ants are holometabolous insects with different food requirements for larval and adult stages (Blüthgen, Gebauer & Fiedler 2003). In accordance with the ecological stoichiometry theory, which refers to the nutritional balance between the consumer and its food (Sterner & Elser 2002), precise food regulation by workers is necessary for larval growth and foraging activities (Mitra 2005; Cook & Davidson 2006; Hillebrand 2009). Many studies on ants and their nutrition ecology have been conducted under laboratory conditions, allowing us to understand their behavioural and physiological demands for the main macronutrients (e.g. Dussutour & Simpson 2009; Cook, Eubanks, Gold & Behmer 2010). However, only a handful studies were conducted at the level of whole communities along wide geographical gradients in the field and using multiple nutrients (see Peters *et al.* 2014; Lasmar *et al.* 2021).

### *The effects of climatic changes on ant communities*

The magnitude of climate change impacts on biodiversity is predicted to be greater in the tropics. The reasons for this assumption are the great number of tropical species with narrow elevational ranges, prevalence of the species that are endemic to cold mountaintops and thermal specialization of most of the arthropods as a result of limited temperature variability (Laurance *et al.* 2011). For tropical mountains, there are three potential effects of global warming on the geographical distributions of species, which include lowland biotic attrition, range-shift gaps and range contraction or mountaintop extinctions (Colwell, Brehm, Cardelus, Gilman & Longino 2008).

For ant species in tropical areas, several predictions have been made based on existing patterns of ant communities along elevational gradients in terms of expected responses to climate change (Sanders *et al.* 2007; Colwell *et al.* 2008; Lach *et al.* 2010). It is most likely that increases in temperature may cause an increase in local ant diversity and abundance since it has been shown that ant diversity and abundance increases with temperature, resulting also to changes in ecological roles of ants in ecosystems (Lach *et al.* 2010).

Most tropical arthropod species are thought to be thermally specialized as a result of limited temperature variability (Laurance *et al.* 2011) and such elevational specialization has generated high diversities of endemic species in cool montane areas in the tropics (McDonald & Brown 1992). Hence, mountains are important areas for conservation (McCain 2009; Laurance *et al.* 2011). Similarly, the high diversification-rates, and endemism that exist along tropical altitudinal gradients can provide insights into the potential effects of species responses to climate change

(Castaneda *et al.* 2010; McCain & Grytnes 2010; Maveety, Browne & Erwin 2011). One of the factors that might be explored in a relatively short time is possible connection of forest disturbance to effects on species elevational ranges, as grasslands and early successional (open) forest habitats differ in environmental temperature and humidity compared to the pristine forests. Further, observations through year (i.e. variance in ant activity between dry are wet season) are valuable, but are usually scarce, as studies sample rather only in one of the seasons or ignore such variance in tropical mountains (but see Bishop, Robertson, Rensburg & Parr 2014; Bishop, Robertson, van Rensburg & Parr 2015; Joseph *et al.* 2019). As different elevations host naturally different ant species with a variable preferences for environmental niches (Bishop *et al.* 2016; Diamond *et al.* 2016), this group is very suitable to explore the changes and assembly mechanisms of their communities in the view of both elevational (climate), successional (forest type, and its age) and temporal (seasonal) changes.

### *Diversity of biota in Papua New Guinea, with particular reference to ants*

Papua New Guinea is a country situated on the eastern half of the New Guinea Island, the most floristically diverse island in the world and a biodiversity hotspot (Mittermeier & Mittermeier 1997; Cámara-Leret *et al.* 2020). A total of 13,634 vascular plant species of which 68% are endemic have been documented on the New Guinea mainland alone and the rate of discovering new plant species is still high (Cámara-Leret *et al.* 2020). The high levels of vegetation diversity and species endemism in New Guinea reflect its complex geological history that has promoted rapid speciation and complex evolutionary patterns of the biota associated with mountain ranges (Toussaint *et al.* 2014). The country vegetation comprises three main zones classified into lower altitude forest, lower montane and upper montane forests, stretching from mangrove forests on the coast to tropical alpine grasslands on the mountain tops (Paijmans 1976; Shearman & Bryan 2011).

The ant fauna of New Guinea is also diverse although it is not probably richer compared to Borneo and the Philippines. A total number of 1392 ant species have been documented in New Guinea and nearby islands, of which 839 have been formally described (Janda 2007). Ants in this region has been described as consisting of some elements of both the Oriental and Australian ant fauna (Wilson 1959). A total of 545 species are likely endemic to New Guinea and its surrounding archipelagos (Janda 2007; Janda *et al.* 2016). Further, there are ten subfamilies and 98 genera in total that have been documented in the region, but only 1% of the genera (i.e., *Ancyridris*) are endemic to the mainland of New Guinea (AntWiki 2020).

Studies on ants conducted at several locations in Papua New Guinea showed one of the highest species diversity at the local scale worldwide for a tropical rainforest. For instance the number of arboreal ant species found to be nesting in two 0.32 ha plots of lowland rainforest (i.e., 0.64 ha area) was 99 species (Klimes *et al.* 2012). Other studies on ants along the Mt. Wilhelm elevational gradient found 67 ant species using baits on understorey plants (Orivel, Klimes, Novotny & Leponce 2018) and 168 species from nests found on trees (Plowman *et al.* 2017; Plowman *et al.* 2020). However, compared to those many studies of vegetation, ground-dwelling sampling was not conducted along an elevational gradient in the region until my work, which documented 118 ground-dwelling ant species along the Mt. Wilhelm gradient (Colwell *et al.* 2016).

### *Variance in species richness and composition of ants along environmental gradients in New Guinea*

Ant studies carried out in tropical lowland and mountain rainforests of Papua New Guinea found in general high differences in ant diversity and composition. Lowlands had higher richness and gamma diversity with low beta diversity, compared to low alpha and gamma with high beta diversity among mountain ranges (Sam, Koane & Novotny 2015; Colwell *et al.* 2016; Matos-Maraví 2016; Moses *et al.* 2021). Similar differences in the species richness have also been observed for arboreal ants in different forest habitat types, for example between secondary and primary forest successions (i.e. higher richness in pristine habitats). However, this pattern varied for beta diversity within different elevations, i.e. high turnover of species among the forest types in the lowlands, but a little difference in high altitudes (Klimes *et al.* 2012; Mottl *et al.* 2019).

The ant assemblages collected from different localities in New Guinea not only consist of native ants but also introduced invasive ant species, for instant *Anoplolepis gracilipes* have been observed to spread widely in the lowlands, but not in the highlands, in disturbed vegetation (Janda *et al.* 2011; Moses *et al.* 2021). Introduced invasive ant species are a threat to the native biodiversity and are ecologically destructive. Studies on interspecific competition have indicated that native ants resist invasion or rather control the rate of spread of invasive ants into natural ecosystems (Hölldobler & Wilson 1990; Lach & Thomas 2008; Rowles & O'Dowd 2009; Dejean *et al.* 2010). However, to date very little is known about the spread and potential threat of invasive ant species to the native biodiversity in New Guinea, and especially Papua New Guinea over a wider geographical scale. In general, we do have now a good information on ant communities and their diversity in the lowlands of Madang province up to higher elevations (Klimes, Fibich, Idigel & Rimandai 2015; Colwell *et al.* 2016; Janda 2016; Plowman *et al.* 2017; Orivel *et al.* 2018; Mottl *et al.* 2019; Mottl, Yombai, Fayle, Novotný & Klimeš 2020; Plowman *et al.* 2020; Moses *et al.* 2021), but no data are available from other provinces of PNG.

### *Aims and scope of this thesis*

This thesis builds upon previous ant dataset used for multi-taxa comparison in Colwell *et al.* (2016) from Mt. Wilhelm sampled by hand-collection and pitfall trapping, but using a novel sets of analyses and hypothesis on leaf-litter effects on the ants (Chapter 1). Furthermore, it brings new unpublished data from the region from other sampling methods conducted at the mountain and contrasting them to two other geographic regions (preferences for six different nutrients; Chapter 3), and from other provinces previously not sampled in Papua New Guinea using baits (Chapter 2).

Thesis aims are to provide insights into ground-dwelling ant communities in tropical rainforest ecosystems, and how they are affected by abiotic and biotic variables, by investigating their distributional patterns and composition along extensive elevational gradients in the tropics. For the first time, we explore these changes in combination with the effects of leaf-litter variance and forest succession in PNG region. In addition, we bring a unique comparison across three different elevational gradients, how ant community patterns and their food preferences change relative to elevation and seasonality.

In **Chapter I** we assess how elevation, leaf-litter and their interaction structure ground-dwelling ant communities at both local and large spatial scales in a tropical pristine primary forest along an extensive elevational gradient (Mt. Wilhelm) in Papua New Guinea. Past studies assessing the effect of leaf-litter on ground-dwelling ant communities on tropical mountains have shown varying trends in ant richness and abundance and did not consider both the simultaneous and interaction effects of elevation and leaf-litter (Olson 1994; Brühl, Mohamed & Linsenmair 1999; Sabu, Vineesh & Vinod 2008; Grimbacher *et al.* 2018). We predict that there will be a peak in ant abundance and richness at sites that have the thickest leaf-litter layer due to higher microhabitat variability and availability and that ant species composition will vary greatly with both elevation and leaf-litter. We used data from pitfall traps and hand collection methods including leaf-litter depth measurements at our sampled sites to test these predictions.

In **Chapter II** we investigate the simultaneous effects of elevation and succession including their interaction on the spatio-temporal distributions of tropical ground-dwelling ant communities along an extensive (315 km long) tropical elevational gradient from 34 to 2620 m above sea level in Papua New Guinea. To date, we know of only two studies conducted along an extensive elevational gradient assessed both the effects of elevation and forest succession on the ants (Tiede *et al.* 2017; Hethcoat *et al.* 2019). We aimed to assess both spatial and temporal trends in the ant communities and whether these changes could serve as indicators towards ecological recovery after human-induced forest disturbance. To investigate this, we used data from tuna baits (ants) and 0.1 ha vegetation plots (vegetation parameters) censused from both the regenerating vegetation and primary forests.

Finally, in **Chapter III** we examine how elevation and seasonality affect the distributional patterns and nutrient preferences of ground-dwelling ant communities along three extensive (each spanned over 2000 m a.s.l.) elevational gradients in the tropics (i.e., Ecuador, Papua New Guinea (PNG) and Tanzania). Several studies on the relative use of nutrients have been conducted in the past on individual tropical mountains (Peters *et al.* 2014; Tiede *et al.* 2017; Orivel *et al.* 2018) but to date, no meta-analysis have been done across regions. In this study, we aimed to assess the elevational trends and the feeding preferences in the ant communities across these different regions. To investigate this, we used data from baiting experiments consisting of six different types of nutrients (i.e., amino acid, CHO, CHO + amino acid, lipid, salt and $H_2O$) exposed to ants.

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# CHAPTER I

**Elevation and leaf litter interact in determining the structure of ant communities on a tropical mountain [*Biotropica*, in press: https://doi.org/10.1111/btp.12914]**

**Elevation and leaf litter interact in determining the structure of ant communities on a tropical mountain**

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## Journal

Published as an original article in Biotropica (Impact Factor: 2.090) – Association for tropical biodiversity and conservation. Accepted on November 22nd, 2020.

## Abstract

Tropical mountains encompass a wide range of environmental conditions and are useful models for studying drivers of community structure. Invertebrate species richness and abundance show various elevational patterns. However, the drivers of these differences are not well understood, although microhabitat complexity is potentially important. We studied ground-dwelling ants using pitfall trapping and hand collection on Mt. Wilhelm (Papua New Guinea) from 169 to 3,795 m a.s.l. We tested for the effects of elevation and leaf litter depth (as a measure of microhabitat complexity) on ant abundance, species richness and composition. We sampled 118 species, with ants present up to 2,331 m a.s.l. Species richness peaked at mid-elevation (~700 m), but the elevational pattern for abundance varied depending on sampling scale. Leaf litter depth negatively affected abundance once elevation had been accounted for, while elevation and litter depth had an interactive effect on species richness. Species richness was positively related to litter depth at lower elevations, but negatively above ~700 m. Species composition varied with elevation and less strongly with leaf litter depth. We speculate that in the lowlands, litter depth rather than temperature limits ant communities. At high elevations, the deeper litter decreases temperature of the litter layer, and temperature becomes limiting. At mid elevations, temperature is not yet too low, and litter is still relatively deep, hence generating a mid-elevation peak in ant richness. Our results may explain differing richness-elevation patterns of litter arthropods around the world, and provide testable predictions for future studies on this topic.

**Keywords**

altitude, elevational gradient, Formicidae, microhabitat availability, mid-elevation peak, rainforest, tropical mountains, Papua New Guinea.

# CHAPTER II

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**Ant succession along a tropical forest elevational gradient in Papua New Guinea [Manuscript]**

## Ant succession along a tropical forest elevational gradient in Papua New Guinea

Jimmy Moses[*1,2,3], Jane Mogina[4], Anita Mosby[4], Rebekah Ilave[4], Martin Mogia[3], Markus Manumbor[3], Elvis Tamtiai[3], Frank Philip[3], John Auga[3], George Dahl[3], Allan Kiatig[3], Kenneth Molem[3], Francesca Dem[3], Pagi Toko[1,2,3], Piotr Szefer[1,2], Vojtech Novotny[*1,2, 3], Petr Klimes[*2]

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Petr Klimes, Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic, Email: peta.klimes@gmail.com.

**Abstract**

The simultaneous response of tropical insect communities to the two key ecological gradients, elevational and successional, remains little understood. Ants are abundant and relatively species diverse taxon in tropical rainforests, and they are known to be sensitive to climatic and forest disturbance changes. We studied how elevation and forest succession (i.e., regeneration after a vegetation clearance in 2012-2014) affect ground-dwelling ant abundance, species richness and composition through time along a 315 km-long forest elevational gradient in Papua New Guinea. We censused ants using baits placed on the ground in 0.1 ha vegetation plots of primary, and regenerating vegetation in 2015 and 2017. In total, 108 ant species were sampled at 1050 baits across 35 elevational sites distributed from 34 to 2620 m a.s.l.

We found a mid-elevation peak in the ant abundance and species richness in both primary and regenerating vegetation. Both elevation and succession affected the abundance and richness, with a significant interaction effects between the two factors. Notably, species richness increased between 2015 and 2017, particularly at mid and high elevations. However, the regeneration phase remained less diverse than primary forest controls. Species composition varied with succession, elevation, tree basal area and tree species richness. The successional ant communities converged slowly (insignificantly) in species composition with those in primary forest between 2015 and 2017. However, there was a significant decline in the abundance of invasive species during this period at the regenerating sites. Hence, even after such a short time (i.e., two years) we were already able to observe directional effects for ground-dwelling assemblages in species diversity, and some but less evident in composition. The recovery of ant community composition may thus take longer than that of the species richness. However, both these attributes are likely to be important for natural ecological processes.

Our study is a unique assessment of the insect responses over such a large spatial scale along both tropical rainforest disturbance and elevational gradients. Our findings suggest that allowing natural regeneration of forests over time encourages recovery of natural ant species diversity through time.

**Keywords:** Forest succession, Formicidae, ants, invasive species, tropical rainforest disturbance, elevation, regenerating vegetation, mid-elevation peak, PNG LNG, secondary succession**.**

# CHAPTER III

**Nutrient use by tropical ant communities varies among three extensive elevational gradients: a cross-continental comparison [Manuscript]**

**Nutrient use by tropical ant communities varies among three extensive elevational gradients: a cross-continental comparison**

Jimmy Moses[1,2,3], Marcell K. Peters[4], Yvonne Tiede[5], Ondrej Mottl[1,6], David A. Donoso[7], Nina Farwig[5], Tom M. Fayle[1], Vojtech Novotny[1,2], Nathan J. Sanders[8], Petr Klimes*[1]

**Affiliations**

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[4]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Würzburg, Germany.

[5]Faculty of Biology, Conservation Ecology, Philipps-Universität Marburg, Marburg, Germany.

[6]Department of Biological Sciences, University of Bergen, Bergen, Norway

[7]Instituto de Ciencias Biológicas, Escuela Politécnica Nacional, Quito, Ecuador

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**Abstract**

**Aim:** While many studies demonstrate that climate limits invertebrates along tropical elevational gradients, we have only a rudimentary understanding of the role of nutrient limitation and seasonality. Here, we examine the relationships among ant community structure, nutrient limitation, and seasonality along elevational gradients.

**Location:** Ecuador, Papua New Guinea (PNG), Tanzania.

**Time period:** Present.

**Major taxa studied:** Ants.

**Methods:** We exposed six types of nutrients along three undisturbed elevational gradients: amino acid (20% L-glutamine), CHO (20% sucrose), CHO + amino acid, lipid (olive oil), salt (1% NaCl) and H2O. In total, we distributed 2370 experimental baits across 38 sites, from 200 m to ~4000 m a.s.l. We used generalized linear models to test for the effects of elevation and season on the ant species richness and occurrences, and relative nutrient use. We also tested, if relative changes in ant trophic guilds corresponded to particular nutrients.

**Results:** Both ant species richness and number of species occurrences decreased similarly with elevation in all regions. However, there were significant interaction effects among elevation, region, and season, as ant activity was higher in drier season in Ecuador and Tanzania, but lower in PNG. The relative nutrient use was inconsistent among regions: preference for some nutrients varied with increasing elevation in Ecuador (decrease in lipid) and Tanzania (decrease in amino acid, salt, and water use), while only season affected utilizations in PNG. Although the trophic guilds varied with increasing elevation, these functional changes did not correspont to the nutrient use patterns.

**Main conclusion:** While ant community structure changed with increasing elevation in a similar way across mountains, both seasonality and nutrient use by ants differed among sites. We argue that regional differences in climate and nutrient availability rather than ant functional composition shape nutrient use by ants.

**Keywords:** altitudinal gradients, elevation, feeding preference, functional group, Formicidae, insects, intercontinental differences, nutrient use, seasonal shifts, tropical forests.

# SUMMARY

## Thesis summary

This thesis explored the diversity and distribution patterns of ground-dwelling ant communities along tropical elevational gradients. The thesis used data from different sampling methods to assess the distributional patterns and composition of ant communities and their responses to abiotic and biotic factors along elevational gradients. Building on previous studies, we successfully disentangled how leaf-litter depth, forest succession and seasonality affect ground-dwelling ant communities across extensive elevational gradients in the tropics.

Findings from this thesis indicate that distributional patterns and composition of ground-dwelling ant communities on tropical mountains are driven by an interplay of environmental factors (abiotic and biotic) such as temperature interacting with leaf-litter depth (i.e., microhabitat variability and availability), forest succession and seasons (dry and wet) on different mountains. Finally, the thesis brings the first cross-continental assessment of the variance in relative nutrient use by the ants along tropical mountain gradients.

Below I summarize our main findings from each chapter and further provide some future perspectives for ground-dwelling ant community ecology research.


## Main findings and conclusion

In **Chapter I**, we found a mid-peak in ant richness and a linear decrease in ant abundance along the elevation gradient, which conforms to other studies (Olson 1994; Lach, Parr & Abbott 2010; McCain & Grytnes 2010; Colwell *et al.* 2016; Longino & Branstetter 2019), particularly at large scale. Further, variations in ant species composition was explained more by elevation and less by leaf-litter. These findings suggest that resource availability (i.e., leaf-litter) is limiting at the lower elevations while temperature has stronger effect at higher elevations. Moreover, the interaction effect of both predictors may be responsible for driving the mid-peak observed in ant richness at our mid-elevational sites. Results from this study may help explain the variations observed in richness-elevation patterns of arthropod communities on tropical mountains.

Further, in **Chapter II**, we observed mid-peak elevational pattern in ant richness similar to those found in **Chapter I** as well as a mid-peak in ant abundance. Moreover, the results indicate a shift in species richness between the 2015 and 2017 regenerating vegetation, particularly at mid and high elevations. Additionally, species composition varied with succession, elevation, tree basal area and tree species richness. Although there was a slow convergence of succession in ant communities between the regenerating and primary species composition, the number of invasive ant species significantly declined after two years at the regenerating sites. Our findings suggest that both combination of temperature via elevation and forest succession affect vegetation structures, which in turn influence ant communities along the elevational gradient. Allowing natural regeneration of forests over time may encourage the recovery of natural ant species diversity through time.

Finally, in **Chapter III**, we used one of our unpublished data set from Mt. Wilhelm and contrasted it with two other different mountain data sets from Ecuador and Tanzania, all equatorial regions. Findings from this study showed that ant species richness and occurrences decreased similarly with elevation, and also the ant trophic guilds occurrences varied similarly with elevation, across the three regions. However, there were inconsistencies in the feeding preferences of ants across the regions. These results indicate that these nutrient use variations are driven by regional differences in climate and nutrient availability rather than by ant functional composition.

## Future perspectives

Changes in ground-dwelling ant communities and their responses to environmental factors have been studied on tropical mountains in the past however, the mechanisms structuring these communities are still less understood (Lach *et al.* 2010; Colwell *et al.* 2016; Longino & Branstetter 2019). While this thesis is unique in its scope in assessing several broad environmental drivers affecting ground-dwelling ant communities along extensive tropical elevational gradients, it is limited in several aspects. For example, this thesis successfully disentangled how leaf-litter, forest succession and seasons affect alpha (species densities) and beta (species turnover) diversity of ground-dwelling ants along elevational gradients, but not yet on the phylogenetic and functional diversity (i.e., traits) of ants. Future studies should take into consideration phylogenetic and functional characteristics of a community (Arnan, Cerdá & Retana 2017), and compare our conclusions based on taxonomic diversity with those based on the other concepts. Phylogenetic diversity reflects the accumulated evolutionary history of a community while functional diversity concerns the association of functional (e.g., foraging rates), physiological (e.g., temperature tolerance) or morphological traits (e.g., body size) of species assemblages to habitat-specific environmental conditions. Such traits reflect environmental filtering for instance, temperature gradients have been observed to be responsible for temperature-tolerant physiological traits, while habitat complexity affect the body size of ant assemblages (Lach *et al.* 2010; Arnan *et al.* 2017). On the other hand, both functional and phylogenetic measures may also indicate competition in the communities, if rather showing over-dispersed than clustered patterns (Arnan *et al.* 2017). Examining the two diversity measures may provide insights to the spatial and temporal changes in community structures. Both have received less scrutiny and their properties are currently less understood than the taxonomic community changes (Gibb & Parr 2010; Bishop, Robertson, van Rensburg & Parr 2014; Arnan *et al.* 2017). Further, an alternative and ideal approach proposed in Colwell *et al.*

(2016) was to use multimodal attractors and phylogenetic structure to illuminate the drivers of the patterns of ant communities on mountain slopes (Machac, Janda, Dunn & Sanders 2011; Bishop *et al.* 2014).

Next, as elevation and leaf-litter were found to be important drivers of ground-dwelling ant communities in this thesis, leaf litter depth variation deserves further investigation across elevational gradients from multiple geographic areas. The complicated relationship between leaf litter depth, elevation and invertebrate communities calls for experimental leaf litter removal and addition in order to understand the role of these factors in shaping communities on tropical mountains (Sayer 2006; Ashford *et al.* 2013; Grimbacher *et al.* 2018).

Further, as we found that within a two years period there was already a slight directional shift in ant species composition between the regenerating vegetation stages (i.e., 2015 and 2017), future studies should incorporate a wider temporal scale in assessing how ants or any taxa respond to rainforest disturbance gradient across wide elevational gradients over a longer time period.

Finally, competition, forest structure and climate are key environmental factors that affect the structure of tropical communities and vary with elevation and degree of forest disturbance. Forest disturbance has a negative effect on richness and structure of insect communities because of the simplified vegetation structure, which usually harbors different, often invasive, dominant species typical for disturbed forests and plantations (Bihn, Gebauer & Brandl 2010; Klimes, Fibich, Idigel & Rimandai 2015). Hence, it is likely that biotic processes within communities, such as competition, are also important in shaping species' observed distributions (i.e., realized niches) (Sheil 2016). This requires experimental manipulation since observations of species occurrence patterns often do not reveal the exclusive roles of competitive and other biotic interactions (forest structure) versus abiotic variables (climate). An ideal approach that has been successfully tested is the translocation of individuals or whole communities to mimic environmental changes (e.g., climate change and forest disturbance) and their effects on community structure. This approach has rarely been utilized (but see Maunsell, Kitching, Burwell and Morris (2015) for insect herbivores and Garibaldi, Kitzberger and Chaneton (2011) for plants). However, recent trial translocation experiments conducted in Papua New Guinea lowlands using artificial ant nests (Mottl, Yombai, Fayle, Novotný & Klimeš 2020) suggest that the ants might be a good model for such cross-elevational experimental manipulations.

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Sheil, D. (2016). Disturbance and distributions: avoiding exclusion in a warming world. *Ecology and Society*, 21.

# CURRICULUM VITAE

# **Curriculum vitae** | Jimmy Moses

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## Education

**University of South Bohemia** **České Budějovice**
*PhD student in Entomology* *2016–present*

**University of Papua New Guinea & New Guinea Binatang Research Center** **Port Moresby**
*MSc. in Research, Tropical Ecology* *2012–2014*

**University of Papua New Guinea & UPNG Remote Sensing Center** **Port Moresby**
*BSc.H, Applied Tropical Ecology* *2010–2011*

**University of Papua New Guinea** **Port Moresby**
*BSc., Biology and GIS/Satellite Remote Sensing* *2006–2009*

## Theses (completed)

**1.Title**: A Tropical Elevational Gradient in Ants (Hymenoptera: Formicidae): Diversity Patterns, Food Preferences and Scavenging Activities on Mt Wilhelm, Papua New Guinea (*MSc. in research*)

**Supervisors**: Vojtech Novotný, Tom M. Fayle, Phile Daur, Regina Kiele and Pius Piskaut

**2.Title**: Understanding cocoa pod borer (*Conopomorpha cramerella*) infestation and distribution using GIS and Remote Sensing in Gazelle Peninsula of East New Britain, Papua New Guinea (*BSc.H*)

**Supervisors**: Regina Kiele, Phil Shearman and Pius Piskaut

## International foreign laboratory visits

**Biocenter, University of Würzburg, Würzburg** **Germany**
*Host collaborator: Dr. Marcel K Peters* *2019 (4 weeks)*

**Royal Belgian Institute of Natural Sciences, Brussels** **Belgium**
*Host collaborator: Dr. Maurice Leponce* *2018-2019 (3 stays, 6 weeks total)*

## Work

**Institute of Entomology, Biology Center, CAS** **České Budějovice**
*PhD student* *2016 - present*

**New Guinea Binatang Research Center** **Madang**
*Course Instructor* *2015*
I worked as an intructor for the International Tropical Ecology course assisting students on their projects especially in entomology and statistics

**New Guinea Binatang Research Center** **Madang**
*GIS Officer* *2015*
Provided all the mapping support for the New Guinea Binatang Research Center and ExxonMobil on Biodiversity Monitoring project in Papua New Guinea

**New Guinea Binatang Research Center** **Madang**
*Postgraduate Coordinator* *2014–2015*
Provided training and supervision of honors and masters students on their various research projects including undergraduate interns from other universities at New Guinea Binatang Research Center

**Department of Environmental Science and Geography, UPNG** **Port Moresby**
*GIS and Remote Sensing Tutor* *2011*
Full-time tutor in GIS and Remote Sensing at the University of Papua New Guinea

## Congresses

- Macro2019: University of Würzburg (March $11^{th}$ – $14^{th}$, 2019), Würzburg (https://www.biozentrum.uni-wuerzburg.de/cctb/research/ecosystem-modeling/events/macroecology-2019/), Germany
- Zoological Days: Czech University of Life Sciences (July $8^{th}$ – $9^{th}$, 2018), Prague (http://zoo.ivb.cz/), Czech Republic
- European Conference of Tropical Ecology (GTO): Tropical Diversity, Ecology and Land Use (February $23^{rd}$ – $26^{th}$, 2016), Gottingen, Germany
- University of Papua New Guinea Science Conference: Promoting Responsible Sustainable Development through Science and Technology ($17^{th}$ – $21^{st}$ November, 2014), Port Moresby, Papua New Guinea
- University of Papua New Guinea Science Conference: Scientific Research, Education and Awareness ($3^{rd}$ – $4^{th}$ November, 2011), Port Moresby, Papua New Guinea

## Publications

- **Moses, J.**, Fayle, M. T., Novotný, V. and Klimeš, P. (2021) *Elevation and leaf litter interact in determining the structure of ant communities on a tropical mountain.* Biotropica. DOI: 10.1111/btp.12914
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## Computer Skills

**GIS**: *Proficient*
**Satellite Remote Sensing**: *Proficient*
**R**: *Proficient*
**LATEX**: *Proficient*
**Python**: *Familiar*
**Relational databasing**: *Familiar*

## Additional Training

### Entomology

- Ant Taxonomy: identification of ants to subfamily, genus and morphospecies (or species whenever possible) levels; Ant and general insect ecology

### Workshops

- Applied Satellite Remote Sensing – Biocenter of the University of Würzburg ($12^{th}$ – $13^{th}$, 2019), Würzburg, Germany
- Meta-Analysis – Faculty of Environmental Sciences, Czech University of Life Sciences ($6^{th}$ – $7^{th}$, 2018), Prague
- AutoCADing - University of Papua New Guinea (November, 2011), Port Moresby, PNG

### Field Courses and Expeditions

- International Tropical Ecology Course - New Guinea Binatang Research Center and University of South Bohemia, 2013
- Papua New Guinea IBISCA (Terrestrial) Expedition, 2012

### School Courses offered by the University of South Bohemia, CAS (2017-2018)

- Biostatistics (Lecturer: doc.RNDr. Jakub Těšitel, Ph.D.)
- Biology of Social Insects (Lecturer: doc.RNDR. Petr Klimeš, Ph.D.)
- Design and Analysis of Ecological Experiments(Lecturer: prof.RNDR. Jan Lepš, CSc.)
- Functional Traits in Ecology (Lecturer: Francesco De Bello, Ph.D.)
- Modern Regression Methods (Lecturer: doc.RNDR. Petr Šmilauer, Ph.D.)

## Volunteer

- Assisted students experiment projects in Bavaria National Park, Germany | 2018
- Taught introductory Biostatistics to postgraduate students at the New Guinea Binatang Research Center within a period of eight weeks and provided examination and certification at the end of the course | 2017

- Collaborated on a grant proposal GIS mapping component with volunteers from Australia and New Zealand for an NGO (OceansWatch: https://oceanswatch.org; grant awarded) in the Solomon Islands | 2016

## Awards

- Distinction in MSc. in research thesis (1st class) – UPNG | 2015
- Distinction in BSc. with Honors in research thesis (2nd upper class) – UPNG | 2012
- First place in GIS and SRS final year undergraduate student project (*Scapanes australis* and *Oryctes rhinoceros* infestation on palms) – UPNG | 2009

## Interests

- Ant ecology, Macro-ecology, Biostatistics, GIS and SRS

## Languages

**English**: Proficient *formal education*
**Melanesian Tok Pisin**: Proficient *creole*
**Kuanua**: Proficient *vernacular*

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