



Diversification of Fijian halictine bees: Insights into a recent island radiation



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ABSTRACT

Although bees form a key pollinator suite for flowering plants, very few studies have examined the evolutionary radiation of non-domesticated bees over human time-scales. This is surprising given the importance of bees for crop pollination and the effect of humans in transforming ecosystems via agriculture. In the Pacific, where the bee fauna appears depauperate, their importance as pollinators is not clear, particularly in Fiji where species diversity is even lower than neighbouring archipelagos. Here we explore the radiation of halictine bees in Fiji using phylogenetic analyses of mtDNA COI sequence data. Our analyses indicate the existence of several 'deep' clades whose divergences are close to the crown node, along with a highly derived 'broom' clade showing very high haplotype diversity, and mostly limited to low-lying agricultural regions. This derived clade is very abundant, whereas the more basal clades were relatively rare. Although nearly all haplotype diversity in Fijian *Homalictus* comprises synonymous substitutions, a small number of amino acid changes are associated with the major clades, including the hyper-diverse clade. Analyses of haplotype lineage accumulation show a steep increase in selectively neutral COI haplotypes corresponding to the emergence of this 'broom' clade. We explore three possible scenarios for this dramatic increase: (i) a key change in adaptedness to the environment, (ii) a large-scale extinction event, or (iii) a dramatic increase in suitable habitats leading to rapid population expansion. Using estimated mutation rates of mitochondrial DNA in other invertebrates, we argue that *Homalictus* first colonised the Fijian archipelago in the middle–late Pleistocene, and the rapid accumulation of haplotypes in the hyper-diverse clade occurred in the Holocene, but prior to recorded human presence in the Fijian region. Our results indicate that bees have not been important pollinators of Fijian ecosystems until very recent times. Post-Pleistocene climate change and anthropogenic effects on Fijian ecosystems are likely to have greatly transformed pollinator suites from the conditions when those ecosystems were first being assembled.

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1. Introduction

Bees are profoundly important pollinators of angiosperms in almost all terrestrial ecosystems (Michener, 2007). The rapid diversification of angiosperms in the mid-Cretaceous is believed to have driven subsequent diversification in their corresponding pollinators (Grimaldi, 1999). Bees are almost entirely dependent on angiosperms (Michener, 1979a), and their diversification can often be tied to coevolutionary relationships with flowering plants (Dötterl and Vereecken, 2010).

The importance of bees as pollinators in island systems, where there are generally reduced levels of species richness but high levels of endemism (Cronk, 1997), can provide very important

insights into the evolution of ecosystems. Plants in island plant–pollinator mutualistic networks often show increased levels of pollinator specialisation, due to an increased plant:pollinator ratio that involves only a narrow range of visiting pollinator groups, some of which are often atypical (Olesen and Jordano, 2002). The result of this reduced interspecific competition between pollinators appears to encourage broadened pollination niches for endemic species, creating 'super generalists' (Olesen et al., 2002) that can act as keystone species, critical to the functioning of the ecosystem.

1.1. Pacific endemism

The islands of the Pacific in particular exhibit some of the highest levels of endemic richness for vascular plants, terrestrial vertebrates, and particularly avian taxa (Kier et al., 2009). Endemic birds have been shown to comprise between 22% and 44% of the known avian diversity in the Solomon Islands, French

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Polynesia, Fiji, and Hawaii (Groombridge, 1992). While insects show even higher levels of endemism in the region (e.g. 67% in Hawaii; Miller and Eldredge, 1996), it is sometimes low (e.g. 11% in the Pitcairn Islands; Groombridge, 1992; Benton, 1995). Raised levels of endemism in the Pacific islands, but reduced pollinator diversity, means the loss of generalist pollinators could constitute a great threat to pollination networks (Memmott et al., 2004). A large proportion of threatened species occur in island systems, due to pressures from habitat degradation and loss (Brooks et al., 2002), natural resource exploitation (Rainbird, 2002), and the introduction of invasive species (Zavaleta et al., 2001; Daehler et al., 2004). Furthermore, island species may compete poorly with introduced continental taxa that have undergone extensive selection over relatively long evolutionary periods (Cox and Elmqvist, 2000), and this may facilitate further introductions (Simberloff and von Holle, 1999). Therefore, for island populations there are not only increased risks of extinction, but indirect threats to the disruption of pollinator interactions critical to their persistence. For island plant–pollinator interactions to remain functional in the face of human-mediated changes to ecosystems, there is a need to understand how pollinator groups originated in these systems, how they have radiated, and how they contribute to ecosystem functioning.

1.2. Dispersal patterns in the Pacific

The evolution of island biota is often strongly influenced by geological history, not only for volcanic oceanic islands that typically have short life spans in archipelagos of varying ages (Whittaker et al., 2008), but also for continental rafts that represent source locations. Thus, understanding how different pollinator groups disperse requires confident geological reconstruction. In regions of complex geological history, such as the volcanic hotspots of the Pacific, this is not always easily achieved. Radiation of bees into island groups has been examined in several regions of the world, but not in the south western Pacific (SWP).

The islands of the Hawaiian archipelago have a relatively recent volcanic origin via a step-wise chain that enabled the expansion and diversification of species as new islands emerged and older islands submerged (Clague and Dalrymple, 1987). Magnacca and Danforth (2006) used molecular phylogenetics to show that the Hawaiian *Hylaeus* bee fauna (family Colletidae) appears to have resulted from a single colonisation event followed by rapid diversification. However, species were not distributed in the same way as many other Hawaiian taxa, where basal species are found on older islands with apical species on younger islands. Magnacca and Danforth (2006) suggested this is the result of the coloniser first adapting to open niches on the island of origin before dispersing to other islands and separating into distinct species. But should the original colonising island now be submerged it is possible that the crown age of the *Hylaeus* clade in Hawaii could predate the oldest extant islands, affecting the time frame and perceived dispersal pattern of subsequent lineages.

It is commonly expected that isolated and species-poor islands tend to harbour a subset of the diversity of islands closer to the source population. In the Kepulauan Seribu island archipelago off the coast of west Java in Indonesia, Spengler et al. (2011) found that although bee and wasp assemblages deviated from a random pattern of species distribution, community nestedness was only weakly developed. Gillespie (2002) showed that *Tetraglathia* spiders from neighbouring islands of the Society Islands, the Marquesas Islands, and the Hawaiian islands were almost completely unrelated, and instead represented repeated colonisation events from the source.

1.3. Geological and recent history of Fiji

Fiji comprises a group of islands that began forming during the Late Eocene with island-arc volcanics and subsequent deposition of shallow water limestones as a result of westward subduction of the Pacific plate, with the earliest emergence of Viti Levu occurring between 29 and 24 Myr (Taylor et al., 2000). By the Mid Miocene (15.97–11.6 Myr) the most significant land mass had formed but it was not until 8–6.5 Myr, after the breakup of the Vitiav trench and attachment of Viti Levu to the Pacific plate, that Vanua Levu formed (Rodda, 1994; Neall and Trewick, 2008). The next largest volcanic islands of Kadavu and Taveuni emerged within the last 3.43–3.35 Myr (Taylor et al., 2000) and 3.0–0.7 Myr (Nunn, 1998; Monaghan et al., 2006) respectively, with the latter comprised of large deposits of magma. Volcanic origins of both primary, Viti Levu and Vanua Levu, and secondary, Taveuni and Kadavu, islands mean they share similar profiles. Large, heavily forested peaks of high rainfall create dry windward areas where drier forests or savanna persist, particularly the northwestern side of the primary islands. Given the geological age for the islands, all pre-human settlement taxa are believed to have arrived via post-Eocene dispersal (Pole, 1994). Reconstructions of Fijian vegetational history have focussed on anthropogenic impacts, but sedimentary samples from Lake Tagamaucia at c. 800 m on Taveuni provide pre-human records to 27,000 years ago revealing mist forests dominated by *Ascarina* and gymnosperms giving rise to Myrtaceae, *Balanops* and *Pandanus* in the mid Holocene (Hope et al., 2009). Recent history of the Pacific saw the rapid human settlement of Melanesia and Polynesia between 3500 and 2500 years ago, followed by a period of extensive land use change via slash-and-burn processes for cultivation (Nunn, 1990). Anthropogenic burning practices have contributed to large-scale conversion of forest to grassland across the SWP islands; however, there is some evidence that suggests the presence of savanna prior to settlement (Latham, 1983; Hope et al., 2009).

1.4. Paucity of Fijian bee fauna

The bee fauna of the south western Pacific (SWP) has been reported as largely depauperate with only 71 species recorded across the four main island groups (Groom and Schwarz, 2011). New Caledonia exhibits a mix of Australian and Indo-Malayan elements, Vanuatu predominantly the latter, and the islands of Fiji and those east of Samoa contain only limited bee diversity (Michener, 1965). However, studies on these island bee faunas have been few and were based on morphology; attempts to determine how well morphological variation reflects species boundaries were limited by restricted sampling areas. The low bee diversity in Fiji suggests that either the extant bee fauna consists of only a small number super-generalist species, that the current records do not reflect the true diversity, or that Fijian angiosperms do not rely primarily on bee-pollinated systems. The rarity of bee-focused studies in the region and tendency of islands to harbour super-generalist pollinator species (Kaiser-Bunbury et al., 2010), such as *Xylocopa darwini* of the Galapagos (McMullen, 1993) or *Bombus canariensis* of the Canary Islands (Olesen, 1985), suggests the former two scenarios are most likely. However, Davies et al. (2013) show that the Megachilidae of Fiji, which represent the next most abundant group after halictines, are likely to be recent anthropogenic introductions.

1.5. *Lasioglossum* (*Homalictus*)

One bee group, subgenus *Homalictus* in the genus *Lasioglossum*, is particularly abundant throughout Fiji and the SWP. Its highest diversity is in Australia (43 recorded species, Walker, 1986, 1997), and Papua New Guinea (PNG) where 37 species have been

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