BEES OF THE SOUTH WEST PACIFIC:

EVOLUTION OF AN ISLAND POLLINATOR GROUP

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SUMMARY

This thesis investigates the assembly and evolution of the bee fauna in the south western Pacific (SWP) islands using molecular phylogenetics. Previous studies have shown that the majority of bee species in the SWP comprise just two families, Halictidae and Megachilidae, both of which have low species diversity despite an otherwise rich island biota. However, previous assessments were largely focussed on single archipelagos during the early 20th century and were based purely on morphology with no implementation of molecular methods since. With potential for many synonymies or undescribed species of a bee fauna critical to the function of threatened ecosystems, the work presented here looks to understand the composition and role of bees in the Pacific.

In this thesis, examination of conspecific and congeneric genetic differences in mitochondrial DNA sequences was the primary method used to explore species diversity in all bee families in the SWP through a variety of phylogenetic methods, whilst Bayesian approaches were used to apply molecular clocks to model diversification and changes in effective population size over time for the endemic halictine bees in the subgenus *Homalictus*.

Results indicated high levels of genetic variation in derived haplotype clades of Fijian halictine bees from low elevations, and indicate that these major diversification changes in these clades arose at a time that coincides with the last glacial maximum (LGM). Basal lineages appear restricted to higher elevations,

suggesting that colonising species were adapted to wet forests. Reconstruction of effective population size changes reveals an increase corresponding to a warming climate post-LGM and radiation through lower elevations.

The dataset of Fijian haplotypes was then expanded and demonstrated almost identical and simultaneous responses to the last glacial maximum in populations of neighbouring archipelagos of Vanuatu and Samoa. Large-scale population declines in cooler climates of the LGM were followed by considerable increases corresponding to a subsequent period of warming.

The presence of at least four species of the family Apidae were also documented in the Pacific, with genetic distances revealing their likely introduction from Australia, Asia, and North America since human colonisation. As long tongued bees, there are large implications for the presence of these genera in the region. Furthermore, bees of the genus *Amegilla* are able to buzz pollinate, meaning a novel method of pollination has been introduced with their arrival. We explore the implication of these introductions in light of our other research findings.

Megachilidae of the Pacific were found to comprise a mixture of species introductions and dispersals from southeast Asia since the last glacial maximum. As species of this family are largely wood boring, it is likely that the arrival of humans in the region and establishment of maritime trade routes has influenced the dispersal of the group.

Considered as a whole these results indicate that the bees of the Pacific are not likely to have played a key role in the development of early island ecosystems, and that since the LGM there has been considerable change in the composition of island pollinator suites. This has large implications for the future management of the region's biodiversity and development of agriculture.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Scott Vernon Charles Groom

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GENERAL INTRODUCTION

Bees are critical pollinators in almost all terrestrial ecosystems, yet their presence in the archipelagos of the south western Pacific appears limited (Groom & Schwarz 2011). Studies of bees have typically shared the belief that species diversity of these islands was considerably less than neighbouring continents, but the majority of these works are many decades old and based solely on morphology (Cockerell 1924; Perkins & Cheesman 1928; Cheesman 1936; Michener 1979; Pauly & Villemant 2009). Islands often have reduced species richness, but the reduced competition allows pollinators on islands to have broadened host-plant ranges (Olesen *et al.* 2002). So if the archipelagos of the south west Pacific (SWP) were to exhibit a low number of endemic pollinators, those that are present are likely to have a critical role in the function of their ecosystem. Determining which pollinators are endemic is therefore important in understanding their relationship with endemic flora and how this has developed over time. Likewise, understanding those species that are non-endemic helps us make informed decisions on their management and potential utility in agriculture.

As the studies of the bee fauna of the Pacific have previously been purely morphology-based, there is great potential in applying molecular techniques to understanding this important pollinator group. As a developing region, the health of pollinator populations in the Pacific islands can have large influences over the health of village communities where subsistence living remains prevalent. Reconstructing the histories of Pacific bee faunas not only gives us insight into the assembly of island ecosystems, but how we might best ensure food security in a developing region.

This thesis endeavours to utilise molecular data to address several of these issues in order to better understand the true diversity and evolutionary history of the bee fauna of the SWP islands. The components of this thesis are presented in the form of five multi-authored chapters, with references formatted for their corresponding journals. Versions of chapters I and II have been published in *Apidologie* (**42**:6, 759-770) and *Molecular Phylogenetics and Evolution* (**68**:3, 582-594) respectively, and these chapters are presented as copies of the final accepted manuscripts. Chapter III is currently accepted pending minor revisions and is presented as a copy of the manuscript submitted to the *Proceedings of the Royal Society B: Biological Sciences*. Chapter IV has been published in *Biological Invasions* and is presented as the final submitted manuscript. Chapter V is currently under review with the *Journal of Insect Conservation* and is presented as the first submitted manuscript.

I was primarily responsible for all data collection, analysis, laboratory work, interpretation/discussion of the results, as well as production and formatting of published material. The following contributions were made by various co-authors: Chapter I benefitted from review of early drafts by Mike Schwarz. Chapter II drew from collections made with the assistance of Mark Stevens and revision of manuscript drafts by Mike Schwarz. Chapter III drew from data collected with the assistance of Mark Stevens. Both Mark Stevens and Mike Schwarz assisted with analyses and multiple revisions of the manuscript. Chapter IV drew from molecular data of Hien Ngo collected from southeast Asia that represented many outgroup taxa and representatives of *Ceratina dentipes*, while Sandra Rehan also provided sequences of this species from Samoa and the Solomon Islands. All co-authors including Posa Skelton, Mark Stevens, and Mike Schwarz contributed to revision of the manuscript. Chapter V drew from molecular data from Hien Ngo that included specimens of *Heriades* sp., *Megachile umbripenne*, *M. australis*, and outgroup species from southeast Asia, while Sarah Hayes helped prepare the resulting dataset. Mark Stevens and Mike Schwarz oversaw analysis of the data and revisions of the manuscript. All five chapters were written with commentary from the candidate's supervisor, Associate Professor Michael Schwarz, and adjunct supervisor Associate Professor Mark Stevens. Funding from grants awarded to Michael Schwarz are also recognised by his inclusion as author. The following paragraphs summarise each chapter.

CHAPTER I: Bees in the Southwest Pacific: Origins, diversity and conservation Provides a summary of the available literature on the bee fauna on the SWP and neighbouring regions. It highlights a distinct drop in species diversity from Indo-Australian region eastwards, with the prevalence of colletid bees in Australia almost entirely absent from the Pacific islands. However, much of the research in the region occurred in the first half of last century, with very few studies completed recently. This leaves a potentially underestimated species diversity for each archipelago and how they relate to one another.

CHAPTER II: Diversification of Fijian halictine bees: insights into a recent island radiation Explores the radiation of halictine bees in Fiji using phylogenetic analyses of mtDNA COI sequence data. These data reveal a high level of haplotype diversity despite only four recorded species. Analysis of synonymous substitutions, haplotype lineage accumulation and changes in effective population size reveals key changes responsible for this genetic diversity. By using estimated mutation rates of other invertebrates we are able to determine the likely time scale of such changes to reveal the magnitude of response to Pleistocene climate change.

CHAPTER III: Parallel responses of bees to past climate change in three isolated archipelagos of the south western Pacific Aims to explore the impacts of glacial cycles on the endemic halictines bees of the SWP. Data from Chapter II shows a dramatic response to the LGM in Fiji, and here we are able to show how population sizes in three isolated archipelagos have fluctuated over the Quaternary. We show that the bee faunas of Vanuatu, Fiji and Samoa all suffered large and near-simultaneous population declines corresponding to the LGM, followed by rapid expansion post-LGM. As key pollinators, the inferred changes in these bee faunas may have been critical in the development of the diverse Pacific island flora.

CHAPTER IV: Multiple recent introductions of apid bees into Pacific archipelagos signify potentially large consequences for both agriculture and indigenous ecosystems Uses DNA barcodes to provide the first detailed account of Apidae bees from Vanuatu, Fiji, and Samoa. We show that most if not all apid species in these archipelagos have been recently introduced from Australia and South East Asia, with a further species introduced from the New World. As long tongued bees, we outline the potentially large threats to endemic plant-pollinator interactions but also possible benefits to regional agriculture.

CHAPTER V: Megachilidae in the south west Pacific: potential impacts of a recent bee fauna on ecosystem development and stability Looks into the most prevalent group of long-tongued bees in the Pacific; the megachilids. Little is known of their origin, but by using mtDNA to measure genetic distances we are able to infer the likely ages and origins of species from Vanuatu, Fiji, and Samoa. Our results suggest a very recent origin for megachilids in the SWP, with many species exhibiting small intra-specific genetic distances. Considered with the outcomes of our other research of bee groups in the region, the results have broad implications for how the Pacific island biota developed.

Finally, the overall conclusions and broader implications of these studies, as well as important avenues for further research, are examined in a General Discussion following Chapter V.

Two further manuscripts are included in Appendices. Appendix A, which comprises the manuscript ‘Origins and diversity of Fijian Leafcutter bees’ published in the journal *Pacific Science* (**67**:4, 561-570) was the result of my supervision of Ms Davies during an undergraduate course. Appendix B includes the manuscript ‘Recent introduction of an allodapine bee into Fiji: a new model system for understanding biological invasions by pollinators’ accepted for publication in *Insect Science* pending minor revision. Although not included as part of this thesis, their results provide important context for the outcomes of this research.

References cited

Cheesman L.E. (1936). Hymenoptera of the New Hebrides and Banks Islands. *Transactions of the Royal Entomological Society of London*, 85:7, 169-195.

Cockerell T.D.A. (1924). Bees from the Tonga and Samoa Islands. *Annals of the Entomological Society of America*, 17:4, 392-394.

Michener C.D. (1979). Genus *Homalictus* in Fiji (Hymenoptera, Halictidae). *Pacific Insects*, 21:2, 227-234.

Olesen J.M., Eskildsen L.I. & Venkatasamy S. (2002). Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions*, 8:3, 181-192.

Pauly A. & Villemant C. (2009). Hyménoptères Apoidea (Insecta) de l'archipel du Vanuatu. *Zoosystema*, 31:3, 719-730.

Perkins R.C.L. & Cheesman L.E. (1928). Hymenoptera - Apoidea, Sphecoidea, and Vespoidea. *Insects of Samoa*, Part V., 1-3