GENERAL CONCLUSION

The research presented here has provided important insights into both the evolution and the history of diversification in the bee fauna of the SWP. A comprehensive review of the available literature is presented in Chapter I, which details the composition of a largely depauperate bee fauna in the Pacific islands despite the region comprising multiple biodiversity hotspots (Myers, Mittermeier et al. 2000). One key feature of the bee fauna of this region is the almost complete absence of the family Colletidae, which comprise over half of the approximately 2000 bee species present in Australia (Michener 2007). Instead, Megachilidae and Halictidae are the predominant families, yet are only represented by a few key subgenera. This suggests that only a few species may be responsible for a considerable proportion of pollination services provided by bees in the Pacific. In light of the lack of understanding of bees in the region, Chapter I highlights how important their populations may be to the sustainability of biodiversity and agricultural production in the region.

The bee family Halictidae in the SWP is almost entirely represented by just one subgenus, *Homalictus* (Groom and Schwarz 2011). In Chapter II, the presence of just four species in Fiji is shown to be very recent relative to the proposed geological age of the archipelago. Previous collections of Fijian *Homalictus* suggested a diversity gradient, as three of the four known species were described exclusively from collections above 800m in altitude. Phylogenetic reconstruction revealed rare basal lineages collected from above this elevation, with derived lineages collected from below this height exhibiting very high haplotype diversity. Exploration of nonsynonymous substitutions revealed this haplotype diversity is the result of only a few key changes, with one large clade comprising many small synonymous changes. Reconstruction of haplotype accumulation curves shows a steep increase in diversification close to the present, which is also evident in effective population size changes. By applying a known rate of mutation in invertebrate mtDNA (Haag-Liautard, Coffey et al. 2008), the timing of these population increases was determined to coincide with the period following the last glacial maximum (LGM) with a likely origin of *Homalictus* in Fiji during the Pleistocene. As *Homalictus* comprise such a large part of the Pacific bee fauna, these findings have major implications for the development of early ecosystems that may have been absent of a key endemic pollinator.

Given the response to the LGM determined in the *Homalictus* of Fiji, there was a clear need to examine whether this climatic event also influenced neighbouring archipelagos. Climatic records in the Pacific are limited (Meckler, Clarkson et al. 2012), and our understanding of ecosystem development in the region is also poor. As the evolution of bees is closely tied to the rise of the angiosperms (Grimaldi 1999), we can gain insight into the assembly of a large part of an island's biota through modelling changes in their bee fauna populations. Chapter III expands on the Fijian *Homalictus* dataset to include additional regions of Fiji, and the neighbouring archipelagos of Vanuatu and Samoa. Haplotype accumulation curves demonstrate almost identical trends to that shown in Fiji, while changes in effective population size show a large decrease followed by considerable increase occurring simultaneously in all three archipelagos. By applying an estimated mutation rate for invertebrate mtDNA as done previously, the decrease in populations sizes is shown to coincide with the beginning of the LGM with the subsequent increase occurring during a period of climatic warming. With parallel responses across a large spatial scale, these results strongly support the hypothesis that the most likely causal factor is climate although it is not certain whether bees are directly responding to this. Palynological records from the region are only confident for recent times, with the one exception being from the highland Lake Tagamaucia of Taveuni in Fiji that covers a pre-LGM time scale. This site indicates a dramatic shift in floral composition from wet forest species, to drier-adapted plants and may provide further indication of a shift in environmental conditions that enabled the expansion of *Homalictus* into lower elevations.

The early records of Pacific bees suggest that the European honeybee (*Apis mellifera*) has been present for up to a century (Cockerell 1924), yet it remained the only record of the Apidae family until recently (Evenhuis 2007). Chapter IV reveals at least four other species are now established in the region, and that extremely low genetic diversity almost certainly confirms their presence is the result of human-aided introductions from Australia, Asia, and North America. As long tongued bees, Apidae are able to pollinate some plants that the endemic short-tongued Halictidae are not. In some circumstances this may be beneficial, such as the provision of agricultural services with the arrival of buzz pollination in *Amegilla*, but it may also be to the detriment of the local ecosystem. The impacts of recent introductions are likely to comprise two major issues in the management of weeds and displacement of endemic pollinators. The spread of novel weeds can be impeded without a suitable pollinator, but the introduction of polylectic bee species might increase their invasive potential considerably (Goulson 2003). Termed ‘sleeper weeds’, there is great potential for any benefits to agriculture via pollination services being offset by the management of invasive weeds (Groves 2006). There is also the potential for resource competition and displacement of native pollinators (Kearns, Inouye et al. 1998, Kato and Kawakita 2004). Islands often harbour reduced pollinator species richness, which can enable endemic pollinators to possess broadened host-plant ranges (Olesen, Eskildsen et al. 2002). The introduction of competing pollinators has the potential to disrupt these interactions to the detriment of both endemic plants and pollinators.

The other most prevalent group in the Pacific comprise species of the family Megachilidae. Phylogenetic analyses in Chapter IV suggest a complex but recent history of the group in the Pacific, with all species likely to have arrived since the LGM. At least twelve species are recorded for the SWP, with at least four confirmed to be likely introductions from south east Asia. The genus *Heriades* had been previously described from the islands of Micronesia, but representatives from Fiji are shown to share almost identical haplotypes with specimens from Asia. While we did not find that same for specimens of *Lithurgus scabrosus* recovered from Vanuatu, it is a known tramp species capable of dispersing and colonising through human mediated avenues (Perkins and Cheesman 1928, Pauly and Munzinger 2003). The remaining species of the genus *Megachile* show evidence of introduction and recent dispersal, although with some potential for insular speciation. The implications of such recent arrivals mean that over half of the Pacific bee fauna appears to have arrived since the LGM. This raises the question of what pollinators were present prior to this period and how the arrival of the current bee fauna has influenced the established relationships of early ecosystems.

The investigations presented in this thesis have shown the Pacific bee fauna to be valuable in understanding the complex histories involved in community assembly. This work highlights the utility of mtDNA in not only understanding species diversity, but also reconstructing the demographic history of a key island pollinator group. Phylogenetic examinations of each family present in the Pacific has revealed a recent but complicated history that has been influenced by two key periods, namely the LGM and arrival of humans.

While the research outlined here represents the most thorough study of Pacific island bees to date, considerable gaps persist in our understanding of the biota of the region. As this work highlights shifts in the composition of Pacific pollinators, there is a clear need to determine if these changes are reflected by historical changes in flowering plant abundances and diversity. Diversification of angiosperms has been closely linked to the evolution of bees, and the findings presented here, that bees represent recent arrivals in the Pacific, suggests that a major change in angiosperm communities may have also occurred. Studies that investigate the assembly of the flora and fauna of the Pacific islands are relatively few, and based on the research here future studies should focus on the central role and development of the regional flora.

Climate has been shown to have considerable impact on the development of ecosystems, as suggested here. Studies of climate change in the Pacific are limited, with most reconstructions comprising extrapolation of trends evident from areas neighbouring the region (Meckler, Clarkson et al. 2012). However, the potential for variation at a local scale means the accuracy of timing and magnitude of changes could be missed. Climate proxies within the region are also few, and largely restricted to palynological studies that only date confidently to periods since the LGM (Hope, Stevenson et al. 2009). Given the influence of the Pacific Ocean over past and future climate shifts, there is a clear need for more detailed reconstructions within the region.

Economic development in the Pacific has seen positive changes in the well-being of human communities. However, it has also resulted in a transition from subsistence village communities to urbanised lifestyles (Ulijaszek 2005). The introduction of mass-produced, poor quality, but cheap food options has seen a drastic rise in diet-related health issues such as heart disease and diabetes (Collins, Dowse et al. 1996, DiBello, McGarvey et al. 2009, Dancause, Dehuff et al. 2011). With growing human populations, there is an increasing demand for arable land that is often to the detriment of native habitat. By ensuring optimal crop yields and availability of a diverse diet, such issues impacting Pacific communities could be mitigated to some extent by ensuring the health of pollinator communities.

Declines in honeybee (*Apis mellifera*) in the Solomon Islands have all but decimated the apiculture industry since the arrival of the *Varroa* mite, meaning the utility of native pollinators has never been more important. Results presented here highlight several species, both endemic and introduced, that might be suitable as 'insurance' against any pollination deficit. However, with almost no studies on the biology of these species, the feasibility of non-*Apis* species filling this role in the Pacific remains largely unknown. Further research must understand the ecological requirements of key species, and particularly their interaction with high value crops such as coconut (*Cocos nucifera*) and papaya (*Carica papaya*) (Tyagi and Datt 2004, Cloin 2005).

By applying these recommendations for future research, and developing local expertise in the process, we lay the foundations to ensure the sustainability of biodiversity and food security in a future of great change while effectively managing some of the most important insects of the Pacific islands.

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