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Biogeography and evolution of Melanesian and South Pacific ants

Ph.D. Thesis

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Annotation

This thesis investigates the systematics, biogeography, and diversification dynamics of a large and ecologically important insect group in SE Asia and the Indo-Pacific region: the ants. This study utilizes a multidisciplinary framework to elucidate the evolutionary history of selected ant clades with the overall aim to shed light on similar ecological and evolutionary processes intervening in ant diversity.

Declaration [in Czech]

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Pável Fortunato Matos Maraví

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Cover image: *Rainforest in Wanang*, photo taken in Papua New Guinea in 2011 by Markéta Aubrechtová

Para mis amadas Markétka y Sofia Mia

List of papers and author’s contributions

The thesis is based on the following papers (listed chronologically):

I. Janda, M., **Matos-Maraví, P.**, Borovanska, M., Zima, J., Youngerman, E., Pierce, N. E., 2016. Phylogeny and population genetic structure of the ant genus *Acropyga* (Hymenoptera: Formicidae) in Papua New Guinea. Invertebrate Systematics 30, 28–40. (IF = 2.155)
[*Pável Matos-Maraví and Milan Janda conceived the study, Matos Maraví participated in DNA extraction and sequencing, analyzed the data, and significantly contributed in writing the manuscript.*]

II. **Matos-Maraví, P.**, 2016. Investigating the timing of origin and evolutionary processes shaping regional species diversity: Insights from simulated data and Neotropical butterfly diversification rates. Evolution 70, 1638–1650. (IF = 4.007)
[*Pável Matos-Maraví conceived the study, analyzed the data, and wrote the manuscript.*]

III. **Matos-Maraví, P.**, Clouse, R. M., Sarnat, E. M., Economo, E. P., LaPolla, J. S., Borovanska, M., Rabeling, C., Czekanski-Moir, J., Latumahina, F., Wilson, E. O., Janda, M. An ant genus-group (*Prenolepis*) illuminates the drivers of insect diversification in the Indo-Pacific. (Manuscript)
[*Pável Matos-Maraví conceived the study, conducted the laboratory work, analyzed the data, and drafted the manuscript.*]

IV. **Matos-Maraví, P.**, Matzke, N. J., Larabee, F. J., Sorger, M., Suarez, A. V., Janda, M. A phylogenetic framework to Wilson's Taxon Cycle: the evolutionary history of *Odontomachus* trap-jaw ants (Hymenoptera: Formicidae: Ponerinae), with a focus on the Indo-Pacific region. (Manuscript)
[*Pável Matos-Maraví conceived the study, conducted the laboratory work, analyzed the data, and drafted the manuscript.*]

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Introduction

Introduction

One of the major challenges for mankind in the XXI century is a climate change and the so-called biodiversity crisis. The rate and magnitude of species losses (extinctions) over the last centuries may have even been comparable to those of the "Big Five" mass extinction events (Barnosky et al., 2011). Modern conservation efforts thus urgently require a multidisciplinary perspective to better understand the factors and processes controlling biodiversity dynamics and its uneven distribution on Earth. A macroevolutionary component in conservation planning needs to be particularly emphasized (Moritz, 2002). It represents our best window to previous paleobiodiversity crises that happened over millions of years ago, and it contributes with important insights on how to anticipate the impact of environmental disturbances on extant ecosystems. Accordingly, the study of paleobiodiversity, the responses of ancient taxa to paleoenvironmental changes, and the historical biogeography of clades, is not only part of basic evolutionary research, but is also a critical task now more than ever.

Tropical islands harbor a large portion of Earth's species diversity, including rare and endemic species (Myers et al., 2000). Due to the discrete nature and size of islands, populations of endemic species are particularly susceptible to drastic and rapid changes in the environment (e.g., climate, landscape, etc). The Indo-Australian Archipelago and the oceanic islands of tropical South Pacific (Figure 1) together encompasses about one third of the total biodiversity recorded on Earth (Keppel et al., 2009). The exceptional pace of habitat degradation and species loss make the region a biodiversity hotspot with high conservation priorities. However, the origin and maintenance of Indo-Pacific biodiversity have rarely been studied under a multidisciplinary framework that includes ecology, comparative phylogenetics, historical biogeography, and diversification rate estimation, from the perspective of insect evolution. The present thesis attempts to provide an alternative view on the radiation and biogeography of a large and successful insect lineage, the ants of the Indo-Pacific. This study aims to bridge towards a better understanding of biodiversity dynamics over space and time using an integrative approach to disentangle the abiotic and biotic factors shaping the extant diversity of insular ants.

1. Island biogeography

Islands have ever amazed evolutionary biologists due to the outstanding array of ecological patterns and biodiversity dynamics encountered in such systems. In fact, the foundations of Evolutionary theory (Darwin, 1859) and Biogeography (Wallace, 1860; Wilson, 1959, 1961; MacArthur & Wilson, 1963) have been established through the study of ecological and evolutionary processes occurring on islands. The proposal of the equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967) was a breakpoint in ecological biogeography research. For the first time, biologists were able to predict biodiversity dynamics and community assembly using a quantitative approach to estimate the number of species that an area could support. Briefly, the MacArthur-Wilson equilibrium model postulates that species richness on island communities are largely regulated by two geographical drivers: remoteness and island size. The number of species on one island is therefore primarily the result of the number of colonizers (immigration rate as a function of island remoteness) and local extinction rate that is inversely correlated with island size and population sizes. As a consequence, remote and small islands would support far less species diversity than large islands that are close to continents (MacArthur & Wilson, 1963).

However, the equilibrium theory of island biogeography in its original form does not take into account the dynamic nature of islands and speciation, thus, it is less predictive at evolutionary and geological timescales (Gillespie, 2004; Whittaker et al., 2008). Moreover, biotic processes such as competition, niche partitioning, or adaptation are neglected, contributing little towards a multidisciplinary framework on the study of processes shaping biodiversity dynamics over time. Recent expansions of the MacArthur-Wilson equilibrium theory (Gillespie, 2004; Whittaker et al., 2007, 2008; Rosindell & Phillimore, 2011) have considered geological progression and evolutionary and ecological responses. These advancements build towards an integrative theory of island biogeography with more realistic predictions: e.g., peak in speciation rate at the early stages of island emergence, followed by gradual decline of speciation and increased extinction rate as niches become saturated and population sizes decline. Nonetheless, the predictions of the extended island biogeography theory have rarely been tested on hyperdiverse and ecologically important clades such as insects.

2. The taxon cycle hypothesis

The taxon cycle is another influential biogeographical concept formalized first by E. O. Wilson (Wilson, 1959, 1961). Contrary to the equilibrium theory of island biodiversity, the taxon cycle predicts a dynamic interplay between ecological and evolutionary forces, and suggests that biodiversity might not be at equilibrium (Ricklefs & Cox, 1972; Ricklefs & Bermingham, 2002). The cycle can be divided into two major phases: expansions and contractions. At early stage, a species with limited geographical range (e.g., primary rainforest) expands its ecological niche and habitat preferences (e.g., it readily occupies open environments close to the seashore). Such adaptation has been originally postulated to be driven by interspecific competition, but certainly other co-evolutionary forces may be invoked (e.g., antagonism-driven (Ricklefs, 2010)). The adaptive shift may lead to ecological release whereby the taxon may successfully establish in marginal habitats where competition can be less intense than in primary rainforests. Geographical expansion to other islands and archipelagos might then be facilitated by such ecological release. However, in the long term, widespread populations across islands may phenotypically and genetically differentiate because of reduced inter-island gene flow. The contraction stage begins, and small, unspecialized populations may compete with new expanding taxa, eventually going extinct or surviving as single-island endemics specialized to other habitats. The cycle begins again with the ecological expansion of those geographically restricted taxa.

Although geographical data and phylogenetic evidence have supported to some extent the expansion and contraction phases postulated by the taxon cycle hypothesis (Sequeira et al., 2000; Economo & Sarnat, 2012; Jønsson et al., 2014; Economo et al., 2015b), a quantitative assessment of the hypothesis is challenging. If indeed the cycles of geographical and ecological expansions exist, these may overlap temporarily across lineages and may leave an intricate biogeographical pattern. Moreover, stochastic extinction of lineages may erase any signal of taxon cycles. In fact, other processes might leave a similar pattern predicted by species' expansion and contraction phases, such as recent climatic fluctuations, adaptation, and disparate dispersal abilities across lineages (Pregill & Olson, 1981; Liebherr & Hajek, 1990). Recent advancements on comparative phylogenetics and ancestral state reconstructions, however, have paved the way for a quantitative test of the taxon cycle, through the estimation of diversification rates, ecological preferences shifts, and historical biogeography. Such macroevolutionary input along with ecological studies, including local community assembly, may offer more insights on the existence of taxon cycles or other biogeographical phenomena acting on insular biota.

3. The tropical SE Asia and South Pacific

Biogeographically, SE Asia and the Indo-Pacific might be subdivided into five major realms (Figure 1): 1) the Indomalayan (including continental SE Asia and the Malay Archipelago), 2) Australian, 3) Melanesian, 4) Micronesian, and 5) Polynesian. From these, the Indomalayan realm is the geologically most-complex region because the formation of most of its terranes and land originated during the collision of the Pacific, Sunda, and Australian plates (Lohman et al., 2011). Recent advances in SE Asian paleogeographical research suggest that subduction around Sundaland resumed at about 45 Ma as a consequence of Australia moving rapidly northwards and approaching SE Asia. Intense volcanic activity and the reorganization of land and sea have been postulated for most of the past 35 Ma, but the approximate timing of emergence and the extent of land in most of the Malay Archipelago remain poorly known (Hall, 2012, 2013). Although most paleogeographical models agree that significant rise of land and orogenic activity happened within the past 10 Ma, it is inconclusive based on the recorded geological evidence that there was ever a chain of short-lived volcanic islands connecting SE Asia and Australia and New

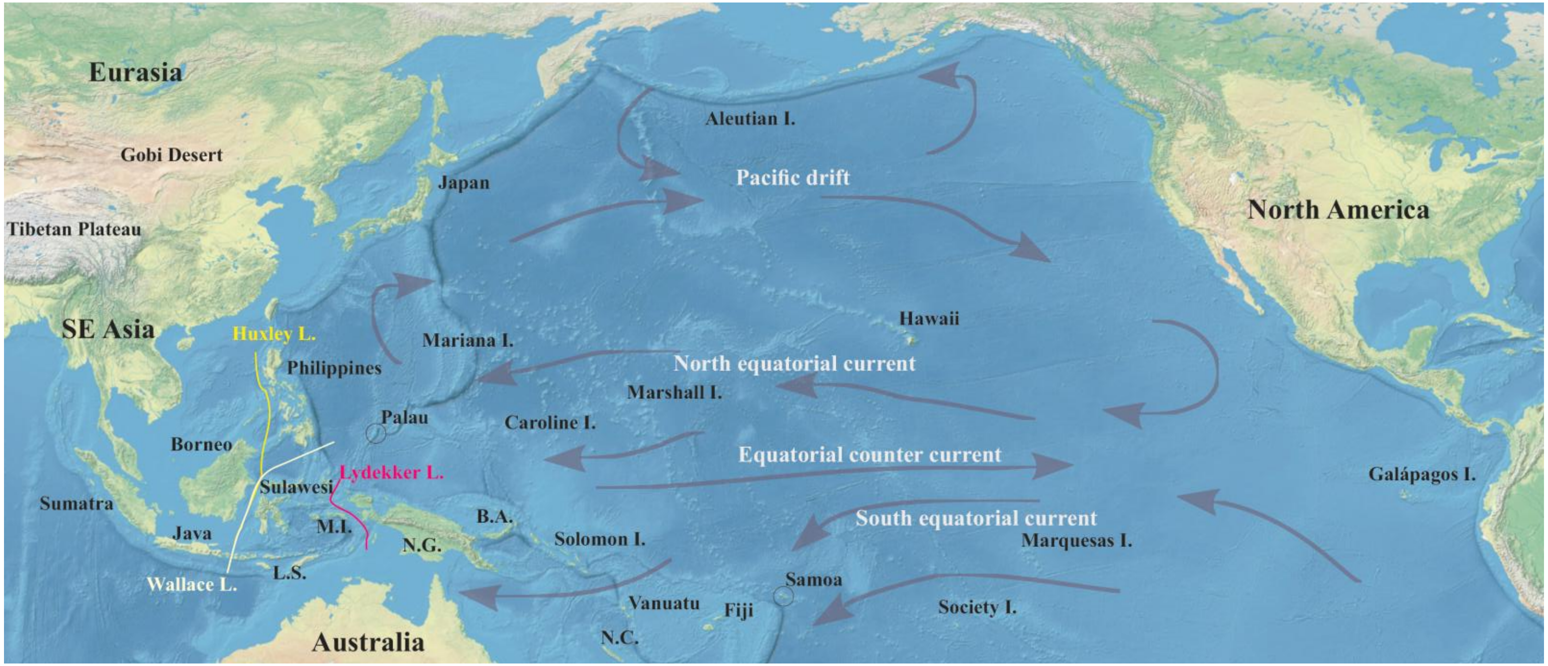

Figure 1. Present-day configuration of the Pacific region. The Indomalayan realm comprises SE Asia and the Malay Archipelago (In map M.I.= Moluccas Islands, L.S.=Lesser Sundas. Melanesia comprises the islands of New Guinea (N.G.), the Bismarck Archipelago (B.A.), Solomon Islands, Vanuatu, and Fiji. Micronesia encompasses Palau, Mariana Islands, Caroline Islands, and Marshall Islands. Polynesia comprises the islands, atolls, and archipelagos in the eastern Pacific, from Samoa to Marquesas Islands. In the Malay Archipelago, three importarnt boundaries were delineated for Asian and Australian taxa, namely Huxley Line (in yellow), Wallace Line (in white), and Lydekker Line (in fucsia). Pacific oceanic currents are depicted as solid lines: westward currents are the North and South equatorial currents, whereas eastward currents are the Pacific drift, the Equatorial counter current, and the West wind drift (not shown) from southern Australia and New Zealand to southern South America. Map adapted from Natural Earth (http://www.naturalearthdata.com). Oceanic currents adapted from Gillespie et al., 2012).

Guinea (Hall, 2001; Baldwin et al., 2012; Stelbrink et al., 2012). However, time-calibrated phylogenies suggested that terrestrial faunal interchange between the two continents might be as old as 25 Ma (Jønsson et al., 2011; Cibois et al., 2014; Georges et al., 2014; Mitchell et al., 2014; Economo et al., 2015b), indirectly supporting the scenario where ephemeral islands across Wallacea may have facilitated stepping-stone dispersal since the Miocene epoch (*ca*. 25 Ma; Figure 2).

From all islands in the Malay Archipelago, New Guinea is the major centre of biodiversity and endemism. New Guinea is the largest tropical island on Earth, and due to its complex tectonic history, volcanism, and glaciation events, a myriad of landscape and climate types allows the co-existence of diverse life forms. The earliest colonization and diversification events of land animals has been dated to the beginning of the Miocene epoch (20–25 Ma) (de Boer & Duffels, 1996; Sharma & Giribet, 2012; Müller et al., 2013). These dates are in agreement with the proto-Papuan archipelago paleogeographical model (Figure 2), which describes short-lived archipelagos of varying geological origin on the northern edge of New Guinea by 25–30 Ma (Jønsson et al., 2011). Nonetheless, the major geographical event that triggered species diversification has been the rapid orogeny of the Central Range during the past 5–10 Ma (Toussaint et al., 2014). Although the Australian and Pacific plates converged at about 12–15 Ma, initiating the Central Range orogeny on the western region and continued to the east until about 3 Ma, elevations comparable to present day were attained only at about 5 Ma (Hill & Hall, 2003; Cloos et al., 2005). However, paleogeographical reconstructions do not entirely agree on where and when substantial land emerged and remained above water until present. On one side, collisional orogeny forming the extant Papuan Peninsula has been reconstructed at about 30–38 Ma (van Ufford & Cloos, 2005). On the other hand, it is believed that most present-day land did not formed until about 5 Ma, concurrent with the Central Range orogeny (Toussaint et al., 2014).

Present-day oceanic islands across the Pacific basin emerged above water during the late Miocene and Pleistocene (i.e., since about 12–15 Ma) (Neall & Trewick, 2008; Gillespie & Clague, 2009; Keppel et al., 2009). In Micronesia, the Caroline Islands are the result of volcanism that began about 15 Ma on the western archipelagos (i.e., Yap, Palau, and Chuuk) and continued until about 1 Ma forming Pohnpei and Kosrae on eastern Micronesia. Two models were proposed for the origin of such islands: 1) the hot-spot model, in light of the progressive age of islands from east (younger) to west (older), similar to the Hawaiian islands (Jarrard & Clague, 1977; Keating et al., 1984); and 2) the fracture-induced volcanism, suggesting the uplift of seamounts and islands as the result of tectonic subduction of the Pacific and Philippine Sea plates (Rehman et al., 2013). On the other hand, in Melanesia, ancient volcanic arcs existed across New Guinea, the Solomon Islands, Vanuatu, and Fiji, but it is unclear when the land above water appeared, and for how long. The Vitiaz Arc Model (Ewart, 1988; Rodda, 1994) suggests short-lived islands extending across the area until about 10 Ma, thus facilitating stepping-stone dispersal from source regions, namely New Guina, SE Asia, or Australia.

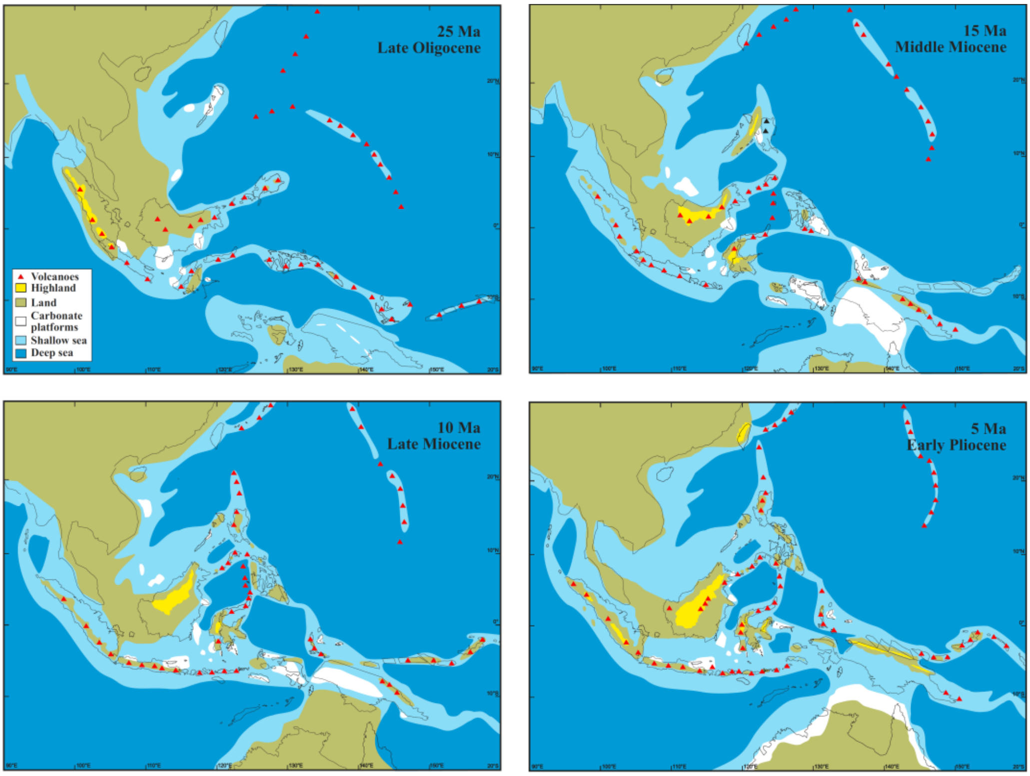

Figure 2. Palaeogeography of the Malay Archipelago of Hall (2012, 2013). Distribution of land and sea during the Neogene Period (last 25 Ma) remains far from complete understanding. Biogeographic patterns may help to clarify the timing of stepping-stone dispersal routes. By the transition between the Oligocene and Miocene (*ca*. 25 Ma), there is evidence of dispersal across the Malay Archipelago from vertebrate and arthropod phylogenies. By 10–15 Ma, Australian and Pacific plates converged, triggering the exposure of land above sea and the orogeny of New

Guinean Central Range. By 5 Ma, substantial land in the Indo-Pacific was exposed and remained above water to present day. Maps were downloaded from (http://www.searg.rhul.ac.uk).

4. The ants

Macroevolutionary research on hyperdiverse clades is critical towards a better understanding of tropical biodiversity. The insects represent the largest faunal radiation in the history of life on Earth (Grimaldi & Engel, 2005). Unfortunately, little is known on the evolutionary history, biogeography, and diversification dynamics of Indo-Pacific insects, paradoxically being the largest component of biodiversity with key roles in ecosystem balance and the most vulnerable to anthropogenic environmental degradation. Within the insects, the order Hymenoptera (ants, wasps, bees) are one of the four largest groups, along with butterflies and moths, flies, and beetles. The evolutionary success of ants (family Formicidae), and social insects in general, is probably the result of its ecological dominance and intricate biological interactions with plants, fungi, bacteria, and other animals. Ants constitute about 15–30% of the total animal biomass in tropical environments (Hölldobler & Wilson, 1990). Moreover, the array of intimate ecological interactions as predators, symbionts, and decomposers, facilitated co-evolution and may have even promoted spectacular diversification on different clades, as for instance the angiosperms (Lengyel et al., 2009).

The about 14,000 described species of ants (estimates of total diversity are around 22,000 species) are classified within 16 extant subfamilies (Bolton, 2016). The tropics harbor the largest portion of ant diversity, while the Malay Archipelago and eastern Australia have one the highest concentration of ant species on Earth (Janicki et al., 2016). Although the extensive fossil record of ants suggests that they evolved for over 100 Ma, ants diversified and became ecologically dominant only within the past 50 Ma (Grimaldi & Agosti, 2000; LaPolla et al., 2013; Ward, 2014). In fact, molecular phylogenetic approaches recovered the origin of extant ants to the early Cretaceous (115–135 Ma) (Brady et al., 2006) or to the late Jurassic (139–158 Ma) (Moreau & Bell, 2013), but the major radiation and increases in diversification rates across major ant clades occurred throughout the Cenozoic (i.e., < 66 Ma; in the four largest subfamilies: Myrmicinae (Ward et al., 2015); Formicinae (Blaimer et al., 2015); Ponerinae (Schmidt, 2013); and Dolichoderinae (Ward et al., 2010)).

Nylanderia sp. VANU001
CR120625-48
Vanuatu: Espiritu Santo Is.
Leg: Christian Rabeling

Pseudolasius sp. PSEU002
MJ9384
Papua New Guinea, Varirata NP
Leg: Milan Janda

Acropyga acutiventris
MJ13919
Papua New Guinea, Varirata NP
Leg: Milan Janda

Odontomachus turneri
874.ODO.1.1
Australia, Northern Territory
Leg: Ronald Clouse

Figure 3. Collage of photographs from the ants studied in the present thesis. Frontal and lateral views of worker ants are shown, and voucher information is detailed below each ant specimen. The genera *Nylanderia* and *Pseudolasius* are both members of the *Prenolepis* genus-group (Formicinae: Lasiini) and are studied along with the remaining siter genera *Paratrechina*, *Paraparatrechina*, *Euprenolepis*, *Prenolepis*, and *Zatania*, in **Manuscript III**. The systematics of *Acropyga* (Formicinae: Plagiolepidini) and population genetics of the species *Acropyga acutiventris* are studied in **Paper I**. The biogeography of the spectacular trap-jaw ant *Odontomachus* (Ponerinae: Ponerini) is investigated in **Manuscript IV**.

Aim and objectives

In order to bridge towards a better understanding of insect evolution and the origin and maintenance of Indo-Pacific biodiversity, this thesis investigates the systematics, biogeography, and diversification dynamics of a large and ecologically important group: the ants. This study utilizes a multidisciplinary framework to elucidate the evolutionary history of selected ant clades with the overall aim to shed light on similar ecological and evolutionary processes intervening in ant diversity. The thesis' main research objectives are:

1) Construct a novel, well-sampled, molecular dataset for selected Indo-Pacific ant clades. The thesis includes some of the most comprehensive Indo-Pacific ant phylogenies to date. The ants' geographical ranges and habitat preferences are assembled from public databases and our own field records.

2) Time-calibrate the ant phylogenies to shed light on the origin and dispersal routes across the tropical South Pacific. The extensive ant fossil record along with cutting-edge statistical approaches are used to infer reliable diversification times and rate dynamics.

3) Tempo and mode of ant evolution are evaluated in a multi-layer framework: a) biogeographic history elucidates shared dispersal corridors and the biodiversity source regions; b) ecological traits shifts (distribution, habitat preferences) may have modulated diversification rates; c) speciation driven by abiotic and biotic factors are assessed using comparative phylogenetics.

4) Evaluate the taxon cycle and its predictions on Indo-Pacific ants. Well-sampled, time-calibrated phylogenies permit the elucidation of geographical patterns in the context of expansion and contraction phases. The existence of taxon cycles, frequencies of cycles, timing of adaptive shifts, and changes in habitat preferences, may all be recognized in a phylogenetic context.

General material and methods

1. Taxon sampling

Ant sampling in the Indo-Pacific region was carried out during 2002–2013 using standard methods for ant collection in the field (Agosti et al., 2000): 1) hand collecting in all possible habitats; 2) baiting techniques using tuna and honey as baits in arboreal vegetation, and ground; 3) Winkler leaf litter extraction; 4) and in New Guinea, methodological and exhaustive hand collection using 1 to 12 plot systems of 20 m × 20 m at each sampling site. Measures of sampling effort for each plot are as follows: 1) for baiting technique, at least 20 bait traps on forest floor and 20 bait traps on understory vegetation exposed for at least one hour; 2) for leaf litter extraction, at least 1 m^2 leaf litter, extracted for 48–72 hours; 3) for direct hand-collection, at least four person-hours a day. The total sampling area at each site ranged about 20–25 km^2. At some localities in New Guinea (Baitabag, Ohu, Madang Lagoon, Weam, Port Moresby), targeted population sampling for this thesis was increased outside the surveys plots, to include ants of the genera *Acropyga*, *Odontomachus*, and those within the *Prenolepis* genus-group. On those sites, plot-based sampling was not possible, and we used direct hand-collecting and/or baiting. The collected ants were stored in 70–100% ethanol and preliminary sorted by genus in the field. Ants were primarily mounted and photographed at the Institute of Entomology, Biology Centre CAS (Czech Republic), and all voucher specimens used in the present thesis are deposited in the Melanesian Ant Collection (Institute of Entomology, Biology Centre CAS), with selected duplicates deposited in the MCZ (Museum of Comparative Zoology, Cambridge, MA, USA).

2. Dataset collection

All laboratory work was done at the Institute of Entomology, Biology Centre CAS. DNA was isolated from two legs or the whole ant specimens, depending on their body sizes, using the Geneaid Genomic Tissue DNA kit (Taiwan). DNA amplifications were carried out using 2–3 μl of isolated DNA, 1x of PPP Master Mix (Top-Bio, Prague), and 0.4 μM of each forward and reverse primers. PCR protocols consisted on 95°C for 5 min, 35 cycles of: 94°C for 30 sec, 50/55°C for 50 sec and 72°C for 90 sec, and the final extension for 5 min at 72°C. Annealing temperatures in the PCR protocols varied from 50°C for the mitochondrial COI and the nuclear genes wingless and LWR, to 55°C for the nuclear genes CAD, EF-1αF1 and EF-1αF2. Primer sequences including the universal primers *T7promoter* and *T3* at the beginning of each sequence are detailed in Table 1. Standard DNA sequencing on both forward and reverse directions was carried out by the company Macrogen (South Korea). DNA editing and alignments were done using the program Geneious v. 8, and datasets for phylogenetic analyses were generated using the web application VoSeq v. 1.7.4 (Peña & Malm, 2012). Voucher information and photographs are publicly available at http://www.newguineants.org, DNA sequences were deposited in GenBank and in BOLD, http://www.boldsystems.org (ASPNA project) databases. All published datasets and phylogenetic trees generated in this thesis may be located in the TreeBASE and Dryad repositories.

3. Phylogenetic methods

The extensive research collaboration established during the course of the present thesis ensured a comprehensive taxon sampling from diverse regions across the Indo-Pacific. This allowed the discovery of a significant number of cryptic and undescribed ant diversity, but the taxonomic treatment of each genus was out of the scope of this study. Preliminary sorting of species was based on morphology coupled with molecular information but are not definitive, instead it awaits a comprehensive taxonomic review of the Indo-Pacific ant fauna. Multi-locus, molecular species delimitation were conducted using three Bayesian approaches: 1) bGMYC (Reid & Carstens, 2012) and 2) bPTP (Zhang et al., 2013) to recover potential boundaries between species; and 3) BP&P (Yang & Rannala, 2010) to validate *a priori* species boundaries based on morphology and the results from bGMYC and bPTP analyses.

Gene region and primer sequences	Direction	Described in
Cytochrome c oxidase subunit I (COI)		
LCO: 5' TAATACGACTCACTATAGGGGGTCAACAAATCATAAAGATATTGG 3'	Forward	(Folmer et al., 1994)
HCO: 5' ATTAACCCTCACTAAAGTAAACTTCAGGGTGACCAAAAAATCA 3'	Reverse	(Folmer et al., 1994)
Internal shorter fragment, LCO326: 5' ATTAACCCTCACTAAAGRGGRGGATAAATWGTTCATCC 3'	Reverse	This study
Internal shorter fragment, LCO215: 5' TAATACGACTCACTATAGGGGGATCYCCTGATATAGCYTACCC 3'	Forward	This study
Carbomyl-phosphate synthase II (CAD). Done in two pieces		
Region 1, CD892: 5' TAATACGACTCACTATAGGGGGYACCGGRCGTTGYTAYATGAC 3'	Forward	(Ward et al., 2010)
Region 1, CD1491: 5' ATTAACCCTCACTAAAGGCCGCARTTNAGRGCRGTYTGYCC 3'	Reverse	(Ward et al., 2010)
Region 2, CD1423: 5' TAATACGACTCACTATAGGGAGGTRATACRATCGGARAGRCCDGA 3'	Forward	(Ward et al., 2010)
Region 2, CD1910: 5' ATTAACCCTCACTAAAGCCGAGRGGRTCRACRTTYTCCATRTTRCAYAC 3'	Reverse	(Ward et al., 2010)
Elongation factor 1-alpha F1 paralog (EF-1αF1)		
F1-1424: 5' TAATACGACTCACTATAGGGGCGCCKGCGGCTCTCACCACCGAGG 3'	Forward	(Schultz & Brady, 2008)
F1-1829: 5' ATTAACCCTCACTAAAGGGAAGGCCTCGACGCACATMGG 3'	Reverse	(Schultz & Brady, 2008)
Elongation factor 1-alpha F2 paralog (EF-1αF2)		
F2-557: 5' TAATACGACTCACTATAGGGGAACGTGAACGTGGTATYACSAT 3'	Forward	(Schultz & Brady, 2008)
F2-1118: 5' ATTAACCCTCACTAAAGTTACCTGAAGGGGAAGACGRAG 3'	Reverse	(Brady et al., 2006)
Long wavelength rhodopsin (LWR)		
LW143: 5' TAATACGACTCACTATAGGGGACAAAGTKCCACCRGARATGCT 3'	Forward	(Ward & Downie, 2005)
LW639: 5' ATTAACCCTCACTAAAGYTTACCGRTTCCATCCRAACA 3'	Reverse	(Ward & Downie, 2005)
wingless		
WG578: 5' TAATACGACTCACTATAGGGTGCACNGTGAARACYTGCTGGATGCG 3'	Forward	(Ward & Downie, 2005)
WG1032: 5' ATTAACCCTCACTAAAGACYTCGCAGCACCARTGGAA 3'	Reverse	(Brady et al., 2006)
28S		
28S-3668: 5' TAATACGACTCACTATAGGGGAGAGTTMAASAGTACGTGAAAC 3'	Forward	(Ward & Downie, 2005)
28S-4395: 5' ATTAACCCTCACTAAAGTCGGARGGAACCAGCTACTA 3'	Reverse	(Brady et al., 2006)

← **Table 1**. List of primer sequences utilized in the present thesis. The universal primers *T7promoter* and *T3* (underlined sequences) were used to facilitate DNA sequencing of multiple gene markers. The gene marker CAD was amplified in two fragments (Region 1 and Region 2), whereas internal primers were developed for the COI gene marker to facilitate amplification of degraded samples.

Phylogenetic relationships were evaluated using primarily model-based approaches, namely Bayesian Inference (Ronquist et al., 2012) and Maximum Likelihood (Stamatakis, 2014). Moreover, time-calibrated species trees and concatenated trees were inferred using the multispecies coalescent model (Heled & Drummond, 2010) and relaxed clock approaches (Drummond et al., 2006) as implemented in the software BEAST (Bouckaert et al., 2014). The extensive ant fossil record in the literature were revised to obtain the most reliable estimate of crown group ages, following best-practice guidelines (Parham et al., 2012). In addition, chronograms of the whole ant family and/or within ant subfamilies were evaluated to extract secondary calibration points for the root of trees or major clades.

4. Ancestral state reconstructions

Ancestral geographical ranges of the ants and the relative probabilities of distributional shifts were inferred using parameterized biogeographical models in a maximum likelihood framework. Extant geographical ranges for each species were retrieved from the literature, taxonomically-curated databases (AntWeb, 2016), and field notes. The package BioGeoBEARS (Matzke, 2014) allows the incorporation of paleogeographical reconstructions as relative dispersal rates across areas over time periods. These characteristics allow flexible models to be tested on a range of abiotic/biotic factors governing biodiversity dynamics. For instance, 1) the rise and fall of geographical barriers – mountain orogeny, emergence of volcanic islands; 2) paleoclimatic fluctuations – dispersal triggered by sea level drops during glaciations, or during major warming events; 3) island sizes over time – explaining diversity differences across islands due to increased immigration, speciation, or species-level carrying capacity as area size increases.

Diversification dynamics and distributional shifts might be affected by shifts in ecological preferences. Ancestral ecological preferences were inferred in BEAST based on extant habitat preferences (e.g., primary rainforests, open environments, semi-disturbed forests, coastal scrubs, etc.) and elevation occurrences. Habitat information for each species were compiled from the literature, public databases, and field annotations. Speciation and extinction rates were estimated using software that account for incomplete taxonomic sampling (DDD (Etienne et al., 2012), BAMM (Rabosky, 2014), TreePar (Stadler, 2011)). Hypotheses of rate shifts were assessed using customized models and null-hypotheses of constant-rate diversification, shifts in speciation and extinction rates, and ecological limits to species richness.

Results and synthesis

1. Diversification methods to study biodiversity dynamics over time

The variation in species richness observed across clades in the tree of life is modulated by speciation and extinction. The interplay between these two evolutionary forces governs the dynamics of biodiversity, its generation and maintenance, in time and in space (Ricklefs, 2007). The study of diversification of lineages in a macroevolutionary framework is thus critical to understand patterns of biodiversity (e.g., latitudinal gradients) and in macroecology (e.g., community composition) (Morlon, 2014). This premise is followed throughout the thesis and is further elaborated in the methodological ***Paper II*** (Matos-Maraví, 2016), where I discuss the importance of phylogenies and the estimation of macroevolutionary variables, such as ecological limits to species richness, speciation, and extinction rates, in biodiversity research. The issue is not new, as it has received much attention theoretically and supported by empirical molecular phylogenies (Nee et al., 1992). However, insights from the perspective of hyperdiverse groups, such as insects, have scarcely been proposed.

Paper II uses primarily simulations of time-calibrated phylogenies to highlight serious shortcomings in recent meta-analyses of time-calibrated phylogenies when neglecting extinction and modeling ecological limits to species richness. Moreover, incomplete taxonomic sampling, poor preservation of fossils, and uncertainties in tree topology and divergence times, add another level of complexity when deciphering actual diversification processes in a clade. Accordingly, quantitative evaluation of alternative diversification models are highly beneficial to unveil the evolutionary and historical processes shaping extant species diversity. As a case study, the empirical dataset in ***Paper II*** focused on the Neotropics as it arguably is the best-studied tropical realm for insect evolution. Nonetheless, the conclusions of ***Paper II*** are applicable to any biogeographical region on Earth, including the Indo-Pacific.

A number of diversification hypotheses have been proposed to explain the origin of Neotropical diversity (Antonelli & Sanmartín, 2011), including the popular rainforest refugia scattered across the Amazon basin (Haffer, 1969). The most comprehensive set of published chronograms of any Neotropical insect group comes from butterfly studies. Therefore, I utilized them to highlight the advantages and limitations of using diversification approaches that incorporate extinction and ecological limits, as well as deal with incomplete taxon sampling. Contrary to recent butterfly meta-analyses that neglected patterns of diversification (Garzón-Orduña et al., 2014), I found evidence that butterflies diversified well before the Pleistocene and that any substantial increase in speciation in the past 2.6 Ma was detected in butterfly chronograms. The main implication for the ant fauna on the Indo-Pacific is that any evaluation of the timing of origin and diversification needs to be done in a phylogenetic framework. The Pleistocene glacial cycles and sea-level fluctuation have been frequently invoked to explain the origin and distribution of Indo-Pacific insects, ever since the early work of E.O. Wilson, P.J.M. Greenslade, and J.L. Gressitt. But without acknowledging extinction or diversity-dependence processes, our interpretations might be seriously mislead, even in the light of divergence time estimations.

2. Origins of Melanesian ants

The major centre of ant diversity across Melanesia is located on the island of New Guinea. Although Australia is the geographically closest continental landmass to New Guinea (and potential source of ant lineages), many ant groups seem to have spread from SE Asia, and even have reached tropical Queensland in Australia (Wilson, 1959). The results of the present thesis along with recent molecular phylogenies provide insights on the timing of colonization and biogeographic history of Melanesian ants. These studies partially confirmed the importance of Asian stocks in the composition of New Guinean species diversity, but they also emphasized other sources as significant contributors, namely Australia and the New World. Below, a summary of such reports in the context of the present thesis is presented:

2.1. Southeast Asian source

In ***Manuscript III***, the biogeographic history and diversification patterns within the *Prenolepis* genus-group (Formicinae: Lasiini) in the Indo-Pacific are analyzed. It was suggested that at least six colonization events to Melanesia from SE Asia occurred, three of them at the early Miocene (15–25 Ma) whereas the remaining three happened at the late Miocene and Pliocene (5–10 Ma). Such "colonization waves" into Melanesia might be explained by the paleogeographical models suggesting uplift of land as ephemeral islands in the Malay Archipelago during the early Miocene (*ca*. 25 Ma), and the significant volcanic activity, which may have uplifted island arcs during the Pliocene (*ca*. 6 Ma) (Hall, 1998). Such biogeographical pattern is reinforced by other time estimates of faunal interchange between SE Asia and Australia. For instance, terrestrial vertebrates might have been able to spread across the Malay Archipelago during the early Miocene, perhaps along small, ephemeral volcanic islands in the area (Jønsson et al., 2011; Cibois et al., 2014; Georges et al., 2014; Mitchell et al., 2014).

The colonization of Melanesia by SE Asian ant lineages seems therefore to have been facilitated by the collision between the Australian, the Philippines and Pacific plates. Such geological events have likely triggered the uplift of landmass, although paleogeographical reconstructions are not clear yet on the timing, extent, and duration of volcanic arcs in the Malay Archipelago. In addition to the colonization of Melanesia by the *Prenolepis* genus-group (***Manuscript III***), at least two ant clades (*Pheidole* (Economo et al., 2015a, 2015b) and *Lordomyrma* (Lucky & Sarnat, 2010)) have invaded New Guinea, Australia, and the South Pacific from SE Asia, coincidentally at around 15–20 Ma, whereas other three *Pheidole* clades appeared to have spread from SE Asia at about 5–10 Ma (Economo et al., 2015b). Moreover, the same dispersal route have been inferred from the molecular phylogeny of *Camponotus maculatus*-like ants (Clouse et al., 2015), although divergence times were not reported in that study.

2.2. Australian source

Australian-endemic lineages seem to have spread to New Guinea more recently than SE Asian lineages. Molecular phylogenies of Dolichoderinae ants largely agree on a late Miocene and Pliocene colonization of New Guinea (*ca* 5–10 Ma) (Ward et al., 2010; Lucky, 2011; Boudinot et al., 2016), contrasting with the long history of ant diversification throughout the Cenozoic in Australia (e.g., the tribe Melophorini (Blaimer et al., 2015)). However, in such cases ecological requirements rather than geographical distance may explain the timing of dispersal into New Guinea. Most of the Australian lineages that invaded New Guinea (e.g., within Dolichoderinae, *Leptomyrmex*, and *Iridomyrmex*) are associated with subtropical-temperate environments (Shattuck, 1992; Lucky & Ward, 2010). On the other hand, the savannah-like environment and dry forest areas that could have acted as a dispersal route for subtropical-temperate ants may have established geologically recently in southern New Guinea (Trans-Fly lowlands, Papuan Peninsula) (Kearns et al., 2011), aided by the global decrease in temperatures after the mid-Miocene climatic optimum (Zachos et al., 2008). In fact, recent dispersal events from southern New Guinea to Australia by ants associated with dry environments have been reported at about 5 Ma (e.g., *Acropyga* in ***Paper I*** (Janda et al., 2016), and *Odontomachus cephalotes* genus-group in ***Manuscript IV***).

2.3. New World source

Although massively separated from Melanesia by the Pacific Ocean, the New World may have been the source of several ant lineages. Three alternative dispersal hypotheses may explain the disjunct distribution of several ant clades on both edges of the Pacific: (a) trans-Antarctica; (b) Boreotropical origin; and (c) direct, passive dispersal via Pacific Equatorial currents.

(a) An Antarctic land corridor have connected Australia and southern South America until about 30–35 Ma (Sanmartín & Ronquist, 2004), and may have facilitated dispersal of cool-adapted ants (Boudinot et al., 2016). However, in the case of Melanesian ants, this hypothesis imply an indirect colonization by groups that first arrived to and radiated in Australia, and further dispersed northwards to New Guinea. Two Dolichoderinae clades show the abovementioned pattern: *Leptomyrmex* (Lucky, 2011; Boudinot et al., 2016), and the large Australasian clade sister to the Neotropical genus *Linepithema* (Ward et al., 2010)(Matos-Maraví et al., *in prep*.).

(b) The Boreotropical hypothesis has not yet been formally suggested for any ant group. Such hypothesis, originally proposed for early Cenozoic Northern Hemisphere plants, suggests an ancestral Holarctic distribution of tropical and warm-temperate lineages until the mid-Eocene (*ca*. 39 Ma) (Wolfe, 1975; Tiffney, 1985). North America and eastern Asia were likely connected by a warm Beringian bridge for most of the Eocene, but the rapid cooling event during the Oligocene glaciation event might have terminated such dispersal corridor at about 34 Ma (Sanmartín et al., 2001). Ant clades that originated in the Northern Hemisphere in the Eocene may have been isolated on both sides of the Pacific Ocean after the demise of the megathermal boreotropical flora. ***Manuscript IV*** discusses further alternatives for the the Boreotropical hypothesis to explain the disjunct distribution of *Odontomachus* lineages in the New World and the Indo-Pacific. Other possible example of an ant lineage that may be explained by this hypothesis is a subclade of the warm-adapted *Anochetus* trap-jaw ants, wherein the split between Neotropical and Indomalayan clades is dated at about 35–50 Ma (Larabee et al., 2016). In such case, the Antarctic land corridor may have been intolerably cold for these tropical/sub-tropical ants.

(c) Direct, long-distance dispersal across the Pacific Ocean have been invoked in a number of ant lineages at various geological times throughout the Neogene Period (*ca*. 0–25 Ma). For instance, mid-Miocene dispersal events from the New World to the Indo-Pacific has been inferred for *Pheidole* (Economo et al., 2015b) and *Odontomachus* lineages (***Manuscript IV***). These colonization events coincide with the major Neogene warming event, but more studies are needed in order to establish a potential link between global shifts in temperatures and ant dispersal along the warm Pacific Equatorial currents. *Odontomachus simillimus*, for instance, seems to have spread directly from the Neotropics into Melanesia across the Pacific Ocean as recently as 5 Ma, thus human-mediated dispersal is unlikely to have happened in such case, but a trans-Pacific long-distance dispersal (***Manuscript IV***). Other examples of apparent disjunct distribution may be explained by commerce, at least until divergence times of closely related taxa are elucidated, as for example a *Camponotus maculatus*-like Pacific lineage that clusters with a New World clade (Clouse et al., 2015).

3. Regional routes for ant dispersal within the Indo-Pacific

Little is known about the paleogeography of the Pacific volcanic islands. It is believed that certain islands of eastern Melanesia, including Vanuatu and Fiji, emerged and remained above water since the Miocene (i.e., for the past 25 Ma) (Keppel et al., 2009; Economo & Sarnat, 2012). However, the extent of their landmasses or the existence of island arcs that temporarily connected them with New Guinea or Australia remains speculative. The Vitiaz Arc biogeographic hypothesis suggests that the earliest colonization of eastern Melanesia occurred by the early to mid-Miocene (15–25 Ma), facilitated by an ancient archipelago across proto-Papua, the Solomon Islands, Vanuatu, and Fiji (Ewart, 1988; Liebherr, 2005). Such paleogeographic scenario predicts Miocene stepping-stone fashion dispersal of terrestrial fauna, until the disruption of the island arc at about 10 Ma. In ***Manuscript III***, the Vitiaz Arc model is supported by two lineages within the genera *Nylanderia* and *Paraparatrechina* that reached Vanuatu and Fiji at about 11 Ma. Similar biogeographic pattern has also been recovered in other ant taxa, namely *Lordomyrma* (Lucky & Sarnat, 2010) and *Pheidole* (Sarnat & Moreau, 2011; Economo et al., 2015b), which colonized and further diversified in the Solomon Islands, Vanuatu, and Fiji at about 9–17 Ma.

The exposure of most present land in the Pacific occurred rather recently, in the late Miocene and Pliocene (i.e., less than 10 Ma). Palau is the most species-rich archipelago along Micronesia and Polynesia (Clouse, 2007). Contrary to the most accepted assumption that the fauna of Palau is the result of single, long-distance dispersal, followed by local diversification (Gressitt, 1984), recent evidence from ant molecular phylogenies suggests instead that multiple dispersal from various sources occurred in the past 4–8 Ma. The Philippines and New Guinea are the two main sources of *Prenolepis* genus-group taxa in Micronesia (***Manuscript III***), whereas dispersal from Vanuatu and Australia was inferred for *Camponotus maculatus*-like ants (Clouse et al., 2015). Eastern Melanesia (i.e., Vanuatu and Fiji) was re-colonized during the Pliocene by younger lineages (*ca*. 5 Ma) from New Guinea (e.g., *Prenolepis* genus-group (***Manuscript III***), *Odontomachus* (***Manuscript IV***)), Australia (e.g., *Camponotus maculatus*-like ants (Clouse et al., 2015)), and SE Asia (e.g., *Pheidole* (Economo et al., 2015b)), in line with the recent re-exposure of most of its land area. Although westward dispersal or migration back to source areas has received little support by the taxon cycle hypothesis, such pattern was recovered in at least two ant clades. In *Camponotus maculatus*-like ants dispersal was reconstructed from Vanuatu to Micronesia, and back to New Guinea (Clouse et al., 2015), whereas *Odontomachus simillimus* seems to have colonized the entire Indo Pacific from Fiji (Janda et al., *in prep*.), a scenario that is consistent with the Neotropical origin of the lineage and subsequent dispersal westwards in the Pacific (Larabee et al., 2016)(***Manuscript IV***).

4. Diversification dynamics in New Guinea

The Central Range orogeny in New Guinea is one of the most important trigger of insect speciation (Toussaint et al., 2014). Such radiation happened relatively rapid (less than 10 Ma) probably by means of allopatric and parapatric differentiation. Ant diversification at lower montane habitats began at about 10–15 Ma (genus *Nylanderia*, ***Manuscript III***), when Australia and the Pacific plates converged and triggered the initial orogeny of Central Range on its western edge. Speciation continued throughout the Miocene and Pliocene on montane environments, along and across the Central Range (e.g., the genus *Odontomachus*, ***Manuscript IV***). Nonetheless, further taxon sampling and a better understanding of the ants' natural history in New Guinea are necessary before attempting to generalize the mechanisms of speciation (e.g., vertical or horizontal segregation by competition (Diamond, 1973), narrow habitat associations along altitudinal bands (Fjeldså & Lovett, 1997), geographical barriers to gene flow across mountains and valleys (Deiner et al., 2011), etc). For lowland ant taxa, strong habitat associations and possible local competitive exclusions may have strengthen differentiation among populations, rather than the Central Range *per se* as a significant barrier to gene flow (e.g., in *Acropyga* (***Paper I***), and in *Leptomyrmex* (Lucky & Ward, 2010)). Biotic interactions, such as ant-plant associations or inter-specific competition, may have also enhanced ant radiation in lowland rainforest (Chomicki et al., 2015). For instance, the Dolichoderinae genus *Philidris* seems to have diversified within the past 5 Ma (Ward et al., 2010) thanks to its association with myrmecophytes (Matos-Maraví et al., *in prep*.). Community assembly in such case contrasts that observed in other ant taxa displaying phylogenetic overdispersion, perhaps mediated by strong competition (Plowman et al., *in prep*.).

5. An integrative Indo-Pacific biogeography – ecology, evolution, and geography

The taxon cycle hypothesis has been one of the most integrative island biogeographic model, coupling ecological (local communities) and evolutionary mechanisms (population dynamics) to explain geographical distributions of taxa. However, a critical further expansion of the taxon cycle has been recently proposed, wherein the phases of expansions/contractions may not only be a single-species phenomenon, but also a broader clade-level pattern (Erwin, 1985; Economo et al., 2015a, 2015b). Such macroevolutionary component was not clear in the original proposal of the taxon cycle hypothesis. The expanded hypothesis then may predict that shifts in ecological preferences on one lineage may eventually lead to ecological release, promoting phenotypic variability and differentiation. Nonetheless, such evolutionary innovation may confer an ecological advantage for expanding lineages (both geographically and ecologically), and may persist even over cladogenetic events. Thus, if further speciation occurred, an entire clade might be considered at the expansion phase. Widespread clades within *Pheidole* (Economo et al., 2015b) and *Nylanderia* (***Manuscript III***), whose members occupy marginal habitats (e.g., coastal environments) have been recently reported. In ***Manuscript III***, furthermore, the analyses of diversification rates suggested that not only expanding clades may exhibit habitat preference shifts, but also those events may have increased speciation rates. Accordingly, shifts in habitat preference (ecological release) may not only favour geographical range expansion, as proposed by the original taxon cycle hypothesis, but it may also trigger species diversification of terrestrial invertebrates.

6. Conclusions and perspectives

This thesis represents a step forward to a better understanding of tropical insect evolution. Indo-Pacific ants offer a great opportunity to study the origin and diversification of taxa on insular landscapes. Standard protocols to collect them along with their abundances in tropical localities make the ants accessible and preferable study organisms. The good fossil preservation of the ants is another advantage when time-calibrating ant phylogenies. Various hypotheses on the success and radiation of ants have been proposed, including the influential taxon cycle. Cutting-edge methods on ancestral state reconstruction and diversification dynamics offer a new avenue to test such hypotheses in a multi-layer framework, including: paleogeography, phylogenetics, biogeography, and ecology. Nevertheless, this thesis might be considered, along with other Indo-Pacific ant biogeographic studies, only the starting point to disentangle the complexity of tropical biodiversity. Further ecological, behavioral, population genomics studies are needed to unveil the mechanisms of diversity generation in the Indo-Pacific. For now, a little bit more is known on the timing and how complex was the origin and maintenance of biodiversity in SE Asia and the tropical South Pacific.

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Chapter I

Phylogeny and population genetic structure of the ant genus *Acropyga* (Hymenoptera: Formicidae) in Papua New Guinea

Janda M, Matos-Maraví P, Borovanska M, Zima J,
Youngerman E & Pierce NE

Invertebrate Systematics 30, 28–40

Chapter II

Investigating the timing of origin and evolutionary processes shaping regional species diversity: Insights from simulated data and Neotropical butterfly diversification rates

Matos-Maraví P

Evolution 70, 1638–1650

Chapter III

An ant genus-group (*Prenolepis*) illuminates the drivers of insect diversification in the Indo-Pacific

Matos-Maraví P, Clouse RM, Sarnat EM, Economo EP,
LaPolla JS, Borovanska M, Rabeling C, Czekanski-Moir J,
Latumahina F, Wilson EO & Janda M

Manuscript

Chapter IV

A phylogenetic framework to Wilson's Taxon Cycle: the evolutionary history of *Odontomachus* trap-jaw ants (Hymenoptera: Formicidae: Ponerinae), with a focus on the Indo-Pacific region

Matos-Maraví P, Matzke NJ, Larabee FJ, Sorger M, Suarez AV & Janda M

Manuscript

Curriculum Vitae

Pável Fortunato Matos Maraví

Personal information

Date and place of birth: 14th October 1986 in Lima, Peru.

Family status: one child born in 2014.

Personal web page: http://pavelmatos.wordpress.com/

Academic record

November 2015. RNDr in Biology (major Experimental Biology), University of South Bohemia, Ceske Budejovice, Czech Republic.

"Causes of endemic radiation in the Caribbean: historical biogeography and diversification of the butterfly genus *Calisto*". *Approved with the highest score*.

The paper was ranked highly-accessed [see article (7) in Publications].

December 2010. MSc in Biology (major Evolutionary Biology), University of Turku, Finland.

"Molecular systematics and evolutionary history of the Neotropical *Taygetis* butterflies". *Eximia cum laude approbatur*. Supervisor: Dr Niklas Wahlberg.

The work resulted in a highly-cited publication [see article (5) in Publications].

September 2009. BSc in Genetics and Biotechnology, National University of San Marcos, Lima, Peru.

Graduated with Honours, top 5 of my class. My active participation in research projects made me elligible to an integral scholarship for the academic year 2008–2009 at the University of Turku, Finland.

During my BSc studies, I have worked as a trainee at different Peruvian research institutions. As a result, several poster presentations in national scientific meetings were produced.

Academic positions

September 2012–now. PhD student, Faculty of Sciences, University of South Bohemia, Ceske Budejovice, Czech Republic.

September 2012–now. Doctoral fellow, Institute of Entomology, Biology Centre, Czech Academy of Sciences.

June 2010–August 2012. Research assistant, Department of Biology, University of Turku, Finland.

June 2009–May 2010. Employed visiting student, Department of Biology, University of Turku (Finland). During this time I worked in three research groups:

> Dr Satu Ramula's group: I managed the standardization of microsatellite markers for the plant genus *Lupinus* (Fabaceae) and I taught molecular methods to post-doc Shouli Li.
>
> Prof Craig Primmer's group: I was involved in the development of INDEL markers for linkage mapping studies in freshwater fishes. Strong collaboration with Dr Anti Vasemägi.
>
> Dr Niklas Wahlberg's group: Butterfly molecular systematics and barcoding of insects.

March 2004– August 2008. During my BSc studies, I joined research teams as a trainee to learn topics on molecular systematics, Neotropical biodiversity, cytogenetics and, overall, the scientific working environment:

> Laboratory of Molecular Systematics and Phylogeography, University of San Marcos: I was supervised by Dr Rina Ramírez in snail's molecular evolution and phylogenetics.
>
> Department of Malacology and Carcinology, Museum of Natural History, Lima: I received training on land snail specimen manipulation, storage, and sampling techniques in the field.

Honor and Awards

2013. Ant Course, Manu Biosphere Reserve, Peru. Travel support (US $975).

2012. Programming for Evolutionary Biology, Germany. Travel support (€300).

2011. Congress of the European Society for Evolutionary Biology (ESEB), Germany. Travel support by the Turku University Foundation, Finland (€800).

2010. EDIT's (European Distributed Institute of Taxonomy) Summer School in Taxonomy, Portugal. All expenses covered by EDIT European Network.

2008–2009. Undergraduate exchange studies. Integral scholarship for the academic year at the University of Turku, Finland. Funded by the North-South-South Higher Education Institution Network Programme, Finnish Ministry for Foreign Affairs (€5,400).

Funded research projects

2016. Marie Skłodowska-Curie Intra-European Research Fellowship (project MARIPOSAS-2015-704035). The aim of the project is to unveil the molecular systematics and biogeography of selected Neotropical butterfly clades (skippers and brush-footed butterflies), using Next-Generation-Sequencing technologies. The project length is for 2 years (€185,857) and will be based at the University of Gothenburg, Sweden, under supervision of Prof. Alexandre Antonelli

2014–2015. "Unraveling the environmental and biotic triggers of insect diversification in the tropical islands of the Pacific". Funded by the Grant Agency of the University of South Bohemia, Czech Republic (200,000 Kč ≈ €7,500). The aim of the project is to integrate macroevolution (above species level) and microevolution (population level) to comprehensively understand the radiation of ants in the Indo-Pacific region. Article (12) is presented in the thesis, article (10) has been published, and articles (13 and 16) will be submitted.

2012. Scientific scholarship to study the diversification of Neotropical butterflies in the tribe Satyrini (Nymphalidae). Funded by the Oskar Öflund Foundation, Finland (€3,000). Articles (2 and 5) are the result of this project.

2012. Young scientist fellowship to study the diversification of Caribbean butterflies in the genus *Calisto* (Nymphalidae: Satyrinae). Funded by the Turku University Foundation, Finland (€9,500). Articles (1, 3, and 7) are the result of this project.

2010. Undergraduate study grant funding my Master thesis project on the molecular systematics of the *Taygetis* group (Nymphalidae: Satyrinae: Euptychiina), a group of butterflies that occurs in the Neotropics. The Finnish Cultural Foundation, Finland (€1,500). Article (5).

Teaching and mentoring

University courses

Spring 2007. "Molecular Biology" (Undergraduate course at the Faculty of Biological Sciences, University of San Marcos, Peru). I took responsibility for the laboratory exercises.

Fall 2007. "Animal Diversity" (Undergraduate course at the Faculty of Biological Sciences, University of San Marcos, Peru). I assisted and taught in field course expeditions.

Mentoring/tutoring of students

as co-supervisor of Master's research projects

2016. Yuliza Tafoya Alvarado. "Genetic patterns in ecological specialization of ants, based on ancient and modern DNA". Thesis at Langebio, Cinvestav Research Centre, Mexico.

as teaching/supervising grad students in molecular laboratory

2010–2012. I taught molecular methods in evolutionary biology to several undergraduate and graduate students at University of Turku, Finland.

Publications in major, peer-reviewed journals.

Article's citation statistics (excluding self-citations) based on Google Scholar.

Citation indices updated to 30th August 2016: **Google Scholar**, 73 citations (excluding self-citations), h-index 5, i10 index 3; **ISI Web of Science**, 53 citations (excluding self-citations), h-index 5.

10. Larabee FJ, Fisher BK, Schmidt CA, **Matos-Maraví P**, Janda M, Suarez AV (2016) Molecular phylogenetics and diversification of trap-jaw ants in the genera *Anochetus* and *Odontomachus* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution* 103: 143–154.

9. **Matos-Maraví P** (2016) Investigating the timing of origin and evolutionary processes shaping regional species diversity: insights from simulated data and Neotropical butterfly diversification rates. *Evolution* 70(7): 1638–1650.

8. Janda M, **Matos-Maraví P**, Borovanska M, Zima J, Youngerman E, Pierce N (2016) Phylogeny and population genetic structure of the ant genus *Acropyga* (Hymenoptera: Formicidae) in Papua New Guinea. *Invertebrate Systematics* 30(1): 28–40. **(1 citation)**.

7. **Matos-Maraví P**, Núñez Aguila R, Peña C, Miller JY, Sourakov A, Wahlberg N (2014) Causes of endemic radiation in the Caribbean: evidence from the historical biogeography and diversification of the butterfly genus *Calisto* (Nymphalidae: Satyrinae: Satyrini). *BMC Evolutionary Biology* 14(1): 199. **(7 citations)**.

6. Li S, Vasemägi A, **Matos-Maraví P**, Ramula S (2013) Development and testing of microsatellite loci for the invasive herb *Lupinus polyphyllus* through 454 pyrosequencing. *Molecular Ecology Resources* 13(4): 760–762. **(4 citations)**.

5. **Matos-Maraví P**, Peña C, Willmott K, Freitas AVL, Wahlberg N (2013) Systematics and evolutionary history of butterflies in the "*Taygetis* clade" (Nymphalidae: Satyrinae: Euptychiina): towards a better understanding of

Neotropical biogeography. *Molecular Phylogenetics and Evolution* 66(1): 54–68. **(27 citations)**.

4. Müller CJ, **Matos-Maraví P**, Beheregaray LB (2013) Delving into *Delias* Hübner (Lepidoptera: Pieridae): fine-scale biogeography, phylogenetics and systematics of the world's largest butterfly genus. *Journal of Biogeography* 40(5): 881–893. **(16 citations)**.

3. Núñez Aguila R, **Matos-Maraví P**, Wahlberg N (2013) New *Calisto* species from Cuba (Lepidoptera: Nymphalide: Satyrinae). *Zootaxa* 3669(4): 503–521. **(1 citation)**.

2. Freitas AVL, Wahlberg N, **Matos-Maraví P**, Marin MA (2012) *Euptychia boulleti* (Le Cerf) n. comb. (Lepidoptera: Nymphalidae: Satyrinae), a rare and endangered butterfly from southeastern Brazil. *Neotropical Entomology* 41(6): 461–467. **(12 citations)**.

1. Núñez Aguila R, Oliva Plasencia E, **Matos-Maraví P**, Wahlberg N (2012) Cuban *Calisto* (Lepidoptera: Nymphalide: Satyrinae), a review based on morphological and DNA data. *Zookeys* 165: 57–105. **(5 citations)**.

Manuscripts in preparation for peer-reviewed journals.

11. **Matos-Maraví P**, Clouse RM, Sarnat EM, Economo EP, LaPolla JS, Borovanska M, Rabeling C, Czekanski-Moir J, Latumahina F, Wilson EO, Janda M. An ant genus-group (*Prenolepis*) illuminates the drivers of insect diversification in the Indo-Pacific.

12. **Matos-Maraví P**, Matzke NJ, Larabee FJ, Sorger M, Suarez AV, Janda M. A phylogenetic framework to Wilson's Taxon Cycle: the evolutionary history of *Odontomachus* trap-jaw ants (Hymenoptera: Formicidae: Ponerinae), with a focus on the Indo-Pacific region.

13. **Matos-Maraví P**, Larabee FJ, Borovanska M, Zima J, Suarez AV, Janda M. Phylogenetic relationships of the trap-jaw ants within the *Odontomachus cephalotes* species group (Hymenoptera: Ponerinae) and population genetics of the Australo-Papuan species *O. cephalotes*.

14. **Matos-Maraví P**, Klimes P, Plowman N, Borovanska M, Janda M. Molecular systematics and diversification of the ant subfamily Dolichoderinae in New Guinea.

15. Penz C, **Matos-Maraví P**, DeVries P, Wahlberg N. Molecular systematics of the Neotropical butterfly tribe Haeterini (Nymphalidae: Satyrinae).

16. Janda M, Borovanska M, Zima J, **Matos-Maraví P**. Phylogeography of the trap-jaw ant *Odontomachus simillimus* (Hymenoptera: Formicidae: Ponerinae).

Conferences and seminars

Talks in international scientific meetings

1. 7th Biennial Conference of the International Biogeography Society (IBS). Bayreuth, Germany (2015) Matos-Maraví et al. "Endemic butterfly radiation on the Caribbean: insights from historical biogeography and phylogenetic diversification". Abstract in *Frontiers of Biogeography* 6(5) supp. 1: 84.

Invited seminars/lectures

1. BIG4 field workshop. Podyji National Park, Czech Republic. (2016) Matos-Maraví "Molecular species delimitation"

2. Ant mini-symposium. Ceske Budejovice, Czech Republic (2016) Matos-Maraví "Diversification and biogeography of Melanesian ants"

3. Department of Zoology, Charles University. Prague, Czech Republic (2015) Matos-Maraví "Macroevolutionary processes of insects on tropical islands, examples from the Caribbean and Melanesian regions"

4. LANGEBIO, National Laboratory of Biodiversity Genomics, Irapuato, Mexico (2013) Matos-Maraví "Biodiversity dynamics of ants in Melanesia and the South Pacific"

5. Faculty of Biological Sciences Seminar Series, National University of San Marcos. Lima, Peru (2012) Matos-Maraví "Evolutionary history and biogeography of tropical insects"

6. SEBDEM Symposium. Turku, Finland. (2011) Matos-Maraví "What can a group of brownish butterflies tell us about the Neotropical Biogeography?"

7. II BIOINT Graduate School Annual Meeting, Jokioinen, Finland (2010) Matos-Maraví et al. "Elucidating the phylogenetic relationships in the group of "*Taygetis*" butterflies (Nymphalidae: Satyrinae: Euptychiina) and dating its phylogeny"

8. XVIII National Scientific Meeting of the Research Institute for Biological Sciences (ICBAR), Lima, Peru (2009) Matos-Maraví et al. "Preliminary results of DNA barcoding in the butterfly genus *Hipparchia* (Nymphalidae: Satyrinae)"

9. V National Congress Genetics and Biotechnology, Lima, Peru (2009). Matos-Maraví & Vasemägi. "Linkage mapping and "Common garden" experiments in Atlantic salmon"

Poster communications

1. Ant Symposium. Munich, Germany (2016) Matos-Maraví et al. "A phylogenetic framework to Wilson's Taxon Cycle: evolutionary history of Melanesian trap-jaw ants (Ponerinae: *Odontomachus*)"

2. XIX European Congress of Lepidopterology. Radebeul, Germany (2015) Rindoš et al. "The historical biogeography of the hawkmoth genus *Ambulyx* (Lepidoptera: Sphingidae) in Indonesia based on mitochondial DNA genes"

3. 17th Congress of the International Union of the Study of Social Insects (IUSSI). Cairns, Australia (2014) Janda et al. "Diversification and dispersal of Australasian ants, from populations to species"

4. Zoologicke dny. Brno. Czech Republic (2013) Zima et al. "All roads lead to South Pacific - a comparative phylogeography of the Asian weaver ant *Oecophylla smaragdina* and the trap-jaw ant *Odontomachus simillinus*"

5. XXXII Meeting of the Willi Hennig Society. Rostock, Germany (2013) Janda et al. "Next-Gen phylogeography of the Asian weaver ant *Oecophylla smaragdina* - combining de novo SNP discovery and genotyping with ddRADseq with mt. DNA"

6. 13th Congress of the European Society for Evolutionary Biology, Tübingen, Germany (2011) Matos-Maraví et al. “Origin and diversification of the Neotropical "*Taygetis*" butterflies (Nymphalidae: Satyrinae)”

7. XVII National Scientific Meeting of the Research Institute for Biological Sciences (ICBAR), Lima, Peru (2008) Matos-Maraví et al. “Preliminary cytogenetics studies in the eadable land snail *Megalobulimus capillaceus* (Mollusca, Gastropoda) from the peruvian Amazonia”

8. 13th Latin American Congress of Genetics and VI Peruvian Congress of Genetics, Lima, Peru (2008) Ramírez et al. “Advances in the mitocondrial genomics knowledge of the edible land snails genus *Megalobulimus* (Mollusca, Gastropoda) from the peruvian Amazonia”.

9. XVI National Scientific Meeting of the Research Institute for Biological Sciences (ICBAR), Lima, Peru (2007) Romero et al. “Populational variation in the shell morphology of *Bostryx scalariformis* (Mollusca, gastropoda)”.

10. XV National Scientific Meeting of the Research Institute for Biological Sciences (ICBAR), Lima, Peru (2006) Ramírez et al. “Biogeographic characteristics of the coastal desert zone Lachay-Casma based on the analysis of mollusc biodiversity”.

Organization of scientific meetings/courses

1. Faculty of Biological Sciences' Seminar Series, University of San Marcos, Lima, Peru (2012). Membership in the steering and programme committee. The seminar series organized at my home university in Peru gave the opportunity to Peruvian researchers studying abroad to talk about their latest projects/results and the research opportunities for undergraduate biology students.

2. SEBDEM **S**ymposium in **E**cology, **B**iological **D**iversity, Genetics, **E**nvironmental and **M**arine biology, Turku, Finland (2011). Membership in the steering and programme committee. The symposium goal was to gather and integrate PhD students of Biology from the two universities in the city of Turku (University of Turku and Åbo Akademy).

3. Course on Plant Biology, Genetics and Biotechnology, and the implications for Peru, Lima, Peru (2007). I assisted in the organization of the course, one of the first in the subject in the country.

4. Theoretical and practical course on Forensic Biology and Genetics, Lima, Peru (2007). I assisted in the organization of the course, where renowned Peruvian investigators took part.

Reviewer services

Biological Journal of the Linnean Society; Peerage of Science; ZooKeys.

Languages

Spanish and English, written and spoken fluently. Czech and Finnish, basic understanding.

Research skills

Laboratory work

- DNA extraction of plant and animal organisms, **P**olymerase **C**hain **R**eaction (PCR), gel and capillary electrophoresis.

- DNA sequencing using Sanger method, fragment analysis of polymorphic markers such as **IN**sertion-**DEL**etion (INDEL) and microsatellites.

- Cytogenetics approaches such as slide preparations and karyotype construction (experience with human and land snails samples).

Software and analytical methods

- Phylogenetic inference and species tree estimation using software TNT, BEAST, *BEAST, MrBayes, RAxML.

- Molecular species delimitation using multi-locus dataset with software bGMYC, PTP, BP&P.

- Ancestral state estimation in model-based environment: Historical biogeography with BioGeoBEARS (in R language) and Lagrange (in C++

programming language). Trait reconstruction using Mesquite, BayesTraits, diversitree and picante (R packages).

- Diversification rate estimations using software BAMM, DDD, TreePar (R packages).

- Population genetic analyses: summary statistics in Arlequin, DnaSP; population structure using structure, BAPS, along with admixture analysis, clustering algorithms and **P**rincipal **C**omponent **A**nalysis (PCA); Demographic reconstructions using Migrate-n, diyABC.

Field and taxonomic work

- Field sampling of ants and butterflies in Peru, Portugal, and Mexico. Samples prepared for molecular work in the field.

- Courses in taxonomic identification of insects (Madeira, Portugal) and ants (Manu, Peru). Able to identify at least at the genus-level several groups of tropical ant and butterfly species.

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