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Multiple recent introductions of apid bees into Pacific archipelagos signify potentially large consequences for both agriculture and indigenous ecosystems

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Abstract The islands of the south west Pacific (SWP) are highly biodiverse, yet records of their bee fauna suggest a region depauperate of a key pollinator suite. Studies of the bees of Fiji based on molecular data have revealed a recent origin with the majority of species having arrived since the last glacial maximum or introduced since human colonization. Here we use DNA barcodes to provide the first detailed account of Apidae bees from Vanuatu, Fiji, and Samoa. We show that most if not all species in these archipelagos have been recently introduced from Australia and south east Asia, with a further species introduced from the New World. Some of these species have become regionally abundant and we discuss the potential impact of introduced pollinators on endemic plant–pollinator associations. Given the wide-reaching role of native pollinators in island systems, yet lack of understanding of SWP pollinator suites, our study highlights the urgent need for more detailed pollinator research in the region.

Keywords Apidae · Anthropogenic introductions · Exotic species · Pollinators · Fiji · Vanuatu · Samoa · South west Pacific

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Introduction

The south west Pacific (SWP) comprises a very large number of islands with highly variable geological histories, many of which are still not confidently resolved. For example, there is evidence that New Caledonia comprises a Gondwanan element that may

or may not have been continuously sub-aerial since rifting from the Australian plate (Grandcolas et al. 2008; Heads 2008; Murienne et al. 2005). Similarly, New Zealand represents a Gondwanan element that rifted from Australia about 80 Mya that may or may not have been entirely submerged (the so-called 'drowning of New Zealand') approximately 25 Mya (Trewick et al. 2007; Waters and Craw 2006; McGlone 2005; Cooper and Cooper 1995). On the other hand, the Fijian islands are thought to have emerged relatively recently but also comprise sea floor crust dating from prior to the Oligocene (Neall and Trewick 2008).

This complex geological history of the SWP provides enormous opportunities to understand how ecosystems are assembled from combinations of vicariance and dispersal events that potentially cover both large periods of time and long distances between landmasses. Knowing when different biotic elements arrived in these regions and being able to identify those species that may have arrived via human activity will have considerable influence over the way we perceive current ecosystems.

Identifying anthropogenic dispersals of biota into a region can be problematic if dispersals predate the accumulation of historical museum records. The coconut (*Cocos nucifera*), for example, was utilized widely in exploration by humans, which resulted in a disjointed pantropical distribution. Until the advent of molecular techniques, determining the origin of this species was impeded by an inability to distinguish between natural and human-aided dispersal events (Gunn et al. 2011). If human colonisation into new regions carries species before documentation of indigenous biota from those regions began, those species might also be mistakenly considered as endemics in early descriptions. This problem can be further exacerbated if either or both early documentation of biota was incomplete or biota from potential source regions is poorly understood. While successful colonisation of bees has been shown to only require a small number of individuals (Zayed et al. 2007). Given the bee species diversity of likely source regions in Asia and Australia and our very incomplete knowledge of bee taxonomy (Batley and Hogendoorn 2009; Chenoweth and Schwarz 2011; Smith et al. 2013), these problems are highly relevant to understanding the biodiversity and biogeography of the bee fauna in the SWP.

Bees are one of the most important groups of invertebrate pollinators and their origin and early radiation are linked to the rise of angiosperms (Engel 2001). Many recent studies have indicated the importance of bees in both natural (Kearns et al. 1998; Allen-Wardell et al. 1998; Bascompte and Jordano 2007) and agricultural ecosystems (Klein et al. 2007; Garibaldi et al. 2013), attributed to their role in sexual reproduction of flowering plants. Therefore, their role in terrestrial ecosystems needs to be carefully considered when attempting to understand how extant ecosystems have come into place and what factors might threaten the function and conservation of those ecosystems (Gonzalez-Varo et al. 2013).

Studies in the SWP have suggested a very depauperate bee fauna (Michener 1965; Perkins and Cheesman 1928; Pauly and Munzinger 2003), and recorded species richness in archipelagos east of the Solomon Islands is very low when compared to the diversity of land plants (Keppel et al. 2009). Groom and Schwarz (2011) reviewed the current descriptions of bee diversity in the region, which is largely represented by two families; Halictidae and Megachilidae. However, assessments of the SWP bee fauna suffer from three major problems: (1) regional studies have often been piecemeal, sometimes separated by long periods of time, and based on limited sample sizes; (2) taxonomic treatments have, for the most part, not considered possible affinities with other island and especially continental faunas from both the New and Old World regions; and (3) studies have relied on morphological data that were frequently reported with minimal, and often idiosyncratic, descriptions in ways that do not allow clear comparisons between putative species from different regions.

Two recent studies have used genetic tools to examine bee diversity in the SWP. Groom et al. (2013) used molecular phylogenetic and coalescent analyses to infer patterns of radiation in the halictine subgenus *Homalictus* (genus *Lasioglossum*) in Fiji. They showed that although this group of bees is now very abundant in Fiji, it is a recent faunal element and likely colonized this archipelago during the mid-Pleistocene. Another recent study by Davies et al. (2013) examined the long-tongued bee family Megachilidae in Fiji and concluded that most, if not all, megachilid species in that region comprised very recent introductions that were likely aided by maritime trade. These two studies therefore indicate that a considerable proportion of the Fijian bee fauna is likely to have a recent origin.

Bees of the bee family Apidae in the SWP have not been subjected to genetic analyses to assess their history in the region. Like the megachilids, apid bees are long-tongued and therefore able to extract nectar from a very wide variety of angiosperms (Michener 2007). The honeybee, *Apis mellifera*, is now widespread in the SWP due to purposeful human introductions because of its utility in honey production and crop pollination. In the first taxonomic checklist of Hymenoptera from Fiji (Fullaway 1957) the only recorded apid species was the introduced *A. mellifera*. In Michener's (1965) comprehensive treatment of bees from Australia and the South Pacific, *A. mellifera* was again the only recorded apid from both Fiji and Vanuatu. However, a checklist of Fijian Hymenoptera compiled by Evenhuis (2007) lists *Amegilla* sp. (tribe Anthophorini), *Braunsapis* sp. (tribe Allodapini) and *Ceratina* sp. (tribe Ceratinini), though collecting localities and dates were not given. Pauly and Villemant (2009) recorded 22 bee species from Vanuatu, but this included only one apid, the introduced *A. mellifera*. Records of apid species from Samoa are even scarcer. *Apis mellifera* was recorded there as an exotic, as early as 1924 (Cockerell 1924), and Rehan et al. (2012) reported two unidentified *Ceratina (Neoceratina)* species.

Records of Apidae bee species from Fiji, Vanuatu and Samoa are, therefore, clearly limited and with the exception of the introduced honeybee, *A. mellifera*, the earliest and only published record is the Fijian hymenopteran checklist by Evenhuis (2007).

Here we use 87 sequences of mtDNA for four species of the bee family Apidae from Vanuatu, Fiji, and Samoa in the SWP to determine whether apid bee species recorded from the region represent anthropogenic dispersals. We discuss whether these species might provide pollination services to angiosperm crops, which could be important if honeybee populations decline with future introduction of parasites and diseases. Conversely, we also consider whether these species might be potential threats to native plant–pollinator relationships and discuss their likely impact on conservation of endemic species.

Methods

Collecting localities

Specimens were collected via sweep netting from flowers of both native and introduced plant species in both natural and developed areas. We collected from the four largest Fijian islands of Viti Levu, Vanua Levu, Taveuni and Kadavu, covering an altitudinal range of 0–906 m above sea level (asl) between July 16 and August 20, 2010. The southern Lau islands of Fiji were sampled between July 6 and August 8, 2011, covering the islands of Ono-i-Lau, Vatoa, Ogea, Vulaga, Namuka, Kabara, Lakeba, Vanuavatu, Moala, Totoya, and Matuku. Collections from Vanuatu were conducted between January 30 and February 18, 2011 across the three largest islands of Santo, Malekula, Efate, and the southern volcanic island of Tanna, covering an elevation range of 0–190 m asl. Samoan specimens were collected between September 11 and 18, 2011 from the two main islands of Upolu and Savaii covering 0–704 m asl. The sampling regimes sought to cover both habitat and geographic variability across all islands. In total 71 Apidae specimens were recovered, excluding *A. mellifera*.

DNA sequencing

Tissue samples, comprising a single leg of each specimen, were processed at the Canadian Centre for DNA Barcoding (CCDB) at the Biodiversity Institute of Ontario. Standard protocols for DNA extraction, PCR, and mtDNA cytochrome oxidase I (COI) sequencing were used (Ivanova et al. 2006). Bidirectional sequencing used the universal primer pair of LepF1/LepR2 (Hebert et al. 2004), which produced approximately 650 bp length of COI. Subsequent trace files were examined using Geneious Pro v5.6.4 (Drummond et al. 2012) and haplotypes that were ambiguous for one or more base pairs in both forward and reverse directions were removed from analyses. Sequences were screened via BLAST database searches for potential *Wolbachia* contamination, but were also checked as part of CCDB sequencing quality controls. All voucher specimens are stored in the Schwarz Bee Collection at Flinders University, South Australia.

COI sequences for additional non-SWP taxa were acquired from GenBank and Barcode of Life Database (BOLD) databases. Many of these haplotypes had only been identified to generic level. Species distinction was supported by the Barcode Index Number system, which applies a COI sequence divergence threshold of 2.2 % as a standard measure of conspecific variation (Ratnasingham and Hebert 2013). This threshold has

been shown to consistently identify to species level, with differentiation between even the most distinctive representatives of a species sometimes being considerably less (Gibbs 2009). However, there are also instances where divergence within an individual may be substantial (Magnacca and Brown 2010) but these remain diagnostic. Accession numbers and locality data for all our haplotypes and for the GenBank/BOLD acquired sequences are given in Table S1.

Phylogenetic analyses

We used two methods to infer phylogenetic relationships among our Apidae specimens (excluding *A. mellifera*): a genetic-distance based analysis and a Bayesian inference (BI) approach. Our genetic distance analysis used a neighbor joining technique applied to uncorrected 'p' distances in PAUP* v4.0b (Swofford 1999). Missing gene fragments were not included when calculating pairwise distances and trees were explored using a heuristic search. Node support for the neighbour-joining distance-based phylogram was not assessed using bootstrapping. Because most of the intra-specific haplotype variation involved only one to several nucleotide differences, bootstrapping procedures are very likely to omit these informative differences in most pseudoreplicates. Instead, we relied on BI, implemented in BEAST, as a further check for phylogenetic topology and to estimate posterior probability (PP) support for the nodes of interest in our analyses.

For the BI analysis we used an MCMC technique implemented in BEAST version 1.6.5 (Drummond and Rambaut 2007). We applied two sequence partitions to the dataset with 3rd codon positions separated from the 1st and 2nd, and we used a GTR + I + Γ model for each partition following a test for most appropriate substitution models using model test 3.06 (Posada and Crandall 1998). Gene partitions were unlinked for substitution parameters and we used an uncorrelated log-normal relaxed clock model and Yule process. The *Amegilla* representatives were constrained as sister to the remaining genera as per the topology of Cardinal et al. (2010) as substitution saturation limited confident reconstruction of deeper nodes. We ran the analysis for 50 million generations, sampling every 10,000 generation. Stationarity in the model parameters was assessed by plotting LnL and parameter estimates against iteration number using

Fig. 1 Neighbour-joining phylogram based on uncorrected 'p' genetic distances between SWP-collected apid bee COI haplotypes. Source regions for haplotypes are colour coded according to the map in the *lower left hand corner*, and haplotype names from the SWP are *right-indented*. *Scale bar* indicates substitutions per nucleotide
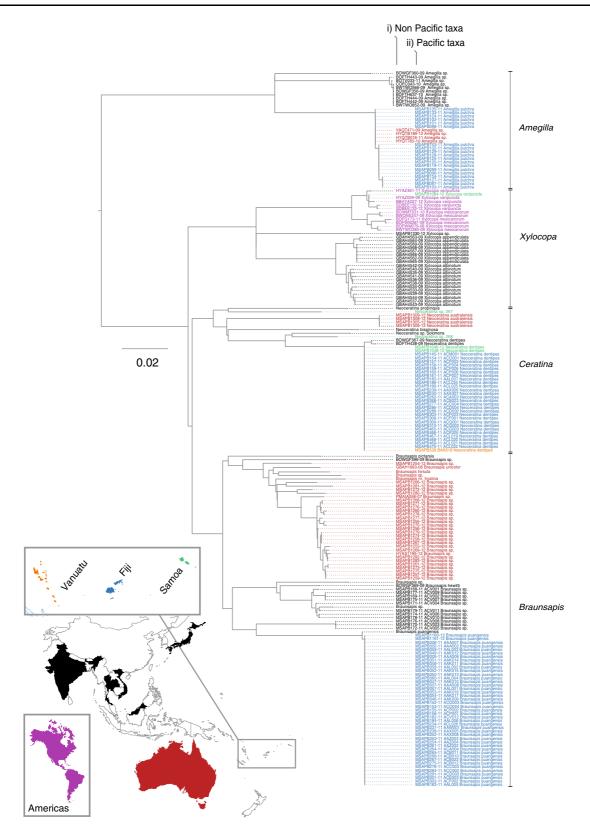
Tracer v.1.5 (Rambaut and Drummond 2007). We used a burnin of 30 million generations; well beyond stationarity as indicated by plotting indicator values.

Results

The genetic distance-based tree is provided in Fig. 1, while the maximum credibility tree with branches proportional to the number of changes from our BEAST analysis along with PP node support values is given in Fig. S1. Both analyses returned highly similar trees and recovered four major clades corresponding to four apid genera, *Amegilla*, *Xylocopa*, *Ceratina* and *Braunsapis*. The relationships between these genera in our analyses correspond to studies using broader taxon sampling (Cardinal et al. 2010; Cardinal and Danforth 2013), where *Amegilla* is a member of the Anthophorini, and *Xylocopa* is sister clade to Ceratinini + Allodapini within the Xylocopinae. In Fig. 1 and Fig. S1 broad localities for each haplotype are colour coded according to SWP and non-SWP regions. We now outline the main features of each of the generic-level clades in our analyses.

Amegilla

Our *Amegilla* haplotypes formed three distinct haplotype clades, with one of these representing a single specimen from Vietnam. The second largest clade comprised specimens from Vietnam and Thailand, and the largest clade comprised just three unique haplotypes shared by our 19 Fijian specimens with four specimens from Australia embedded within it. Uncorrected p-distances among haplotypes in this clade ranged from 0 to 0.31 % across 655 bp of COI sequence (Table 1), and the four Australian specimens shared identical haplotypes with six Fijian specimens. This exceedingly low level of haplotype variation in the combined Australian and Fijian specimens is consistent with a very low level of intraspecific variation for the geographic distance between the populations. Fijian specimens were confirmed to be

Table 1 Summary of uncorrected p-distances for each species with the number of specimens per species, average and maximum distance values

Species	Representatives	Av. genetic distance (%)	Max. genetic distance (%)
Amegilla pulchra	23	0.12	0.31
Braunsapis puangensis	42	0.00	0.00
Ceratina (Neoceratina) dentipes	32	0.30	0.30
Xylocopa varipuncta	6	0.27	0.59

Amegilla pulchra, an Australian species with a continent-wide distribution (R. Leijs pers comms.).

Xylocopa

We recovered only a single *Xylocopa* specimen, belonging to the subgenus *Neoxylocopa*, from Samoa. The haplotype for this specimen was nested within five haplotypes from Arizona and California classified as *X. varipuncta*, and these were closely allied to six haplotypes from the Central American species *X. mexicanorum*. Uncorrected 'p' distances for the six haplotypes within the *X. varipuncta* clade, including the Samoan specimen, ranged from 0 to 0.59 % and averaged 0.27 % (Table 1). Interestingly, the value of 0 %, or complete sequence identity, was for the Samoan specimen and the BOLD haplotype HYAZ029 from Arizona. It is therefore highly likely that the Samoan specimen represents an introduction from the New World, likely from south western North America.

Ceratina

Our analyses indicate three *Ceratina* (*Neoceratina*) lineages in Samoa whose pairwise genetic distances range from 8.23 to 10.07 %, indicating very clear species distinctness. Two of these lineages are represented by unique haplotypes whereas the third lineage comprises two Samoan specimens that have an identical haplotype to our Fijian specimens and another specimen from Vanuatu, and are closely related to a specimen from Thailand and another from Vietnam identified as *Ceratina* (*Neoceratina*) *dentipes*. The maximum and average sequence divergence in this clade is only 0.3 % (Table 1), with only the Vietnamese and Thai specimens differing from the single Pacific haplotype. Such low genetic divergence across a large spatial scale clearly indicates a recent introduction, likely from south east Asia.

There is only a single species of *Neoceratina* recorded from Australia (Michener 2007), *Ceratina (Neoceratina) australensis*, and our SWP *Ceratina* haplotypes are unrelated to this species (Fig. 1), indicating that *Ceratina* species in the SWP represent multiple dispersals from the Asian or Indo-Papuan regions.

Braunsapis

We recovered a large number of specimens identified as *Braunsapis puangensis* (Reyes 1991) from Fiji, most from Viti Levu, but one specimen each from the islands of Vanua Levu and Taveuni. We also included a single specimen of *B. puangensis* collected by us from southern India, where the species was described. Although our Bayesian analysis (Fig. S1) suggests some haplotype variation among the SWP specimens, this is due to small differences in available COI sequence lengths, and uncorrected 'p' distances within this clade were all 0 % (Table 1; Table S2), suggesting that introduction to Fiji has not been old enough for haplotype variation to accumulate. An examination of woody shrubs on the University of South Pacific campus in Suva in July 2013 revealed many hundreds of nests in the space of only a few hours searching. The absence of published records of *Braunsapis* from Fiji prior to 2007 despite its current abundance suggests a dramatic population expansion despite an apparently very recent introduction to Fiji, and its current presence on at least three islands in the Fijian archipelago indicates an ability to readily cross short distance water barriers, either naturally or via human activity.

Discussion

The lack of any haplotype differences for the large number of SWP specimens of both *N. dentipes* and

B. puangensis, combined with an absence of SWP records of these species prior to 2007, strongly suggest that both species have only recently arrived in the SWP. Our collections indicate that *B. puangensis* has been able to disperse among three Fijian islands, indicating an ability for rapid cross-water dispersal in this archipelago.

Unlike *B. puangensis* which was restricted to Fiji, specimens of *C. dentipes* were also found in Samoa and Vanuatu. Both later samples had identical haplotypes to the Fijian specimens, indicating that this species is able to rapidly disperse over major ocean barriers. Interestingly, *C. dentipes* has also been recovered from Mauritius, where its presence is likely due to maritime trade between Mauritius and Asia (Rehan et al. 2010). *Ceratina dentipes* was described from Java in 1914 by Friese and is widely distributed in the south east Asian and Indo-Malayan regions, including the Solomon Islands (van der Vecht 1952). Its presence in Mauritius and the zero genetic distances between our specimens from Fiji, Samoa, Vanuatu, and very low distances from Thailand and Vietnam suggests it has become a tramp species spread widely by anthropogenic means.

Haplotype variation in our specimens of *A. pulchra* confirm that the SWP specimens are extremely close to Australian specimens, with six SWP specimens having an identical haplotype to Australian samples, and the other 13 SWP haplotypes differing by ≤0.31 % from Australian haplotypes. This supports an Australian origin for Fijian *Amegilla*, either one that was long enough ago for some minor haplotype variation to accumulate in the Fijian population, or else introductions of more than one female from Australia.

Our record of *Xylocopa* is the first for Samoa and we found a zero genetic distance between our Samoan specimen and one recorded from Arizona, with very minor haplotype differences from specimens in Central America. This suggests a very recent introduction from the New World, and presents an opportunity to examine how this recent arrival subsequently spreads in a newly colonized island.

Lastly, the only evidence we found that may indicate pre-human dispersals of Apidae into the SWP involve two *Ceratina* species in Samoa, both basal to *C. dentipes*. Both species were rare (we obtained only one specimen of each). For one specimen the recovered sister haplotype was from India (*Ceratina propinqua*) and, for the other, the sister haplotype was an unidentified species from the Solomon Islands. We do not know if either of these Samoan species represents recent dispersals, and a major impediment here is the dearth of barcode data from Asia and the poor taxonomic understanding of the genus in this region.

Implications for a recent arrival of Apidae in the SWP

Our analyses indicate that most, if not all, species of Apidae in Fiji, Vanuatu and Samoa represent very recent introductions. The only long-tongued bees apart from Apidae are the Megachilidae. Davies et al. (2013) showed that most, if not all, megachilids in Fiji comprise very recent arrivals with likely anthropogenic origins. Consequently, it appears that long-tongued bees comprise very recent arrivals in the SWP, and that most or all have anthropogenic origins. Importantly, some of these recently arrived species have relatively high local abundances. Given the contrast between a lack of non-*Apis* records in the SWP prior to 2007 and our data indicating locally high abundance, it seems likely that introduced apid species will continue to spread and become regionally abundant.

The introduction and spread of exotic bee species in novel environments raises many important issues. In some cases, they have been viewed as being beneficial as effective crop pollinators (e.g. *A. mellifera, Megachile rotundata*), but they are also thought to be potentially major threats to endemic ecosystems (Goulson 2003). We now discuss two potentially major implications of recent apid introductions to the SWP.

1. *Awakening 'sleeper' weeds.* The full impact of invasive plant species that have colonized islands may be inhibited by the absence of suitable pollinators (Stokes et al. 2006 Diversity and Distributions). For example, many potential weed species such as Solanaceae require buzz-pollination for full seed set (Dafni et al. 2010), but only a few bee groups are able to buzz-pollinate. Buzz pollination is not performed by *Homalictus*, but is done so by the recently introduced bee genera *Amegilla* and *Xylocopa*. The presence of these

introduced genera therefore has the potential to increase the invasive capacity of novel weeds that require buzz pollination, and pose a threat to pasture-based industries or agriculture. Furthermore, in weed species with long corolla tubes only insects with long glossae can access nectar. Endemic SWP bee species in the subgenus *Homalictus* are short-tongued and consequently have limited or no access to such nectar rewards. Invasive plants with long corolla tubes are therefore likely to have higher seed sets in the presence of long-tongued apid bees (Goulson 2003).

2. *Displacing native pollinators.* It seems likely that many angiosperm species in the SWP have evolved pollination systems that involve indigenous pollinators. Newly introduced apid species that have a wide range of host plants and potentially huge population sizes have the capacity to compete with such native pollinators, possibly with negative impacts on the latter's long-term viability (e.g. Kato and Kawakita 2004). A further problem arises if introduced bee species are able to exploit floral resources of endemic angiosperms but do not effectively pollinate them in the process (Gross et al. 2010; Simpson et al. 2005). This problem has been reported many times for exotic bee species in other parts of the world (summarized in Traveset and Richardson 2006).

There is a clear lack of insect pollination studies in the SWP, so the above possibilities are speculative. In terms of exotic species management strategies, the possible negative effects of introduced wild bees will also have to be weighed against their possible beneficial effects on crop pollination, especially given the recent concerns about declining *A. mellifera* populations in other regions. These issues have been unexplored in the SWP, but our study suggests that they might now require urgent attention.

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